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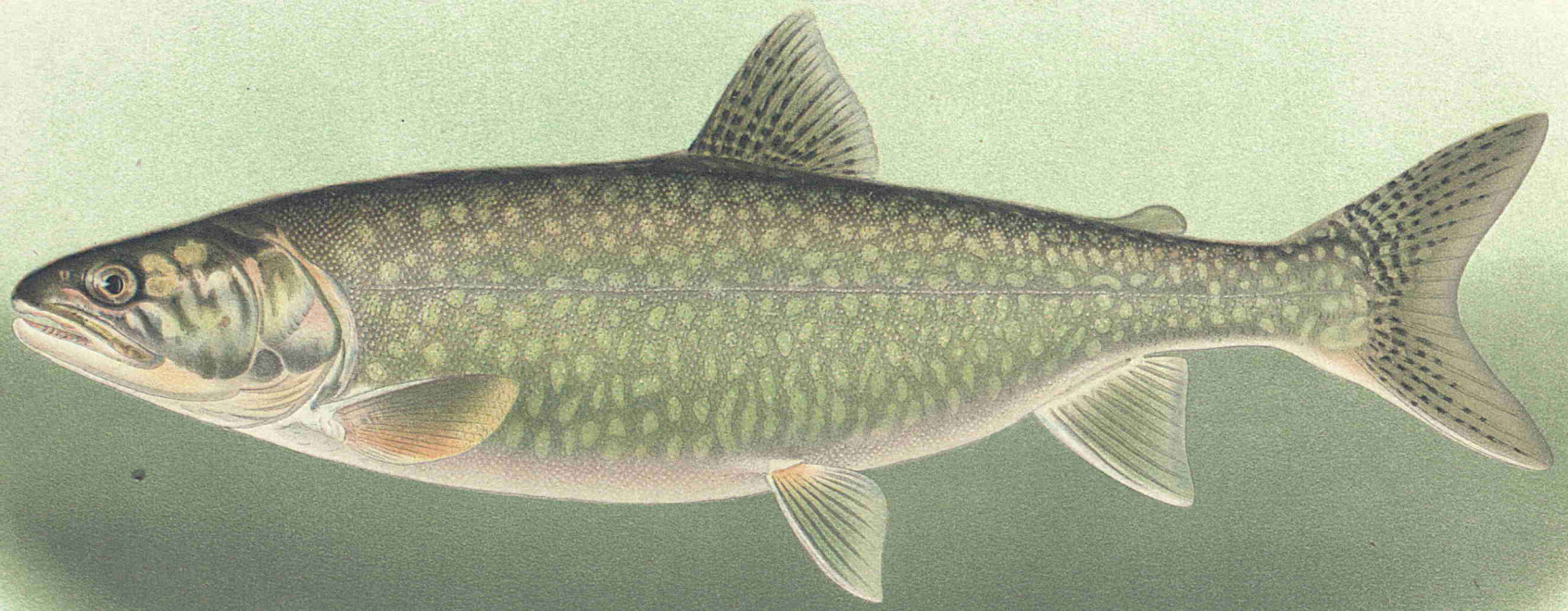
A REVIEW OF THE SALMONOID FISHES OF THE GREAT LAKES WITH NOTES ON THE WHITEFISHES OF OTHER REGIONS

By David Starr Jordan and Barton Warren Evermann



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LAKE TROUT; MACKINAW TROUT
Cristivomer namaycush (Walbaum)

A REVIEW OF THE SALMONOID FISHES OF THE GREAT LAKES, WITH NOTES ON THE WHITEFISHES OF OTHER REGIONS.

By DAVID STARR JORDAN and BARTON WARREN EVERMANN.[a]

In the investigations of the fisheries of the Great Lakes region conducted in 1908 and 1909 by the International Fisheries Commission the writers had opportunity to examine great numbers of specimens of the food fishes and especially of the Coregoninæ, known as whitefish and lake herring. It has been clearly shown that the fauna of each of the Great Lakes exhibits peculiarities of its own, and especially that each lake has one or more species of the group called lake herrings or ciscoes peculiar to itself. In this paper the species of these and other groups of fresh-water Salmonidæ are treated and figured somewhat fully. The specimens described are in the United States National Museum, with series of duplicates in the museum of Stanford University. The following species are described as new:

Leucichthys supernas, Leucichthys cyanopterus, Leucichthys manitoulinus, Leucichthys ontariensis, Leucichthys harengus arcturus.

Three others from the same collections have been previously described and figured (Proc. U. S. Nat. Mus., vol. xxxvi, p. 165–172) by Jordan & Evermann:

Leucichthys huronius, Leucichthys eriensis, Leucichthys zenithicus.

Genus SALVELINUS (Nilsson) Richardson.

Salvelinus fontinalis (Mitchill). *Eastern Brook Trout.*

The common brook trout occurs in all cold streams and in some lakes throughout this region. It occurs freely in Lake Superior but not in any other of the Great Lakes. In the streams of Isle Royale a variety almost jet-black in color is said to occur.

[a] In the preparation of this paper the authors have had the assistance of William Francis Thompson, of Stanford University. Most of the text figures were drawn by William Sackston Atkinson, and the colored plates are from paintings made by Charles Bradley Hudson.

Genus CRISTIVOMER Gill & Jordan.

Cristivomer namaycush (Walbaum). *Lake Trout; Great Lakes Trout; Mackinaw Trout; Togue; Longe; Namaycush; Siscowet.* (Pl. 1.)

The Great Lakes trout or Mackinaw trout occurs throughout the Great Lakes region, and in the lakes northwestward to the Yukon and the Arctic Sea. It is subject to many variations in color and in degree of plumpness, but we find no tangible differences on which the genus can be separated into species or subspecies.

A notable variant is found in the siscowet (*Salmo siscowet* Agassiz, Lake Superior, p. 333, 1850; *Salmo siskawitz* Agassiz in Herbert, "Frank Forester's Fish and Fishing, p. 143, fig. on p. 144, 1849). This is a pale trout, excessively fat and with the skeleton feeble for its size, found in Lake Superior and in waters of 50 to 80 fathoms. It is never seen in shallow water. It differs in no technical respect from the ordinary lake trout, and it is connected with the latter by perfect intergradations known locally as half-breeds. The siscowet is taken in schools of the deep-water ciscoes, the bluefin (*Leucichthys cyanopterus*), the cisco (*L. supernas*) and the Lake Superior longjaw (*L. zenithicus*), themselves also soft-bodied and very fat. There is every reason to believe that the siscowet is an ordinary trout which has fed

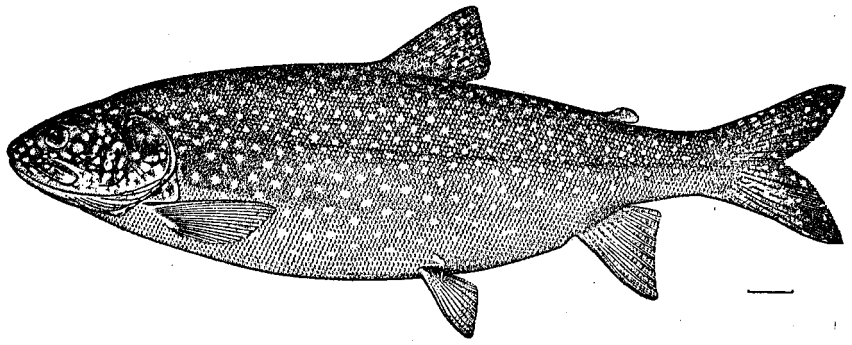


FIG. 1.—*Cristivomer namaycush siscowet.* Siscowet. (Drawn from specimen 18 inches long, taken in Lake Superior off Marquette, Mich.)

on these soft fat fishes and which has followed them into deep water. If so, it should not be regarded as a distinct species or subspecies.

The siscowet is not badly flavored but too fat to be digestible, and it almost melts away in frying. Salted, it is more satisfactory, but there is little market for it. Sometimes the walls of the abdomen are over half an inch in thickness.

Our text figure is taken from a small but very fat example of the typical siscowet taken in a school of bluefins in about 60 fathoms off Marquette. The colored plate is from a typical lake trout from Lake Michigan off Berrien County, Mich.

Commercially the lake trout is of great importance. The catch in American waters for the Great Lakes in 1908, according to the Bureau of the Census, was as follows:

State.	Pounds.	Value.
Indiana	129,600	$9,640
Michigan	6,798,000	424,080
Illinois	150,400	12,550
Minnesota	215,000	11,690
Wisconsin	4,710,100	340,360
Total	12,003,100	798,320

Genus LEUCICHTHYS Dybowski.

The Lake Herrings.

Argyrosomus Agassiz, Lake Superior, p. 339, 1850 (*"clupeiformis"* of De Kay, not of Mitchill=*harengus*); not of M. de la Pylaie, which, according to Doctor Gill, is *Pseudosciæna aquila.*

Leucichthys Dybowski, Fische des Baikal-Wassersystemes, Verh. K. K. Zool.-Bot. Gesell. Wien, bd. XXIV, 1874. p. 390 (*Salmo omul* Pallas).

Allosomus Jordan, Manual Vertebrates, ed. 2, p. 361, 1878 (*Coregonus tullibee* Richardson).

Thrissomimus Gill Ms., November, 1909 (*Coregonus artedi* Le Sueur).

Cisco Jordan & Evermann, new subgenus (*Argyrosomus nigripinnis* Gill).

We are indebted to Prof. Theodore Gill for the information that the name *Argyrosomus* was first given to the "maigre" of the Mediterranean, and in advance of its use by Agassiz for the genus of lake herring. The maigre should therefore stand as *Argyrosomus aquila* instead of *Pseudosciæna aquila.* The following statement is given by Professor Gill:

The name *Argyrosomus* first appears in the "Comptes Rendus du Congrès Scientifique de France," 2nd session in 1834, pages 524 to 534 (published in 1835). The article is entitled "Recherches en France sur les poissons de l'Océan pendant les années 1832 et 1833, par. M. de la Pylaie de Fougères."

On page 534, Professor Gill informs us, M. de la Pylaie has the following:

Sous le tribu des Persèques, nous voyons . . . l'*Argyrosomus procerus*, nouveau genre que j'ai formé avec le *Sciæna aquila* Cuv., et auquel j'associe une nouvelle espèce, l'*Arg. sparoides*, de la baie de Bourg Neuf.

No other reference is made to *Argyrosomus* or these species. The species *Sciæna aquila* must be taken as the type of *Argyrosomus.* The name thus antedates *Pseudosciæna* Bleeker, given in 1863 to the same species, *aquila.*

The name *Leucichthys*, first given by Dybowski in 1874 to two Siberian species of the genus *Argyrosomus* Agassiz, must apparently replace the latter for the lake herring ciscoes with their old world congeners. *Leucichthys*, based on *Coregonus omul* and *Coregonus tugun*, is separated by Dybowski from *"Coregonus sensu strictiore"* by the terminal mouth. The first species named, *Coregonus omul*, may be taken as its type.

Dybowski thus records these species:

2. Gruppe, *Leucichthys*, Der Mund vorderständig oder halb oberständig. Die Symphyse des Unterkiefers mit einer höckerartigen Anschwellung.

19. Art. *Leucichthys omul* Pall., l. c., Taf. VIII, Fig. 2. Der Kopf nach vorn zugespitzt, die Schnauze verlängert. Der Unterkiefer ein wenig vorstehend. Die Nase schwach gewölbt, etc.

20. Art. *Leucichthys tugun* Pall. Der Kopf nach vorn zugespitzt, die Schnauze wenig verlängert, der Unterkiefer etwas vorstehend, etc.

In both these species the jaws and tongue are said to be "mit schwacher Zähnchen besetzt."

Pallas, however, says of *L. omul*, "os plane edentulum," and of *L. tugun*, "maxilla . . . utraque edentula." We find no teeth in the jaws of the American species, and only minute asperities on the tongue. There is no hook on the end of the lower jaw in any of our species, although a slight prominence in *L. johannæ*, *L. prognathus*, and *L. cyanopterus* suggests it. In view of all this there is some doubt as to whether our American species should be referred to the same genus as *Leucichthys omul.* We may note, however, that both Guldenstadt and Pallas deny the presence of teeth in *Stenodus leucichthys.* Our specimens of the latter from the Volga River at Sammara, Russia, show small teeth in both jaws and on the vomer, palatines, and tongue, as supposed by Doctor Günther and as shown by the American species, *Stenodus mackenzii.* The use of *Leucichthys* as a generic name by Dybowski may indicate that he had this species, *Stenodus leucichthys*, in mind as the type of *Leucichthys.* But he mentions only the two species *omul* and *tugun.* As both of these are said to have teeth, and to have the lower jaw produced and hooked, it may be that they constitute a separate subgenus, intermediate between *Stenodus* on the one hand and the American on the other. To this subgenus the European species *Leucichthys vandesius* may possibly belong, as that species is said to have minute teeth on the jaws and tongue, and a projecting lower jaw and uncurved chin as in *Leucichthys omul.* On the other hand, the British species, *Leucichthys pollan*, much resembles the American species.

We therefore provisionally adopt the name *Leucichthys* for the entire group, considering the subgenus *Leucichthys* proper as composed entirely of old world species, and placing the American species in three subgenera, *Thrissomimus*, *Cisco*, and *Allosomus*.

We further note that in *Leucichthys omul* 6 to 8 rows of pearly bodies are present in the breeding season, as in certain species of *Coregonus*. None of the American species of lake herring shows these structures, although slight warty elevations are shown in some of our specimens of *L. johannæ*.

This genus *Leucichthys* includes the species known in America as lake herring, cisco, and tullibee, and the corresponding forms in northern Europe and northern Asia, known as laksild, sik, vendace, pollan, etc. These forms are related to the whitefish, *Coregonus*, agreeing with the latter in the large silvery scales and obsolescent teeth. In *Leucichthys*, however, the mouth is larger, with longer jaws, the lower jaw being at least as long as the upper, and the premaxillaries set nearly horizontally. The gillrakers are long and slender, about 30 on the lower limb. The jaws are toothless in all of our species. There are no teeth on the palate but minute teeth are seen on the tongue when dry.

The species are much more active than those of *Coregonus* and feed more generally on small fishes. In general, they are less valued as food than the whitefishes, but at least one of them ranks with the very best of food fishes. The group separates naturally into three subdivisions which may be called subgenera.

To the first of these, *Thrissomimus* (which is the earlier *Argyrosomus* of Agassiz, the name unfortunately preoccupied), belong the typical lake herring, or laksild, both of Europe and America, fishes with slender bodies, silvery scales, relatively firm flesh and firm skeleton, and the general form of herring, to which these fishes bear much external resemblance that indicates no real affinity. All the species of *Thrissomimus* have the jaws toothless, which separates them from the Asiatic genus or subgenus *Leucichthys*. None of this group or the next one is found in the basin of Lake Winnipeg, which includes the Lake of the Woods, the Saskatchewan, the Rainy River, and the Red River of the North. The only species of the genus in this vast basin is the tullibee, *Leucichthys tullibee*.

To the second group, which we call *Cisco*, belong the ciscoes, bluefins, blackfins, bloaters, and longjaws, species living in 50 or more fathoms of water, with the mouth larger than in the lake herring, and with the skeleton relatively feeble and the flesh softer, often saturated with fat. These forms are all very closely related and probably sprang from a common stock which is near the species called *L. supernas*. It is not clear that they are derived from any of the existing shore species.

To the third group, *Allosomus*, belong the tullibees, robust, compressed fishes with the tail very short, the mouth small and the color in general more dusky than silvery. The scales are firm and the texture of the flesh more solid than in the lake herrings. The species of this group are mostly confined to the region northwest of Lake Michigan, and they are found mainly in the smaller lakes to the northwestward of Lake Huron, their distribution being chiefly in the Winnipeg basin. The tullibees are not greatly valued as food fishes, the flesh being soft and watery and inferior to that of most other Salmonidæ.

The Siberian species, *Leucichthys peled* (Lepechin) (= *Salmo cyprinoides* Pallas) is doubtless a tullibee or typical *Allosomus*.

Besides the species found in the Great Lakes region, we give here an account of all the species of *Leucichthys* known from North America. It may be noticed that the species of each group are closely related to one another, that the differences are more evident in the mass, as in a boat or fish market, than in individual preserved specimens, that measurements are liable to fluctuation, that individual differences are unusually great, and finally, that in those characters usually most trustworthy in fishes, such as the number of scales, fin-rays, gillrakers, etc., the different species are practically in agreement.

ANALYSIS OF SPECIES OF LEUCICHTHYS FOUND IN THE GREAT LAKES REGION.

a. Caudal peduncle relatively long and slender, its length along lateral line above last ray of anal more than .75 length of head, its length from last ray of anal to first of caudal more than its depth; scales silvery, more or less loosely inserted; body more or less elongate, the depth 3.25 to 5.5 in length; minute teeth on tongue, none on jaws or palatines.

THRISSOMIMUS:

b. Species of shore waters, spawning in late autumn, the flesh firm, the skeleton well developed, the mouth small, the maxillary not reaching past middle of eye.

c. Adipose fin very small, usually shorter than eye; body elongate, the caudal peduncle slender, its least depth about 3 in head; body slender, the depth 4.33 to 4.66 in length; body anteriorly long, the pectoral not reaching nearly halfway to ventrals; back lustrous bluish in life, usually not marked with lengthwise streaks..... *harengus; osmeriformis*

cc. Adipose fin well developed, longer than eye.

d. Body elongate, the depth 4.33 to 4.5 in length; caudal peduncle slender, its least depth about 3 in head; body anteriorly long, the pectoral not reaching halfway to ventrals in the adult; back dark lustrous blue in life, usually marked with dark lengthwise streaks.

e. Body subcylindrical, little compressed, its depth about 4.5 in length, its greatest depth usually before dorsal..... *sisco; huronius*

ee. Body more robust and more compressed, its depth about 4 in length, the greatest depth usually near insertion of dorsal.... *ontariensis; lucidus; laurettæ; alascanus; pusillus*

dd. Body deep and compressed, the depth 3.33 to about 4 in length; caudal peduncle stout, its least depth nearly half head; pectoral reaching more than halfway to ventrals; adipose fin larger, longer than eye; back olive-gray, without distinct dark streaks.

f. Body moderately robust, depth 3.5 to 4 in length; angle at the nape slight, scales relatively thin and loosely attached..... *artedi; bisselli*

ff. Body very robust, depth 3.33 to 3.5 in length, with a strong angle at the nape; scales large, regular, and firmly attached; flesh rich, of excellent flavor..... *eriensis*

CISCO:

bb. Deep-water forms found in 50 fathoms and upward, spawning in midsummer, the flesh soft and fat, the skeleton relatively feeble, the mouth relatively large; adipose fin rather large.

g. Mouth moderate, the maxillary not extending to middle of eye; premaxillary nearly horizontal, the upper jaw not truncate; head broad, the width between temples rather more than half length of top of head; caudal peduncle stout.

h. Lower jaw distinctly projecting, its tip somewhat produced upward; head thick; eye large; pectoral extending more than halfway to ventrals; depth about 4 in length; adipose fin small; fins with little dark.

i. Head short and slender, 4.66 in length; mouth relatively small; adipose fin rather small ..... *supernas*

ii. Head long and thick, 4 to 4.25 in length; mouth large; adipose fin small.

j. Gillrakers more than 40..... *prognathus*

jj. Gillrakers fewer than 40..... *johannæ*

hh. Lower jaw included; head long, about 4.5 in length; body moderate, the depth about 4.2 in length; caudal peduncle thick; fins all broadly edged with black.

k. Gillrakers 16 to 19+31 to 35..... *nigripinnis*

kk. Fins slightly bluish or dusky at tip; gillrakers 14+25..... *cyanopterus*

gg. Mouth larger, the maxillary extending about to middle of eye; snout long, subtruncate at tip, the premaxillaries more or less vertically placed, lower jaw included; body slender, the depth more than 4 times in length; caudal peduncle slender; head slender, its breadth at temples half its length above. Color pale, often some dark on fins except the ventrals.

l. Pectoral not reaching halfway to base of ventrals; snout about equal to eye, about 4 in head; depth of tail much greater than snout; snout more truncate than in next species; scales about 70; color very silvery.... *hoyi*

ll. Pectoral reaching more than halfway to base of ventrals; depth 4.6 to 4.66 in length; snout less truncate than in *L. hoyi*, 3 to 3.5 in head, longer than eye; depth of tail not equal to snout; scales about 77. Color brassy-silvery, with dark points on all fins save ventrals.... *zenithicus*

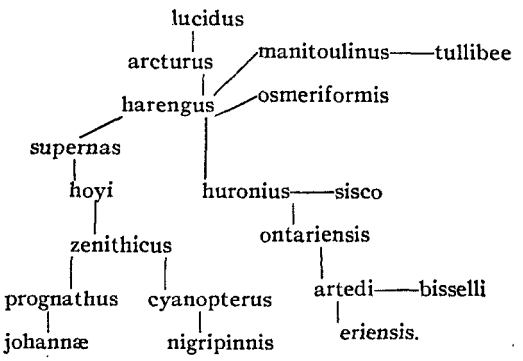
ALLOSOMUS:

aa. Caudal peduncle short and thick, its length along lateral line above last ray of anal about half head, its length from last ray of anal to first of caudal less than its depth; skeleton and flesh firm; scales dusky, firmly inserted; body deep, compressed, the depth 2.25 to 3.4 in length; no teeth. Colors dark, back and fins dusky.

m. Depth 3.2 to 3.33 in length; adipose fin very small, shorter than eye; caudal peduncle moderate, its depth 2.5 in head ..... *manitoulinus*

mm. Depth 2.5 to 3 in length; adipose fin large, longer than eye; body short and deep; caudal .peduncle very short and deep, its depth 2 to 2.25 in head ..... *tullibee*

The relationships of the species may be indicated graphically as follows:



Subgenus THRISSOMIMUS Gill.

Leucichthys harengus (Richardson). *Saginaw Bay Herring; Georgian Bay Herring.*

Salmo (Coregonus) harengus Richardson, Fauna Boreali-Americana, III, p. 210, pl. XC, fig. 2, 1836, Georgian Bay at Penetanguishene, Ontario.

Coregonus clupeiformis, Agassiz, Lake Superior, p. 339, 1850, the Pic (Michipicoten Island); not of Mitchill.

Coregonus albus, Agassiz, op. cit., p. 342, the Pic; not of Le Sueur.

Argyrosomus artedi, Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 305, pl. 21, in part, Bayfield, Wis.

Distribution: Bays and shallow waters of Lake Huron and Lake Michigan; Georgian Bay, Saginaw Bay, Green Bay, etc.

The herring of Georgian Bay, hitherto confounded with *Leucichthys artedi*, is a distinct species, well separated from all the other species of this group found in the Great Lakes by the very small adipose fin, length of which is about 5 in head. This character is well shown in Richardson's figure of the species. In form the Georgian Bay herring is much more slender than *L. artedi*, approaching in that regard the herring of Lake Huron (*Leucichthys sisco huronius*). As a food fish *Leucichthys harengus* is distinctly superior to either *L. artedi* or *L. sisco huronius*, though by no means equal to *A. eriensis*.

Doctor Richardson's specimens came from Penetanguishene at the southern end of Georgian Bay. We obtained many specimens from the neighboring port of Collingwood, one of which we have figured, and which is the type of the following description. This may be regarded as typical of *Leucichthys harengus*. We have seen specimens from near Mackinac which seem to belong to this species.

The herring of Saginaw Bay is also in all respects identical with the specimens from Collingwood. It is not only slender, as usual in this species, but reaches only a small size, the average weight when mature being 6 ounces, those examined by us, from Bayport, ranging from 2.5 to 9.5 ounces. The maximum length is 12 inches and the usual from 9 to 10.

A small copepod which Dr. Charles B. Wilson is describing as a new species of Lernæopoda is parasitic on the gills of the Saginaw Bay herring.

Of all the species of *Leucichthys* this must be the most numerous in individuals, occupying as it does most of the open waters of Lake Huron and Lake Michigan. It is taken in great abundance in Saginaw Bay, where it is largely salted for commercial purposes. It is the most important fish in the fisheries of Saginaw Bay, the catch in 1908 amounting to 3,871,345 pounds, while the total catch of all species was 7,104,703 pounds.

This species is said to range down the shores of Lake Huron to Port Huron, and to be taken occasionally in Lake Erie, having come down the Detroit River. It is also said that the shore lake herring of Green Bay in Lake Michigan are of the same type. These Saginaw herring differ from the ordinary blueback of Lake Huron and Lake Michigan in their gray color, less cylindrical body, smaller size, and especially in the much smaller adipose fin.

Specimens from near Pine, Ind., at the southern end of Lake Michigan, seem to belong to this species rather than to *Leucichthys sisco huronius*. These are small in size, gray in color, and with the adipose fin not larger than in *L. harengus*.

Head 4.33 in body without caudal; depth 4.33; length of caudal peduncle measured from last anal ray to first of caudal, 2.12 in head; depth 3; eye 4; snout 3.75; interorbital space 3.75; maxillary measured from tip of snout 3; dorsal 11, anal 12; scales 10–83–9, between occiput and dorsal, 33; branchiostegals 9; gillrakers 16+31, length 0.87 eye diameter.

Body elongate, not much compressed, more cylindrical than in most species. Width 1.75 in its depth, more convex ventrally; caudal peduncle long, terete, not deep nor much compressed; back above occiput

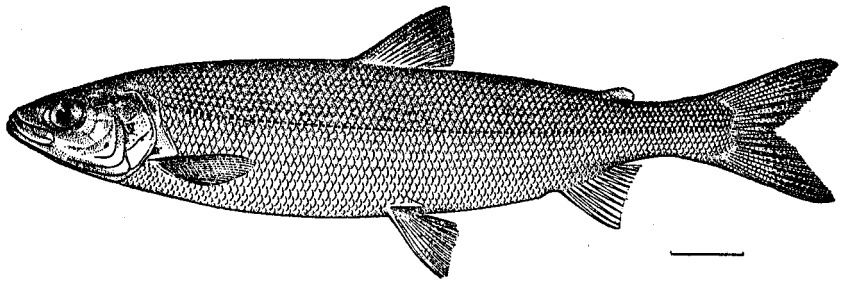


FIG. 2.—*Leucichthys harengus* (Richardson). Saginaw Bay herring. (Drawn from a specimen 11 inches long, collected in Georgian Bay, Lake Huron, Collingwood, Ontario.)

only moderately arched; head small; under jaw projecting somewhat; maxillary not quite extending below the anterior edge of pupil, thrice as long as broad; teeth on tongue only, very minute and few in number; distance from snout to occiput always less than half distance from occiput to dorsal insertion; dorsal inserted midway between snout and base of caudal, somewhat small, its longest ray 1.75 in head, its base about half length of head, usually shorter than eye, rarely longer; adipose small, its length from insertion to tip 5 in head, low, its height 0.33 its length, but variable in different specimens; in general its greatest length is 4 to 4.5 times in the distance from the depressed tip of the dorsal to its base; ventrals somewhat shorter than pectoral, the latter about 0.66 length of head; anal small, its base equal to that of dorsal, its longest ray 2.33 in head; lateral line straight; scales moderate in size.

Color in spirits, dark along the center of the back and on the dorsal surface of the head, coffee-colored on the remainder, silvery laterally and colorless ventrally; dorsal black on distal half; caudal dark, edged with black; pectoral and ventral lightly touched with dark along first rays; anal dark on distal half.

Specimens from Blind River on the North Channel of Lake Huron differ from the Collingwood specimens in having the colors darker, the surface suffused by dusky, as usual in "muskeeg" waters, or water darkened by drainage from sphagnum swamps. These are also more slender and smaller, but do not differ otherwise. A figure of one is presented.

The ordinary herring of Lake Superior are placed provisionally under *Leucichthys harengus*, of which they constitute a tangible variety or subspecies, distinguished by the larger size, the more cylindrical

form, and in general by the still smaller adipose fin. But these characters are average only, and are subject to much variation, hence we refrain from regarding the Lake Superior herring as a distinct species. Specimens having these characters were taken at Sault Ste. Marie, both above the Rapids (Point aux Pins) and below (St. Marys River). Specimens exactly similar were secured from Peter Anderson, a fisherman at Marquette. These are rather larger than the specimens from Collingwood, but exactly like them in form and color. The figure of Evermann & Smith taken from a specimen from Bayfield, Wis., seems to be the same, although named *Argyrosomus artedi* in their plate.

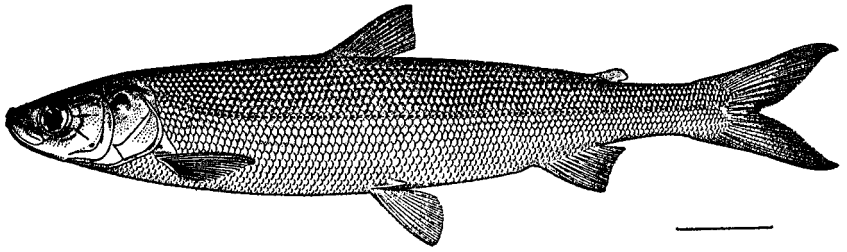


FIG. 3.—*Leucichthys harengus* (Richardson). Saginaw Bay herring. (Drawn from a young example, 9 inches long, collected in Blind River, North Channel, Lake Huron.)

In the work of the International Fisheries Commission it was claimed by the fishermen about Duluth that a mesh of less than 2.5 inches was necessary for the capture of the lake herring. The fishermen about Marquette were entirely satisfied with this mesh. It was claimed at Duluth that the herring there were more slender than those to the eastward of Keweenaw Point. Examination of specimens shows this to be true. The lake herring examined from Duluth, Knife River, Port Arthur, and all points on the northwest shore of Lake Superior, are more slender, less compressed, and more spindle-shaped than those from Georgian Bay and Marquette. On a single specimen no great difference is shown, but in a boat load of herring it is notable. Possibly the difference is due to scantier food on

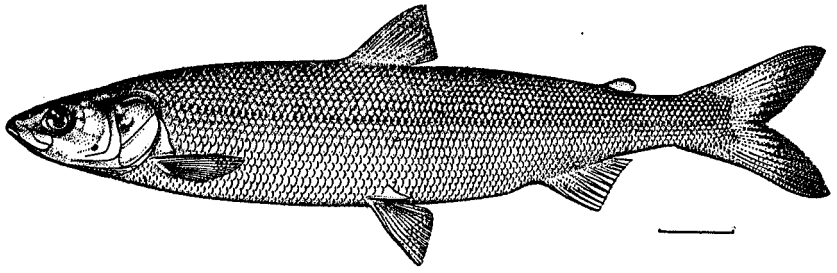


FIG. 4.—*Leucichthys harengus arcturus* Jordan & Evermann, new subspecies. (Drawn from the type, a specimen 11.5 inches long, collected in Knife River, Lake Superior, near Duluth.)

the narrow rocky shelf inhabited by these fishes along the north shore. Possibly it has a certain taxonomic value. The lake herring is a shore fish, and the great depth of the waters of Lake Superior more or less completely isolates the fishes of Isle Royale and neighboring shores from those of the eastern and southern part of the lake.

We present a figure of a specimen from Knife River, near Duluth, typical of the subspecies which we call *Leucichthys harengus arcturus*. This form agrees exactly with the ordinary *harengus* of Georgian Bay in the small size of the adipose fin. The fishes from Michipicoten Island ("the Pic") in Lake Superior, called by Agassiz *Coregonus albus*, may belong to this slender type.

Comparison of specimens of Leucichthys harengus.

	Lake Huron. *L. harengus.*		Lake Superior. *L. harengus arcturus.*			Lake Michigan. *L. harengus.*	
	Collingwood.	Blind River.	Marquette.	Knife River.	Duluth.	Pine, Ind.	
Specimen no.	5267	5283	5271	5256	5210	5288	5290
Length without caudal ..... *mm.*	243	215	255	253	238	215	245
Dorsal rays	10	11	10	11	11	10	10
Anal rays	12	11	12	12	12	12	12
Scales	10–83–9	9–85–9	9–80–8	10–79–8	9–86–8	9–90–8	9–80–8
Scales between occiput and dorsal fins	33	34	34	33	35	38	38
Branchiostegals	9	9	9	9	9	9	8
Gillrakers	16+31	16+29	16+30	16+30	16+30	18+35	17+31
Comparative measurements:[a]							
Head	0.23	0.22	0.225	0.23	0.22	0.23	0.235
Depth of body	.23	.20	.21	.22	.20	.21	.205
Caudal peduncle, length from anal to point of caudal rays	.10	.12	.12	.11	.11	.11	.103
Caudal peduncle, depth (least)	.075	.07	.07	.07	.07	.07	.07
Eye	.055	.05	.05	.05	.05	.05	.05
Snout from eye	.055	.05	.06	.06	.05	.055	.06
Interorbital space	.065	.06	.065	.065	.06	.06	.065
Maxillary length from tip of snout	.075	.07	.08	.08	.075	.07	.075
Snout to occiput	.16	.15	.16	.155	.15	.155	.16
Ventrals to pectorals	.35	.31	.32	.32	.32	.325	.31
Pectoral length in ventral-pectoral distance	2.25	2.20	2.125	2.25	2.00	2.00	2.00
Pectoral length	.16	.14	.15	.14	.155	.155	.16
Ventral length	.14	.13	.14	.14	.14	.15	.15
Dorsal height	.14	.12	.135	.135	.14	.14	.15
Adipose length	.05	.04	.055	.055	.06	.05	.055
Anal height	.09	.085	.09	.08	.09	.09	.09

[a] Measurements in hundredths of body lengths unless otherwise specified.

Leucichthys osmeriformis (Smith). *Seneca Lake Herring; Seneca Lake Smelt.*

Coregonus osmeriformis Smith, Bull. U. S. Fish. Comm., vol. XIV, 1894, pl. 1, 2, Seneca Lake; Skaneateles Lake. Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 305, 1896; same specimens.

Distribution: Lakes of central New York, tributary to Lake Ontario.

We have examined the type (from Seneca Lake, New York) and the 4 cotypes (from Skaneateles Lake, New York) of this species, which is locally known as smelt. It is one of the smallest species and is allied to *Leucichthys harengus*, with which it agrees in the slender body and very small adipose fin. It differs from that species, however, in the considerably longer maxillary, longer and decidedly projecting lower jaw, larger eye, and longer head.

The following is the substance of the account given by Doctor Smith, whose figure we copy (fig. 21, p. 40):

Head 3.9; depth 5; eye 3.9; dorsal 9; anal 13; scales 9–83–10; maxillary 2.6. Body elongate, slender, back not elevated; head rather large, its width equal to half its length; length of top of head 2.25 in distance from occiput to dorsal; greatest depth considerably less than length of head; eye large, equal to snout; gillrakers very long and slender, as long as eye, 20+35; dorsal fin rather high, its height equal to 0.8 depth of body and 1.5 times length of base of fin, its origin nearer base of caudal than snout, its free margin nearly vertical, straight; longest anal ray 0.8 length of base of fin; ventral long, equal to height of dorsal, its length equal to 0.75 of distance from ventral origin to vent; ventral origin midway between base of caudal and pupil; adipose dorsal very small, described as long and slender, of same width throughout, its width 0.33 its length. Mouth large, the lower jaw projecting, the snout straight; maxillary 3 in length of head, its posterior edge extending to line drawn vertically through anterior margin of pupil; mandible 0.5 length of head, its angle under the pupil; teeth present on the tongue. Color above grayish silvery; sides bright silvery; below white; tips of dorsal and caudal dark. Length 10 inches. Known from Seneca and Skaneateles lakes, but probably occurring in other deep lakes of central New York.

Leucichthys sisco (Jordan). *Cisco of Lake Tippecanoe.*

Argyrosomus sisco Jordan, Amer. Nat. 1875, p. 135, Lake Tippecanoe at Warsaw, Ind.; collector, J. H. Carpenter; Rept. Geol. Survey Indiana, 1876, p. 4, with a crude figure, Lake Tippecanoe, Lake Geneva.
Argyrosomus artedi sisco, Jordan & Evermann, Fishes North and Mid. Amer., pt. 1, 1898, p. 469, and elsewhere.

Habitat: Small glacial lakes of northern Indiana and southern Wisconsin formerly tributary to Lake Michigan (lakes Tippecanoe, Barber, Shriner, James, Oconomowoc, Green, La Belle, etc.).

Comparison of the Lake Michigan herring with the "sisco" of Lake Tippecanoe convinces us that no specific difference can be made out by which the two can be separated.

The cisco of Lake Tippecanoe is merely a landlocked form of the ordinary Michigan herring, smaller, softer in flesh, and more plump, but showing no technical differences whatever. This was the judgment of Jordan & Evermann in 1898, but we then made the mistake of supposing the Lake Michigan species to be the true *artedi*. If the common Michigan herring is to receive a distinctive name, it may be provisionally called *Leucichthys sisco huronius*. As a matter of fact, however, *sisco* is the variety and in strictness each separate lake has its own variety of "cisco," as such changes as the form has undergone since post glacial times must have taken place separately in each of the several lakes in which the

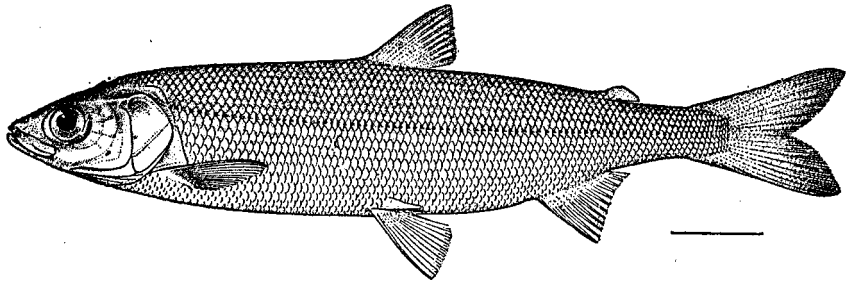


FIG. 5.—*Leucichthys sisco* (Jordan). Cisco of Lake Tippecanoe. (Drawn from specimen 9 inches long, collected in Lake Geneva, Wisconsin.)

cisco is left. As a whole this species differs little from *L. harengus* except in the larger adipose fin, which is, however, subject to considerable variations. In general it is longer than the eye and is contained 3.5 times in the distance from the depressed tip of the dorsal to its base. On the whole *harengus* is the more slender fish and paler in color. Ultimately *ontariensis* and *sisco*, with possibly the deep water *supernas*, may be regarded as subspecies of *harengus*.

The name *Argyrosomus sisco* was applied in 1875 to the cisco of Lake Tippecanoe, a small lake herring, inhabiting the depths of the glacial lakes in northern Indiana and southern Wisconsin, formerly tributary to Lake Michigan. These fishes are known to occur in lakes Tippecanoe, Barber, Crooked, Shriner, Twin, Cedar and James in northern Indiana, and in lakes Geneva, Oconomowoc, and La Belle in Wisconsin. If these are relics of an earlier fauna, as is probable, the cisco in Indiana and the cisco of Wisconsin must have been separately derived from a common ancestor of which *huronius* is the direct descendant, and from which neither has obviously changed. The name *sisco* applied to the first species of fish described by the present senior writer is much older than that of *huronius*, and as elsewhere stated, the common lake form must stand as the subspecies if the two are separated. We do not know the origin of the word "cisco" nor do we know whether it is related to "siscowet." We now adopt the current spelling of "cisco" instead of "sisco," the form under which the cisco of Lake Tippecanoe first became known to us. The following is the substance of the original description of the type of *A. sisco* from Lake Tippecanoe:

Head 4.33 to 5 in length; depth 4.1 (4 to 4.25); eye 3.6 in head; maxillaries 3.33 in head, not reaching center of eye; length of mandible 2.125 in head, much more than least depth of tail; scales 84; dorsal 9 or 10; pectoral 15; ventral 12; anal 12. Form regular, spindle-shaped, slightly elevated at beginning of the dorsal, the form essentially as in the common Lake Michigan herring. Lower jaw the longer; distance from occiput to snout 2.33 in distance from occiput to dorsal; depth at occiput

1.5 in length of head. Scales thin but firm. Dorsal short, rather high, its height 1.5 in head, the longest ray 3 times the shortest; adipose fin "rather slender," reaching slightly beyond anal; pectoral long and pointed, not reaching nearly to ventrals; ventrals more than 0.66 length of head, falling much short of vent, the accessory scale short and triangular, not half length of fin; depth at vent 5.75 in body; caudal deeply forked; vent to base of caudal below, 4.6 times in length.

Color, deep steel blue, becoming gradually paler below to lateral line, where it changes to silvery; scales above dotted with black, with traces of lines along rows of scales; vertical fins and tips of paired fins also thickly punctate; dark dots on skin of head. Length 9.5 inches. Said occasionally to reach a weight of 1.5 to 2 pounds.

A single specimen from Lake Geneva was described at the same time as more slender; the depth 5, the head 4.66 in length, and the eye 4 in head; maxillary 2.87 in head, the depth at the vent 6.75 in length, the distance from the vent to base of caudal below 4 times in length. Scales 77.

The following account was given of the habits of the fish in Lake Tippecanoe by Judge Carpenter:

Some years ago, probably five, these fish were discovered on the north side of Tippecanoe Lake by Isaac Johnson, and at each return of their spawning season, which is the last of November, they have reappeared in large numbers. They are not seen at any other season of the year, keeping themselves in the deep water of the lakes. The general opinion is that they will not bite at a hook, but Mr. Johnson says that he has on one or two occasions caught them with a hook. To my knowledge they have never been found in but two of our lakes, Tippecanoe and Barber, which are both large lakes and close together, as will be seen by reference to the map.

The spawning season lasts about two weeks and they come in myriads into the streams which enter the lakes. There are large numbers of persons who are engaged night and day taking them with small dip nets. They are caught in quantities that would surprise you, could you witness it. Those who live in the neighborhood put up large quantities of them, they being the only fish caught in the lakes that will bear salting. Some gentlemen who have been fishing to-day (Dec. 8) inform me that the run is abating and that in a few days the fishes will have taken their departure for the deep water of the lakes and will be seen no more until next November.

We here present a description of a specimen in the U. S. National Museum, from Lake Geneva, with a figure taken from the same fish. It will be noticed that the differences already noted between Wisconsin and Indiana specimens do not hold in this case, and the same specific name must suffice for both. In the specimen before us the ventral seems to be placed farther forward than in the Michigan herring. This appearance is doubtless fallacious, due to the flabbiness of the fish after spawning and the now rather soft condition of the specimen. In life it would doubtless appear more elongate.

Specimen from Lake Geneva, Wisconsin: Body length without caudal, 8 inches; head 4.33 in body; depth 4.33; length of caudal peduncle 2 in head, its depth 3.33; eye 4 in head; snout 4; interorbital space 3.66; maxillary measured from tip of snout 4; width of opercle 4 in head, subopercle 6.5; dorsal 10; anal 12; scales 8–80–8, between occiput and dorsal 36; branchiostegals 10; gillrakers 18+32.

Body elongate; dorsal and ventral outlines similar, nearly parallel in central third of body; caudal peduncle slender, long, little compressed; head moderate in size, pointed; dorsal outline straight; lower jaw longer than upper; maxillary extending under anterior edge of pupil; teeth on tongue only, very small and few; distance from snout to occiput more than twice in distance from occiput to dorsal.

Scales thin, rather small, not varying much in size between anterior and posterior; lateral line straight, nearest to dorsal contour.

Dorsal inserted slightly nearer caudal than tip of snout, its ray 1.66 in head (specimen mutilated, probably slightly longer); adipose from insertion to tip contained 4 in head, its height 10; anal truncate, its longest ray 2.75 in head; ventral insertion below first rays of dorsal; length 1.66 in head, its scale 2.33 in ventral length; pectoral short, 2.33 in distance between pectoral and ventral bases; caudal deeply forked.

Color in spirits light, darker above, silvery on sides from slightly above lateral line, colorless ventrally; all fins colorless (as far as can be seen in the poor state of specimen).

We have also received three fine specimens of the Indiana cisco, from Lake James, Steuben County, Ind., through the courtesy of Willis S. Blatchley, state geologist of Indiana. These specimens agree with the preceding accounts and we are quite unable to see that they differ in any regard whatever from examples of *huronius* from Port Huron. The adipose fin varies somewhat, but in all it is a little

longer than eye, and 3.5 times in the distance from the depressed dorsal to its base. The gillrakers are 16 to 18+31 or 32. The eye, as in *huronius*, is smaller than in the original *sisco* from Lake Tippecanoe.

It is astonishing how long the slight characteristics of the Lake Michigan and Lake Huron herring (*huronius*) persist in these separated waifs of the glacial lakes, once part of this lake system.

Leucichthys sisco huronius (Jordan & Evermann). *Lake Huron Herring.* (Pl. II.)

Argyrosomus huronius Jordan & Evermann, Proc. U. S. Nat. Mus., XXXVI, p. 167, fig. 2, March 3, 1909, Port Stanley, Ontario.

This is the common blueback or Michigan herring of Lake Huron and Lake Michigan. It occasionally enters Lake Erie, where it is recognized as the Lake Huron herring. We found no specimens in Lake Superior, but have recently received 4 from Wiarton, on Georgian Bay, through the kindness of the Doyle Fish Company, of Toronto. The original type of *huronius* figured by Jordan & Evermann was obtained at Port Stanley, on the north shore of Lake Erie, where about a dozen of this species were found mixed with about a thousand of *Leucichthys eriensis*. We have also specimens obtained at Erie, Pa., by Dr. Seth E. Meek, and numerous young examples from Lake Michigan. We are not able to see that these differ from Lake Huron specimens. Numerous specimens were taken at Port Huron and Mackinac. These vary considerably in the number of scales (80 to 90), but the form and general coloration of lustrous blue is seen in all examples. In all, the adipose fin is large, and the space between pectoral and ventral more than twice length of pectoral. The caudal peduncle is almost as

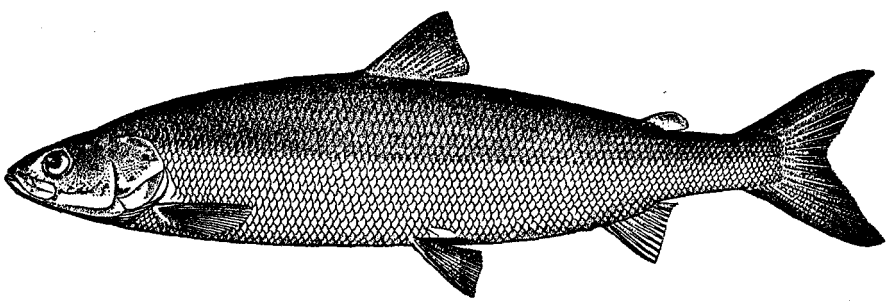


FIG. 6.—*Leucichthys sisco huronius* (Jordan & Evermann). Lake Huron Herring. From the type.

slender as in *harengus*. We may note that but a single specimen of *artedi* as accurately determined has been seen by us from Lake Huron.

The Lake Huron herring may be described as follows: Head 4.66 in length to base of caudal; depth 4.25; length of caudal peduncle from anal to first caudal rays 2 in head; depth of caudal peduncle 2.9; eye 5; snout 4; interorbital space 3.33; length of maxillary from tip of snout 3; dorsal 10 or 11; anal 11 or 12; scales in lateral line 75 to 85; between lateral line and origin of dorsal 8; between occiput and dorsal 36; gillrakers 14 to 16+29 to 31.

Body notably elongate, elliptical, with slender, pointed head and slender tail, less compressed than in the other species of the genus; head small, the snout long and pointed, distance from tip of snout to posterior edge of orbit equaling 0.5 length of head;[a] lower jaw not closing within the upper, but extending slightly beyond it; maxillary reaching a point below center of pupil, its width contained 3 times in the length; teeth on tongue only, minute, seen only by drying; gillrakers on first arch very slender, those near angle equal in length to diameter of eye; lateral line almost straight; scales large and rather loosely attached; dorsal inserted midway between anterior border of eye and base of caudal; height of first ray contained about 1.6 times in length of head; adipose fin large, longer than eye; length of base about equal to its height; origin of ventrals below middle of dorsal, the rays slightly shorter than those of dorsal; length of first anal ray 2.5 in head; caudal deeply forked; pectoral short, about 1.5 in head.

[a] Our drawing is not accurate as to this character.

Color in life, clear metallic blue above, silvery below; in spirits, silvery, dusky above, light below; a very indistinct, narrow, dusky stripe along each row of scales on upper half of body; dorsal with a broad dusky margin; caudal largely dusky; a mere trace of dark color on paired fins and the anal.

The type, no. 62516, U. S. National Museum, a female, measures 14.75 inches in length and was taken at Port Stanley, Ontario, by the writers, on July 29, 1908. A cotype, no. 13082, Stanford University collection, measuring 17 inches long, has 10 rays in the dorsal and a slightly longer pectoral.

The flesh of this species is rather dry and flavorless, something like that of the Menominee whitefish, *Coregonus quadrilateralis*, and it is not to be compared as a food fish with the Erie herring.

Comparison of specimens of Leucichthys sisco huronius.

	Erie, Pa.		Port Huron.		
Specimen no.	4932	4912	5226	5222	5224
Length without caudal ..... *mm*	310	290	290	325	220
Dorsal rays (fully developed)	10	10	10	10	11
Anal rays	12	11	11	12	12
Scales	8–84–7	8–85–7	8–75–7	8–82–7	8–82–8
Scales between occiput and dorsal fin	34	38	35	38	36
Branchiostegals	9	9	9	9	9
Gillrakers	16+31	16+31	14+29	14+29	16+31
Sexual condition	Spawning ♀	Spawning ♀	.....	.....	.....
Ova diameter ..... *mm*	1.8	1.8	.....	.....	.....
Comparative measurements: [a]					
Head	0.21	0.22	0.22	0.22	0.23
Depth	.24	.24	.21	.21	.22
Caudal peduncle, length from anal to first caudal rays	.10	.11	.12	.125	.11
Caudal peduncle, depth	.07	.07	.075	.07	.07
Eye	.045	.04	.045	.04	.055
Snout	.05	.055	.055	.055	.06
Interorbital space	.065	.06	.065	.06	.065
Maxillary length from tip of snout	.075	.075	.075	.075	.07
Snout to occiput	.14	.15	.15	.15	.16
Ventrals to pectorals	.35	.35	.34	.28	.33
Pectorals in pectoral-ventral distance	2.50	2.33	2.20	2.00	2.20
Pectoral length	.14	.14	.15	.15	.15
Ventral length	.14	.14	.14	.14	.14
Dorsal height	.125	.13	.14	.135	.14
Adipose length	.065	.06	.06	.06	.065
Anal height	.08	.09	.095	.095	.08

[a] Measurements in hundredths of body length unless otherwise specified.

Leucichthys ontariensis Jordan & Evermann, new species.

Coregonus clupeiformis, De Kay, New York Fauna, Fishes, p. 248, pl. 60, fig. 198, 1842, Lake Ontario; not of Mitchill.

Habitat: Lake Ontario and Cayuga Lake, New York.

The ordinary lake herring of Lake Ontario is allied to *Leucichthys artedi*, but is more elongate, the caudal peduncle more slender, the pectoral not reaching nearly halfway to ventrals and the color much darker, the back, as in *Leucichthys sisco huronius*, being lustrous blue. In all these regards the form stands intermediate between *L. sisco* and *L. artedi*, though doubtless nearer the former, toward which it seems to vary. The adipose fin, as in *huronius* and *artedi*, is large. From *huronius* it differs in being more compressed and stouter in every part.

The specimens before us, five in number, were taken by Dr. Seth E. Meek at Deseronto, Ontario, the Bay of Quinte. The type is no. 64673, U. S. National Museum (collector's number 29–2). This description is based on the type and four other specimens from Deseronto.

Head 4.5 in body without caudal; depth about 4 (3.75 to 4.25); length of caudal peduncle from last rays of anal to first of caudal 2.5 in head, depth 2.66; eye 4.75 in head; snout 4; interorbital space 3.75; maxillary, measured from tip of snout, 3; width of opercle 3.66 in head, subopercle 6.75; dorsal 10; anal 11; scales 9–76–8, between occiput and dorsal 35; branchiostegals 9; gillrakers 14+27.

Body elongate, more so than in *Leucichthys artedi;* dorsal and ventral outlines similar, convex; body compressed, width 2.12 in depth; depth varying in other specimens to 4 in body length, in which case the width is 1.75 to 2 in depth; caudal peduncle not greatly compressed, longer than deep; head

pointed, lower jaw slightly projecting, not usually included in the upper; maxillary extending to below anterior edge of pupil, its width 3 in its length, supplementary bone 3 in its length. Very minute teeth on tongue, none elsewhere. Scales moderate, not firmly attached, nearly equal in size posteriorly above anal, but not quite to those above tip of pectoral; lateral line nearly straight. Dorsal inserted midway between snout and caudal, its longest ray 1.66 in head; adipose fin moderate, measured from insertion to tip 4 in head, its height 9; anal concave, its longest ray 2.5 in head; ventral length 1.62 in head, its scale 2.5 in ventral length; pectoral short, reaching less than halfway to insertion of ventrals, its length 2.33 in distance between pectoral and ventrals.

Color in spirits dark; a dark blue shading under the scales dorsally, silvery laterally and colorless ventrally; dorsal darkened on distal end; caudal dark, edged with darker; anal, ventrals, and pectorals nearly clear.

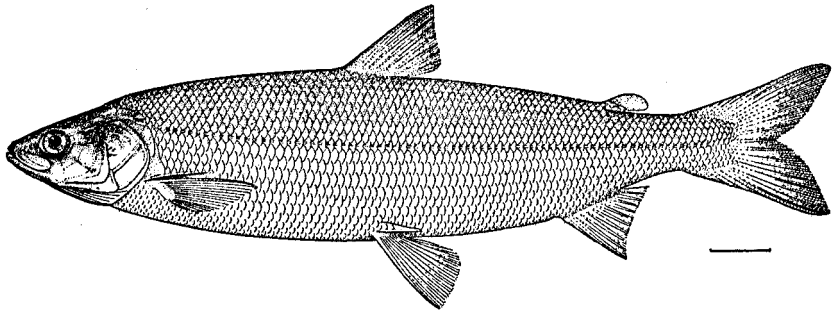


FIG. 7.—*Leucichthys ontariensis* Jordan & Evermann, new species. (Drawn from a specimen 13 inches long, collected in Lake Ontario off Deseronto, Ontario.)

This species is intermediate between *sisco* and *artedi*, differing from the latter chiefly in the greater elongation of the body and the relatively shorter pectoral fin. It is claimed by fishermen that a mesh of 2⅜ inches is required for these fishes, while 3⅛ is adequate for the capture of *artedi* or *eriensis*.

Reed & Wright[a] say that this fish, which they identified as *L. osmeriformis*, is taken in Cayuga Lake in fairly large numbers, but that it is not as common as formerly. They were informed by old fishermen that it has never been abundant since the introduction of the alewife, which occurred about 1872, or earlier.

Comparison of specimens of Leucichthys ontariensis from Deseronto.

Specimen no.	495	492	4918
Length without caudal ..... *mm.*	300	300	310
Dorsal rays	10	10	11
Anal rays	11	11	13
Scales	9-76-8	8-72-7	9-77-7
Scales between occiput and dorsal fin	35	31	35
Branchiostegals	9	10-8	9
Gillrakers	14+27	16+29	16+29
Comparative measurements:[b]			
Head	0.22	0.21	0.22
Depth	.28	.24	.28
Caudal peduncle, length from anal to first of caudal	.095	.11	.09
Caudal peduncle, depth	.08	.08	.09
Eye	.05	.05	.05
Snout from eye	.06	.05	.06
Interorbital space	.06	.06	.06
Maxillary length from tip of snout	.075	.07	.07
Snout to occiput	.15	.15	.15
Ventrals to pectorals	.34	.34	.37
Pectoral length in pectoral-ventral distance	2.33	2.33	2.66
Pectoral length	.14	.15	.15
Ventral length	.14	.15	.15
Dorsal height	.14	.14	.15
Adipose length	.055	.065	.06
Anal height	.08	.085	.10

[a] The vertebrates of the Cayuga Lake basin, New York, by Hugh D. Reed & Albert H. Wright, Proceedings American Philosophical Society, vol. XLVIII, no. 193, 1909, p. 398.

[b] Measurements in hundredths of body length unless otherwise specified.

Leucichthys lucidus (Richardson). *Great Bear Lake Herring.*

Salmo (*Coregonus*) *lucidus* Richardson, Fauna Bor.-Amer., vol. III, p. 207, pl. XC, fig. 1, 1836, with figure, Great Bear Lake.

Coregonus lucidus, Günther, Cat., vol. VI, p. 198, 1866, Great Bear Lake. Gilbert, Bull. U. S. Fish. Comm., vol. XIV, 1894, p. 24, Great Bear Lake.

Argyrosomus lucidus, Jordan & Evermann, Fishes North and Mid. Amer., pt. I, p. 471, 1898; after Gilbert. Scofield Report Fur-Seal Invest., pt. III, p. 495, 1898, Arctic Sea off Herschel Island.

Habitat: Mackenzie River Basin.

The herring of Great Bear Lake is known from Richardson's description and excellent figure, and from specimens taken in 1893 by the artist, Miss Elizabeth Taylor. From these specimens now before us the following description has been prepared. Two specimens were also obtained by Scofield & Seale in the Arctic Sea off Herschel Island. The species has a very long, compressed body and a large adipose fin. It is nearest in its relationship to *L. ontariensis*, but the differences are obvious. In Richardson's figure the adipose fin is represented as far too small and too far back, but it is to be remembered that this figure is taken from a dried skin.

Head small, 5 to 5.33; depth 4.33 to 4.6; eye 5; dorsal 11 or 12 developed rays; anal 11 or 12; scales 85 to 87, 11 or 12 in an oblique series downward and forward from front of dorsal to lateral line. Eye slightly less than length of snout, 1.5 times in interorbital width. Body slender, elongate, the curve of back and belly about equal, the greatest depth exceeding length of head; snout narrow, almost vertically truncate when mouth is closed, the lower jaw fitting within the upper, but the mouth not inferior; distance from snout to nape 2.60 to 3 in distance between nape and front of dorsal; head much smaller in one of our specimens than in the other; mouth oblique, with rather slender maxillary, which extends to vertical midway between front and middle of pupil, its length from tip to articulation equaling distance from end of snout to front of pupil, and contained 3.66 to 3.8 in length of head; supplemental maxillary bone probably broader than in *L. artedi*, from .6 to .66 greatest width of maxillary; suborbitals very narrow, their least width less than half diameter of pupil; supraorbital bone large, its width 2.5 to 2 66 in its length. Gillrakers very long and slender, the longest slightly more than .66 length of eye, 16+28 in number in each specimen. Front of dorsal slightly nearer tip of snout than base of upper rudimentary dorsal rays (the fins are mutilated, so that their length can not be given); adipose fin large, inserted vertically above last anal rays, its height from tip to posterior end of base equaling vertical diameter of eye. Color silvery. As pointed out by Doctor Günther, this northern form differs from *L. artedi* in its shorter head and smaller eye. It seems also to have the premaxillaries placed at a greater angle than in *L. artedi*.

Leucichthys laurettæ (Bean). *Lauretta Whitefish.*

Coregonus laurettæ Bean, Proc. U. S. Nat. Mus., vol. IV, 1881, p. 156, Point Barrow, Alaska; type no. 27695; coll. Capt. Calvin L. Hooper.

Argyrosomus laurettæ, Jordan & Evermann, Fishes North and Mid. Amer., pt. III, p. 471, 1898. Evermann & Smith, Rept. U. S Fish Comm. 1894, p. 374, pl. 25 (1896) Point Barrow. Evermann & Goldsborough, Bull. Bureau Fisheries, vol. XXVI, 1906 (1907), p. 235, Point Barrow, Port Clarence, Yukon River at Nulato, Meade River, Kuaru River, Elson Bay, Nushagak River, Naknek River.

Habitat: Lakes and streams of northern and western Alaska.

This species is apparently common in northern Alaska. It seems to be an ally of *L. lucidus*, having the adipose fin large, the caudal peduncle slender, and the pectoral not reaching halfway to ventrals. The fins are perhaps larger than in *L. lucidus*, the head smaller and the body deeper.

The following is the substance of Doctor Bean's account of this species:

Head 5; depth 4; eye 4.5 to 5; dorsal 12; anal 11; ventral 12; scales 10–84 to 95–10, 84 to 87 in specimens examined. Body robust, the back elevated; head small and slender, the small eye not longer than snout; distance from nape to front of snout 2.5 times in its distance from dorsal; maxillary about reaching middle of eye, 3.5 in head, its supplemental bone half its length; lower jaw very slightly longer than upper; mandible 2.33 in head; lingual teeth present; gillrakers long and numerous, 10+25; ventral scale not half length of fin; pectoral short, not reaching halfway to ventrals. Scales smaller than in *L. artedi*, 16 cross series under base of dorsal. Alaska, from Yukon River northward to Point Barrow, generally common. Apparently very close to *L. lucidus*, but the base of dorsal longer.

Leucichthys alascanus (Scofield). *Arctic Lake Herring.*

Argyrosomus alascanus Scofield, in Jordan & Evermann, Fishes North and Mid. Amer., pt. III, p. 2817, Nov. 28, 1898, and in Jordan, Report Fur-Seal Invest., pt. III, p. 495, pl. XLII, 1898, Point Hope, Grantley Harbor, Arctic Sea.

Habitat: Arctic Alaska, entering the sea.

This species is allied to *Leucichthys sisco*, but has the body less elongate and the caudal peduncle stouter. The pectoral, as in *L. artedi*, reaches more than halfway to the ventrals. The adipose fin is said to be large, but in Scofield's type and as shown in his figure, it is slender and moderately long, midway in size between *sisco* and *harengus*. The ventrals are short, but they reach more than halfway to the anal, a character which will probably separate the species from *harengus*.

It is not certain that this species differs from *Leucichthys laurettæ* of the same region. The body in the latter is deeper and the head smaller, but these may not be trustworthy characters.

The species is known only from the specimens taken by Scofield & Seale. It is described as follows by Scofield:

Head 4.25; depth about 4; dorsal 12; anal 12; scales 10–85–9; eye a little shorter than snout, 5 in head, 1.33 in interorbital space; head wedge-shaped, the upper and lower profiles straight and meeting with a sharp angle at the snout. Viewed from above the snout is blunt, almost square, the narrow, pale, rounded tip of the lower jaw slightly projecting; mouth oblique, the distance from tip of snout to tip of maxillary equal to distance from tip of snout to center of pupil; the maxillary from its anterior articulation is contained 3.5 in the head, its width 3 in its length, its upper anterior edge closing under maxillary; mandible 2.33 in head, its articulation with the quadrate bone beneath the posterior edge of the eye; width of supplemental bone a little more than .5 width of maxillary; preorbital broad, its greatest width equaling .37 of its length, or diameter of pupil; width of supraorbital equaling .28 of its length; gillrakers 12 to 14+21 to 23, long and slender, the longest .66 diameter of the eye; tongue, vomer, and palatine without teeth; distance from tip of snout to nape equaling .5 distance from nape to front of dorsal, or .66 length of head; adipose fin large, ventral scale .5 length of fin; longest dorsal ray 1.5 in head; longest anal ray 2 in head; pectoral reaching more than halfway to ventrals; ventrals reaching .66 distance to vent; caudal forked for a little more than .5 its length. Color dusky above, silvery beneath; the dorsal, adipose fin, tips of caudal rays, and upper side of anterior pectoral rays dusky; fins otherwise pale. But three specimens of this fish were obtained—one in salt water at Point Hope, the other two in brackish water at Grantley Harbor. The largest one is 10.5 inches in length.

Leucichthys pusillus (Bean). *Least Lake Herring.*

Coregonus pusillus Bean, Proc. U. S. Nat. Mus., vol. XI, 1888, p. 526, Kobuk River, Alaska, type, 38366; coll. Chas. H. Townsend.

Argyrosomus pusillus, Jordan & Evermann, Fishes North and Mid. Amer., pt. I, p. 470, 1898, after Bean. Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 312, pl. 23 (1896). Scofield, Fur-Seal Invest., pt. III, p. 494, 1898, Grantley Harbor, Barter Island, Naknek River, Nushagak River. Evermann & Goldsborough, Bull. Bureau Fisheries, vol. XXVI, 1906 (1907), p. 235, Lake Bennett at Caribou Crossing; coll. Jordan & Evermann, with description.

Habitat: Lakes of Yukon basin and Alaska generally.

This is one of the smallest of the American species, rarely reaching a foot in length, and the flesh, which is said to be bony, is mainly used as food for dogs. The fish is said to be widely distributed throughout northern and western Alaska. Our specimens are from Grantley Harbor. Scofield & Seale found it in the Arctic Sea and about Bristol Bay. It is a slender species with long lower jaw, large adipose fin, the pectoral reaching more than halfway to the ventrals, and usually the dorsal fin is spotted and the fins are all high. It is a well-marked species, probably nearest *L. alascanus*.

The following is the substance of Doctor Bean's account:

Head 5; depth 5; eye 3.75 in head; dorsal 10; anal 12; ventral 11; scales 10–91–9. Body rather elongate, compressed. Form of mouth as in *L. artedi*, the lower jaw considerably projecting; maxillary broad, with rather broad supplemental bone, three times as long as wide, extending not quite to middle of the very large eye, its length 3.33 in head; preorbital extremely narrow; mandible 2.33 in head. Teeth none, or reduced to minute asperities on the tongue. Gillrakers numerous, very long and slender, 49 in all. Dorsal very high, much higher than long, its last rays rapidly shortened, the first rays twice length of base of fin; caudal large, well forked; anal small; ventral inserted under middle of dorsal, very long, .83 length of head; pectoral the same length. Scales as in *L. artedi*. Steel-bluish

above, with many dark points; belly white; dorsal and caudal mostly blackish; pectorals and ventrals tipped with black; eye blackish, the iris silvery. Length a foot or less. Yukon River to Bering Sea and northward, ascending rivers.

To this Evermann & Goldsborough add the following from specimens from Lake Bennett at Caribou Crossing:

Head 4.67 in body; depth 5.5; eye 3.75 in head; dorsal 10; anal 12; ventral 11; scales 10–90–8.

Body rather elongate, compressed; mouth oblique, gape rather small, extending back about half the length of the maxillaries; lower jaw considerably projecting; maxillary broad, somewhat curved, not extending much beyond the anterior margin of orbit, its length 3.13 in head; mandible long, reaching to below middle of pupil, 2.3 in head; teeth almost microscopic in both jaws, none on tongue; gillrakers long, slender, and numerous, 10+26 and 13+28; dorsal high, its longest ray (about the third) about 1.3 in head and about twice length of base; base of dorsal 2.5 in head; dorsal rays shortening rapidly after third and fourth, leaving the margin of the fin very slightly concave; insertion of dorsal midway between tip of snout and a point about halfway between adipose and caudal fins; caudal large, equally forked, both lobes and indentation acutish; anal low, its longest ray 2.25 in head, its base 2 in head, its posterior margin slightly concave; ventrals inserted somewhat behind origin of dorsal, reaching about .66 distance to origin of anal, the length of their longest rays about 1.3 in head; pectoral equaling ventral.

Bluish above, with minute black punctulations; sides below lateral line and a short distance above silvery, belly white; dorsal and caudal almost imperceptibly dusky; other fins wholly plain; iris silvery a narrow blackish ring about the orbit plainest above and below.

Leucichthys artedi (Le Sueur). *Lake Herring; Erie Herring; Common Lake Herring; Grayback.*

Coregonus artedi Le Sueur, Journ. Ac. Nat. Sci. Phila., vol. 1, 1818, p. 231, Lake Erie (at Buffalo) and Niagara River (Lewistown); description inadequate. Jordan & Gilbert, Synopsis, p. 301, 1883.

Argyrosomus artedi, Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 305, in part (not plate). Jordan & Evermann, Fishes North and Mid. Amer., pt. 1, p. 468, 1898. Of recent authors generally.

Coregonus clupeiformis, Günther, Cat., vol. VI, p. 198 (not *Salmo clupeaformis* Mitchill).

The name *artedi* applied by Le Sueur to specimens from near Buffalo must be retained for the common lake herring of Lake Erie.

This species is characterized by its relatively deep elliptical form with compressed sides and rather stout caudal peduncle, in connection with the large adipose fin. All the other species of this subgenus, *bisselli* and *eriensis* excepted, are much more slender in all their parts. The average length of this species in Lake Erie is 12 to 14 inches and the weight about 14 or 15 ounces. The fishermen of Lake Erie are in general entirely satisfied with a mesh of 3⅛ inches to catch *artedi* and *eriensis*, while for the other species a mesh of 2½ inches is required, and this is too coarse for the form called *supernas*. This species is also paler in color than any of the others, *eriensis* excepted, and lacks the blue shades characteristic of *huronius* and *ontariensis*. The flesh in *artedi*, as in *huronius*, is much inferior to that of *eriensis*.

This is the most abundant of the lake herrings so far as market fishing is concerned. It abounds in Lake Erie, especially in its southern parts. It ascends to Lake St. Clair, and we have one fine example from Lake Huron at Port Huron, where it was taken with a multitude of *huronius*. We have also examples obtained by Dr. Seth E. Meek at Toronto. As Doctor Meek was present at the capture of the Toronto specimens, there is no doubt that they came from Lake Ontario, but we know also that whitefish and herring fry have been often transferred from Lake Erie to other lakes, and it is possible that *L. artedi* is not native to Lake Ontario.

The specimens here figured are from Cleveland and Toronto. The fish from the latter place is a ripe female with unusually deep body. Others at hand for comparison are five from Erie, one from Port Maitland, three from Toronto, and one from Port Huron (Lake Huron). The presence of a specimen at the latter locality indicates the tendency of these closely allied species to invade one another's territory.

The Lake Erie herring is described as follows, from eleven specimens, between 8.3 inches and 11.8 inches long, from Lake Erie off Cleveland:

Head 4.4 in body to base of caudal; depth of body 3 to 4; length of caudal peduncle from last rays of anal to first of caudal 2 to 2.75 in head, its depth 2 to 2.5; eye about 4.4; snout 4; interorbital space slightly greater than length of snout; maxillary measuring from tip of snout 2.87 in head;

width of opercle 3.33; dorsal rays (fully developed) 10 or 11; anal 12; scales 8—69 to 75—7, between occiput and dorsal 30 to 35; branchiostegals 8 or 9; gillrakers 15 or 16+27 to 31 on first gill-arch.

Body not elongated, but somewhat compressed and usually deep; dorsal and ventral outlines similar and usually symmetrical, greatest depth at insertion of dorsal; width about 2.12 in depth; caudal peduncle compressed, deep, frequently deeper than long. Head small, pointed, with narrow snout; jaws subequal, the premaxillaries variably oblique; maxillary moderate in length, extending to or slightly beyond perpendicular from front margin of pupil, its width about 3 in length; supple-

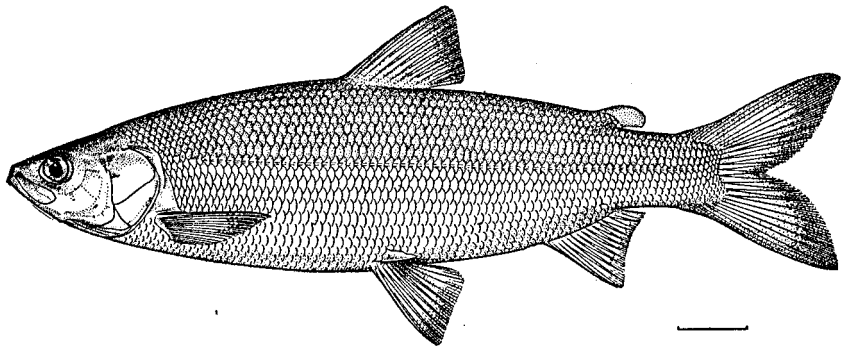


FIG. 8.—*Leucichthys artedi* (Le Sueur). Lake herring. (Drawn from a specimen 12 inches long collected in Lake Erie off Cleveland.)

mentary bone large, well developed; very minute teeth on tongue, absent elsewhere; distance from snout to occiput less than half distance from occiput to dorsal. Scales moderately large, firm, slightly broader anteriorly; lateral line straight, prominent, nearer back than belly.

Dorsal fin inserted midway between snout and base of caudal, its base about 2 in head, its height about twice maxillary length, but variable, margin truncate or slightly concave; adipose large, its length from insertion to tip contained 3 to 4 in head; pectoral usually long, reaching at least half

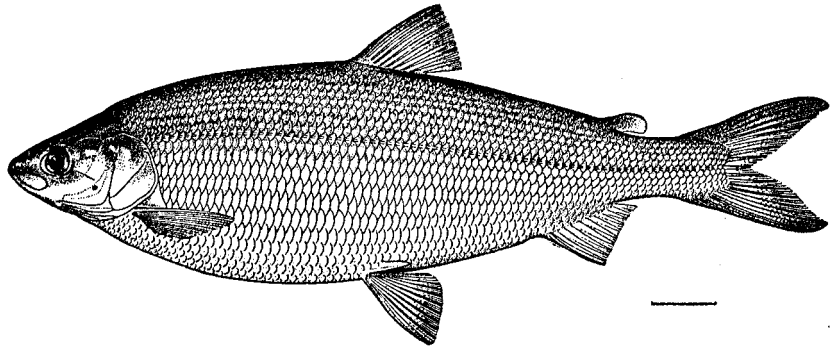


FIG. 9.—*Leucichthys artedi* (Le Sueur). Lake herring. Female. (Drawn from a specimen 12 inches long from the Toronto market.)

distance to ventrals (contrasting with *L. ontariensis*), but very variable; ventral equal or slightly less in length than height of dorsal, rather shorter than usual; anal very short, its longest ray usually somewhat longer than depth of caudal peduncle, its base about equal to that measurement, margin concave; caudal rather short, not very deeply forked.

Color in spirits silvery, darker above; somewhat less silvery and colorless ventrally; dorsal and caudal slightly edged with black, but comparatively pale; pectorals, anal, and ventrals colorless, save for an occasional stipple of black.

Comparison of specimens of Leucichthys artedi.

	Cleveland.		Erie, Pa.	Port Huron.	Port Maitland.	Toronto.	
Specimen no.	5252	5251	523	5223	5225	4930	4937
Length without caudal ..... *mm.*	252	245	260	235	200	262	205
Dorsal rays	11	11	10	11	10	10	11
Anal rays	12	12	12	12	12	11	12
Scales	8-74-7	8-76-7	8½-71-7	9-69-8	8-72-7	8-71-7	8-75-7
Scales between occiput and dorsal fin	33	35	33	30	31	31	30
Branchiostegals	8	8	9	8	8	9	8 or 7
Gillrakers	16+27	16+29	16+29	Evisc.	15+29	16+29	16+31
Comparative measurements:[a]							
Head	0.22	0.23	0.23	0.235	0.23	0.225	0.24
Depth	.28	.30	.30	.26	.23	.28	.27
Caudal peduncle—							
Length[b]	.092	.11	.09	.10	.095	.11	.11
Depth	.10	.10	.10	.09	.085	.09	.09
Eye	.05	.05	.055	.055	.055	.05	.05
Snout from eye	.055	.055	.06	.055	.055	.06	.06
Interorbital space	.065	.07	.07	.065	.06	.065	.06
Maxillary length from tip of snout	.08	.08	.08	.09	.075	.08	.08
Snout to occiput	.15	.155	.16	.165	.155	.145	.15
Ventrals to pectorals	.31	.34	.33	.335	.30	.35	.31
Pectoral length in ventral-pectoral distance	2.00	2.00	2.00	1.89	1.75	2.00	1.89
Pectoral length	.17	.175	.17	.17	.17	.165	.17
Ventral length	.17	.175	.17	.17	.17	.165	.17
Dorsal height	.18	.19	.18	.16	.175	.16	.17
Adipose length	.07	.08	.06	.06	.07	.075	.07
Anal height	.105	.12	.115	.10	.12	.05	.10

[a] Measurements made in decimal fractions of body length without caudal unless otherwise specified.
[b] Length from anal to first caudal rays.

Comparison of L. artedi and L. eriensis.

	L. artedi, Erie, Pa.		*L. eriensis*, Port Stanley.
Specimen no.	491	493	13083 (cotype).
Length without caudal ..... *mm.*	285	305	310
Dorsal rays (fully developed)	10	10	11
Anal rays	11	11	11
Scales	8-65-7	8-73-7	7½-81-8
Scales between occiput and dorsal fin	29	31	33
Branchiostegals	8	9	9
Gillrakers	14+31	14+31	17+32
Sexual condition	Spawning.	Spawning.	Not ripe.
Ova diameter ..... *mm.*	2	2	.....
Comparative measurements:[a]			
Head	0.22	0.22	0.22
Depth	.32	.34	.28
Caudal peduncle—			
Length[b]	.09	.08	.08
Depth	.10	.11	.095
Eye	.05	.055	.04
Snout	.055	.05	.05
Interorbital space	.065	.07	.065
Maxillary length from tip of snout	.075	.075	.07
Snout to occiput	.14	.15	.14
Ventrals to pectorals	.34	.36	.33
Pectorals in pectoral-ventral distance	2.00	2.20	2.00
Pectoral length	.17	.17	.165
Ventral length	.165	.17	.15
Dorsal height	.16	.17	.15
Adipose length	.065	.075	.075
Anal height	.11	.11	.12

[a] Measurements in hundredths of body length to base of caudal.
[b] From last anal to first caudal rays.

Leucichthys artedi bisselli (Bollman). *Rawson Lake Herring; Bissell's Herring.*

Coregonus tullibee bisselli Bollman, Bull. U. S. Fish Comm., vol. VIII, p. 223, 1888, Rawson Lake and Howard Lake, Michigan.

Argyrosomus tullibee bisselli, Jordan & Evermann, Fishes North and Mid. Amer., pt. I, p. 473, 1898.

Habitat: Glacial lakes of southern Michigan once tributary to Lake Erie.

A large plump lake herring was described by Charles Harvey Bollman in 1888, from Rawson and Howard lakes at Schoolcraft, Kalamazoo County, Mich., in connection with his survey of the fish fauna of southern Michigan. Because of its robust form it was regarded by Bollman as a subspecies of *the tullibee*. Its relationships are, however, wholly with *artedi*, of which it may be regarded as a subspecies. The accompanying description and figure are taken by us from Bollman's type, no. 40619, U. S. National Museum:

Head contained 4.5 in length without caudal; depth 3.5; depth of caudal peduncle 2.33 in head; eye 5.2; snout 5; interorbital space 3.66; length of maxillary from tip of snout 3.25 in head; dorsal 11; anal 11; scales in lateral line 77, between dorsal and lateral line 10, between ventral and lateral line 9, and between occiput and dorsal 30; branchiostegals 9. Gillrakers 16+29, 0.75 diameter of eye in length.

Body strongly compressed, its width from side to side contained 1.83 in head; dorsal outline arched upward strongly from head; ventral outline convex; head flat dorsally, pointed; snout rounded;

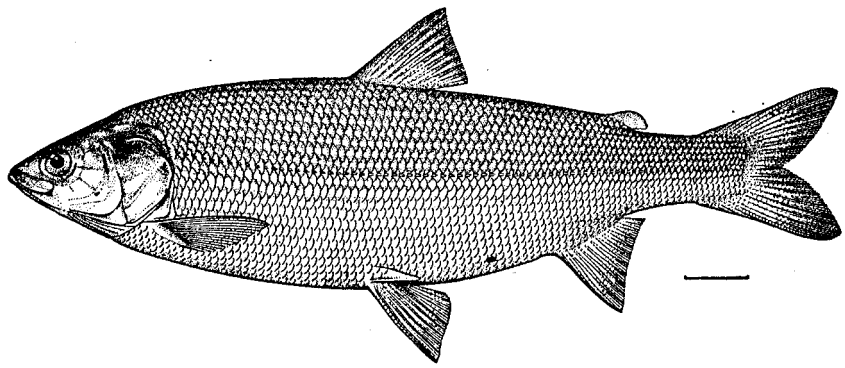


FIG. 10.—*Leucichthys artedi bisselli* (Bollman). Rawson Lake herring. (Drawn from a specimen 13 inches long, collected in Howard Lake, Michigan.)

lower jaw slightly longer than upper; maxillary extending to below anterior edge of pupil, the supplemental parts three times as long as broad; width of opercle 3 in head. Dorsal inserted midway between snout and caudal base, its longest ray 1.5 in head; adipose base 6 in head, length from insertion to tip 3.33 in head; anal base 2.33 in head, longest ray 2.25, and its scale 2.5 in ray length.

Color in spirits, light olive, somewhat darker above; sides silvery; dorsal fin clear, edged with dark, other fins clear.

This subspecies is slightly more robust than *L. artedi*, but no differences of importance set it off from the lake form from which it is no doubt derived.

Leucichthys eriensis (Jordan & Evermann). *Jumbo Herring; Erie Great Herring.*

Argyrosomus eriensis Jordan & Evermann, Proc. U. S. Nat. Mus., vol. XXXVI, March 3, 1909, p. 165, fig. 1, Lake Erie at Port Stanley.

Habitat: Lake Erie, northward.

This species inhabits especially the north shore of Lake Erie, where it is extremely abundant. As a food fish it is far superior to the other lake herrings and is as good as the best whitefish. The original type came from Port Stanley. Besides the type we have examples from Port Burwell and Point Rondeau. Reports of jumbo herring from Toronto have reached us, but these probably refer to large examples of the local species. As the fishes from Port Stanley are largely sold in Toronto, it is possible that the reference is to Lake Erie examples of the present species.

The jumbo herring has been confounded with the tullibee, with which it has nothing in common save the robust form. The name "mongrel whitefish" belongs to *eriensis*, not to the tullibee. The nearest relative of *L. eriensis* is *L. artedi*, from which it differs in the much more robust form, deeper nape, smaller head, and firmer scales.

The following is the original account:

Head 4.4 in length, measured to base of caudal; depth 3.4; depth of caudal peduncle 2.2 in head; eye 5.2; snout 3.75; interorbital space 3.25; length of maxillary from tip of snout 3; dorsal 10; anal 12; scales in lateral line 71; between lateral line and origin of dorsal 8; between occiput and dorsal 32.

Body very deep, its width contained 1.4 times in head; dorsal outline curved abruptly upward behind occiput; dorsal contour of head straight; snout pointed, though rather blunt at tip; jaws about equal, the lower closing just beneath the upper at tip; maxillary extending to a point beneath anterior edge of pupil, the supplemental part about 3 times as long as wide. Gillrakers on first arch 16+29, very slender, the longest equal in length to diameter of orbit. Scales firmly attached. Dorsal inserted about midway between tip of snout and base of caudal, the highest (first) ray contained 1.5 times in length of head; height of adipose dorsal equal to 1.5 times the length of its base; height of anal contained 2 times in length of head; outline of both dorsal and anal slightly concave; origin of ventral below anterior part of dorsal, length of fin contained 1.5 in head; pectoral 1.4 in head.

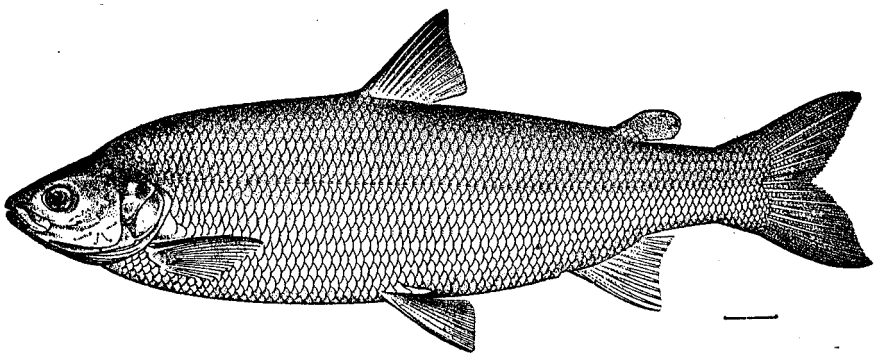


FIG. 11.—*Leucichthys eriensis* (Jordan & Evermann). Lake Erie Herring; Jumbo Herring. From the type.

Color in spirits silvery, dusky on upper parts, but without blue shades in life; distal portion of dorsal, outer part of caudal, and edge and tip of pectoral dusky; other fins white.

Type (no. 62515, U. S. Nat. Mus.) from Lake Erie at Port Stanley, Ontario, measuring 16½ inches in length, and collected by the writers. This represents the maximum size of the species as seen by us. Its weight when fresh was 2¾ pounds. A cotype, 14½ inches long, no. 13083, Stanford University collection, obtained at the same time, is a little smaller and slightly darker in color, the anal having a terminal dusky cloud. It has 11 dorsal and 11 anal rays.

This species is very abundant along the northern shore of Lake Erie about the first of August. It is also occasionally taken in the southern part of Lake Huron, but it seems to be unknown in Lake Superior, and we did not hear of it in Lake Ontario. On the date of our visit to Port Stanley, July 29, 1908, about 1,500 pounds were taken in the gill nets. The largest of these weighed 2¾ pounds and were about 18 inches in length. The bulk of the catch was, however, about 14 inches in length. It is said of this species that there is a "great spurt," or large run, in the spring and a short one in the autumn before the spawning time in November.

The jumbo herring was also seen at Port Burwell, where large numbers are smoked, having an excellent flavor as thus prepared. Many others from Point Rondeau, Ontario, were seen in the Detroit market.

Leucichthys eriensis is characteristic of the northern part of Lake Erie, although other species, *Leucichthys artedi*, the common lake herring, and *Leucichthys sisco huronius* are found in the same lake. It is said to have been virtually unknown until ten years ago, but is rapidly increasing in abundance.

Fishermen claim that it is found in middle water, not at the surface nor at the bottom. As a food fish it is far superior to any other lake herring, being as delicate and rich as the best whitefishes, *Coregonus albus* and *Coregonus clupeaformis*. It is therefore a species worthy of careful attention from the propagators of fishes. Most of the fishermen claim never to have seen examples of 2 or 3 pounds until within four or five years. It is locally known as the jumbo herring because it reaches a larger size than any other lake herring except the tullibee of the northwestern lakes (*Leucichthys tullibee*).

It is believed by many fishermen that the jumbo herring is the product of a cross between the Erie whitefish (*Coregonus albus*) and the lake herring (*Leucichthys artedi*). This belief is without foundation. It rests on the fact that at the Put-in Bay hatchery attempts have been made to fertilize whitefish eggs with the milt of the lake herring, in default of the milt of its own species. To test this matter Mr. Frank N. Clark, of the hatchery at Northville, Mich., undertook the same experiment under carefully prepared conditions. In no case was the egg of a whitefish fertilized by the milt of the lake herring, and the hybridization of the two species is quite improbable.

Subgenus CISCO Jordan & Evermann, new subgenus.

Cicso Jordan & Evermann, new subgenus (type, *Argyrosomus nigripinnis* Gill).

The depths of the Great Lakes are inhabited by species of *Leucichthys*, locally known as blackfin, bluefin, cisco, longjaw, bloater, kiyi, chub, etc., differing somewhat from any of the shore species of the genus. In nearly every favorable locality three forms of these fishes are found, representing the three principal species, *prognathus* (with *supernas* and *johannæ*), *nigripinnis* (with *cyanopterus*), and *hoyi* (with *zenithicus*). These fishes are much softer in flesh and more delicate than the ordinary lake herring. They spawn earlier, in summer, and are rarely taken in water of less than 60 fathoms. None has been found in Georgian Bay or Lake Erie. They inhabit the western part of Lake Ontario, the northwestern part of Lake Huron, the whole length of Lake Michigan, and the middle southern part of Lake Superior.

Leucichthys supernas Jordan & Evermann, new species. *Cisco of Lake Superior.*

Type, no. 64679, U. S. National Museum, a specimen about 11 inches long, from Lake Superior off the mouth of Knife River, near Duluth; coll., Doctor Jordan.

Habitat: Deep waters of Lake Superior.

The cisco, as it is called about Lake Superior, is a fine silvery species, found in waters of 50 fathoms or more, and is regarded as an excellent food fish. It is near *Leucichthys prognathus* and *L. johannæ*

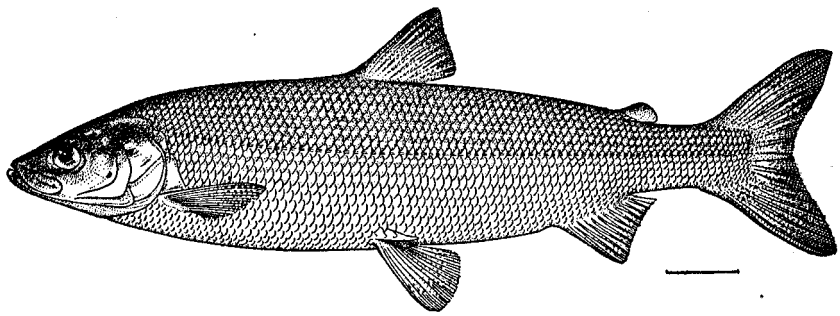


FIG. 12.—*Leucichthys supernas* Jordan & Evermann, new species. Cisco of Lake Superior. (Drawn from the type, a specimen, 11.5 inches long, collected in Knife River, Lake Superior, off Duluth, Minn.)

but is a better food fish than these, is of firmer flesh, and reaches a larger size. It also approaches somewhat *Leucichthys harengus* of the shore waters of the same region.

Leucichthys supernas is especially characteristic of the waters to the west of the Keweenaw peninsula, where it is found in company with the bluefin, *Leucichthys cyanopterus*, and the longjaw, *Leucichthys zenithicus*, and also the siscowet, which preys on all three. The bluefin is a still better fish, reaching a larger size, while the longjaw is inferior and much less fat

Description of type: Head 4.4 in body to base of caudal fin; depth of body 4; length of caudal peduncle from last anal to first caudal rays 2 in head, its depth 2.87; eye 4.6; snout 3.87 to 4; interorbital space 3.5; length of maxillary from tip of snout 2.87; dorsal 10 (developed rays); anal 12; scales 8–76–7; branchiostegals 9; gillrakers 15+29, length .66 eye diameter.

Body somewhat elongate, moderately deep, and compressed, very much resembling *L. artedi;* arched between snout and insertion of dorsal more than from insertion of dorsal to caudal, slightly more convex ventrally; caudal peduncle long, not deep as in *L. artedi* (some specimens of which it approaches, however), and compressed; head smaller than in *L. prognathus*, not full at nape; snout pointed, compressed, its outline continued by premaxillaries, lower jaw slightly projecting; maxillaries short in proportion to snout, reaching to anterior edge of pupil; distance from snout to occiput slightly less than half distance from occiput to dorsal insertion.

Lateral line straight, scales moderate, thin.

Dorsal fin inserted midway between snout and base of caudal, low, more so than in *L. artedi*, its longest ray a trifle less than .66 head, its base .66 of ray length; adipose fin rather small, as long as snout, measuring from insertion to free end; caudal widely forked; anal rather low, its longest ray 2.3 in head, its base equal to ray length, its margin nearly truncate; pectorals and ventrals rather shorter than in *L. artedi*, being slightly longer than longest dorsal ray, the former not reaching more than half way to ventrals.

Color in spirits silvery, slightly darker above, especially on removal of scales; cheeks silvery; dorsal fin dark on distal half, caudal broadly edged with black, other fins colorless save for very slight stipple on pectoral.

As already indicated, this species, although a deep-water form, is very close to *L. harengus*, of which it is probably a deep-water variant. It is perhaps through *L. supernas* that the other deep-water forms are derived. Compared with *L. harengus*, *L. supernas* has a slightly deeper tail and the body is less slender. Two specimens of cisco, from off Knife River, near Duluth, differ from the others in the number of gillrakers, the number being about 11+21. Such variations were also noted by Evermann & Smith. These specimens are a little more robust than the others, with the adipose fin perhaps a trifle larger. For the present we can only record them as a variant of *L. supernas*. They differ from *L. johannæ* in the slightly shorter snout, broader interorbital space, deeper body, and firmer scales.

A copepod, apparently the same, is parasitic on both *L. supernas* and *L. harengus*.

Leucichthys prognathus (H. M. Smith). *Cisco of Lake Ontario; Ontario Longjaw; Bloater; "Chub."*

Coregonus prognathus Smith, Bull. U. S. Fish Comm., vol. XIV, 1894, p. 4, pl. 1, fig. 3, Lake Ontario at Wilson, New York; type no. 45568, U. S. National Museum; coll., John S. Wilson.

Argyrosomus prognathus, Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 314, 1896, pl. 26, Lake Ontario; Jordan & Evermann, Fishes North and Mid. Amer., pt. 1, p. 471, 1898 (after Smith).

Habitat: Deep waters of Lake Ontario, in depths of 60 fathoms and more.

This species is abundant in the western part of Lake Ontario in deep water. Whether any fishes from Lake Huron or Lake Michigan (here recorded as *L. johannæ*) should be referred to this species is uncertain. It is distinguished by its projecting lower jaw and by the thick body. When taken from deep water the viscera become inflated under reduced pressure, hence the name "bloater" given to this and to the related species in the upper lakes. Our specimens of this species were taken by Dr. Seth E. Meek in Lake Ontario off Toronto.

The following description is from a ripe female, 8¼ inches long, from off Toronto, no. 4922 in the table on page 26.

Head 4 in length to base of caudal; depth 3.5 (greater on account of ripe condition); length of caudal peduncle from last anal to first caudal ray 2.5 in head, depth nearly 3.5; eye 4; snout 4; interorbital space 3.57; length of maxillary from tip of snout 2.6; dorsal 10 (developed rays); anal 11; scales 8–71–7; branchiostegals 8; gillrakers 15+29.

Body moderately elongate, more convex ventrally, appearing, despite ripe condition of specimen, deeper than specimens from Lake Huron; caudal peduncle slender, tapering much, especially on ventral outline from anus; head large, thick at opercle, nape full and humped or strongly curved from occiput

to insertion of dorsal; snout bluntly rounded, broad; lower jaw projecting markedly, a slight angle at symphysis of dentaries, giving jaw a slightly hooked appearance; premaxillaries not breaking contour of head noticeably; lateral projection of anterior ends of preorbitals and maxillaries greater than usual; maxillaries extending to below middle third of eye, their supplementals one-half their breadth and length; distance from snout to occiput long, half distance between dorsal and occiput; opercular breadth equal to snout.

Lateral line rising slightly anteriorly, but nearly straight; scales moderate, slightly larger anteriorly, easily detached.

Dorsal fin inserted nearer base of caudal than snout, moderately high, its longest ray about 1.5 in head, its base 2.5, its margin truncate; adipose moderate (somewhat shrunken in preservation), slightly shorter from insertion to tip than snout; ventrals and pectorals a trifle, the latter noticeably, longer than dorsal, pectoral reaching half way to ventrals; anal slightly concave; adipose eyelids and pectoral fold not prominent; caudal forked widely but not deeply.

Color in spirits, suffused with brownish, darker above than in Lake Huron specimens; lateral line marked with line of distinct black in specimen at hand; fins clear, dorsal and caudal dusky on distal halves; ventrals, anal, and pectorals with only slight traces of black stipples on first rays and margins.

From the bloater of Lake Michigan, which we here call *Leucichthys johannæ*, the Ontario fish differs in its darker coloration, the more projecting lower jaw, the slenderer caudal peduncle, the greater depth of the body, and the greater distance between the pectorals and ventrals. From typical examples of *Leucichthys johannæ*, it also differs in the much larger number of gillrakers. But as stated later, part of our specimens from Lake Huron, referred to *L. johannæ*, have the gillrakers much as in *L. prognathus*. What this difference means is a matter demanding further study.

Leucichthys johannæ (Wagner). *Lake Michigan Cisco; Bloater of Lake Michigan.* (Pl. III.)

Argyrosomus johannæ Wagner, Science, n. s., vol. XXXI, no. 807, p. 957–958, June 17, 1910, Lake Michigan, in about 25 fathoms, some 18 miles off Racine, Wis. Type no. 372d, Wisconsin Geological and Natural History Survey.

The bloater is very common in the northwestern part of Lake Huron in deep water, and also for the whole length of Lake Michigan. On these lakes it is not often taken to the markets, and is not highly valued as food. It is a great nuisance to the fishermen, large schools entering the nets and tangling them, although the mesh is large enough to allow escape.

Whether the form in Lake Huron and Lake Michigan is really distinct from the *prognathus* of Lake Ontario is a matter we can not finally determine. Some examples of *johannæ* may be known at once by the few gillrakers, but this character is lost in Lake Huron examples, which, for the present, we are forced to refer to the same species.

The following is a description from four specimens, 7 to 10 inches in length, two from Lake Michigan near Chicago and two from Lake Huron off Cheboygan, Mich.:

Head 4.2 in body length to base of caudal; depth of body equal to head; length of caudal peduncle from last anal to first caudal ray 2.4 in head, its depth 3.5; eye 4.4; snout 3.75 in head; interorbital space equal to snout; length of maxillary from tip of snout 2.66 in head; dorsal 11 (developed rays); anal 12; scales 8–76–8 (8–74 to 80–7 or 8), branchiostegals 9; gillrakers on first arch 11+23.

Body moderately elongate, not greatly compressed nor deep, its depth 1.66 its width; more convex ventrally (possibly on account of being brought from a depth and blown out by reduced pressure); without nuchal hump; caudal peduncle long, not deep, somewhat compressed; head moderately long, somewhat less than the average of *L. zenithicus;* distance from snout to occiput moderately long, equal to half distance from occiput to insertion of dorsal; eye moderate; maxillary rather long, reaching to below anterior third of pupil, without decurving strongly on free edge from junction with premaxillaries; premaxillaries continuing contour of head at but slight angle; snout rather long and rounded, lower jaw projecting beyond it somewhat with a small symphyseal angle; suborbitals narrow, preorbitals rather broad. Lateral line straight, scales moderate in size, thin and flexible. Dorsal fin inserted midway between snout and base of caudal, moderately high, border truncate, adipose moderate, from insertion to free end somewhat longer than snout; pectoral and ventral rather short, latter not

reaching beyond halfway to former, about equal to distance between snout and occiput. Anal rather short, 2.4 in head, concave.

Color in spirits silvery, suffused with brownish and slight dark above lateral line, below silvery white or colorless, cheeks silvery; fins colorless, save for slight edging of black on dorsal and caudal.

Besides these specimens, which resemble each other closely and belong to the same species, we have others not differing at all externally, in which the average number of gillrakers runs from 12+25 to 14+28. All these are from Lake Huron, off Cheboygan, and approach *Leucichthys prognathus*. Evermann & Smith (Report U. S. Fish Commission for 1894, p. 311) note the finding of similar examples, five from Lake Michigan and three from Lake Superior, which they refer provisionally to *hoyi*, although recognizing the close relation to *prognathus*. They say: "In the numerous specimens of *hoyi* examined, the average number of gillrakers was found to be 39, while for the 8 specimens here considered the average is but 31½." These specimens from Lake Michigan we refer to *L. johannæ*, those from Lake Superior provisionally to *L. supernas*. The specimens from Lake Michigan which differ from the type of *Leucichthys johannæ* we may regard for the present as a variation of the latter. We here present a description of this form.

Description of the bloater of Lake Huron with many gillrakers (*Leucichthys johannæ*, var. B.):

Seven specimens from 6.25 to 9 inches in length; one 8.5 inches in length, no. 5277 here described; all from Lake Huron, off Cheboygan, Mich.

Head 4 in length to base of caudal; depth 4; length of caudal peduncle from last ray of anal to first of caudal 2.4 in head, depth 3.25; eye 4; snout 3.57; interorbital space 4; length of maxillary from tip of snout 2.3 in head; dorsal 10 (developed rays); anal 12; scales 8–79–7; branchiostegals 9; gillrakers 14+26.

Body moderately elongate, more convex in ventral outline, not greatly compressed, its width 1.66 in body depth; caudal peduncle rather long and slender, its width 1.5 in depth; ventral outline along base of anal tapering more abruptly to caudal peduncle than dorsal outline; head long as in *L. zenithicus;* dorsal surface slightly arched from snout to occiput, and from eye to eye; snout bluntly rounded, not tapering much; underjaw projecting; dentaries meeting at a slight angle to form a dorsal tubercle at symphysis; premaxillaries breaking contour of head but slightly; anterior ends of preorbitals and maxillaries protruding laterally somewhat to give bluntly rounded appearance to snout; maxillaries not lying closely to head along their whole length, extending to below middle third of eye; supplementals 0.5 maxillary breadth (in other specimens 0.66); distance from snout to occiput long, from 0.5 to 0.57 of distance between occiput and dorsal fin; opercular breadth slightly more than length of snout; lateral line straight; scales moderate in size, easily detached, and smaller posteriorly.

Dorsal fin inserted nearer base of caudal than tip of snout, moderately high, its longest ray about 1.5 in head, its base 2.5, border truncate; adipose moderate, from insertion to tip nearly equal to snout, its height 0.33 length; ventrals and pectorals as long as dorsal ray, pectorals reaching halfway to ventrals; anal somewhat concave; caudal forked widely.

Color in spirits not very silvery, suffused with brownish, but slightly darker above; fins clear, save for dusky margin of dorsal and caudal; slight trace of black on pectorals; lateral line sometimes marked distinctly, sometimes very faintly with a line of black.

Whether *Leucichthys johannæ* can be separated as a species from *L. prognathus* is uncertain; as there can be no connecting forms, it is a distinct species or nothing.[a]

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[a] The following is Mr. Wagner's original description of this species:

Head, 4.1 in length to base of caudal; depth, 3.8; eye, 6.5 in head; depth of caudal peduncle, 3.1; snout, 3.4; maxillary, 2.6; mandible, 2; height of dorsal fin, 1.5; distance from snout to dorsal, 1.9 in length; gillrakers, 10+19; longest, 1 in eye; dorsal, 10; anal, 12; scales, 9–80–8.

Body deep, not greatly compressed, back strongly arched, rising rapidly for one-half the distance from snout to dorsal, then more gradually. Caudal peduncle high, not greatly compressed. Head small, sharply wedged-shaped, its height at occiput 1.9 in height of body. Eye small. Lower jaw even with upper; maxillary reaching nearly to center of eye. Gillrakers coarse and widely set. Lateral line straight. Scales large and thick, nondeciduous.

Color (in formalin): Lips and head pale; body dark above but not nearly to lateral line; quite pale below. Dorsally some indication of stripes, longitudinally. Dorsal and caudal fins with black edges, other fins pale.

Comparison of Leucichthys prognathus and Leucichthys johannæ.

	L. prognathus, Toronto.	*L. johannæ*, Cheboygan.			
Specimen no.	4922	5280	5281	5279	5277
Length to base of caudal ..... *mm.*	205	210	164	160	215
Dorsal rays	10	10	11	9	10
Anal rays	11	12	12	11	12
Scales	8–71–7	8–78–7	8–70–7	8–73–7	8–79–7
Branchiostegals	8	9	8	8	9
Gillrakers	15+29	12+25	13+26	14+28	14+26
Sexual condition	Ripe ♀	?	?	Ripe ♂	Unripe ♀
Comparative measurements:[a]					
Head	0.26	0.26	0.26	0.26	0.25
Depth	.30	.27	.26	.25	.23
Caudal peduncle—					
Length	.095	.105	.095	.11	.11
Depth	.07	.08	.075	.075	.08
Eye	.065	.06	.07	.072	.06
Snout	.068	.07	.075	.07	.07
Interorbital space	.07	.065	.065	.07	.065
Maxillary from tip of snout	.10	.10	.105	.105	.11
Opercular breadth	.07	.07	.075	.075	.07
Subopercular breadth	.03	.02	.03	.03	.035
Snout to occiput	.185	.185	.19	.19	.185
Ventrals to pectorals	.39	.36	.35	.35	.34
Pectorals in pectoral-ventral distance	2.125	2.20	2.00	1.80	2.00
Pectoral length	.19	.17	.17	.19	.18
Ventral length	.18	.17	.18	.19	.18
Dorsal height	.165	.17	.17	.19	.165
Adipose length	.06	.07	.07	.08	.08
Anal height	.11	.10	.11	.11	.10

[a] Measurements in hundredths of body lengths unless otherwise specified.

Leucichthys nigripinnis (Gill). *Blackfin of Lake Michigan.* (Pl. IV.)

Argyrosomus nigripinnis Gill Ms., in Hoy, Trans. Wis. Ac. Sci., 1, p. 100, 1872, Lake Michigan off Racine; name only. Hoy, Rept. U. S. Fish Comm. for 1872–73 (1874), p. 87, Lake Michigan off Grand Traverse. Jordan, Rept. Geol. Surv. Ind. 1875, p. 5, Lake Michigan. Jordan & Evermann, Fishes North and Mid. Amer., pt. 1, p. 472, 1898, Lake Michigan, Lake Mendota, and Lake Miltona, Wisconsin. Evermann & Smith, Rept. U. S. Fish Com. 1894, p. 317, pl. 27 (1896), Lake Michigan.

Habitat: Deep waters of Lake Michigan and certain small lakes in Wisconsin.

This is the largest of the deep-water ciscoes, and is a food fish of fine quality and of large commercial importance in Lake Michigan. It reaches a larger size than any of the other species of *Leucichthys* except *eriensis*, and is readily known by its black fins, in connection with its plump body and rather large eye and mouth. In Lake Michigan the fins are all chiefly black and the fish is called blackfin. In Lake Superior the species is replaced by the paler closely allied bluefin, *Leucichthys cyanopterus*.

The following description is from our single specimen, 13 inches long, taken in Lake Michigan, off Kenosha:

Head slightly less than 4 in body length to base of caudal; depth slightly more than 4; length of caudal peduncle from last rays of anal to first of caudal 3 in head, depth slightly greater; eye 4.66; snout 4; interorbital space 3.5; maxillary from tip of snout 0.5 longer than snout, 2.66 in head; dorsal 11 (fully developed rays); anal 12; scales 8–75–8, between occiput and dorsal 34; branchiostegals 8; gillrakers 18+33.

Body moderately elongate, dorsal and ventral outlines symmetrical, not greatly compressed, its width 2.33 in greatest depth; caudal peduncle short and deeper than its length. Head moderate in length; snout not conical viewed from above, but rounded and broad; premaxillaries projecting very obliquely forward; lower jaw longer, with slight symphyseal angle; maxillary not quite reaching anterior edge of pupil; distance from snout to occiput short, less than twice in distance from occiput to dorsal, and 2.5 times opercular breadth, which is slightly shorter than snout. Lateral line straight, nearer dorsal outline; scales moderate, of equal size anteriorly and posteriorly.

Dorsal inserted slightly nearer head than base of caudal, relatively high, equal in length of first developed ray to the distance between the snout and occiput, a trifle more than 1.5 in head, all ray tips

coinciding when fin is supine, edge truncate, nearly perpendicular, base 2 in head; adipose moderate, equal in length, from insertion to tip, to interorbital space; caudal broad, widely forked, anal moderately high, its edge concave, first developed ray not reaching tip of last when supine; ventrals long, slightly more so than dorsal; pectoral still longer, 1.66 in distance from pectoral to ventrals.

Color in spirits silvery, dark blue-black above, on tip of mandibles and snout, black on all fins, saving their bases, which are clear; ventrals, pectorals, and anal with less black than other fins; body colorless ventrally.

Leucichthys cyanopterus Jordan & Evermann, new species. *Bluefin.*

Type, no. 64672, U. S. National Museum, a specimen 16 inches long, from Lake Superior, off Marquette, Mich.; coll., Mr. August J. Anderson.

Habitat: Deep waters of Lake Superior.

This species, closely allied to the blackfin, *L. nigripinnis*, is here described from the type and 9 cotypes from off Marquette in Lake Superior.

Head a trifle less than 4 in body length to base of caudal; depth of body 3.75; length of caudal peduncle from last anal ray to first of caudal 2.25 in head, its depth 2.8; eye 5; snout 3.5; interorbital space slightly more than snout; length of maxillary from tip of snout 2.8 in head; dorsal 10 or 11 (developed rays); anal 11 or 12; scales 8–76 to 87–7, between occiput and dorsal about 33; branchiostegals 9; gillrakers 13 or 14+24 to 27.

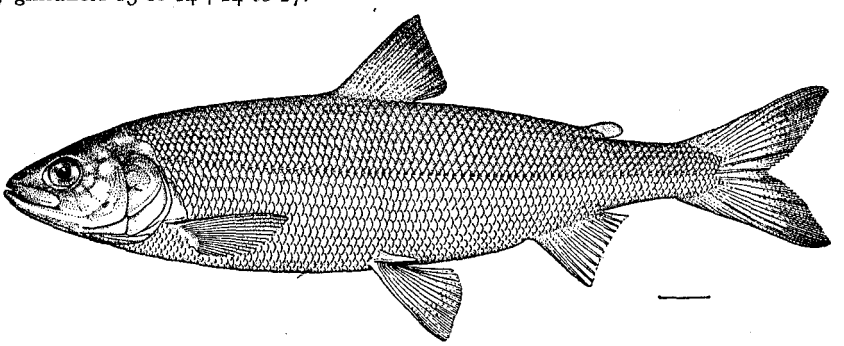

FIG. 13.—*Leucichthys cyanopterus* Jordan & Evermann, new species. Bluefin. (Drawn from the type, a specimen 16 inches long, collected in Lake Superior off Marquette, Mich.)

Body less elongate than usual, dorsally and ventrally equally curved; depth greater than usual not greatly compressed; width of body a trifle over twice in depth; caudal peduncle moderately long and deep, tapering from the proximal end to the caudal, and not more compressed than the body; head somewhat smaller than in related deep-water forms, but larger than in *L. artedi;* snout rounded, lower jaw usually the longer, but meeting the projecting premaxillaries; maxillaries extending nearly to a vertical from the front margin of pupil, and lying close to dentaries, so as to give them an oblique relation to the ventral body plane, distance from snout to occiput slightly more than half the distance from occiput to insertion of dorsal; opercular breadth about equal to snout or somewhat greater; eye rather large, less than interorbital space, the latter very slightly convex, straight in profile; snout slightly arched in profile.

Lateral line straight, slightly nearer dorsal outline; scales moderate in size, equal, save on the caudal peduncle and on belly, showing blue-green luster when magnified. Dorsal fin inserted nearer snout than base of caudal, moderately high, its longest ray about 1.66 in head, its base somewhat over 2, its margin straight or slightly concave, first and last ray tips coinciding when supine; adipose rather large but variable, about 4.33 in head, and moderately high; caudal broad, widely forked, moderately deep; anal similar to dorsal in shape, but about 0.66 its height, its margin more concave, its base about equal to that of dorsal; ventrals long, reaching 0.75 distance to anal, and broad; pectoral also long, reaching halfway or more to insertion of ventrals, and longer than the latter.

Color in spirits silvery, darker above, with a bluish tint; dorsal fin dark on first ray and on distal half, but not dense black, as in *L. nigripinnis;* caudal broadly margined with black in varying degrees;

pectorals and anal margined with fainter black, the latter less; ventrals usually pale, but not always.

This species is exceedingly close to *Leucichthys nigripinnis*, from which it differs by a somewhat shorter snout, fewer gillrakers (18+33 in our specimen of *L. nigripinnis*) and the less pronounced black of the fins. In the measurements given by Evermann & Smith in the Report of the U. S. Commission of Fish and Fisheries for 1894, page 318, the gillrakers for 17 specimens of *L. nigripinnis* of Lake Michigan ranged from 16+30 to 19+34, whereas in our specimens (10 in number) of *L. cyanopterus* the range is from 13+24 to 14+27. From *L. zenithicus*, to which it is almost as closely related as to *L. nigripinnis*, it differs in the shorter maxillary, smaller mouth and deeper body.

The most marked differences are in the length of the maxillary, which in *L. zenithicus* ranges from 0.10 to 0.11 of the body length, while in *L. cyanopterus* it is only 0.083 to 0.095, and in the greater depth of body, the former ranging between 0.21 and 0.245 (with one specimen 0.26), while the latter varied from 0.245 to 0.28. All our specimens of *L. cyanopterus* were taken at Marquette, whence they were sent us by Mr. August J. Anderson, a prominent fish dealer at Marquette. Four specimens of *L. zenithicus* came from Marquette and 6 from near Duluth. The length of our specimens of *L. cyanopterus* is in every case greater than that of any specimen of *L. zenithicus*. In quality of flesh there is a marked difference, the *L. cyanopterus* taken at Marquette being very fat with thick abdominal walls, while *L. zenithicus* is generally lean and with thin abdominal walls. The greater depth of *L. cyanopterus* may be due to accumulations of fat.

Other specimens are from Duluth and from off Knife River, at the head of Lake Superior. The species abounds in the deep waters of the lake, its value exceeding that of the other deep-water species. A large specimen apparently belonging to *L. cyanopterus* was found in the Toronto market. Its fins were almost without dark markings. It must have come from Wiarton, on Georgian Bay. It is very unlikely that any Lake Superior fish would be mixed with these.

Comparison of specimens of Leucichthys cyanopterus from Marquette, Lake Superior.

Specimen no.	5242	5228	5246	5243	5248	5247	5244	5240	5245	5249
Length without caudal.....*mm.*	285	295	305	322	325	330	335	340	345	345
Dorsal rays	10	10	11	10	11	10	11	11	11	10
Anal rays	11	12	12	11	14	12	11	12	11	11
Scales	8-79-7	8-78-7	8-86-7	8-85-7	8-82-7	8-87-7	8-81-8	8-76-7	8-83-8	8-82-7
Scales between occiput and dorsal fin	35	32	35	35	33	36	32	32	33	33
Branchiostegal	9	9	9	9	9	9	9	9	9	9
Gillrakers	14+27	.....	13+24	14+24	13+24	14+27	14+27	13+25	14+26	14+26
Sex	♀	♀	♀	♀	♀	♀	♀	♂	♀	♀
Comparative measurements:[a]										
Head	0.24	0.265	0.255	0.245	0.24	0.25	0.262	0.25	0.23	0.245
Depth	.25	.245	.28	.26	.27	.275	.265	.26	.25	.27
Caudal peduncle—										
Length	.10	.115	.12	.11	.115	.10	.10	.115	.12	.115
Depth	.075	.07	.08	.08	.085	.08	.08	.075	.08	.085
Eye	.05	.05	.054	.05	.052	.052	.052	.05	.05	.05
Snout	.07	.08	.07	.067	.07	.067	.075	.065	.065	.07
Maxillary from tip of snout	.09	.095	.09	.087	.083	.095	.095	.09	.09	.09
Snout to occiput	.17	.18	.18	.17	.165	.175	.18	.18	.165	.173
Pectoral length	.17	.19	.17	.19	.175	.18	.185	.19	.19	.195
Ventral length	.165	.16	.17	.18	.16	.18	.17	.17	.175	.16
Dorsal height	.15	.155	.15	.16	.15	.165	.15	.15	.14	.14
Adipose length	.065	.07	.07	.07	.06	.065	.065	.075	.062	.07
Anal height	.10	.095	.105	.10	.10	.10	.10	.10	.10	.11

[a] Measurements in hundredths of body lengths unless otherwise specified.

Leucichthys hoyi (Gill). *Cisco of Lake Michigan; Kiyi; Chub; Mooneye Cisco.* (Pl. v.)

Argyrosomus hoyi Gill Ms., in Hoy, Trans. Wis. Ac. Sci., vol. 1, 1872, p. 100, Lake Michigan off Racine; no description. Milner, Rept. U. S. Fish Comm. for 1872–73 (1874), p. 86; in part; no description. Jordan, Rept. Geol. Surv. Ind. 1875, p. 5, Racine, Wis., specimen received from Doctor Hoy. Jordan & Evermann, Fishes of North and Mid. Amer., pt. 1, p. 469, 1898, Racine and Kenosha. Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 310, pl. 22 (1896), Lake Michigan.

Habitat: Lake Michigan, in deep water.

This beautiful cisco is very abundant in the deep waters of Lake Michigan and is an excellent food fish, very delicate in flavor. We have examined specimens from Racine (Doctor Hoy's type),

from Kenosha (here figured), and from Green Bay, off Escanada. Thus far it has not been certainly recognized outside of Lake Michigan, the closely related *L. zenithicus* replacing it in Lake Superior and probably in Lake Huron.

Description of *Leucichthys hoyi* from a cotype, a specimen 11 inches in length taken off Kenosha, Lake Michigan, sent to Doctor Jordan by Doctor Hoy, no. 11919, Stanford University collection:

Head about 4 in body length without caudal; body depth equal to head; length of caudal peduncle from last anal to first caudal rays 2.2 in head, depth of same 3.25; eye 4.5; snout 3.5; interorbital space slightly less than snout; maxillary 2.5 in head; dorsal 10 (fully developed rays); anal 11; scales 7–72–7; branchiostegals 9; gillrakers 14+25 (gill-arch mutilated slightly, however).

Body somewhat elongated and compressed, yet not deep; dorsal and ventral outlines similar, without nuchal hump or fullness; caudal peduncle long, somewhat compressed, and not deep; head moderately large (not as long as in *L. zenithicus* or *L. prognathus*, but larger than in *L. harengus* or *L. artedi*); snout rather long, blunt, because of almost vertical position of premaxillaries, which approach those of a true *Coregonus* in position; jaws subequal, the lower slightly included; maxillaries broad and long, extending slightly beyond vertical from center of pupil; eyes fairly large; distance from snout to occiput long, 0.5 distance from occiput to dorsal fin insertion. Gillrakers numerous, their length 0.5 eye diameter, slightly serrated on edges. Lateral line straight, scales moderate, smaller

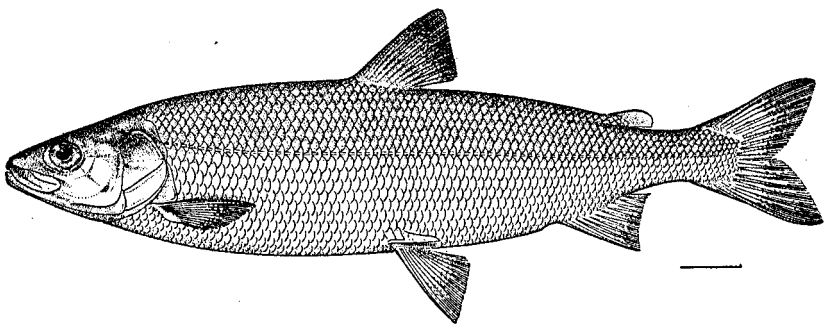

FIG. 14.—*Leucichthys hoyi* (Gill). Cisco of Lake Michigan. (Drawn from a specimen 11.5 inches long, collected in Lake Michigan at Kenosha, Wis.)

posteriorly. Dorsal fin inserted midway between snout and base of caudal fin, low, its longest ray 1.2 in head, its base 0.66 ray length, its margin truncate; adipose rather small; caudal widely forked; anal low, its longest ray 2.6 in head, its base slightly shorter or equal; pectorals and ventrals equal in length, and equal to longest dorsal ray, the former not reaching quite half way to ventrals in specimen at hand.

Color in spirits silvery, slightly darker above; cheeks silvery; fins colorless, save for slight black on edge of dorsal and caudal.

Leucichthys zenithicus (Jordan & Evermann). *Longjaw of Lake Superior.*

Argyrosomus hoyi, Milner, Rept. U. S. Fish Comm. 1872–73 (1874), p. 86, Lake Superior at Outer Island, Wisconsin; not of Gill, Hoy, or Jordan, and not original type.

Argyrosomus zenithicus Jordan & Evermann, Proc. U. S. Nat. Mus., vol. XXXVI, March 3, 1909, p. 169, fig. 3, Lake Superior, between Duluth and Isle Royale.

Habitat: Lake Superior, in deep water; possibly in other lakes.

Description of *Leucichthys zenithicus*, from 11 specimens, 8.5 to 12 inches in length, 4 from Marquette, Lake Superior, and 7 from Duluth, Lake Superior:

Head 3.8 to 4 in length to base of caudal; depth 4 to 4.75; length of caudal peduncle from last anal ray to first caudal 2.2 to 2.5 in head, depth about 3.5; eye, 4.6; snout, 3.5; interorbital space about equal to snout; length of maxillary from tip of snout 2.6 in head; dorsal 10 or 11 (developed rays); anal 11 or 12; scales 8–77 to 83–7, between occiput and origin of dorsal, 32 to 34; branchiostegals 9; gillrakers 14 to 16+24 to 28.

Body rather elongate, somewhat compressed, its width about 2.4 in length of head; depth greatest cephalad of insertion of dorsal, seeming to taper posteriorly from somewhat larger head, but not always; caudal peduncle moderately elongate and not deep, compressed; head rather large, larger than in *L. cyanopterus* on average, but about same as *L. prognathus*, which is larger than usual; snout proportionately long; maxillaries long, extending almost to below center of pupil, gape large; lower jaw equal to or longer than upper; distance from snout to occiput long, slightly more than half distance from occiput to dorsal. Eye large in proportion to the larger head; dorsal surface of head slightly arched and convex between orbits. Lateral line straight near center of body, scales moderate in size, loosely attached. Dorsal inserted nearer base of caudal, high, its longest ray about 1.6 in head, its base 2.5, its margin straight or slightly concave, the longest, first developed ray reaching beyond tip of last ray when supine; adipose rather large, but variable; caudal deeply forked; anal short, its longest ray about 0.66 that of longest dorsal ray; ventrals long, reaching about 0.66 distance to anal; pectoral longer, reaching more than halfway to ventrals, the fin length variable, merging into that of other closely related species.

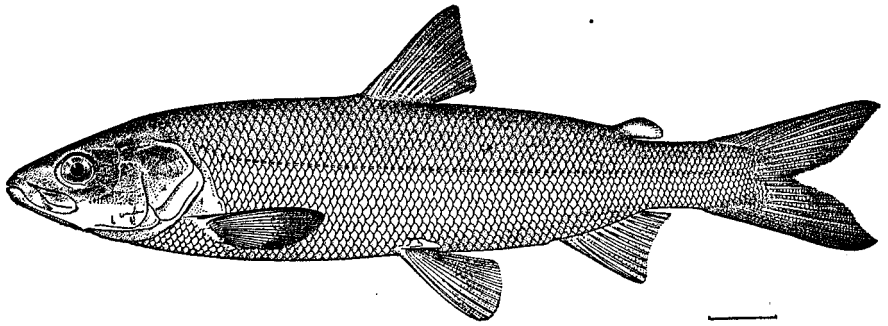

FIG. 15.—*Leucichthys zenithicus* (Jordan & Evermann). Lake Superior Longjaw. From the type.

Color in spirits silvery, darker above, no stripes clearly visible along rows of scales; dorsal and anal broadly edged with dusky; other fins clear, save for occasional stipples of black. In life, clear metallic blue above, silvery below.

Comparison of specimens of Leucichthys zenithicus.

	Marquette, Lake Superior.				Duluth, Lake Superior.						
Specimen no.	5238	5236	5241	5237	5215	5221	5219	5216	13084	5269	5257
Length without caudal.....*mm*	230	247	252	253	205	255	235	240	275	240	250
Dorsal rays	11	11	10	10	11	11	11	10	11	11	10
Anal rays	11	11	11	12	11	11	12	12	11	11	12
Scales	8-80-7	8-78-7	8-77-7	8-83-7	77	83	81	78	79	80	77
Branchiostegals	9	9	9	9	9	9	9	9	9	9	9
Gillrakers	16+26	14+28	14+26	15+26	14+26	14+25	14+24	14+26	14+27	14+26	14+26
Sexual condition	♀	♀	Ripe ♀	♀	♀	Ripe ♀	♀	♀	Ripe ♀	♀	♀
Comparative measurements: [a]											
Head	0.26	0.25	0.26	0.25	0.26	0.26	0.26	0.255	0.25	0.26	0.253
Depth	.21	.23	.26	.21	.22	.245	.22	.22	.21	.225	.21
Caudal peduncle—											
Length [b]	.10	.115	.105	.11	.11	.105	.11	.11	.10	.115	.11
Depth	.07	.075	.075	.075	.075	.08	.08	.075	.075	.075	.07
Eye	.06	.055	.055	.06	.06	.06	.06	.055	.055	.058	.055
Snout	.075	.07	.075	.075	.075	.075	.075	.07	.075	.08	.08
Maxillary from tip of snout	.10	.11	.11	.10	.105	.10	.11	.10	.105	.11	.105
Snout to occiput	.19	.18	.18	.20	.185	.18	.185	.185	.18	.18	.19
Pectoral length	.17	.18	.175	.19	.17	.17	.19	.185	.16	.17	.17
Ventral length	.155	.17	.17	.18	.17	.17	.17	.17	.15	.165	.17
Dorsal height	.15	.16	.165	.16	.17	.16	.165	.16	.15	.16	.17
Anal height	.10	.10	.11	.09	.10	.09	.10	.11	.095	.10	.10

[a] Measurements in hundredths of body lengths unless otherwise specified. [b] From last of anal to first of caudal.

Subgenus ALLOSMUS Jordan.

Leucichthys manitoulinus Jordan & Evermann, new species. *Manitoulin Tullibee.*

Argyrosomus tullibee, Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 320, pl. 28; in part.

Type no. 64670, U. S. National Museum, a specimen 11 inches long, from Blind River, North Channel, Lake Huron; coll., Dr. Seth E. Meek.

Habitat: North Channel of Lake Huron and probably lakes of Minnesota.

Head 3.89 in length without caudal; depth 3.4; depth of caudal peduncle 2.5 in head; eye 4.5; snout 4; interorbital space 3.25; length of maxillary from tip of snout 2.75; dorsal 12; anal 13; branchiostegals 7 or 8; scales 8–71–8; between occiput and dorsal 24; gillrakers 16+29.

Body somewhat over twice as deep as broad, comparatively elongate, more so than in *Leucichthys tullibee*, symmetrically elliptical; dorsal contour of the head straight; snout rounded, tapering; lower jaw slightly longer; maxillary extending to beneath anterior third of the eye, the supplementary bone three times as long as broad; teeth on tongue very minute, none on jaws, vomer, or palatines; width of opercle 4 in head, that of subopercle 7.5, measuring from anterior edge overlapped by opercle; gillrakers 0.87 diameter of eye in length; lateral line straight, ascending a little at the anterior end; scales moderate in size, not deciduous, yet easily removed. Dorsal inserted midway between nares and base of caudal, its height moderate, the longest ray 1.33 in head; adipose fin smaller than in the true tullibee, being

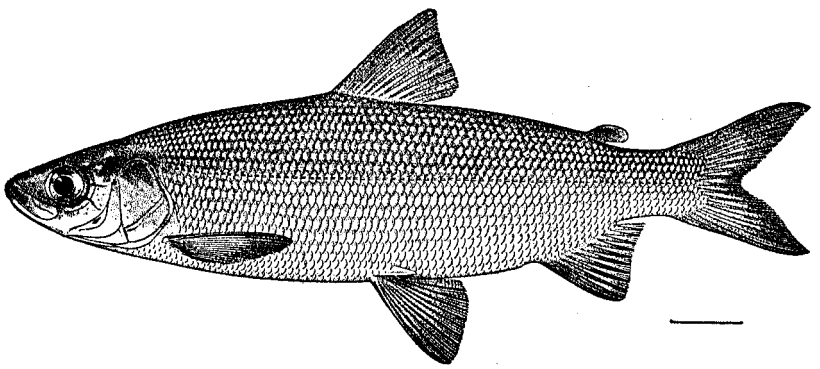

FIG. 16.—*Leucichthys manitoulinus* Jordan & Evermann, new species. Manitoulin tullibee. (Drawn from specimen 11 inches long, collected at Blind River, North Channel of Lake Huron.)

contained 4.25 to 6 in head, measured from insertion to free end; anal base one-half length of head and equal to its longest ray; ventral insertion not much posterior to that of dorsal, its longest ray 1.5 in head, its scale contained 2.75 in its length; length of pectoral 1.33 in head.

Color in spirits, dark on dorsal surface of head and body above lateral line, silvery below, all fins blackish but darker on the border; general hue suffused with smoky, as usual in fishes from waters colored by "muskeeg" or the wash of sphagnum and of peaty substances.

This species is close to *L. tullibee*, from which it may be distinguished by the longer head, longer snout, more slender body, larger eye, and longer and larger maxillary.

This description is based on three specimens, the type and two cotypes, at Stanford University, all taken by Doctor Meek at Blind River on the north side of the North Channel of Lake Huron Another specimen, smaller and more slender, is in the same collection. It is evidently one of the tullibee group, but it is not identical with the tullibee of the northwestern lakes, differing in the more elongate body and tail and in the smaller adipose fin.

All these characters and every other one shown by the species are approximations toward characters shown by *Leucichthys harengus*, the common lake herring of the same waters. We were told about the Manitoulin Islands that the tullibee was occasionally taken, but we saw no specimens other than these three.

Mr. Charles W. Triggs, a dealer in fish in Chicago, tells us that he recently had a consignment of fish of this species sent from the North Channel to Chicago. There was no sale for them. The flesh was poor and flavorless, almost worthless as food, in comparison with the other fishes of the Great Lakes. This is said to be the only species of the tullibee type, or *Allosomus*, found in the Great Lakes, and it is confined to the northern region of Lake Huron and perhaps of Lake Superior and the smaller lakes of Minnesota

Leucichthys tullibee (Richardson). *Tullibee; Tulipi.*

Salmo (Coregonus) tullibee Richardson, Fauna Boreali-Amer., vol. III, p. 201, 1836, Cumberland House, Pine Island Lake (near Lake Winnipeg).
Coregonus tullibee, Günther, Cat., vol. VI, p. 199, 1866, Albany River. Jordan & Gilbert, Synopsis, p. 301, 1883.
Argyrosomus tullibee, Evermann & Smith, Rept. U. S. Fish Comm. 1894, p. 320, pl. 28, 1896. Jordan & Evermann, Fishes North and Mid. Amer., pt. I, p. 473, 1898.

Habitat: Winnipeg basin, perhaps entering Lake Superior.

We have critically examined the following specimens of the tullibee type: One 13.75 inches long; from Waubegon Lake at Oxdrift, Ontario; one 12.5 inches long, from Rainy Lake at Rainier, Minn., one 9 inches long, from Lake of the Woods at Warroad, Minn.; a specimen 18 inches long, presumably from Minnesota, figured by Evermann & Smith in their whitefish paper; one 14 inches long, sent to

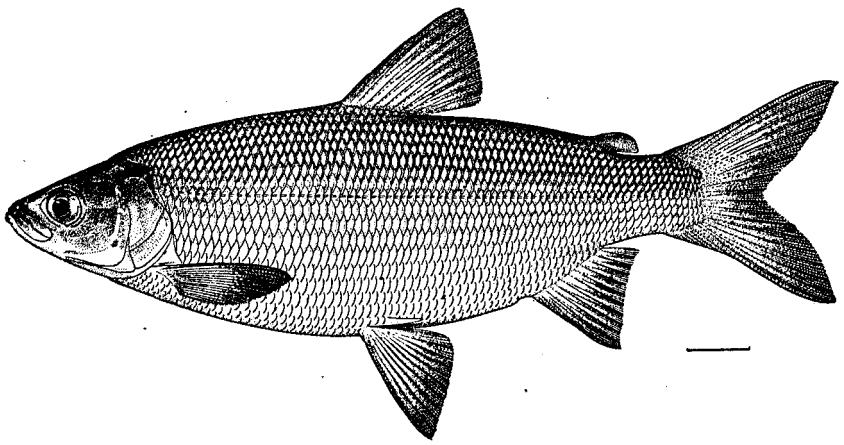

FIG. 17.—*Leucichthys tullibee* (Richardson). Tullibee. (Drawn from specimen 12.5 inches long, collected in Rainy Lake, Rainier, Minn.)

the Bureau of Fisheries by Dr. G. A. MacCallum of Dunnville, Ontario, presumably from Lake Simcoe; one 14 inches long, from Oneida Lake, N. Y.; two specimens 4.62 and 5.5 inches long, from Kettle Falls, Minnesota.

Head 4 in body without caudal; depth 3; depth of caudal peduncle 2.5 in head, its length 3, as measured from last ray of anal to first of caudal; eye 4; snout 4; interorbital space 1.25 in eye, 3.5 in head; length of maxillary from tip of snout 3; dorsal 12; anal 12; scales in lateral line 67 to 72; between dorsal fin and occiput 28; branchiostegals 9; gillrakers 16+34.

Body very deep, elliptical, its width a little less than half the depth; dorsal outline convex, curved strongly upward from the snout; ventral outline nearly as convex as dorsal; head arched slightly dorsally from snout to occiput, premaxillaries continuing the curve of the head; jaws nearly equal in front but the lower contained in the upper; maxillaries extending to below the anterior edge of the pupil, their supplementaries 2.5 times as long as wide and about half their width; scales large, rather firm, lateral line nearly straight.

Dorsal truncate, inserted midway between the occiput and adipose fin, its highest ray 1.33 in head; adipose fin large, its base equal to its height, measured from insertion to free tip, 3.5 in head; longest

anal ray 1.87 in head, anal outline concave; longest ventral and pectoral rays 1.33 in the head; ventral scale 3.5 in ventral length; caudal widely but not deeply forked.

Color in spirits, light olive, silvery laterally, dark above; dorsal, anal, and caudal fins bordered with dark; ventral and pectoral clear, slightly stippled with black.

The specimen from Rainy Lake differs in being much darker in coloration, the lower fins largely black, a few more scales (72) in the lateral line, slightly narrower opercle and subopercle, and slightly larger adipose fin and ventral scale. The specimen from Warroad, Lake of the Woods, differs noticeably in nothing but a darker coloration, more nearly approaching that from Rainy Lake, and the larger eye, correlated with the smaller size.

We have taken as the basis of this description a tullibee from Waubegon Lake at Oxdrift, Ontario, a tributary of Lake Winnipeg, as being nearest the type locality of the species, which is Pine Island Lake, at Cumberland House, a tributary of the Saskatchewan which flows into Lake Winnipeg. We present figures of specimens from Rainy Lake at Rainier and Lake of the Woods at Warroad. In the specimens from the coffee-colored waters of Rainy Lake and Lake of the Woods the coloration is very dark, as is usual with other species in the same locality. The only important differences are

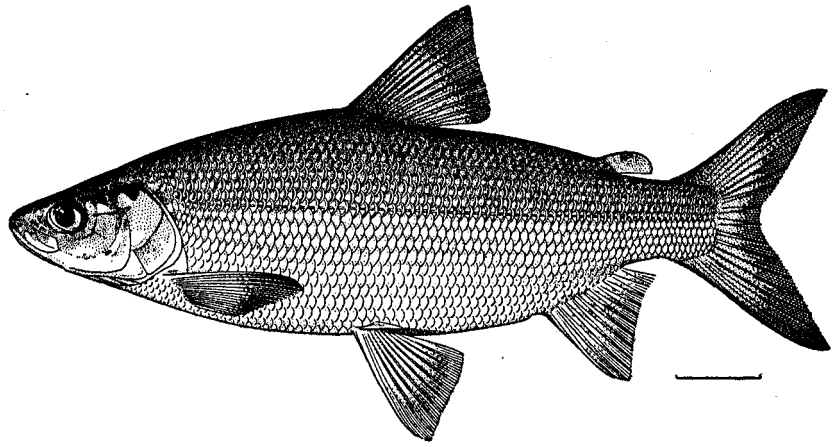

FIG. 18.—*Leucichthys tullibee* (Richardson). Tullibee. (Drawn from a specimen 9 inches long, collected in Lake of the Woods at Warroad, Minn.)

shown in the figures. The caudal peduncle is relatively thickest in the largest examples. The subopercle in the Rainy Lake example is narrower than in the others. These are no doubt individual differences.

Comparative measurements of all of the specimens are given in the following table:

	Waubegon Lake.	Rainy Lake.	Lake of the Woods.	Minnesota.	Kettle Falls.		Simcoe Lake.	Oneida Lake.
Length in inches..	13.75	11.25	9	18	4.625	5.5	14 ♀	14 ♀
Gillrakers.....	.....	.....	.....	.....	14 or 15+28	17+32 L	17+31	17+31 L
					14 or 15+28	17+31 R	17+31	17+29 R
Head.....	4	4.18	4	4.28	3.95	3.65	4.6	4.25
Depth.....	3	2.89	3.25	3.2	4.12	3.65	3.25	2.83
Eye.....	4	4+	5—	5	3.5	3.55	5	5
Snout.....	4	4.25	4.25	4	4	4	5	4+
Maxillary.....	3	.....	.....	.....	.....	.....	.....	.....

The tullibee or tulipi is the most abundant fish in the lakes tributary to Lake Winnipeg, its young forming a large part of the food of the wall-eyed pike or yellow pike, *Stizostedion vitreum*. It is not highly valued as food, its flesh being rather watery and tasteless. In the summer it is largely infested with worms, which are found in the flesh of the back. In winter it is more esteemed.

The southern distribution of the tullibee is unknown. It occurs in certain small lakes of Minnesota and is reported in those of Wisconsin. Eastward *Leucichthys artedi bisselli* and *Leucichthys eriensis*, species not at all related, have been confounded with it. Doctor Bean records it from Onondaga Lake, in New York. We have seen no specimens of the true tullibee from the Great Lakes, but we are told that it occurs in Lake Superior and the North Channel of Lake Huron. Doubtless these statements refer to *L. manitoulinus*. The "mongrel whitefish" of Lake Erie, once supposed by the present writers to be the true tullibee, proves to be *Leucichthys eriensis*.

Comparison of species of Allosomus.

	L. tullibee.			*L. manitoulinus*, Blind River.	
	Oxdrift.	Lake of the Woods.	Rainy Lake.		
Specimen no.	5229	5272	499	5273	5284
Length without caudal....*mm*	330	210	270	245	205
Dorsal rays (fully developed)	12	12	12	12	12
Anal rays	12	12	12	13	13
Scales	8–67–8	9–67–9	9–72–8	8–71–8	8–77–8
Scales between occiput and dorsal fin	30	30	30	24	31
Branchiostegals	9	9	9	8	9
Gillrakers	Evisc.	16+28	16+29	16+29	16+31
Comparative measurements: [a]					
Head	0.24	0.25	0.26	0.25	0.25
Depth	.32	.33	.35	.28	.27
Caudal peduncle—					
Length [b]	.07	.07	.11	.085	.09
Depth	.10	.105	.115	.10	.10
Eye	.06	.06	.065	.06	.06
Snout	.055	.055	.06	.06	.06
Interorbital space	.07	.075	.08	.07	.075
Maxillary length from tip of snout	.075	.085	.09	.09	.08
Opercular breadth	.07	.07	.065	.065	.065
Subopercular breadth	.04	.04	.03	.025	.03
Snout to occiput	.17	.17	.17	.17	.18
Ventrals to pectorals	.28	.295	.32	.31	.31
Pectorals in pectoral-ventral distance	1.55	1.50	1.60	1.66	1.75
Pectoral length	.18	.20	.20	.19	.17
Ventral length	.18	.20	.20	.17	.17
Dorsal height	.19	.21	.21	.17	.17
Adipose length	.08	.08	.08	.04	.055
Anal height	.14	.14	.15	.12	.10

[a] Measurements in hundredths of body lengths to base of caudal unless otherwise specified.
[b] Length from anal to first caudal rays

Genus COREGONUS (Artedi) Linnæus.

Subgenus COREGONUS.

Coregonus clupeaformis (Mitchill). *Labrador Whitefish; Sault Whitefish; Lake Superior Whitefish; Manitoba Whitefish; Musquaw River Whitefish; Whiting of Lake Winnepesaukee; Shad of Lake Champlain.*

Salmo clupeaformis Mitchill, Amer. Monthly Mag., vol. II, 1818, p. 321, Falls of St. Mary, northern extremity of Lake Huron; coll., Col. Samuel Hawkins, who called it "whitefish of the lakes."

Coregonus clupeaformis, Jordan & Evermann, Proc. U. S. Nat. Mus., vol. XXXVI, 1909, p. 171, Sault Ste. Marie; not *Coregonus clupeiformis*, Jordan & Evermann, Fishes North and Mid. Amer., pt. I, p. 466, 1898, which is chiefly based on *Coregonus albus*.

Salmo otsego [a] Clinton, Account of the *Salmo otsego* or the *Otsego basse*, 1822, p. I, with plate, Otsego Lake.

Coregonus labradoricus Richardson, Fauna Bor.-Amer., vol. III, p. 206, 1836, Musquaw River, Labrador, and of many subsequent authors.

Salmo (Coregonus) sapidissimus Agassiz, Lake Superior, p. 344, 1850, Lake Champlain (type), after Zadock Thompson; Lake Superior.

Coregonus latior Agassiz, Lake Superior, p. 348, 1850, Lake Superior.

Coregonus neohantoniensis Prescott, Amer. Journ. Sci. Arts, vol. XI, 1851, p. 343; Lake Winnepesaukee, New Hampshire.

? *Coregonus richardsonii* Günther, Cat. Fish., vol. VI, p. 185, 1866, Arctic North America; locality unknown.

This species is the common whitefish of all the Great Lakes, Lake Erie excepted. It is also found in many of the smaller lakes tributary to these. The Otsego whitefish (*Salmo otsego* Clinton) is apparently identical with this species, as is also the whiting of Lake Winnepesaukee.

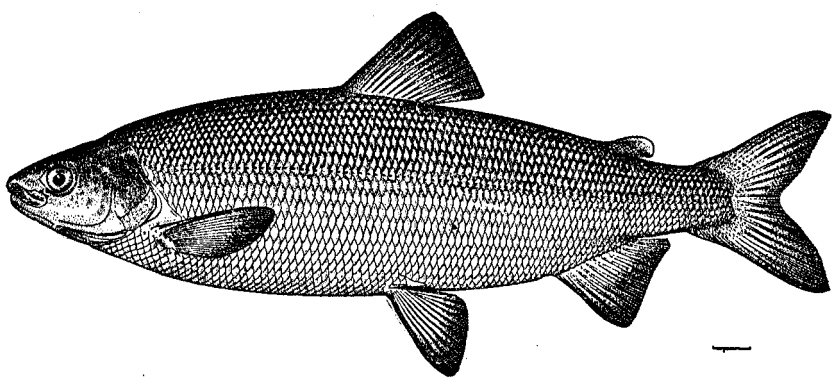

FIG. 19.—*Coregonus clupeaformis* (Mitchill). Labrador whitefish. (Drawn from a specimen 21 inches long, collected at Rainy Lake, Rainier, Minn.)

This whitefish is generally recognizable by the compressed elliptical form, rather pointed snout, the absence of a hump at the nape except in very large examples, and by the presence of a dusky shade on the back, forming more or less distinct streaks along the rows of scales. It varies much in size, being

[a] This description is accredited by authors to the Medical & Philosophical Register, 1844, vol. III, p. 188. The correct title of this publication is "Annals of Medicine, Natural History, Agriculture and Arts, in four volumes, by J. W. Francis & D. Harack, published in 1814". The description and figure appear in a printed "Account of the *Salmo otsego*, or the *Otsego basse* in a letter to John W. Francis, M. D., professor of obstetrics and the diseases of women and children in the University of New York, by De Witt Clinton, LL. D., governor of the state of New York; published by C. T. Winkle, 101 Greenwich street, 1822."

According to Doctor Evermann, who has examined the copy in the Library of Congress, the printed matter is on pages 1, 3, 4, 5, and 6. Preceding the title page, p. 1, is a full-page cut of the fish described. Following the words "Otsego basse" has been written in lead pencil "*Coregonus clupeiformis*". The cut, although crude, plainly shows *Coregonus clupeaformis*. The form is elliptical, and the back shows the dark streaks along the rows of scales usually characteristic of that species.

mature at about 2½ pounds, and growing to the weight of 8 to 12 pounds in Lake Superior. These very large whitefish are known as bowbacks. The species is one of the most valuable of all of our food fishes. It is probably the only large whitefish native to the Great Lakes system, Lake Erie excepted.

In Jordan & Evermann's Fishes of North and Middle America, the upper lakes were supposed to be inhabited also by the Erie whitefish, and on this supposition the name *clupeiformis* was retained for the latter, while the present species was called *Coregonus labradoricus*. There is very little difference between these two species, if species they really are. In general, *Coregonus clupeaformis* can be told at once by its more elongate, more compressed and more symmetrical body, deepest at the dorsal fin, and scarcely elevated at the nape, by its dark and streaked back, and by its longer pectorals, which reach more than halfway to ventrals. The flesh of the Lake Erie fish is fatter and softer.

The whitefishes from the basin of Lake Winnipeg, or Manitoba whitefish, show the general traits of *Coregonus clupeaformis*. In general, however, these are more robust, with larger head, deeper body, and longer fins. The caudal peduncle is deeper than long (the gillrakers are mutilated in all our specimens). Those from the dark or "muskeeg" water are unusually dark, with dark streaks above and black fins. Those from the milky waters of Lake Winnipeg (about the mouth of the Red River of the North) are all very pale, as pale as the whitefish of Lake Erie. As the water of Lake Erie is similarly milky, discolored by muddy, clay-bottomed streams, it is a question whether this feature of coloration is really a specific character. Perhaps *Coregonus albus*, as well as this Manitoba form, may be "ontogenetic species," or forms dependent on the food and the character of the water. Of the Manitoba form of *Coregonus clupeaformis* we have examined hundreds of examples and have preserved examples from Rainy Lake at Rainier, Lake of the Woods at Warroad, Lake Winnipeg at Fort Alexander, Lake Playgreen, and Lake Waubegon at Oxdrift.

We figure the example from Rainy Lake.

The following description of *Coregonus clupeaformis* is taken from numerous specimens, mostly from Lake Superior:

Head, 4.5 to 5 in body length to base of caudal; body depth 3.5 to 4; eye 4.5 to 5.5 in head; snout 3.5 to 4.5; maxillary to tip of snout 3 to 4; interorbital space 3 to 3.8; caudal peduncle length from last rays of anal to first of caudal 1.8 to 2.5 in head, its least depth 2 to 2.5, but usually less than its length; dorsal 10 to 12 (fully developed rays); anal 10 to 14; scales 72 to 86 (usually over 75), between occiput and insertion of dorsal 30 to 34; branchiostegals 9 or 10; gillrakers 9 to 11+16 to 18 (25 to 28 in all) on first gill-arch.

Body moderately elongate, increasing considerably in depth with age, deepest under dorsal; compressed, its width about 2.5 in its depth; dorsal profile sometimes arched from occiput to insertion of dorsal fin, sloping gradually to caudal peduncle, the latter deep, nearly as deep as long, sometimes deeper than long, compressed strongly; head small, conic, square at tip, premaxillaries directed backward so as to place mouth on lower side of projecting snout; lower jaw included, mandible reaching to midway between pupil and hind margin of eye, about 2.6 in head; maxillary broad and short, extending to anterior margin of eye, supplementaries broad, short, not as broad as long; distance from snout to occiput about 2 in distance from occiput to insertion of dorsal; teeth on tongue only, very minute, barely visible, except when dried.

Origin of dorsal about midway between snout and base of caudal; moderate in height, between 0.8 and the whole of the head length, almost always greater than distance from snout to occiput, its base 1.66 in head; adipose moderate or rather large, from insertion to free end contained about 2 to 3 in head; pectorals and ventrals equal to longest dorsal rays in length (former reaching over halfway to vent in forms from Lake of the Woods, Rainy Lake, and Lake Waubegon); anal low, its longest ray 1.66 in head, its base 1.75 or 2. Lateral line straight, scales moderately large.

Color in spirits pale, darker above, always showing more or less distinct streaks along the rows of scales; vertical, pectoral, and ventral fins usually colorless, save for dark margin of dorsal and caudal, although others are sometimes dusky.

Comparison of Coregonus albus and C. clupeaformis.

	C. albus, Lake Erie.				*C. clupeaformis*, Lake Ontario.				
Specimen no.	494	5255	5254	5253	4933	4914	4913	4936	4911
Body length.....*mm*	340	355	315	290	275	265	350	190	265
Dorsal rays	11	10	11	11	11	11	12	11	11
Anal rays	12	14	12	11	11	11	10	11	11
Scales	9-80-8	9-86-8	10-81-8	10-79-9	10-79-9	9-82-8	10-82-8	10-80-8	10-81-8
Branchiostegals	9	9	9	9	9	9	9	9	9
Gillrakers	10+16	11+16	9+18	10+18	10+18	10+19	10+18	9+16	10+18
Comparative measurements:[a]									
Head	0.20	0.225	0.215	0.215	0.21	0.20	0.22	0.225	0.21
Body depth	.30	.325	.29	.30	.27	.26	.29	.265	.29
Caudal peduncle—									
Length	.105	.10	.085	.08	.09	.10	.10	.125	.115
Depth	.10	.095	.10	.105	.085	.085	.09	.09	.09
Eye	.045	.04	.045	.04	.05	.05	.045	.05	.057
Snout	.04	.06	.05	.052	.05	.05	.055	.05	.05
Maxillary from tip of snout	.055	.065	.06	.06	.06	.06	.065	.065	.07
Distance snout to occiput	.14	.15	.15	.16	.15	.15	.15	.16	.15
Pectoral length	.18	.19	.18	.18	.163	.17	.19	.165	.18
Ventral length	.18	.20	.18	.18	.165	.17	.17	.17	.17
Dorsal height	.195	.18	.185	.18	.175	.17	.17	.185	.17
Anal height	.12	.13	.13	.13	.12	.11	.12	.115	.115

[a] Measurements in hundredths of body lengths unless otherwise specified.

Comparison of specimens of Coregonus clupeaformis.

	Lake Superior.	Lake Huron.		Lake Michigan.	Lake of the Woods.	Lake Waubegon.		Rainy Lake.
Specimen no.	5227	4927	13112	528	11918	5231	5259	A
Body length.....*mm*	283	370	285	190	420	365	270	445
Dorsal rays	12	12	11	11	11	11	12	13
Anal rays	12	11	11	11	11	14	11	14
Scales	10-84-8	10-79-8	10-78-9	10-79-8	10-70-8	10-74-9	81	86
Branchiostegals	9	9	9	9	9	9	9	10
Gillrakers	10+18	10+16	8+17	10+16	Evisc.	Evisc.	Evisc.	Evisc.
Comparative measurements:[a]								
Head	0.20	0.21	0.21	0.225	0.23	0.225	0.235	0.235
Body depth	.25	.26	.26	.25	.37	.37	.29	.32
Caudal peduncle—								
Length	.105	.10	.12	.11	.085	.105	.09	.09
Depth	.08	.09	.09	.085	.11	.11	.10	.10
Eye	.04	.04	.05	.05	.045	.045	.05	.045
Snout	.05	.06	.05	.06	.055	.06	.06	.065
Maxillary from tip of snout	.055	.06	.05	.065	.075	.065	.07	.068
Distance snout to occiput	.15	.155	.15	.17	.16	.167	.165	.16
Pectoral length	.16	.18	.15	.17	.21	.21	.20	.20
Ventral length	.16	.18	.16	.175	.20	.20	.20	.19
Dorsal height	.16	.20	.16	.195	.21	.21	.20	.17
Anal height	.11	.13	.11	.13	.16	.14	.15	.12

[a] Measurements in hundredths of body lengths unless otherwise specified.

Coregonus albus Le Sueur. *Lake Erie Whitefish; Common Whitefish.* (Pl. VI.)

Coregonus albus Le Sueur, Jour. Ac. Nat. Sci. Phila., vol. 1, 1818, p. 232, Lake Erie. Jordan & Evermann, Proc. U. S. Nat. Mus., vol. XXXVI, 1909, p. 171, Lake Erie. And of many other authors.

Habitat: Lake Erie and Lake St. Clair; introduced into other lakes.

This species is the common whitefish of Lake Erie. It is very close to *Coregonus clupeaformis*, the whitefish of the other lakes, differing only in form and color. Compared with the latter, the Erie whitefish has a smaller head, higher nape, more angular form, and the color is almost pure olive-white, without dark shades or dark stripes along the back. The flesh is softer, containing more fat. All these differences may be correlated with the fact that Lake Erie is shallow and its southern shore is fed by warm, shallow, muddy, or milky rivers. The difference shown by the wall-eyed pike of the different lakes is supposed to rest on the same variation in environment. As no difference appears

in technical characters, we regard *Coregonus albus* as a doubtful species, its distinctions being perhaps purely ontogenetic. On the other hand, it is claimed that the fry of the two can be readily separated. Mr. Harry Marks, superintendent of the United States hatchery at Sault Ste. Marie, claims that the eggs of *Coregonus clupeaformis* are larger and darker than those of the Lake Erie whitefish. The fry are also livelier and are marked by two dark lines on the side, while those of *C. albus* are plain silvery.

The Lake Superior whitefish takes the hook readily, large numbers being taken every day in season in the locks at Sault Ste. Marie by local anglers. *Coregonus albus* is not known to take the hook.

The eggs of the Lake Erie whitefish have been planted in all the other lakes, and we have recognized specimens we call *Coregonus albus* from Lake Champlain, Lake Ontario, and Lake Superior among the Apostle Islands. The close resemblance between the whitefish, fat, plump, and pale, from the milky waters of Lake Winnipeg and those of Lake Erie has been noticed by many fish dealers. We doubt if anyone could distinguish individual specimens from these two localities, although on the average they are different. Possibly *Coregonus albus* is merely an "ontogenetic species," its peculiarities being due to the conditions of food and water in Lake Erie.

According to the figures issued by the Bureau of the Census, the total catch of whitefish in United States waters of the Great Lakes for the calendar year 1908 was 7,482,800 pounds, valued at $507,310. The following table shows the catch by states:

State.	Pounds.	Value.
Pennsylvania	451,200	$36,290
Ohio	732,200	60,010
Michigan	4,768,500	339,230
Indiana	51,800	4,990
Wisconsin	1,274,500	56,320
Minnesota	204,600	10,470
Total	7,482,800	507,310

Coregonus nelsoni Bean. *Alaska Whitefish.*

Coregonus nelsonii Bean, Proc. U. S. Nat. Mus., vol. VII, 1884, p. 48, Nulato, Alaska; type 29903; collector Edward W. Nelson.

Habitat: Rivers and lakes of Alaska and Mackenzie River region.

This species resembles the Lake Erie whitefish, but has a smaller mouth and the flesh is said to be dry and bony.

Subgenus PROSOPIUM Milner.

Numerous species of river whitefish occur in the United States. These belong to the subgenus *Prosopium*, distinguished by the elongate form, the thick gillrakers, and the moderate or large scales. In some of these the males have pearl organs or tubercles on the scales in spring. In some the adipose fin is enormously developed. In some the snout in the male is much produced, and in one the scales are much enlarged. Each of these types should perhaps stand as a distinct subgenus, the typical species of each being *quadrilateralis* (*Prosopium*), *williamsoni*, *coulteri* and *oregonius*.

Coregonus quadrilateralis (Richardson). *Menominee Whitefish; Pilotfish; Round Whitefish; Shadwaiter.* (Pl. VII.)

Coregonus quadrilateralis Richardson, Franklin's Narrative, p. 714, pl. XXV, fig. 2, 1823, Fort Enterprise, British America.

Coregonus nov-angliæ Prescott, Am. Jour. Sci. Arts, vol. XI, 1851, p. 342, Lake Winnepesaukee N. H.

Habitat: Alaska and upper Great Lakes to New England, in lakes.

This species is common in Lake Superior and the northern parts of Lake Huron and Lake Michigan. It may be known at once by its short head and elongate, little compressed body. It is not highly valued as food, ranking even inferior to lake herrings in this regard, and agreeing with them in size and form. It is destructive to the spawn of the whitefish.

The species is recorded by Evermann from Lake Bennett, Yukon Territory, where it was taken by the writers in 1903. It is also recorded from various other localities on the Yukon and from Wood River (Bristol Bay). As the species certainly does not occur in the Winnipeg basin, it may

be questioned whether this Yukon fish is not a distinct species of *Prosopium* separate from the ordinary *Coregonus quadrilateralis*. Our specimens are from Mackinac, Cheboygan, Marquette, and Blind River.

Description of a specimen of *Coregonus quadrilateralis* 15.5 inches long from Blind River, North Channel, Lake Huron:

Head 5.5 in body length to base of caudal; depth 4.5; eye 5 in head; snout 3.6; interorbita breadth 3; maxillary from tip of snout somewhat longer than eye diameter; caudal peduncle length 1.28 in head, its depth one-half its length; dorsal 11 (fully developed rays); anal 12; scales 8–90–7, between occiput and origin of dorsal 35; branchiostegals 8; gillrakers 6+10.

Body elongate, little compressed, more terete than in any other species of the genus, its greatest depth and width in anterior portion of body, hence space from snout to insertion of dorsal more strongly arched than remainder; caudal peduncle long, little compressed, half as deep as long; head small, pointed; snout moderately short; post-orbital and sub-orbital bones broad; maxillary very short, broad, not reaching eye; supplementary bone very narrow; mandible short, three in head, not reaching posterior edge of pupil, included within upper jaw; dorsal contour arched somewhat, although not greatly; distance from snout to occiput 2.5 in distance from occiput to dorsal insertion. Dorsal insertion nearer snout than base of caudal, its longest ray equal to distance from snout to occiput, its base about 1.5 in head; adipose small; caudal short; pectorals short, somewhat longer

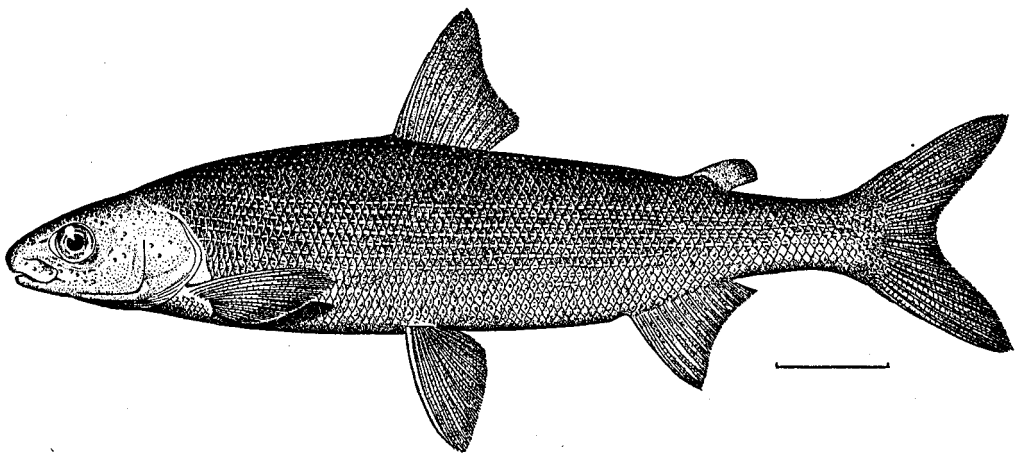

FIG. 20.—*Coregonus stanleyi* Kendall. From the type.

than dorsal rays, inserted low, reaching halfway to ventrals; ventrals very short, considerably more so than pectorals; anal base somewhat more than 0.5 head, its longest ray 1.66 in head. Lateral line straight, scales rather small.

Color in spirits, rather dark on sides and back, colorless ventrally; a line or streak of dark along edges of longitudinal rows of scales, especially just below lateral line; fins pale, except for borders of dorsal and caudal, which are dark

Coregonus kennicotti Milner. *Kennicott's Whitefish.*

Coregonus kennicotti Milner, in Jordan & Gilbert, Synopsis Fishes North Amer., p. 298, 1883, Fort Good Hope, British America.

Habitat: Mackenzie River, Canada, Yukon River, and other streams of the Alaskan region. Recorded by Evermann from Lake Bennett, Alaska, where it is probably common.

Coregonus stanleyi Kendall. *Stanley's Whitefish.*

Coregonus stanleyi Kendall, Bull. U. S. Fish Comm., vol. XXII, 1902 (1904), p. 366, with figure, thoroughfare between Mud and Cross lakes, Aroostook County, Me.

Habitat: Lakes of northern Maine.

This species, provided with pearly bodies on the scales in the breeding season, seems nearest to the Rocky Mountain whitefish, *Coregonus williamsoni*.

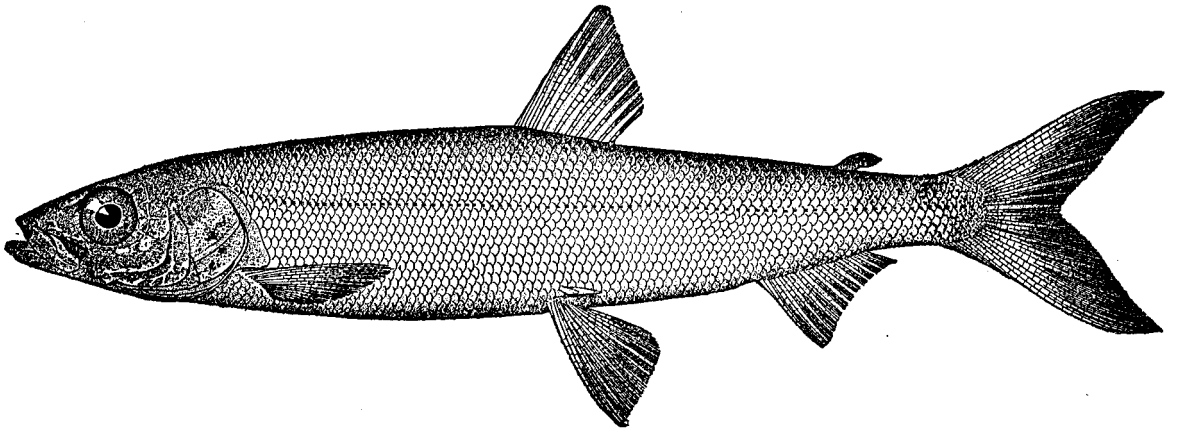

FIG. 21.—*Leucichthys osmeriformis* (H. M. Smith). Smelt. From the type, a specimen 10 inches long, taken in Seneca Lake, New York.

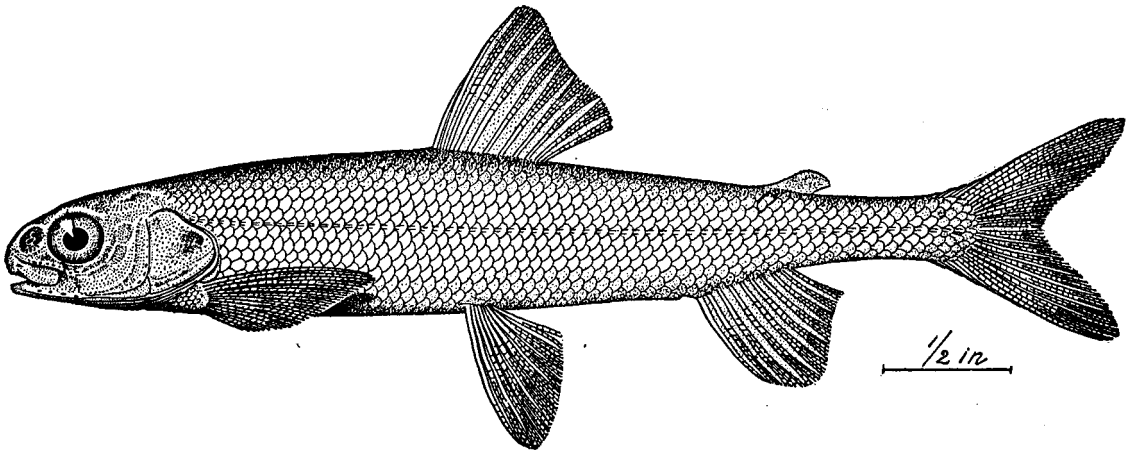

FIG. 22.—*Coregonus coulteri* Eigenmann & Eigenmann. Coulter's Whitefish. From a specimen, 4 ⅓ inches long, one of the types, collected in Kicking Horse River, at Field, British Columbia.

Coregonus williamsoni Girard. *Rocky Mountain Whitefish.*

Coregonus williamsoni Girard, Proc. Ac. Nat. Sci. Phila. 1856, p. 136, Des Chutes River, Oregon.

Habitat: Rivers of the Sierra Nevada and west slope of the Rocky Mountains, from the Fraser and the Columbia to the Truckee and other streams of the Lahontan basin of Nevada; abundant especially in lakes of northern Idaho, western Montana, and Washington. One of the most delicious of food fishes, and reaching a weight of 4 pounds.

Coregonus cismontanus Jordan. *Yellowstone Whitefish.*

Coregonus williamsoni cismontanus Jordan, Bull. U. S. Fish Comm., vol. IX, 1889, p. 49, pl. 9, fig. 8, 9, Horsethief Creek, Madison River, Montana; coll., E. R. Lucas.

Habitat: Streams of the Rocky Mountain region tributary to the upper Missouri.

It is very doubtful if this fish differs at all from *Coregonus williamsoni* which replaces it on the west side of the Rock Mountains.

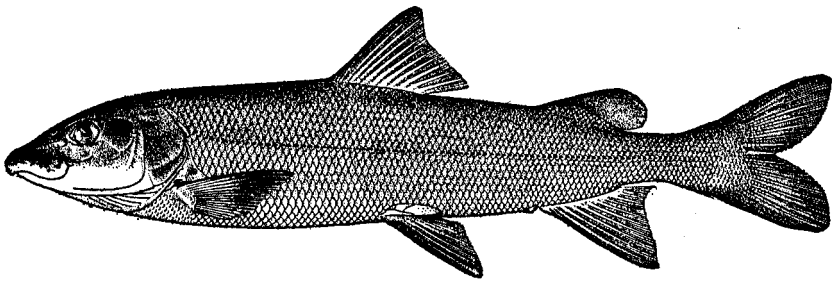

FIG. 23.—*Coregonus oregonius* Jordan & Snyder. Oregon Whitefish. From the type.

Coregonus coulteri Eigenmann & Eigenmann. *Coulter's Whitefish.*

Coregonus coulterii Eigenmann & Eigenmann, Amer. Nat., Nov., 1892, p. 961, Kicking Horse River at Field, British Columbia.

Habitat: Headwaters of the Columbia.

A strongly marked species easily recognized by its large scales (60 to 63).

Coregonus couesi Milner.

Coregonus couesii Milner, Rept. U. S. Fish Comm. for 1872–73 (1874), p. 88, Chief Mountain Lake, Montana; coll., Elliott Coues.

Habitat: Headwaters of Saskatchewan River.

This is a strongly marked species, allied to *Coregonus oregonius*, and very improperly confounded with *Coregonus williamsoni* by Jordan & Evermann.

Coregonus oregonius Jordan & Snyder. *Chisel-mouth Jack; Oregon Whitefish.*

Coregonus oregonius Jordan & Snyder, Proc. U. S. Nat. Mus., vol. XXXVI, 1909, p. 425, with fig., Mackenzie River, Oregon.

Habitat: Lower Columbia River basin.

A well-marked species, agreeing with *C. couesi* in the long snout, and further distinguished by the very high adipose fin.

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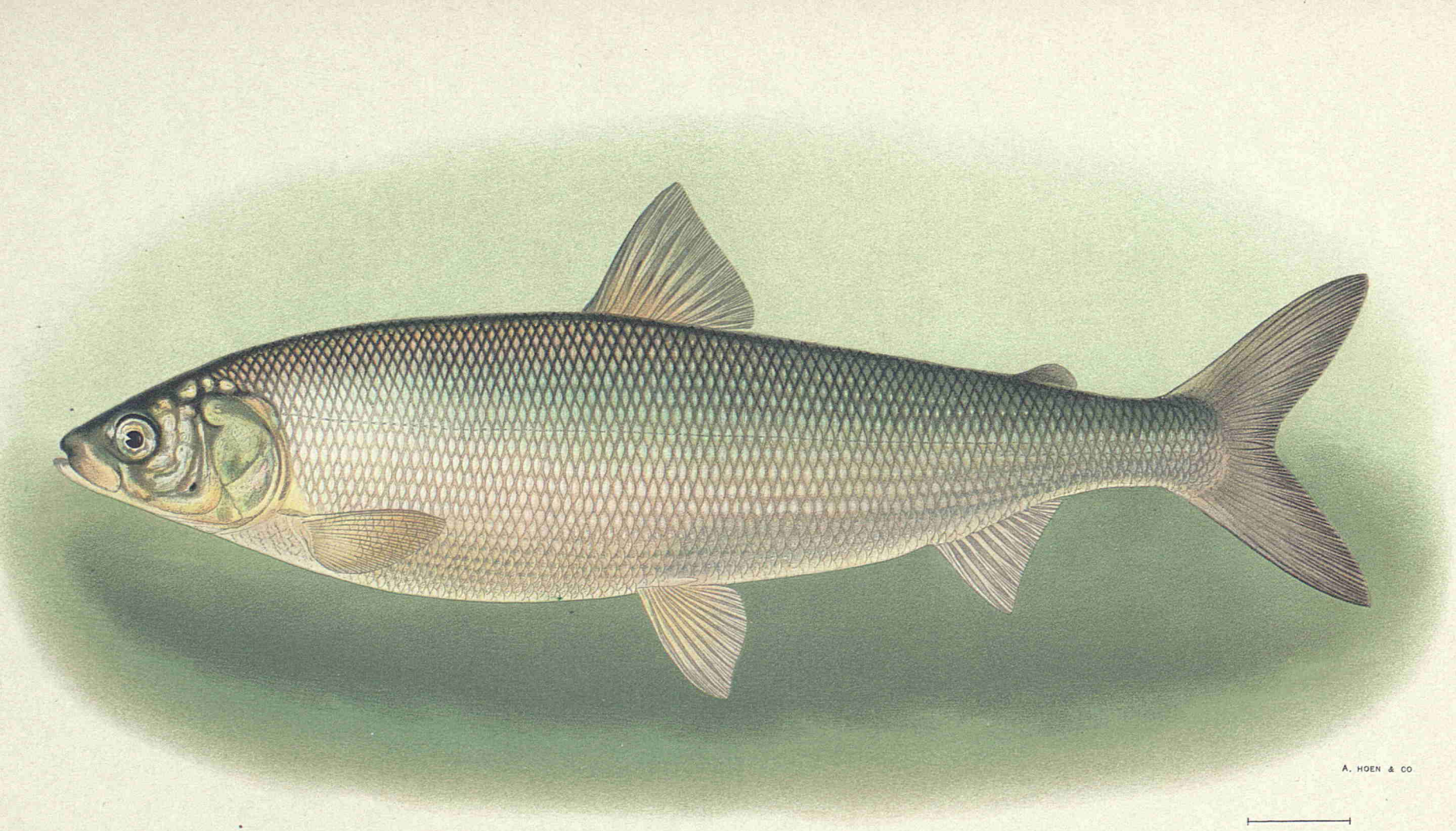
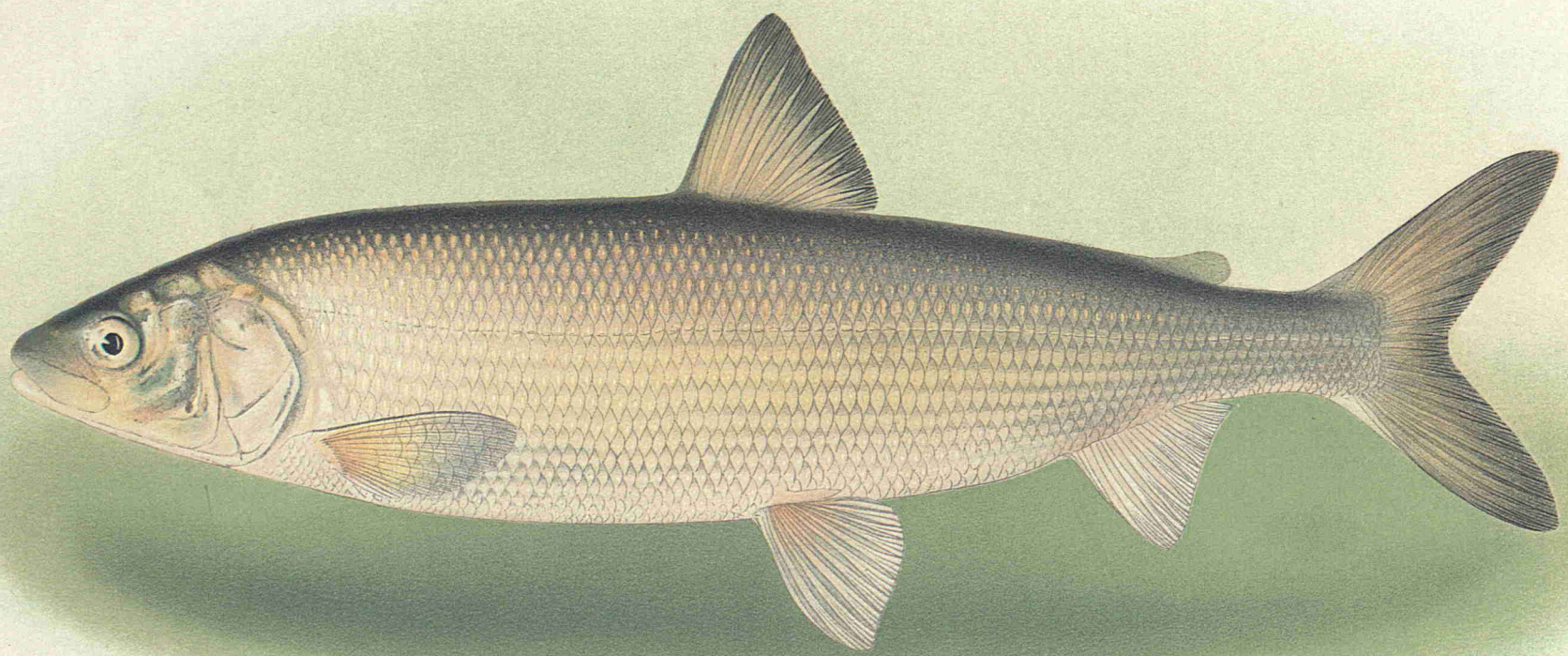


A. HOEN & CO

Drawn by Charles B. Hudson

LAKE HURON HERRING

Leucichthys sisco huronius (Jordan & Evermann)



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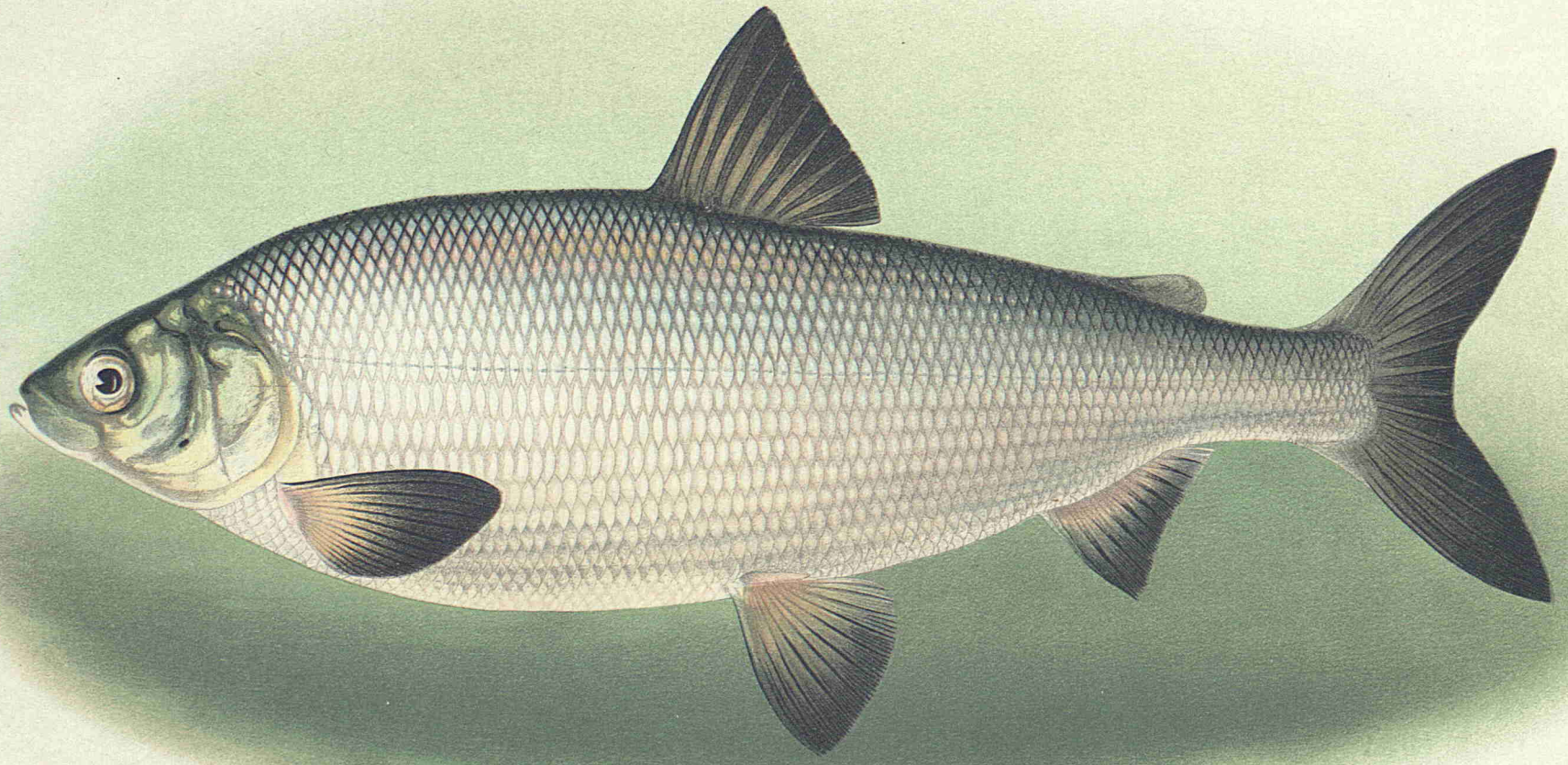
BLOATER OF LAKE MICHIGAN
Leucichthys johannæ (Wagner)



A. HOEN & CO

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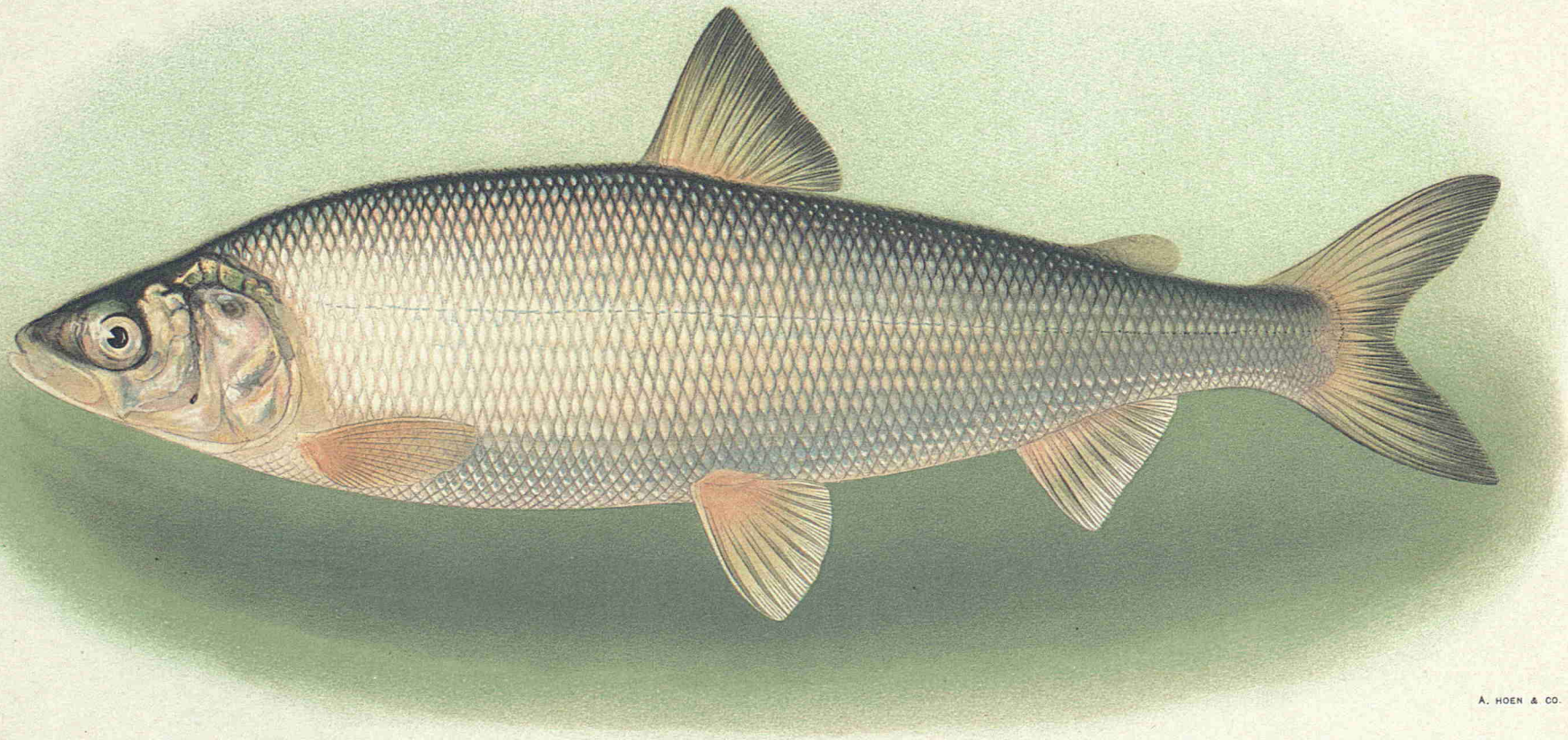
BLACKFIN OF LAKE MICHIGAN
Leucichthys nigripinnis (Gill)



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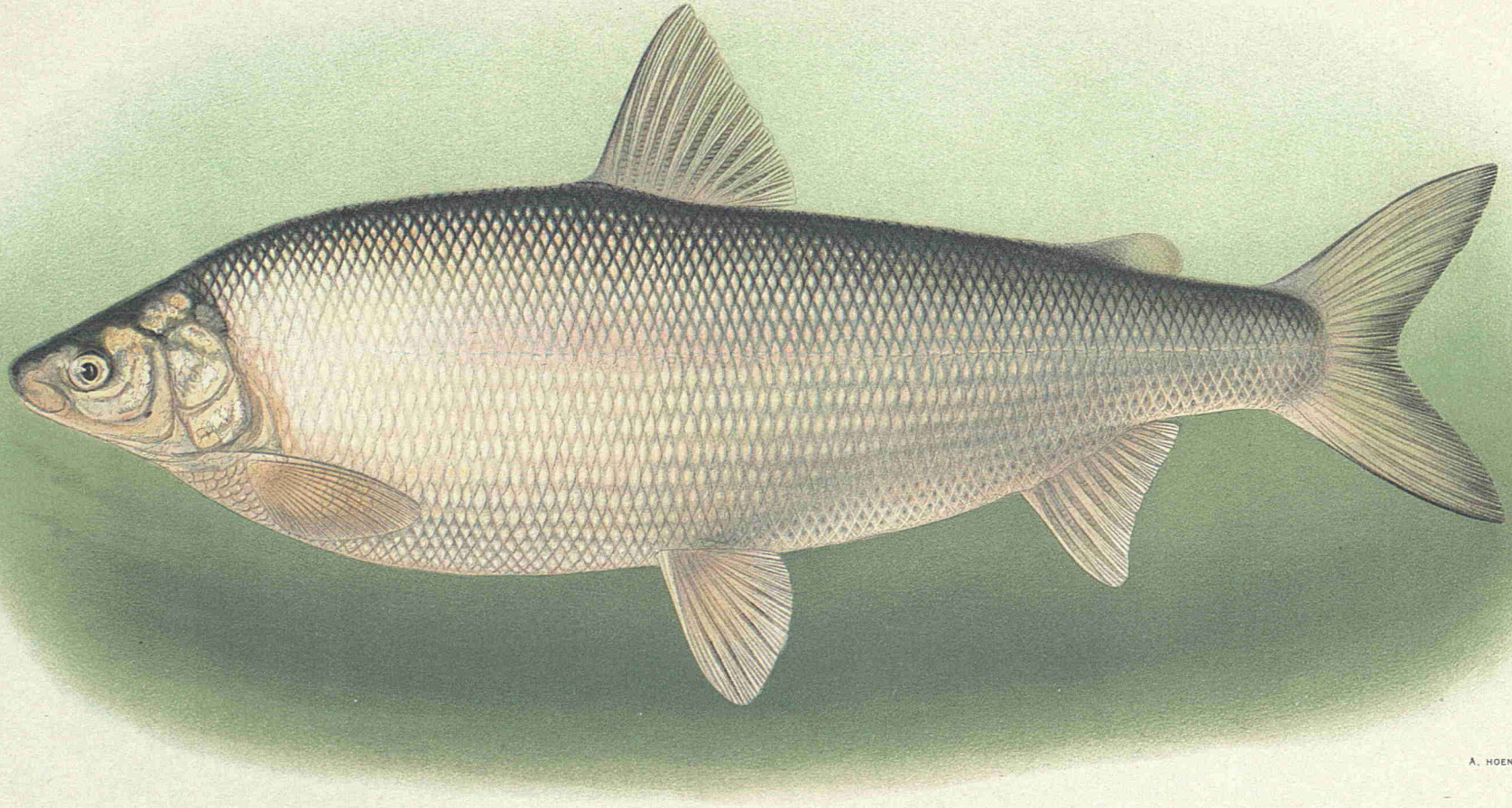
CISCO OF LAKE MICHIGAN
Leucichthys hoyi (Gill)



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COMMON WHITEFISH OF LAKE ERIE
Coregonus albus (LeSueur)

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MENOMINEE WHITEFISH; ROUND WHITEFISH
Coregonus quadrilateralis (Richardson)

INFLUENCE OF THE EYES, EARS, AND OTHER ALLIED SENSE ORGANS ON THE MOVEMENTS OF THE DOGFISH, MUSTELUS CANIS (MITCHILL)

By G. H. Parker, S. D.,

Professor of Zoology, Harvard University

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INFLUENCE OF THE EYES, EARS, AND OTHER ALLIED SENSE ORGANS ON THE MOVEMENTS OF THE DOGFISH, MUSTELUS CANIS (MITCHILL).

By G. H. PARKER, S. D.,
Professor of Zoology, Harvard University.

The common occurrence of the smooth dogfish, *Mustelus canis* (Mitchill), in the waters about Woods Hole, the success with which this fish can be kept in confinement, and the ease with which it resists the adverse effects of operations led me to undertake a study of its more important sensory reactions. This paper deals with the effects of the following sense organs on the movements of the dogfish: Eyes, ears, lateral-line organs, the ampullæ of Lorenzini, and the organs of touch. The work was carried out at the United States Fisheries Laboratory, Woods Hole, Mass.

CLASSES OF MOVEMENTS.

The more obvious external movements of the dogfish fall into four classes. The first class consists of the movements of the eyeballs, either backward and forward, as for instance when the fish is swimming, or rolling movements such as occur when the animal is rotated on its long axis. The second class of movements are those of the false eyelid or nictitating membrane, which can be made to rise from the ventral edge of the orbit and thus cover the surface of the eyeball ordinarily exposed. The third class of movements are the respiratory movements of the gill region. These vary much in rate dependent upon the momentary state of the animal. In a large resting fish they vary from about 35 to 45 movements per minute. The same fish when swimming slowly will respire 50 to 55 times per minute. In vigorous swimming the rate is doubtless still more rapid. The fourth class of movements are the locomotor movements which are carried out in the main by the fins. The specific gravity of the dogfish is slightly greater than that of sea water and when the fish ceases to swim it sinks to the bottom. As it has no swim bladder, it is incapable of floating in the water as many teleosts do, and whenever it is off the bottom it maintains its position necessarily by active swimming. In this operation all the fins are concerned, but of these none is so important as the caudal fin. If one dorsal fin or the anal fin is removed, the fish swims apparently as well as ever. If

all three fins, i. e., the two dorsal and the anal, are removed the efficiency in swimming is somewhat reduced though not as much so as when the caudal fin alone is removed. The removal of all the median fins leaves the fish still capable of forward locomotion but only with excessive effort, largely because of the small amount of surface that can be opposed to the water. The removal of the paired fins from one or both sides has very little effect on the swimming of the fish, though its ability to turn accurately is much reduced. The removal of all fins both median and lateral leaves the animal still capable of wriggling through the water, though with a somewhat rolling motion. It is probable that under normal conditions the lateral fins correct this roll. Of all the fins the caudal is the one chiefly concerned with locomotion; the others serve mainly as keel-like guides and rudders, though the median fins other than the caudal certainly supplement this fin in the movements of swimming.

THE EYES.

When a normal dogfish is first put into even a large aquarium, it swims about with much awkwardness, colliding with such objects as the dark walls and glass sides of the aquarium and avoiding only the more conspicuous bodies, such as light-colored rocks, etc. The impression given to the observer is that the dogfish has very poor vision, and this opinion is current among many fishermen. After a few hours, however, such a dogfish will adjust itself to its new quarters and will swim about with only an occasional collision. That this condition is not dependent upon its acquaintance with the currents, etc., in the aquarium is shown from the fact that if the dogfish is etherized and its optic nerves are cut, it will swim slowly about bumping its nose continually against solid objects precisely as a blinded animal might be expected to do. Nor does it ever recover in any very marked degree from this state. It therefore seems clear that a normal dogfish possesses fair vision and that it is capable of adjusting its responses to the stimuli in its retinal fields with such precision that its locomotion is in large part guided by these stimuli. The relation of the two eyes in these responses is clearly seen when only one optic nerve is cut. Under this condition the dogfish will still swim much as a normal one does, though collisions will occasionally occur on its blinded side. Such a fish never moves in circles, as many of the lower animals do, showing that the directive discrimination in one retinal field is of more importance in its locomotion than the mutual relation of the two retinas.

Not only does a blinded dogfish fail to recognize the detailed illumination of its surroundings, but its remaining sensory apparatus is apparently unstimulated by light. If a beam of concentrated sunlight is thrown on any part of the skin of a blinded dogfish, no response is obtained, showing that the integumentary nerves of these fishes, unlike those of the young lamprey (Parker, 1905 *b*) and many amphibians, are not stimulated by light.

Another feature to be observed in the blinded dogfish as compared with the normal one is the region of its swimming. A normal dogfish will swim indiscriminately through an aquarium, whereas a blinded one remains usually near the bottom and swims about in

such a way as to be almost continually in contact with some solid surface, as though relying on its sense of touch for its location.

If the nictitating membranes of a dogfish are drawn across the eyes and stitched to the upper eyelids, the fish does not respond as a blinded fish does, but swims about in the most brightly illuminated part of the aquarium. This is usually the top, but it may be the bottom if light is admitted from low down on the sides. Such fishes are liable to collide with solid bodies in their paths of motion and are doubtless reduced to the condition of many lower animals in which the visual organs are not image-forming eyes but mere direction eyes, i. e., the fishes are reactive to the presence or absence of light and to the direction of a chief source, without, however, being able to respond to the details of illumination in their surroundings. This condition is doubtless dependent upon the fact that the intercepting nictitating membranes are at best only slightly translucent and thus prevent the formation of efficient retinal images.

When a bright light is brought to the glass side of an aquarium otherwise dark, normal dogfishes and those whose eyes are covered with the nictitating membranes will gather near it. Very likely a submerged light in clear water could thus be made a lure for dogfishes in the night. These reactions, however, cease in a generally illuminated field such as surrounds the dogfish during daytime. As might be expected from what has already been observed, blinded dogfishes show no response to a single light in an otherwise dark field.

From these observations it is clear that the only part of the dogfish sensitive to light is the eye and that the retinal image is an important factor in guiding the locomotion of these fishes. In an otherwise unilluminated field dogfishes will swim toward a single light, i. e., they are positively phototropic.

THE EARS.

The original function attributed to the vertebrate ear was of course that of hearing. In 1828 Flourens recorded observations that led to the belief that the ear was also concerned with equilibrium, and this opinion, though not without its opponents, has been supported by Goltz, Mach, Breuer, and others. In 1891 Ewald advanced the view that the ear likewise had to do with the maintenance of muscular tonus. These three functions are the chief ones ascribed to the vertebrate ear. To what extent they are characteristic of the ears of the dogfish will now be discussed.

In a previous paper (Parker, 1903), on hearing in fishes, I made the statement, recently confirmed by Lafite-Dupont (1907), that the ears, lateral-line organ, and skin of the dogfish were not open to stimulation by vibrations such as are produced by a bass-viol string and transmitted to this fish through the water. But I also noted that this fish was responsive to the same vibrations when it rested on a solid transmitting base. It would seem from these observations that the smooth dogfish is at best only slightly sensitive to material vibrations, and my subsequent work has shown the correctness of this opinion. To test the question of hearing in the dogfish, I followed the plan previously adopted for *Fundulus* (Parker, 1903), and experimented in the main with three classes of fishes: (1) Normal individuals; (2) those with the eighth nerve cut but

with the surface of the skin normally sensitive, and (3) those with the ears intact but with the surface of the skin rendered insensitive.

When a normal dogfish is placed in a large wooden aquarium, it at first swims about in a disturbed and irregular manner. After half an hour or so it becomes so far accustomed to its new quarters as to move about with apparent complacency. If, while the dogfish is swimming through the water and is not in contact with the sides or bottom of the aquarium, a fairly vigorous blow is struck with a mallet on the wooden wall of the aquarium, the dogfish will almost invariably respond with a sudden jump forward. This can be repeated many times provided that a few minutes intervene between the trials. If the blow is not very vigorous the response may be only a slight waving of the fins, best seen on the posterior edges of the pectorals.

To get some measure of this response, I suspended on a stout cord from the ceiling of the room in which the experiments were conducted a large spherical iron weight so that it formed the bob of a pendulum which, when at rest, just touched the middle of one of the wooden sides of the aquarium. By drawing this iron bob away from its position of rest and letting it swing squarely against the wooden side of the aquarium, a noise was produced that would be louder or fainter depending upon the distance between the bob and the aquarium side when the bob was liberated. The momentum with which the blow given by the bob was struck was taken as a rough measure of the noise produced. As the whole apparatus was a simple pendulum, it was comparatively easy to make the necessary calculations for a scale to be placed next the cord of the pendulum to indicate the positions from which the bob must be liberated in order to generate given momenta. The length of the pendulum was 260 centimeters and the weight of its bob was 3,800 grams. The momenta used in the experiments and expressed in centimeter-gram-second units were (1) 83,600, (2) 125,400, (3) 167,200, (4) 250,800, and (5) 334,400, or, calling momentum (1) unity, they could be more conveniently designated as 1, 1.5, 2, 3, and 4.

Normal dogfishes when swimming freely in the water of the aquarium occasionally responded by pectoral fin movements to the sound generated by the bob of the pendulum striking the wall of the aquarium with a momentum of 1, and invariably responded when the momentum was 1.5. The range from 1 to 1.5 was therefore taken as the range of minimum stimulus for a normal fish.

Six dogfishes, which had previously been tested to ascertain that they were normally responsive, were now subjected to the operation for cutting the eighth nerve, and after recovery they were again tried for their responsiveness. None reacted to the sounds produced when the ball struck the side of the aquarium with a momentum of less than 3, and they responded invariably only when the momentum was 4.

At first sight this considerable reduction in the sensitiveness of the fish might be taken to be a final answer to the question of the significance of the ear as a receptive organ for sound, but it is possible that its real explanation lies in the reduced physiological state of the animal as a result of so severe an operation as that of cutting the eighth nerve. I therefore repeated these tests on several dogfish in which for other purposes the optic nerves had recently been cut, and I found that notwithstanding the

severity of the operation these fishes were as sensitive to sounds as normal fishes are. I therefore believe that the loss of sensitiveness in dogfishes whose eighth nerve has been cut is not due to the severity of the operation, but to the actual loss of the ear as an effective sense organ.

As it has often been maintained that the responses of fishes to sounds depend upon stimulation of the skin and not of the ears, I prepared another set of dogfishes in which I endeavored to render the nerves of the whole integument insensitive to mechanical stimulation. As in the case of *Fundulus*, so in the dogfish, I cut the fifth and seventh nerves as well as the lateral-line nerves. I also pithed the animals by cutting off the tail, plugging the caudal artery and vein with a ball of absorbent cotton so as to prevent excessive bleeding, and inserting a wire into the spinal canal and twirling it as far forward as the neck region so as to destroy the spinal cord. After recovery from these operations the skin of the dogfish was found insensitive to mechanical stimuli except in the region of the gills and pectoral fins. In my experiments on *Fundulus* this region was also of necessity left sensitive to mechanical stimulation and might therefore serve as a receptive surface for sound vibrations. In reporting my results on *Fundulus* I noted this fact with regret, and it has been used as an argument against the validity of my results by a recent critic, Körner (1905). It seemed to me therefore highly important to ascertain whether this region of the skin played any important part in the reception of sound, and for this purpose I attempted to render it insensitive without, however, interfering with the nervous control of its underlying muscles.

To accomplish this end I endeavored to cut the dorsal roots of the spinal nerves of this region, but my efforts were unsuccessful. I finally found in cocaine a means of accomplishing my purpose. If a 2 per cent solution of cocaine is applied to a tactile area on a dogfish's skin, in from fifteen to twenty minutes the area becomes somewhat mottled and loses its sensitiveness. I therefore placed, on a frame in the open air, a dogfish in which the appropriate nerves had been cut, and after having started a current of sea water through its mouth and gills for respiration I covered the remaining sensitive part of its skin in absorbent cotton soaked in 2 per cent cocaine. Before the application of the cocaine the dogfish responded by movements of the pectoral fins to mechanical stimuli applied to these fins, but after a quarter of an hour these responses ceased. After half an hour's treatment the dogfish was taken from the frame and suspended by its anterior dorsal fin in the sea water of the wooden aquarium and subjected to sound stimuli. The animal occasionally responded by movements of the pectoral fins to the sound produced when the bob of the pendulum hit the side of the aquarium with a momentum of 1 and it invariably reacted when the momentum was 1.5 or more; in other words, the animal, so far as its responses to sound were concerned, differed in no essential respect from a normal dogfish. Three other dogfish were tested in like manner and gave similar results. I therefore conclude that the skin of a dogfish is not essential to its response to sound.

To check these conditions in relation to the ear, two of the four dogfishes with insensitive skins were subjected to the further operation of having their eighth nerves

cut. On testing these with sounds before the effects of the cocaine had disappeared they were found not to respond to any sounds produced by the pendulum apparatus. It therefore seems clear that the relatively slight response that the smooth dogfish shows to sounds is mainly dependent upon the ear and that this fish, like *Fundulus* (Parker, 1903), *Carassius* (Bigelow, 1904), and *Cynoscion* (Parker, 1910), may be said to hear.

Having ascertained that the smooth dogfish is capable of hearing, I next endeavored to determine what part of its ear is concerned with this function. The deep seat of this organ and its relatively small size made my task so difficult that I was at last obliged to abandon it, but one set of experiments in this direction are not without value. Following the directions given by Lyon (1900) for cutting cranial nerves, I found that the sacculus of the ear of the dogfish was accessible for operative purposes through the roof of the mouth and that this organ could be exposed in favorable cases without causing bleeding. I made this exposure in seven dogfishes with the intention of opening the sacculus and washing out its otolith with a fine current of sea water. In four cases the operation was successful on both sides. These four dogfishes were given time to recuperate and then were tested. All were strong and vigorous in their swimming and, contrary to what would be expected from the statement made by Kreidl (1892), they were absolutely indistinguishable from normal individuals in their equilibrium. In their reactions to sounds produced by the pendulum apparatus they resembled fishes in which the eighth nerves had been cut in that they were responsive only to sounds made by a blow of the bob with a momentum of 3 or more.

Objections might be raised to these results, at least so far as equilibrium is concerned, because the animals tested had had both otoliths removed, and in fact Loeb (1891 *a*) has already declared that when only one otolith is taken out the animals show disturbed equilibrium in that they swim with the operated side low. I removed a single otolith from each of three dogfishes, but though I kept them under observation several days I was never able to make out any characteristic irregularity in their equilibrium. These results show that the large friable otoliths of the dogfish's ears, like those of *Siredon* and the frog (Laudenbach, 1899) and *Cynoscion* (Parker, 1908), are not essential to equilibrium, but are, as in the case of *Cynoscion* at least, concerned with hearing.

That the ears of the dogfish have to do with equilibrium is so well attested by previous investigators that this aspect of the subject calls for no special reconsideration. After having had their eighth nerves cut, some smooth dogfishes will acquire the ability to swim slowly in normal equilibrium—a condition which, as experiments have shown, is certainly in part dependent upon the eye and perhaps in part upon the sense of touch; but these animals when made to swim with ordinary rapidity lose equilibrium and present a condition of irregular locomotion such as characterizes the majority of operated animals at all times.

Possibly exceptional cases of this kind influenced Sewell (1884) and Steiner (1886, 1888) in their opinion that the ear of the dogfish was not concerned with equilibrium—an opinion that has been set at naught by the more recent work of Loeb (1891 *b*), Kreidl (1892), Lee (1892, 1893, 1894, 1898), Bethe (1899), Gaglio (1902), and Quix (1903).

Although some of these investigators differ among themselves as to the details of their conclusions, they all agree in ascribing a function of equilibration to the ear, and this conclusion is abundantly borne out by my own observations. If both eighth nerves of a smooth dogfish are cut, the animal becomes profoundly disturbed in equilibrium. It usually swims in irregular spirals and will rest on the bottom in any position, dorsal or ventral side up. When only one nerve is cut, the disturbance is much less pronounced. After such an operation a dogfish will often swim and rest in the usual position and be almost indistinguishable from a normal individual. If such animals are made to swim rapidly, however, they usually show much unsteadiness and may even lose equilibrium. A comparison of dogfishes in which one nerve has been cut with those in which both have been severed makes it perfectly evident that the loss of one ear can be largely compensated for by the other and that it is only after the loss of both ears that profound disturbance of equilibrium can be looked for with certainty. These conditions are so uniform and clear that the conclusion is fully justified that the ear of the dogfish is a receptive organ from which emanate impulses that influence its locomotor mechanism so far as to retain the equilibrium of a body that is naturally in a somewhat unstable state.

A dogfish in which one of the eighth nerves has been cut is slightly weaker after the operation than before it, and one in which both eighth nerves have been cut is invariably very much weaker than it was previously. These differences are very noticeable in handling the fishes, and they are characteristic of operations involving the eighth nerves. Where, for instance, the second nerves have been cut, this diminution in muscle tonus does not occur. It is, as Ewald (1892) has pointed out, a distinguishing feature of the eighth nerve.

From these various observations and experiments on the ears of the smooth dogfish, I conclude that these organs, like the ears of the higher vertebrates, are concerned with hearing, equilibrium (Flourens), and muscular tonus (Ewald), and that the otoliths are not essential to equilibrium, but are in some way concerned with hearing.

THE ORGANS OF THE LATERAL LINE.

As I have elsewhere shown (Parker, 1905 *a*), the lateral-line organs of the smooth dogfish can be stimulated by material vibrations of low frequency. This stimulation gives rise to movement of the fins, especially of the caudal fin, and to actual locomotion in which the fish swims, where possible, downward into deeper water. Lee (1898) has maintained on the basis of the movements of the fins as a result of the direct stimulation of the lateral-line nerves that the lateral-line organs are concerned with equilibrium and that in this respect they are closely related to the ear. I have repeated Lee's experiments so far as possible, but with rather different conclusions.

Lee states that if the lateral-line nerve is cut near its anterior end and stimulated centrally, perfectly coordinated, definite movements of the fins occur. Thus if the left lateral-line nerve is stimulated, the dorsal fins and caudal fin move to the right, the right pectoral and pelvic fins move downward and the left upward. It is true that if

the lateral nerve is exposed and directly stimulated electrically precisely these movements occur. They also occur if the lateral line on the surface of the body is stimulated electrically. But none of these movements take place if previous to the stimulation of the regions mentioned the spinal cord is destroyed. If the spinal cord of the dogfish is destroyed from the tail to the neck region and the animal allowed to recover, no amount of stimulation of the lateral line or its nerve in the region in which the cord has been destroyed will, in my experience, call forth the fin movements described by Lee; but if the lateral-line nerve is cut anteriorly these movements may be induced by stimulating any spot along the appropriate side of the body, provided the stimulus is applied anterior to the pelvic fins. Thus the responses described by Lee depend on a stimulation of spinal nerves, not of lateral-line nerves. As Lee nowhere states that he took steps in his experiments to eliminate the spinal nerves, I suspect that he mistook reactions dependent upon these nerves for true lateral-line reactions. Thus the evidence that he has brought forward for the equilibrium function of the lateral-line organs falls to the ground.

Although the lateral-line organs, in my opinion, do not influence the fin movements in the way that Lee believed, they are capable of effecting important responses. If the skin of a dogfish whose spinal cord has been destroyed is pressed upon above or below the lateral line, no reaction occurs; if, however, the pressure is brought to bear on the lateral line itself, there is a considerable slowing in the respiratory rate or even a temporary cessation of movement. This respiratory response can also be obtained when a current of water is played on the lateral line, but it disappears permanently on cutting the lateral-line nerve. With the lateral-line system intact it is, however, so invariable in its occurrence that I believe that pressure may be regarded as one of the normal means of stimulating this system. This view has already been advanced by Fuchs (1894) as a result of his experiments on *Raja*.

The influence which the lateral-line organs of the dogfish have on its respiratory rate is not limited to the side stimulated. A stimulus applied either to the right lateral line or to the left one will effect a change in the whole respiratory mechanism.

The experiments thus far carried out show that the lateral-line organs of the dogfish are stimulated by vibrations of low frequency and by simple pressure, both mechanical forms of stimuli, and that these organs can influence the respiratory rate and the locomotion of the animal, but not in a way especially concerned with equilibrium.

THE AMPULLÆ OF LORENZINI.

The head of the dogfish is marked with symmetrically placed clusters of minute pores which are often mistaken for lateral-line pores. Each of these pores opens into a long, narrow tube which makes its way below the skin and ends in a bulb-like enlargement. These are the ampullæ of Lorenzini. They have long been suspected of being related to the lateral-line organs, an opinion that is supported by their innervation. So far as I am aware, no experimental evidence has thus far been obtained concerning their function. As the region in which they occur is covered with a skin filled with

tactile organs and penetrated by certain parts of the lateral-line system, it was necessary first of all to eliminate these sense organs before conclusive experiments could be made on the underlying ampullæ. To effect this elimination, I painted the skin over a given patch of ampullæ with a 2 per cent solution of cocaine, hoping thereby to destroy the receptiveness of the superficial tactile and lateral-line organs and leave that of the deep-seated ampullæ. After half an hour I tried various stimuli on this surface and I found that pressure upon this spot was accompanied by a momentary slowing or cessation of the respiratory movements. As I had also obtained this reaction from the lateral-line organs and as these organs were possibly involved here, I abandoned this method of procedure for another. This consisted in dissecting off the skin over a patch of ampullæ and thus removing the tactile and lateral-line endings completely. If, now, into the mass of ampullæ thus exposed, a blunt glass rod is gently pressed, the same partial or complete respiratory inhibition takes place as was seen in the earlier experiment. As this ceased on cutting the bundle of fine nerves that supplied the cluster of ampullæ, I conclude that pressure is a normal stimulus for the ampullæ of Lorenzini, and that these organs are in truth closely related to lateral-line organs.

THE ORGANS OF TOUCH.

The whole outer surface of a smooth dogfish, like that of many higher vertebrates, is open to stimulation from a deforming pressure, i. e., it is sensitive to touch. As a result of this stimulation no alteration in the respiratory rate has been observed, but movements of the nictitating membrane and fins have been called forth. The fin movements often appear in coordinated groups such as would result in normal locomotion. Wherever tactile stimulation occurs, electrical stimulation is also usually effective, with this difference, however, that the electrical stimulation may call forth a much more vigorous response than the purely tactile does.

The surface of the dogfish's body may be divided into some five tactile regions characterized mainly by the responses that result from their stimulation. The first of these regions is the part of the head anterior to the hindermost limits of the orbit. So far as the fins are concerned tactile stimulation of this region results in only slight irregular movements. When the stimulus is applied to a considerable stretch in front of the eyes, or above or below them, or to a very restricted area behind them, quick closing movements of the nictitating membrane occur. These movements, which are the really characteristic ones of this region, are strictly homolateral in that mechanical stimulation of the appropriate region on one side of the head never calls forth movements in the nictitating membrane of the opposite side, but only in that of its own side. Since they originate from a stimulus that in most cases is anterior to the eye and result in a closure of the nictitating membrane, they may be regarded as primarily concerned with the protection of the corneal surface of the eye-ball. Strange to say, they do not occur with anything like the certainty when the cornea is touched as when the adjacent skin is stimulated. This protective winking movement can be called out so far as I am aware only by mechanical stimulation; the nictitating membrane is not moved when intense

sunlight is thrown into the eye or the surface of the cornea is bathed with even so stimulating a solution as normal sulphuric acid. The protection apparently is only against mechanical injury.

The second general tactile region includes the whole surface of the fish from the posterior edge of the orbits to the pelvic fins except the ventral surfaces of the pectoral fins and the skin on the breast between these fins. The second region is bilaterally divided and a stimulus applied to any part of one side may call forth a movement of the two dorsal fins, the caudal fin, and the anal fin away from that side, an upward movement of the pectoral and pelvic fins of the stimulated side, and a downward movement of those of the opposite side, a group of coordinated movements already described by Lee (1898). These movements are undoubtedly concerned with guiding the fish in swimming.

The third general tactile region extends from the pelvic fins to the end of the tail. This region, like the preceding one, is bilaterally divided. The same fins that respond to the stimulation of the second region also respond to stimuli applied to this region, but the response is in the reverse direction. A stimulus applied to one side of this region calls forth a movement of the median fins toward that side, a downward movement of the paired fins of the same side, and an upward movement of those on the opposite side. Comparing this condition with that of the second region, it is clear that the fin responses produced by stimulating a given side in the second region agree with those called forth by stimulating the opposite side of the third region. This diagonal relation is probably significant in the swimming movements of the dogfish.

The fourth tactile region is the ventral surfaces of the pectoral fins and the breast region. Mechanical stimuli applied to almost any part of these surfaces call forth a fairly symmetrical ventral approximation of the pectoral fins. At times there is almost an overlapping of the posterior median edges of the two fins, but never a scissors-like movement, such as Sheldon (1909) has demonstrated by chemically stimulating the breast region.

The fifth region is the ventral surfaces of the pelvic fins. When these surfaces are stimulated a symmetrical movement of the pelvic fins toward the median plane takes place, thus closing the cloaca. There is some correlation between the response of this region and that of the fourth, though in the main the two regions are independent.

The movements of the fins produced from the fourth and fifth region partake of the nature of protective movements in that they wipe surfaces or close apertures. They probably have little to do with locomotion. The reactions initiated in the second and third regions are chiefly locomotor and probably have little significance otherwise. In this connection the movements of the posterior dorsal fin are significant. This fin moves with extreme freedom and in such a way that its posterior finger-like tip is wiped over the back of the animal on the side stimulated as though it were intended to remove some offending body. If, however, a weak stimulus is applied to a point low down on one side of the body, the fin thus made to move slightly to one side, and then a strong stimulus is applied between the dorsal line and the fin, the fin instead of wiping back over the newly stimulated part turns still further away from the dorsal line and vigorously wipes a part of the skin to which no stimulus whatever has been applied. It is

therefore evident that the direction of the movement of this fin is dependent upon the stimulation of any part of a given side and is not related to particular spots on that side. Hence the movement probably subserves a general function like swimming rather than a special one like the protection of the surface.

Not only are these fin movements called forth by the obvious tactile stimulation of given areas of skin, but, as Lyon (1900) first pointed out, they can be induced by moving certain parts of the body. If the end of the tail of a dogfish is seized symmetrically and turned to a given side, the dorsal and anal fins bend toward that side as though a tactile stimulus had been applied to that side in what has been called the third tactile region. That this reaction is really dependent upon a mechanical stimulation of the skin and not upon the activity of more deeply seated sense organs, is seen from the fact that the reaction disappears when the skin of the tail is rendered insensitive by about twenty minutes' treatment with a 2 per cent solution of cocaine. Not only can these correlated fin movements be called forth by turning the tail, but they can also be induced by moving the head. If the head of a dogfish is taken hold of symmetrically and turned toward a given side the median fins, particularly the anterior dorsal, turn toward that side. Thus the tactile surfaces of the dogfish are most intimately concerned with the correlated movements of this animal's fins and in such a way that they are undoubtedly significant factors in the animal's locomotion.

CONCLUSIONS.

The eyes of the smooth dogfish are the only receptive organs for light possessed by this animal. The dogfish reacts with sufficient accuracy to the details of its retinal images to show that it has moderately sharp vision. When the sharpness of its vision is greatly reduced, it becomes simply positively phototropic.

The ears of the dogfish are organs of hearing and are concerned with equilibrium and muscular tonus. The removal of their otoliths interferes with hearing but not with their two other functions.

The lateral-line organs are stimulated by vibrations of low frequency and by pressure. They are relatively insignificant as organs for the control of equilibrium.

The ampullæ of Lorenzini are stimulated by pressure and are doubtless closely related in origin and function to the lateral-line organs.

The whole integument of the dogfish is a receptive organ for mechanical stimuli. From it arise impulses for the movement of the nictitating membrane, and for a complicated system of correlated fin movements most of which are concerned with locomotion and equilibrium.

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BARNACLES OF JAPAN AND BERING SEA

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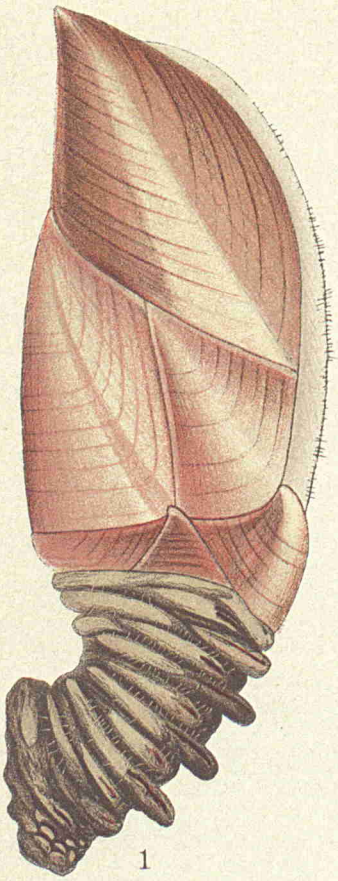

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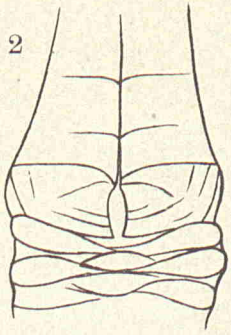

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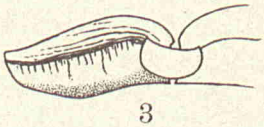

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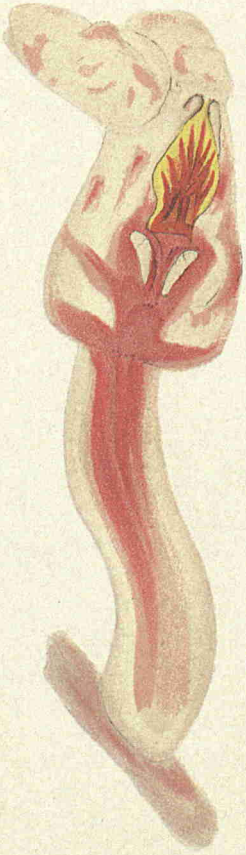

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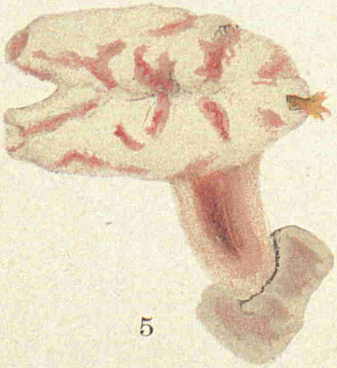

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BARNACLES OF JAPAN AND BERING SEA.

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The Cirripedia described herein were collected by the United States Fisheries steamer *Albatross* during the expedition of 1906. With a single exception, all are from Japanese waters and Bering Sea. The stations occupied are described in Bureau of Fisheries Document No. 621.

Little has been published on the barnacles of the northwest Pacific and adjoining seas; our knowledge of littoral and deep sea forms alike is scant. If the profusion of other invertebrates has any significance, we may expect a rich and varied fauna of Cirripedia off the Japanese east coast. Yet it must be admitted that the work of the *Challenger* and that of the *Albatross* have given no evidence of unusual richness in this cirripede fauna. An interesting feature brought out by the work of the *Albatross* is that a number of species of *Scalpellum* and *Pachylasma* live upon the stalks and pinnules of crinoids.

In Japan, acorn barnacles (Balanus sp.) are extensively used as manure. Bunches of bamboo collectors, similar to those used for oyster spat, are planted in the tide flats of Ariake Bay. After sixty to one hundred days they are taken up and the barnacles are beaten off. The annual yield is 400,000 bushels, valued at 30,000 yen.[a]

Family SCALPELLIDÆ.

Genus MITELLA Oken.

Mitella mitella (Linnæus).

1851. *Pollicipes mitella* Linnæus, Darwin, Monograph on the Cirripedia, Lepadidæ, p. 316.

Locality, Matsushima, on shore.

Genus SCALPELLUM Leach.

GROUP OF S. SCALPELLUM.

Scalpellum stearnsii Pilsbry. [Pl. IX, fig. 1 (young).]

1907. *S. stearnsii*, Pilsbry, U. S. National Museum Bulletin No. 60 p. 14.
1907. *S. stearnsii*, Hoek, Siboga Expeditie, Monographie XXXIa, Cirripedia, p. 69, with var. *gemina* and *robusta*.

This species was originally described from the Pacific coast between the Bay of Tokyo and the Inland Sea. The *Albatross* has taken specimens at the following stations:

Museum number.	Station number.	Locality.	Depth in fathoms.
38663	4940	Kagoshima Gulf	115
38665	4941	.....do	117
38664	4942	.....do	118
38677	4943	.....do	119
32875	3704	Seno Umi, off Hondo I	94

[a] K. Mitsukuri, Bulletin of the Bureau of Fisheries, vol. XXIV, p. 287.

A specimen taken at Nagasaki by Lischke has been figured by Hoek. The same author has described a variety *robusta* from the Malay Archipelago. This form has a broader capitulum and is said to have a longer peduncle. In the latter character, at least, the Japanese form does not differ from the Malaysian, as will be seen by the following measurements:

Station number.	Length of capitulum.	Breadth of capitulum.	Length of peduncle.	Number of rings of scales.	Remarks.
	mm.	*mm.*	*mm.*		
4942	50	32	64	20	Very plump.
4942	44	28.5	55	22	
4940	40	26	35	17	
4941	47	33	58	30	

A dry specimen in the collection of the Academy of Natural Sciences of Philadelphia has a very short peduncle; length of capitulum 44, width 28.5, length of peduncle, 20 mm. with 14 close scale rings. In dry specimens the peduncle contracts a good deal, bringing the spaced scale rings close together. The type originally figured by me was a dry specimen, which probably had originally a peduncle fully as long as any of the variety *robusta*. It has about 26 rings of scales.

Scalpellum stearnsii var. *gemina* Hoek (=*Scalpellum inerme* Annandale) I regard as a distinct species.

A young specimen (pl. IX, fig. 1) from station 4942 shows some suggestive features. The capitulum is 8.5 mm. long, 4.5 wide. The umbo of the scutum is apical, and that of the carina is nearly so, being within 1 mm. of the apex, the total length of the carina being 7 mm. The inframedian latus is comparatively much narrower than in adult individuals, and is somewhat contracted in the middle, the umbo being situated below the middle near the rostral border. In shape this plate reminds one of that of *S. idioplax* and its allies. The carinal latera project very little below the carina. No rostrum is visible. The plates are closely juxtaposed, without the wide chitinous sutures of the adult stage. These several characters, especially the positions of the umbones and the shape of the inframedian latus, approximate to the structure of *Arcoscalpellum*, and inasmuch as they probably represent an ancestral condition, they indicate that the typical group of *Scalpellum* is a divergent phylum, *Arcoscalpellum* being a more conservative group. The specimen figured is no. 38678 U. S. National Museum.

SUBGENUS ARCOSCALPELLUM HOEK.

GROUP OF SCALPELLUM VELUTINUM.

This group was defined in Bulletin 60, U. S. National Museum, page 26, where the American species are described. The following species belong here, all being deep-water forms:

Scalpellum velutinum Hoek.
S. regium Wyville Thomson.
S. regium latidorsum Pilsbry.
S. regina Pilsbry.
S. darwini Hoek.
S. gigas Hoek.
S. giganteum Gruvel.
S. moluccanum Hoek.
S. rubrum Hoek.
S. antarcticum Hoek.
S. sociabile Annandale.
S. alcockianum Annandale.
S. pedunculatum Hoek.
S. indicum Hoek.
S. hirsutum Hoek.
S. hawaiiense Pilsbry

Scalpellum rubrum Hoek. [Pl. VIII, fig. 1, 2, 3, 4.]

1883. *S. rubrum* Hoek, Challenger Report, Zoology, vol. VIII, p. 91, pl. 4, fig. 18.

This species was described from one specimen with the capitulum 5 mm. long, taken by the *Challenger* at station 204, near Luzon, in 100–115 fathoms. This specimen is described as "beautifully red and white colored", but without details as to the pattern. Its valves are "not covered by distinct membrane," and nothing is said of cuticular hairs. The internal organs were not examined.

A series of ten specimens was taken by the *Albatross* at station 4934, Eastern Sea, off Kagoshima Gulf, 30° 58′ 30″ N., 130° 32′ E., 152 fathoms, rocky bottom. (No. 38680 U. S. National Museum.) These show that the *Challenger* example was a very young one. I have therefore thought it well to describe the adult stage.

The occludent margin of the scutum is slightly convex, that of the tergum a trifle concave. The plates are crimson, passing into a dull yellowish tint. The pattern varies somewhat, but there is usually a ray of the paler tint down the middle of each of the three larger plates, while the borders have crimson rays. In some examples nearly the whole scutum is yellowish. The plates of the lower whorl are generally crimson. The narrow sides and rounded ribs bordering the roof of the carina are milk white. The flat, sunken roof has a crimson stripe bordering each lateral rib, the middle being pale. The plates are covered with a very thin cuticle which is most minutely downy.

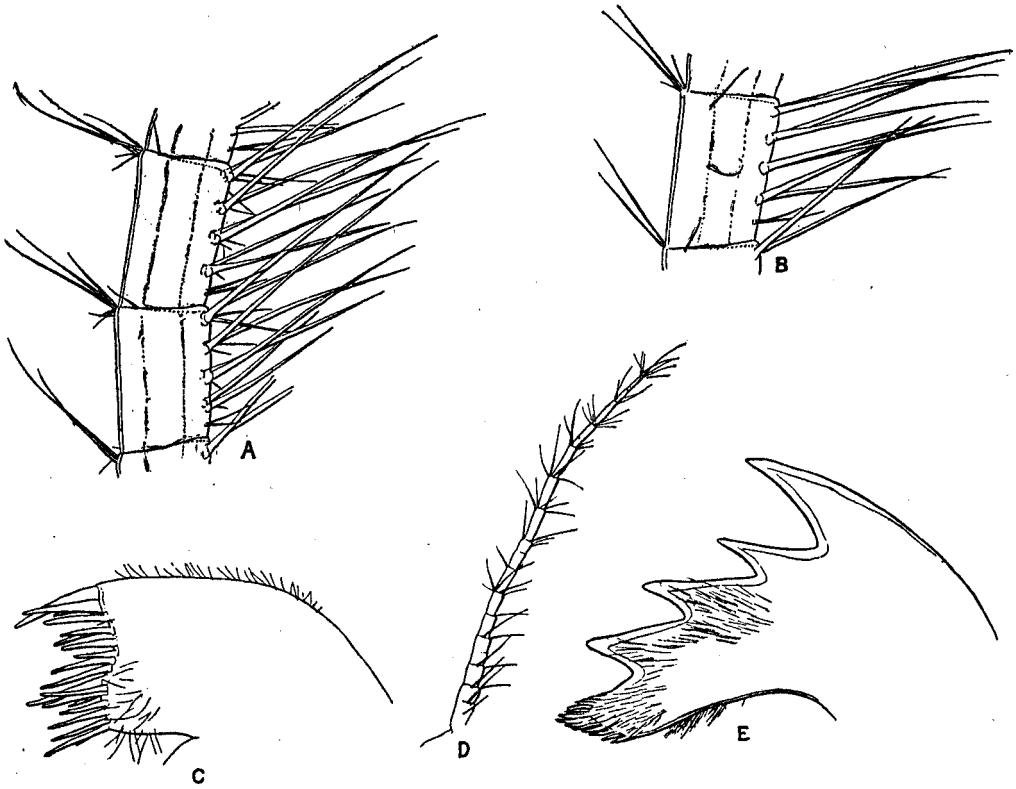


FIG. 1.—*Scalpellum rubrum* Hoek. A, 15th and 16th segments of outer ramus of cirrus V; B, 11th segment of inner ramus of cirrus V; C, maxilla; D, terminal appendage; E, mandible.

The scutum and tergum each has a low median diagonal riblet running from umbo to the baso-carinal angle. On both sides of this the surface is sculptured with low, irregular growth-wrinkles, and extremely minute growth-striæ; and weak fine radial striæ may be seen in suitable lights. A low rib runs along the scutal border of the upper latus, which is sculptured with growth-wrinkles and indistinct radial striæ, like the other plates.

The carina is very long, reaching upward beyond the upper fourth of the length of the carinal border of the tergum: and its apex is thrust between the terga, which diverge at the tips. On the roof the fine growth-striæ are broadly V-shaped.

The visible portion of the rostrum is small and triangular or oblong (pl. VIII, fig. 2).

A dissected specimen shows that the true shape of the rostrum is very unlike its externally visible face. It is wider than high, with concave upper and convex lower margin, as shown in figure 3, an inside view of rostrum and rostral latera.

The inframedian latus is triangular, the base slightly longer than the sides.

The peduncle is short, with six rows of large erect scales, five to seven scales in each row. It is rather copiously hairy. The scales are dull olive-yellowish, those of the carinal and adjacent rows edged with crimson.

The measurements of three individuals follow:

Length of capitulum.	Breadth of capitulum.	Length of carina.	Diameter of carina.	Length of peduncle.
Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
16.0	9.7	17.0	3.1	9.0
17.0	9.2	17.0	3.0	8.0
17.0	10.0	18.5	3.0	12.0

The mandible (fig. 1, E) has four teeth and a multispinose lower point. There is a very small beard on the lower edge.

The maxilla (fig. 1, C) has a slightly sigmoid edge, closely spinose.

The first cirrus has very unequal rami of 8 and 11 segments, which are densely hairy. The other cirri are of the usual slender form. The second cirrus has many spines on the inner faces of the cirri, and five pairs on the anterior side. The third and fourth cirri have a row of about 3 small spines on the inner face. The fifth cirrus has rami of about 27 segments, the median ones with four pairs of large and one of small spines, and the usual tufts at the posterior sutures (fig. 1, A, 15th and 16th segments of outer ramus cirrus v); besides these, the inner ramus has 1 to 3 small spines on the inner face of some of the median segments (fig. 1 B, 11th segment). The terminal appendages have 17 segments (fig. 1, D).

The penis is extremely long and slender, with some short, very sparsely scattered hairs.

GROUP OF SCALPELLUM ALBUM.

A group of *Arcoscalpellum;* rostral latera rather high; inframedian latus narrowly triangular with apical umbo; carinal latus high, with incurved apical umbo. Scales of the peduncle well developed, in few (5 or 6) regular longitudinal rows. Small forms, living so far as we know on the pinnules of crinoids. The following species belong here:

a. Rostrum well developed; carina extending downward V-like between the carinal latera.

Scalpellum album Hoek, Malay Archipelago, 500 fathoms.

S. weltnerianum Pilsbry, off southern Japan.

S. pentacrinarum Pilsbry, off Havana, Cuba.

b. Rostrum minute or wanting; carinal latera enormously long, united in a suture below the carina

Scalpellum balanoides Hoek, 5° 42′ S., 132° 25′ E., 126 fathoms.

S. gonionotum Pilsbry, Goto Islands, Japan.

Scalpellum weltnerianum Pilsbry. [Pl. IX, fig. 5, 6, 7.]

Type no. 32679 U. S. National Museum.

Type locality: Albatross Station 4918, 30° 22′ N., 129° 08′ 30″ E., 361 fathoms, about 90 miles WSW. of Kagoshima Bay, Japan; one specimen on a crinoid pinnule.

The capitulum is fully twice as long as wide; the occludent border is straight, the dorsal border arched. The plates are white, with an extremely thin, not hairy, cuticle, and those of the upper whorl are separated by distinct but rather narrow chitinous spaces which isolate the carina and upper latus except at their bases. All of the plates are sculptured with radial striæ or fine riblets, which are weaker and worn near the apices; and there are some spaced impressed lines indicating growth periods.

The scutum is narrow, with the beak reaching over the base of the tergum. The basal margin makes a right angle with the occludent margin, and is less than half its length. The diagonal ridge is acute in its lower part.

The tergum is about three times as long as wide, with straight occludent and basal margins. The carinal margin is straight except near the lower angle, where it becomes convex. The apex of the carina lies in the middle of the carinal margin. The surface of the plate is lightly concave near the occludent margin.

The carina is regularly and strongly arched throughout, with rounded roof. In section it is U-shaped. The sides are wide near the base, pass gradually into the roof and taper regularly toward the apex, near which an extremely narrow intraparietal area is visible through the cuticle. The lines of growth descend V-like on the roof.

The upper latus is quadrangular, more than twice as long as wide. The scutal border is much the longest and is concave; tergal border straight, somewhat serrate; carinal border slightly convex; basal border very oblique and straight. The lower angle of the plate is concealed under the apex of the inframedian latus. The umbo is terminal above.

The visible part of the rostrum is lozenge-shaped or rather narrowly pointed-oval, with regularly convex sides and a ridge down the middle.

The rostral latus is about as high as wide, with straight and equal scutal and lateral borders meeting at an angle of about 60°. The basal margin is very short, and the rostral margin is concave.

The inframedian latus is narrowly triangular, the height more than double the basal width. It is longer than the adjacent edge of the rostral latus, and toward the apex it curves slightly toward the carina.

The carinal latus is higher than wide, with the acute apical umbo curving scutad and situated at the suture between carina and upper latus. The carinal border is longest, strongly arched; upper border concave; the lateral margin is somewhat concave. The surface of the plate is divided by a curved diagonal line from the apex to the baso-lateral angle separating the sunken lateral area from the strongly convex carinal area. In carinal view, the carinal latera meet at the base, their carinal edges forming a long V.

The peduncle tapers strongly toward the base. It is closely covered with strongly imbricating and laterally interlocking subtriangular white scales, which under a high power are seen to be finely striated from summit to base. The scales form six regular longitudinal rows, of fourteen scales each.

Length of the capitulum 11 mm.; greatest width 5 mm. Length of the carina 8.2 mm.; width near the base 1.5 mm. Length of the peduncle about 4 mm.

A single example was taken. In order to preserve this entire, I was compelled to forego examination of the internal organs. It is closely related to *S. album* Hoek described from the Malay Archipelago in 500 fathoms, but that species seems from the description and figure to be smoother, more compressed, and larger. Hoek writes of *S. album:* "surface smooth * * * when studied with the microscope the beautiful striation of the valves distinctly appears". In *S. weltnerianum* the costation is distinctly visible to the naked eye. *S. weltnerianum* is also related, though rather distantly, to *Scalpellum pentacrinarum* Pilsbry,[a] a West Indian species also living on the pinnules of crinoids. The peculiar armor of the peduncle is the same in the two species, which further agree in the structure of the carina and the general shape of the other plates; but the sculpture and proportions of the individual plates are quite diverse. The very sparsely scattered hairs mentioned in my preliminary description are, I am now disposed to think, foreign growths.

This species is named in honor of Herr W. Weltner of the Museum der Naturkunde in Berlin, author of several useful papers on cirripedes.

Scalpellum gonionotum Pilsbry. [Pl. IX, fig. 2, 3, 4.]

Type no. 38678, U. S. National Museum.

Type locality: Albatross station 4901, 32° 30′ 10″ N., 128° 34′ 40″ E., 10–20 miles southwest of the Goto Islands.

[a] U. S. National Museum Bulletin no. 60, p. 55, fig. 20.

The capitulum is narrow and long, widest near the middle, tapering toward both ends, with no perceptible cuticle or pubescence. Occludent margin straight, carinal margin obtusely angular in the middle. The plates are white, everywhere closely juxtaposed, with sculpture of rather widely spaced grooves indicating former growth-periods.

The scutum is long, with straight, subparallel occludent and lateral margins; basal margin straight, at a right angle with the occludent margin.

The tergum is longer and larger than the scutum, with slightly convex basal and carinal margins, the apex erect.

Carina very short, nearly straight, with apical umbo at the upper fourth of the carinal margin of the tergum. Roof flattened; sides rounded, narrow, of nearly equal width throughout. Upper latus triangular, the sides and angles subequal.

Rostrum very narrow, separating the rostral latera in the upper half of their length.

Rostral latus somewhat wider than high, quadrangular, divided into triangular areas by a low diagonal ridge.

The inframedian latus is triangular, the apex curving toward the occludent margin. The basal width is about half the height.

The carinal latus is enormously lengthened, as long as the carina. The two latera meet behind in a straight suture, diverging only near the apices, which curve ventrad. The carinal outline of the plate is convex; the lateral border is divided into two concave arcs, a point between them projecting toward the occludent margin.

The peduncle tapers rapidly to the small base. It is densely covered with ivory-like scales arranged in five regular longitudinal rows, of which one is carinal, two on each side lateral. The carinal row has 14 scales, which are not so wide as those of the other rows. In the largest specimen a few additional scales are interposed between the lateral rows near the base of the capitulum.

Length of the capitulum 7.3 mm.; breadth 3.5 mm. Length of the carina 3.5 mm.; length of the peduncle 4.2 mm. A second specimen is slightly smaller; length of the capitulum 6 mm.

This curious little species is closely related to *S. balanoides* Hoek, taken by the *Challenger* in 5° 42′ S., 132° 25′ E., in 129 fathoms. A number of specimens were seated on a crinoid arm, none of them so large as *S. gonionotum*, the capitulum being only 4.5 mm. long, peduncle with five rows of seven scales each. *S. balanoides* has no rostrum; the dorsal margin is regularly curved, not hunchbacked like *S. gonionotum*, and the inframedian latus is very much narrower. Moreover, the roof of the carina is flat in *S. gonionotum*. The two species seem therefore to be quite distinct. The two specimens of *S. gonionotum* were detached when received, but from the shape of the impression near the base of the peduncle, they were attached to some narrow object, probably a crinoid pinnule.

GROUP OF SCALPELLUM JAPONICUM.

The species of this group have one or more longitudinal rows of spines on the segments of the posterior cirri, besides the usual pairs on the anterior and along the posterior margins. The posterior side is also minutely spiculose. The somewhat allied *S. imperfectum* Pilsbry has similar segments.

This group seems to be rather richly developed off southeastern Japan. The species are variable, and many more forms probably await the dredge.

Scalpellum japonicum Hoek. [Pl. x, fig. 1 to 5, 9.]

1883. *Scalpellum japonicum* Hoek, Challenger Report, VIII, Cirripedia, p. 67, pl. 3, fig. 9, 10 (type locality, Challenger Station 235, lat. 34° 7′ N., long. 138° E., in 565 fathoms).

1907. *Scalpellum japonicum metapleurum* Pilsbry, Proc. Acad. Nat. Sci. Phila., 1907, p. 360 (type locality Albatross station 4972).

This species was based upon a single example with the capitulum 13.5 mm. long, taken in the Pacific off Japan south of the middle of Hondo Island in deep water.[a] Since the published drawing does not show clearly the shape of the calcified portion of the upper latus, I have given a view of the right side

[a] The shell upon which this barnacle is seated was thought by Hoek to be perhaps a species of *Rissoa*, but from its size and shape, as shown in Hoek's drawing, I think it may be a *Bathybembix* (*Turcicula*).

(pl. x, fig. 9) from a camera lucida sketch of the type which I owe to the kindness of Mr. W. T. Colman, of the British Museum. These show the calcified area to be irregularly oblong, with subparallel scutal and basal borders, and with two short subequal, straight facets opposed to the carina and the carinal latus, respectively. The peduncle is described as 4.5 mm. long, with about 8 longitudinal rows of 7 scales each. The two sides of the type are alike.

The *Albatross* took two specimens of *Scalpellum* at station 4972, south of Hondo, 33° 25′ 45″ N. 135° 33′ E., in 440 fathoms, which agree in the main with *japonicum*, but differ a little in shape of the upper latus. These specimens may be referred to as no. 38684 and no. 38685.

No. 38684 (pl. x, fig. 1, 2, 3) has a capitulum 17 mm. long, 9.5 wide, peduncle 5 mm. long. The calcified portion of the upper latus on the right side (fig. 1) forms a quadrangular band transverse to the length of the capitulum, with an oblong tongue projecting beyond the umbo. There is no calcified lobe along the scutal margin, and it differs from the type of *S. japonicum* in having no straight face opposed to the carinal latus. On the left side, the upper latus has a slightly waved lower margin, approaching in a slight degree to the condition in specimen no. 38685, and to typical *S. japonicum*. The other

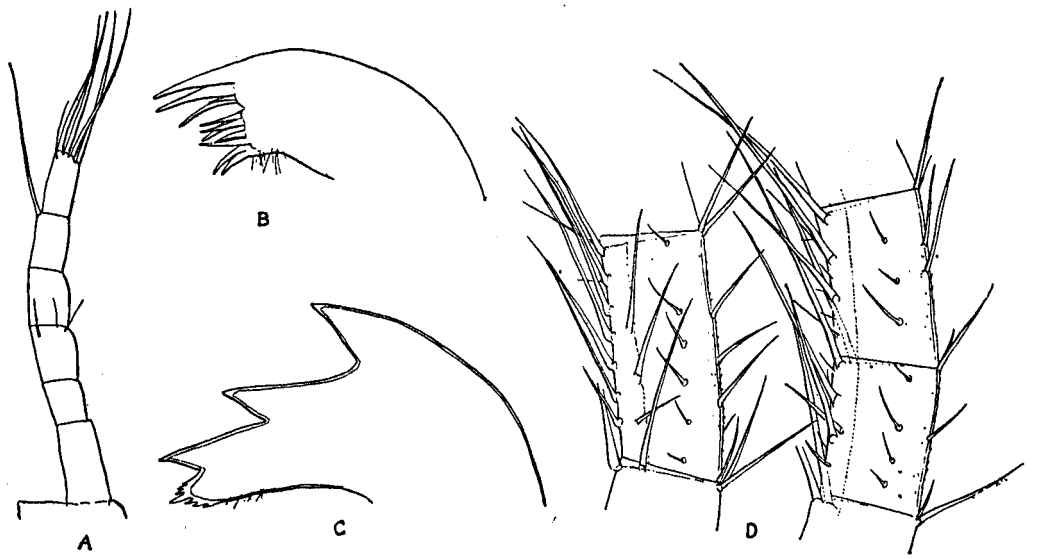


FIG. 2.—*Scalpellum japonicum*. A, terminal appendage; B, maxilla; C, mandible; D, segments from both rami of cirrus v.

plates are substantially as in the type of *S. japonicum*. The peduncle has 8 longitudinal rows of about 7 large scales each, therefore like that of *S. japonicum*. This is the specimen I called var. *metapleurum*, which name will now become a synonym of *japonicum*.

Specimen no. 38685 measures, length of capitulum 15, width 9, length of peduncle 6 mm. On the left side the upper latus is shaped substantially as in no. 38684, but on the right it is narrower, and abruptly attenuated near the carinal end (pl. x, fig. 4). The rostrum is a trifle smaller (pl. x, fig. 5). The scales of the peduncle are less numerous, only 4 or 5 in each longitudinal row. Both of the above specimens are clothed with a very thin, finely pilose cuticle, which has been mainly ignored in the figures, in order to show the outlines of the calcified valves more clearly.

Specimen no. 38684 was opened. The mandible (fig. 2, C) has three acute points and a seven-spined lower point. There are a few scattering hairs below, but elsewhere the borders are very smooth, simple, and clear-cut.

The maxilla (fig. 2, B) has very few spines, a few hairs below but none on the upper margin.

The first cirrus has unequal rami of about 7 and 12 segments, but they are not distinct in my preparation. The second cirrus has subequal rami, is profusely bristly, with 6 or more pairs of large spines

on the anterior margin of each segment The fifth cirrus has branches of 33 and 27 segments. The posterior edges are set with minute spines The outer branch has three pairs of large and one of small spines along the anterior border. There are two or three very unequal spines posteriorly at each suture, and one or two between the sutures. There is also a row of short spines along the inner face of the ramus. The inner branch has longer segments, with more spines along the anterior border—as many as 6 or 7 pairs. There are two rows along the inner face of the ramus (fig. 2, D, 12th segment of inner ramus and 13th and 14th segments of outer ramus of cirrus v).

The terminal appendages (fig. 2, A) have 6 segments, with very few bristles except for a group of long ones at the apex. Its length, not measuring the apical bristles, is 2.25 mm.

At Albatross station 4901, southwest of the Goto Islands, Eastern Sea, 139 fathoms, a minute barnacle was taken, which I believe to be the young stage of *S. japonicum* or some closely related form. It is figured on plate x, figures 6, 7, 8. The capitulum is 6.3 mm. long. The carina is separated from the tergum and upper latus by a narrow chitinous space, the other plates being closely juxtaposed. There is a narrow rostrum. The umbo of the inframedian latus is near the lower third. The carina has a rather broad roof. The peduncle has rather large scales, sparse except on the dorsal side. If mature this barnacle would be thought a member of the group of *Scalpellum idioplax;* but its characters are just what one would expect in young of the *S. japonicum* group. The specimen is no. 38688, U. S. National Museum.

Scalpellum japonicum biramosum. New subspecies. [Pl. xi, fig. 1, 2, 3.]

Type no. 38686, U. S. National Museum.

Type locality: Albatross station 4972, south of Hondo Island, Japan, 33° 25′ 45″ N., 135° 33′ E., 440 fathoms.

This form was associated with the two specimens of *S. japonicum* described above. It differs from them in the following respects: The umbo of the carina is nearer the upper end of the plate. The upper latus has a lobe extending down along the scutal border; this lobe is bifid on the right (fig. 1), simple on the left side (fig. 2). The hour-glass-shaped inframedian latus is less excavated along its upper border than in *japonicum.* The rostral latus is much higher. The rostrum is reduced to a punctiform vestige. The peduncle has 10 longitudinal rows of about 7 scales each. Length of capitulum 17.5 mm., width 9.3 mm., length of carina 17 mm., diameter at base 2 mm. Length of peduncle 4 mm.

Whether this form will prove to be within the range of normal variation of *S. japonicum* or not remains to be determined by future collections.

Scalpellum molliculum. New species. [Pl. xi, fig. 4, 5.]

Type no. 38687, U. S. National Museum.

Type locality: Albatross station 4967, south of Hondo Island, Japan, 33° 25′ 10″ N., 135° 37′ 20″ E., in 244 fathoms.

A species allied to *S. curiosum* and *S. japonicum.* The oblong capitulum is widest in the middle, tapering toward both ends, the occludent and carinal margins about equally arched. The calcified portions of the valves are white, the chitinous portions yellowish. The very thin cuticle is nowhere hairy.

The scutum has an arcuate occludent margin, and a short projection at the tergo-lateral angle. The baso-lateral margin is rounded.

The tergum is V-shaped, the occludent limb narrower and much shorter than the carinal.

The carina is regularly and strongly arcuate, with a flat roof and slightly projecting angles. The sides are narrow, a little wider above; they meet above the umbo, which is removed a very short distance from the upper end of the plate.

There is no externally visible rostrum.

The upper latus is triangular, the umbo quite near the apex. The carinal margin is very short, the basal margin irregular.

The rostral latus is oblong, the lateral margin longer than the rostral; upper and lower margins subparallel.

The inframedian latus is fan-shaped, wide in the upper part, tapering from the middle to the very narrow base, where the umbo is situated.

The carinal latus is triangular, the umbo projecting a little at the baso-carinal angle. There is a short, straight face opposed to the upper latus and a long, slightly concave margin opposed to the inframedian latus.

The peduncle is closely covered with rather small scales in about 15 rows of 12 to 15 scales each. Some of the longitudinal rows do not reach to the base of the peduncle, the scales being somewhat irregularly arranged in places.

Length of the capitulum, 19.5 mm.; width, 11 mm.; length of the carina, 19 mm.; diameter at base, 3 mm.; length of the peduncle, 6.5 mm.

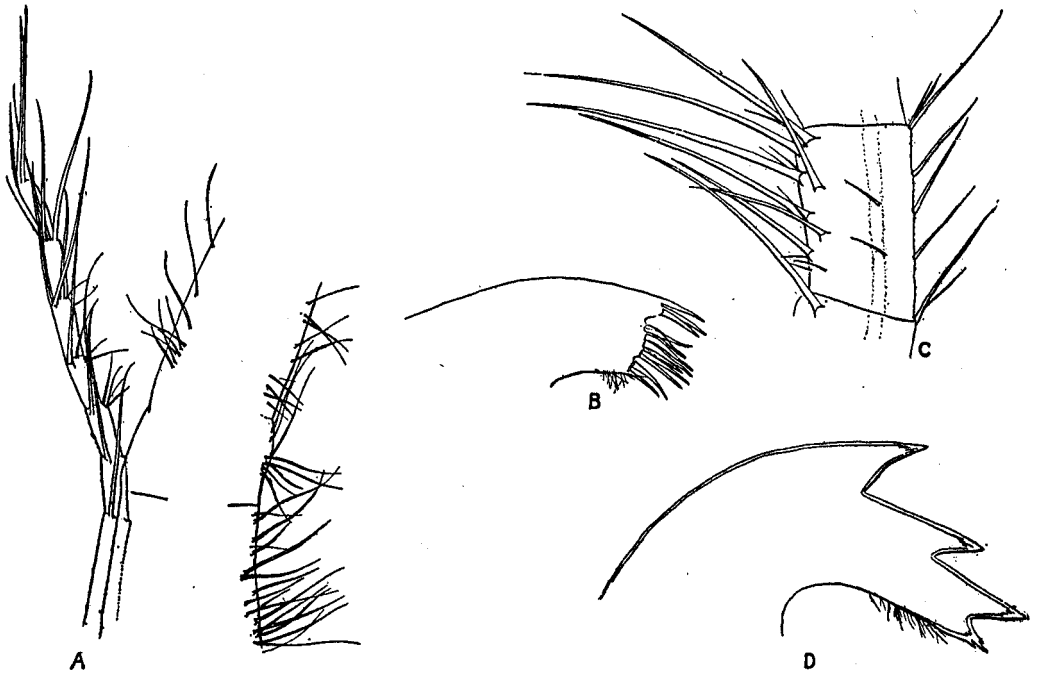


FIG. 3.—*Scalpellum molliculum*. A, basal segments of cirrus VI with terminal appendage; B, maxilla; C, 16th segment of cirrus V; D, mandible.

The type specimen was dissected. The mandible is very similar to that of *S. japonicum*, differing only in being a little more slender, with fewer spines at the lower point (fig. 3, D).

The maxilla (fig. 3, B) is also like that of *S. japonicum*. As in that species, the upper spine stands alone, then two great spines diverge from a common base.

The first cirrus has unequal rami of 8 and 11 segments. The later cirri have segments with four pairs of large and one of minute spines at the anterior edge. They do not differ materially from those of *S. japonicum* (fig. 3, C, 16th segment of cirrus V).

The terminal appendages consist of 9 segments, the last 6 copiously spinose at the articulations. The total length, exclusive of the terminal spines, is nearly 4 mm.

This species differs from *S. japonicum* by the shapes of the upper, inframedian, and rostral latera, and especially by the more numerous scales of the peduncle. The plates are also more fully calcified,

although the specimen is larger. In *S. japonicum* the larger specimens have the calcified portions comparatively more reduced than the smaller ones. The internal organs closely resemble *S. japonicum* except that the terminal appendages are quite unlike. *S. molliculum* has also much in common with *S. curiosum* Hoek, from the Malay Archipelago; but that barnacle has the carina less arched, with the umbo farther from the apex, the scales of the peduncle are far larger, the shape of the carinal latus differs, and there is a small rostrum. *Scalpellum subflavum* Annandale is also related, but it has far larger scales on the peduncle, a more broadly triangular tergum, etc. Only one specimen of *S. molliculum* was taken.

Family LEPADIDÆ.

Genus LEPAS.

Lepas anserifera Linné.

Locality: Albatross station 4920, near Kusakaki-jima, about 90 miles WSW. of Kagoshima Gulf, surface, on pumice.

Lepas anatifera Linné.

Locality: Albatross station 4758, 70 miles W. of Cape St. James, Queen Charlotte Island, surface.

Lepas pectinata Spengler.

Locality: Albatross station 4897, 10–20 miles southwest of Goto Islands, Japan, surface.

A much inflated and unusually smooth variety of this species occurs at Bering Island. It has been figured in Bulletin 60 of the U. S. National Museum, plate VIII, figures 5, 6. This form may be known as *Lepas pectinata beringiana*, n. subsp.

Genus OCTOLASMIS.

Octolasmis orthogonia (Darwin). [Pl. XI, fig. 6 and 7.]

1851. *Dichelaspis orthogonia* Darwin, Monograph on the Cirripedia, Lepadidæ, p. 130, pl. 2, fig. 10 (locality unknown.)

1907. *Dichelaspis orthogonia* Darwin, Hoek, Siboga-Expeditie, Monographie XXXIa, Cirripedia, p. 25, pl. 2, fig. 14–18; pl. 3, fig. 1, 1^a, 1^b, 10^b, Malay Archipelago.

The type locality of this species was unknown, but the typical form was rediscovered in the Malay Archipelago by the Siboga Expedition, where it was taken at several stations, in 40 to 112 meters. Two other forms very closely related to *orthogonia* were taken by the *Siboga*, *Dichelaspis weberi* Hoek and *D. versluysi* Hoek. Three specimens of *O. orthogonia* were taken by the *Albatross* at station 4936, off Kagoshima Gulf, in 103 fathoms, seated on *Heteralepas*. Two of these are figured (pl. XI, fig. 6, 7, no. 38676 U. S. National Museum) to show the variation in shape of the plates, chiefly of the terga. In the larger specimen (fig. 7), length from apex to base of carina 10 mm., the median and occludent lobes of the base of the tergum are rather short and acute on the left side, as figured, but noticeably longer and less acute on the right side. The other example figured (fig. 6) has a capitulum 9.3 mm. long. The basal lobes of the tergum are very long and finger-shaped. The third example of the group has a tergum intermediate in shape between the two extreme forms figured. The basal disk of the carina is formed about as Darwin figures for *D. orthogonia*.

The variations observed among these three individuals, which clung in a group to the peduncle of an *Heteralepas*, show that there is considerable variation in the shape of the terga among adult egg-bearing individuals. It seems not impossible that the three described species of this type, *orthogonia*, *weberi* and *versluysi* might better be looked upon as variations or local races of a single widely distributed species.

The terga in these specimens are pink-tinted, and the valves are not much covered by cuticle.

Genus CONCHODERMA.

Conchoderma auritum (Linné). [Pl. VIII, fig. 5, 6, 7.]

1767. *Lepas aurita* Linnæus, Syst. Nat., ed. XII, p. 1110.
1851. *Conchoderma aurita* Linnæus, Darwin, Monograph on the Cirripedia, Lepadidæ, p. 141.
1907. *Conchoderma auritum* Linnæus, Pilsbry, Bull. 60 U. S. Nat. Mus., p. 99, pl. IX, fig. 2.

Specimens adhering to *Coronula* were taken from the throat of a humpback whale in Plover Bay, Siberia, by Dr. W. H. Dall in 1865, and are now in the U. S. National Museum. Color sketches made by Doctor Dall from life are reproduced on plate VIII. In Atlantic *C. auritum* the stripes and spots are dark purple, but these examples are striped and mottled with deep rose color and rose-pink. In structural characters they agree with Atlantic *C. auritum*. Small scuta and a very minute carina are developed.

The Californian specimens described by Doctor Dall (1883) as *Otion stimpsoni* were marked with purple, like the Atlantic *C. auritum*.

Genus HETERALEPAS.

Heteralepas japonica (Aurivillius).

Alepas japonica Aurivillius, Kongl. Sv. Vet. Akademiens Handlingar, bd. 26, no. 7, p. 28, Hirado Strait, Japan, 80 fathoms.

Locality: Albatross station 4986, off Hokkaido Island, Japan; 43° 01′ 40″ N., 140° 22′ 40″ E. in 103 fathoms. No. 38683 U. S. National Museum.

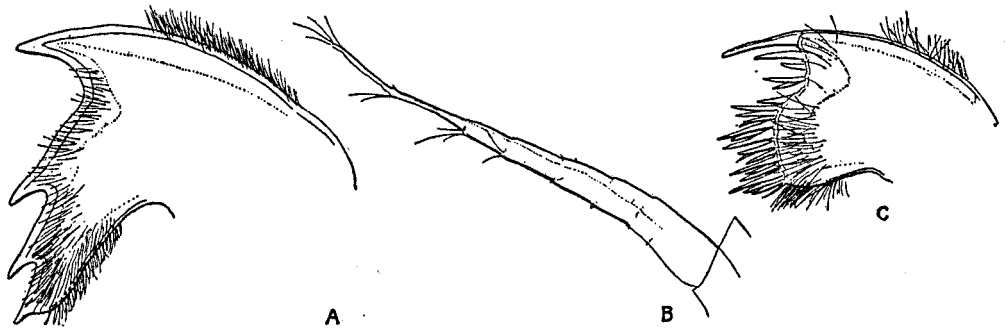


FIG. 4.—*Heteralepas japonica*. A, mandible; B, terminal appendage; C, maxilla.

Two specimens taken agree in the main with the above-named species, but differ in certain details noticed below. The extent of individual and local variation in species of this group is unknown, since a majority of the species are known from one lot from a single place, or at best from very few lots.

The size of two apparently mature specimens is somewhat smaller than *japonica*—length of capitulum 10 mm., width 8.5 mm.; length of peduncle 4 mm., length of orifice 3.5 mm. The capitulum is plump, with only the weak trace of a carina toward the summit. There are three low dorsal tubercles, two on the back of the capitulum and one on the peduncle at the base of the capitulum. The peduncle is shorter than in *japonica*.

The mandible (fig. 4, A) has three slender teeth and a lower point below which the border protrudes. Near the edge it is hairy, and both upper and lower margins are bearded.

The maxilla (fig. 4, C) is deeply excavated below the two great upper spines.

The first cirrus has about 11 and 23 segments, though the rami are not very unequal in length. The second, third, and fourth cirri are long with subequal rami, of about 70 segments in the fourth cirrus. The fifth and sixth cirri have the inner rami very small, less than half the length of the outer rami, and composed of 17 segments.

The terminal appendages (fig. 4, B) are very short, 2.75 mm. long, of 7 segments.

The penis is very long, sparsely hairy, with a small terminal tuft.

The principal differences of these specimens from the types of *H. japonica* are that while the animal is somewhat smaller, there are more joints in the cirri, and the teeth of the mandible are more slender.

Heteralepas vetula, new species. [Pl. XII, fig. 1, 2, 3.]

Type no. 38689, U. S. National Museum.

Type-locality: Albatross station 4934, off Kagoshima Gulf, in 152 fathoms.

The capitulum is oval, plump, somewhat tubular toward the orifice, which is more than one-third the length of the capitulum, and has thin, flaring lips, but slightly crenulated. Along the back a subacute and rather high keel runs from peduncle to summit. The crest of the keel, while irregular, shows no tubercular prominences or nodes. A stout cord-like ridge runs along each side. These ridges meet at the baso-carinal extremity of the capitulum, and converge again at the apex, defining a broadly lanceolate dorsal area, which is somewhat smoother than the slightly wrinkled surface in front of the ridge. No scuta are visible. The capitulum passes rather gradually into the short peduncle, which is transversely wrinkled.

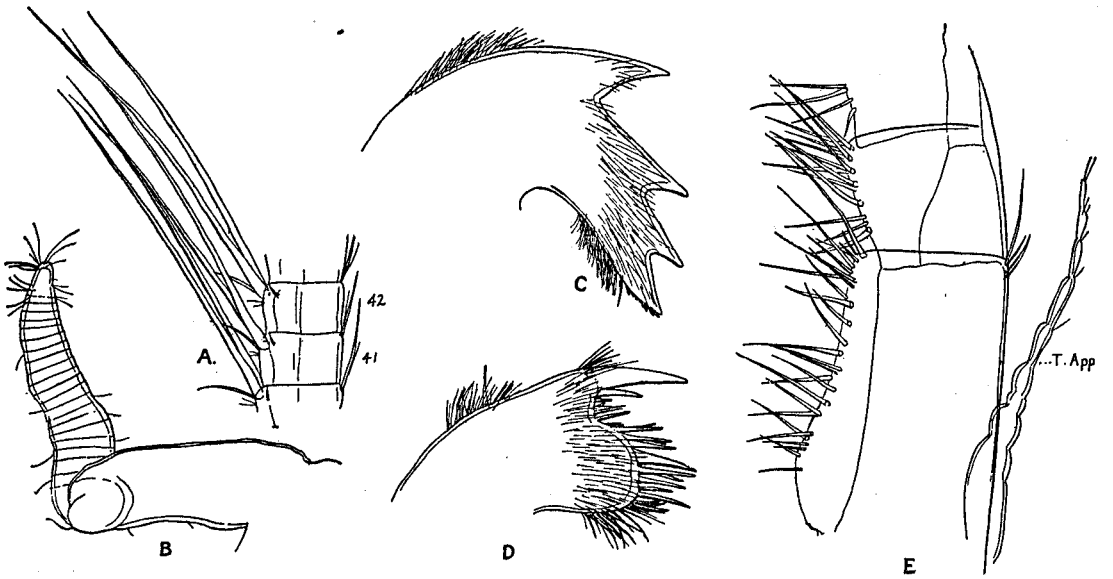


FIG. 5.—*Heteralepas vetula.* A, forty-first and forty-second segments of cirrus v; B, penis; C, mandible; D, maxilla; E, basal segments of cirrus VI and terminal appendage.

Length of the capitulum 11 mm.; breadth 8 mm.; length of the peduncle 5 mm.; breadth 4.5 mm.

The type specimen was dissected. The mandible (fig. 5, C) has three long conic teeth and a lower point, the latter with three short spines below the terminal point.

The maxilla (fig. 5, D) has a deep recess below the major spine. Its edge is profusely spinose, the spines giving place to hairs at the lower angle.

The first cirrus has very unequal rami of 13 and 23 segments, each with a distal circle of hairs. Cirri ii to iv have equal rami of very numerous segments, as usual in *Heteralepas*. Cirrus v has rami 11 and 4.5 mm. long, composed of 57 and 22 segments. The outer ramus bears a pair of long spines at the anterior distal angle of each segment, with several very small ones, and two delicate small spines at the posterior distal angle (fig. 5, A, forty-first and forty-second segments of cirrus v). The smaller ramus bears only a few very small and delicate spines. The sixth cirrus resembles the fifth.

The terminal appendage is very minute, not quite 2 mm. long, and consists of nine segments. There are a few small hairs at the distal articulations, and two at the end (fig. 5, E, t. app.).

The penis is very small, about 5 mm. long. It has comparatively few annuli, and is very sparsely hairy (fig. 5, B).

This species has an external recognition mark in the lateral cords, defining a dorsal escutcheon. Internally the few-jointed inner rami of cirri v and vi, the reduced terminal appendages, and the comparatively small number of annuli of the short penis, are characteristic.

A single small example from Albatross station 4892, southwest of the Goto Islands in 181 fathoms, seems to be referable to *H. vetula*. It is no. 38685 U. S. National Museum.

Heteralepas, species undetermined. [Pl. xi, fig. 8, 9.]

Locality: Albatross station 5049, off the east coast of Hondo Island, Japan, 38° 12′ N., 142° 02′ E., in 182 fathoms.

A single specimen, no. 38682 U. S. National Museum, externally perfect, but the internal organs wholly wanting, seems to represent an undescribed species.

The capitulum is oval; the carinal border is almost evenly arched and is rounded, with no trace of a keel; rostral border strongly convex below the orifice. There is a pair of minute narrow, yellowish scuta; elsewhere the surface is smooth and somewhat transparent. It is flattened laterally, the sides being even a little concave. The orifice is very small, about one-sixth the length of the capitulum, and not in the least tubular. Below it the rostral surface is smooth and rounded, not superficially slit as in *Alepas pacifica*. The peduncle is narrow, very short, and coarsely wrinkled transversely.

Length of the capitulum 11 mm.; width 8 mm.; length of the peduncle 4 mm.; width 3 mm.

The figures will serve to call attention to this species, which I refrain from naming on account of the imperfection of the single specimen.

Family BALANIDAE.

Genus BALANUS Da Costa.

SECTION D.

Balanus rostratus Hoek. [Pl. xii, fig. 6.]

1883. *Balanus rostratus* Hoek, Challenger Report, Zoology, vol. viii, p. 152, pl. 13, fig. 16–22.

This species was described from off Kobe, Japan, in 8 and 50 fathoms. The type specimens were small, the largest 9 mm. high, 7 mm. in diameter of base. The types were not furrowed exteriorly, and the orifice is small. A series from Tokyo Harbor (no. 1814 collections of Academy of Natural Sciences of Philadelphia) shows that the species attains a far larger size, up to 27 mm. high and 37 mm. in basal diameter. Some notes on the adult examples may be useful. While usually almost smooth, or only irregularly roughened, the outer wall is sometimes ribbed in places. The walls and opercular plates are invariably white throughout, and the egg-shaped orifice is generally about half as long as the base, which is strong and flat. The basal ends of the parietes show square holes, exactly as figured by Darwin for *B. porcatus* of the north Atlantic. The large size of the rostral and diminution of the carino-lateral pieces has been duly emphasized by Hoek. The radii are deeply sunken below the parietes, appearing as small, narrowly triangular or wedge-shaped spaces, which are delicately and closely striated transversely.

The opercular plates agree with those described by Hoek, but are less transparent than his figures indicate, though still thin. The longitudinal striation of the scutum is very distinct and beautiful though fine, and the transverse ridges are almost lamella-like on the lower part of the plate. They project along the occludent margin. The terga show only weak traces of the depressor-muscle crests. Externally there are some very weak longitudinal striæ near the carinal margin. The band leading to the spur is smooth except for transverse growth-lines; and the surface on both sides of it has extremely weak oblique riblets, quite narrow and hardly raised above the level surface.

This species, I have little doubt, is identical with "some fine, brilliantly white specimens (without opercula) from the coast of China" which Darwin alludes to as possibly a species distinct from *B. porcatus* (Monograph on the Cirripedia, Balanidæ, p. 259).

B. rostratus agrees with *B. porcatus* Da Costa in the porose parietes, solid radii and base, but differs in having the adductor ridge of the scutum wholly free from the articular ridge, and by the absence of any distinct articular furrow. In *B. porcatus* and *B. nubilis* the articular furrow of the tergum is deep. The wholly white plates are a further distinguishing feature. In *B. porcatus* the tergum usually has a purplish spot on the inner face, and a purplish beak.

Balanus rostratus apertus, new subspecies. [Pl. XII, fig. 4, 7; pl. XIII, fig. 1, 2, 8, 9.]

Cotypes no. 38667, 38668, 38669, U. S. National Museum, all from station 4778.

Type locality: Albatross station no. 4778, Bering Sea, N. lat. 52° 12′, E. long. 179° 52′ in 43 fathoms. Living embedded in sponges. Also stations 4777 and 4779, on Petrel Bank, Bering Sea, in 52 fathoms.

The shell is white, subcylindric or conic, with convex sides and a large, triangular-ovate orifice, frequently as large as the base. The parietes are marked with fine, waved, transverse striæ, and

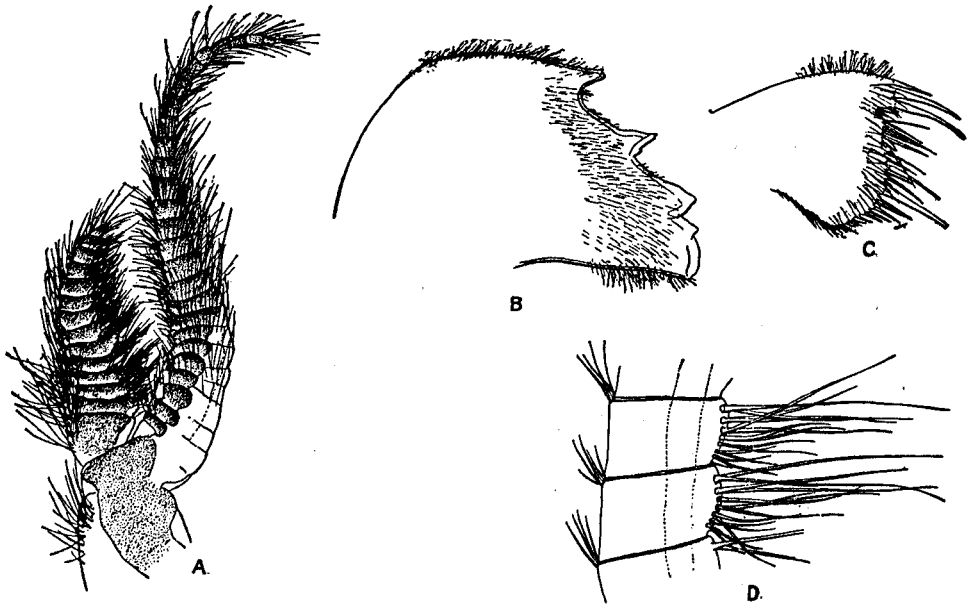


FIG. 6.—*Balanus rostratus apertus.* A, 1st cirrus; B, mandible; C, maxilla; D, 15th and 16th segments of cirrus V.

sometimes bear short, acute spines projecting outward and downward, each prolonged upward in a short rib. These spines appear in groups and are not numerous when present. The radii are much wider than in *B. rostratus*, transversely striated, with the upper edges parallel to the base. They are only very little sunken below the parietes. Internally the plates are deeply, closely, and sharply sulcate, and the bases of the parietes have square holes as in *B. rostratus*. The smooth sheath is nearly half the length of the shell. The stout, poreless, calcareous base is generally concave externally. The rostrum is very wide, about as wide at its summit as at the base. Two specimens measure, (a) height 46, greatest diameter 33, length of aperture 19 mm., length of tergum 22 mm.; (b) height 45, greatest diameter 31, diameter of base 24 mm., length of aperture 26 mm.

The scutum is extremely strongly ridged transversely, the ridges much narrower than the intervals; deeply and closely striated longitudinally, the striæ weaker near the edges. Inside there is a rather narrow, not very high, articular ridge, but only the trace of an articular furrow. The adductor ridge is rather well developed, long, and wholly free from the articular ridge throughout. The

adductor and depressor muscle scars are moderately deep. It differs from the scutum of *B. rostratus* only in being somewhat more solid, with the adductor ridge a little better developed.

The tergum is thin, rather fragile, narrow, its greatest width contained about 2½ times in the length. Spur wide at the base, tapering to an obtuse, truncate end; situated close to the scutal margin; decidedly longer than that of *B. rostratus*. External sculpture of narrow oblique riblets, much stronger than in *B. rostratus*, the intervals faintly, weakly striate longitudinally. There is no groove from spur toward beak, only a flat, longitudinally and transversely striated band. The interior is white throughout. Articular ridge rather narrow, arched, not much more than half the length of the valve, stronger than in *B. rostratus*. Articular furrow only weakly indicated. Crests for the depressor muscles rather weak and irregular, but much stronger than in *B. rostratus*.

Both of the opercular plates have a thin, yellowish cuticle, whitish in young specimens.

The mandibles of no. 38667 have three rather stout short teeth, then a minute tooth and an obtuse lower angle. The upper tooth is minutely bifid at the tip. The upper and lower borders are densely and very finely hairy, as are also the intervals between the teeth (fig. 6 B).

The maxillæ do not differ materially from those of *B. rostratus* as figured by Hoek, except that there are several small spines above the two great spines (fig. 6 C).

The first cirrus (fig. 8 A) has very unequal rami of 15 and 27 segments, those of the posterior branch strongly protuberant at the anterior side, with dense hair-tufts. The second and third cirri also have unequal branches, the segments of both strongly protuberant, with dense tufts. Cirrus ii has 15 and 19 segments; cirrus iii, 12 and 19. Cirri iv to vi are of the usual slender and elongate shape, with subequal branches of about 35 segments. These segments are convex anteriorly, each with 6 or 7 pairs of spines, and having the usual posterior sutural groups of small spines. (Fig. 6 D, 15th and 16th segments of cirrus v.)

The penis is very long, over 20 mm., purplish, densely and conspicuously annulated, with a very few short hairs near the end. There is a blunt projection on the dorsal base. The cirri and mouth parts of the largest specimen in group no. 38670 agree fully with no. 38667.

In this race the radii are scarcely sunken below the parietes. In the type lot the walls form a subcylindric shell, but in a group of seven individuals seated on a scallop shell, from station 4779, 54 fathoms, the shell is more conic and smoother, the parietes yellowish or dirty white, the radii pure white. The largest specimen in this group measures 55 mm. high, 45 mm. in greatest diameter of the base. This group, no. 38670 U. S. National Museum, is figured in plate XII, figure 4.

The cirri of the types of *B. rostratus* are not fully described. The first cirrus as described by Hoek agrees with *B. rostratus apertus*, except in having fewer segments, probably owing to its immature condition or smaller size. The change in shape between the third and fourth cirri in *B. rostratus apertus* is quite abrupt.

Balanus crenatus Bruguière. [Pl. XIV, fig. 1–9.]

1853. *B. crenatus* Darwin, Monograph on the Cirripedia, Balanidæ, p. 261.

Localities: Union Bay, Bayne Sound, British Columbia shore, specimens no. 38671 and 38672 U. S. National Museum; Albatross station no. 5008, Aniwa Bay, Saghalin Island, 24 fathoms, specimen no. 38674 U. S. National Museum; Albatross station no. 5038, near Urakawa Light, south coast of Hokkaido, 175 fathoms.

Two forms of this species were taken on shore in Bayne Sound, British Columbia: No. 38671, a smooth, conic form with triangular parietes and delicately striate opercular plates, the specimen illustrated having a basal diameter of 14 mm. (pl. XIV, fig. 1, 2, 3); and no. 38672, in which the shell is more prism-shaped, or columnar with prominent angles, the old ones generally supporting a crop of younger barnacles at the summit. The opercular plates are much worn and are rather strongly striate. The figured group is 42 mm. high (pl. XIV, fig. 4–9). The examples from station 5008 are small and conic, but more rugged than no. 38671.

SECTION E.

Balanus cariosus Pallas.

Localities: Dutch Harbor, Alaska; Thyedin, on shore, June 13, 1906.

Balanus evermanni Pilsbry.

1907. *Balanus evermanni* Pilsbry, Bulletin of the Bureau of Fisheries, vol. XXVI, p. 203.

In 1906 this fine barnacle was taken at the following stations: Station 4792, near Bering Island, in 72 fathoms, museum no. 38661; stations 4803 and 4804, off Cape Rollin, Simushir I., Kuril Islands, in 229 fathoms, museum no. 38658, 38659, 38660, 38662. It has apparently a general distribution from Alaska to the Kuril Islands.

The specimens agree in essential features with those originally described, but show some variation in the shape of the cup, such as is to be expected in any lengthened acorn barnacle. In a few examples it flares toward the mouth, like some liliaceous corolla (fig. 7, A, mus. no. 38661). In others

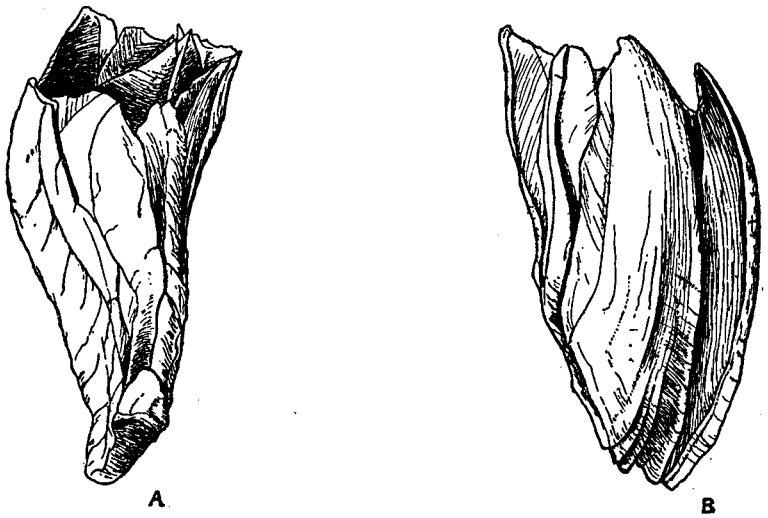


FIG. 7.—*Balanus evermanni*, x ½.

it is shortened and wide (fig. 7, B, mus. no. 38662). In these stumpy examples the rostrum or the carina may become longitudinally ribbed, the ribs rounded and not very prominent.

These specimens from the northwestern Pacific agree with those from Alaska in the characters differentiating the species from the North Atlantic *Balanus hameri* Ascanius.

SECTION G.

Plates of the wall solid, without pores and without radii; base membranous, sometimes with a calcareous peripheral rim, which is poreless.

This group was instituted by Dr. Hoek for two species, *Balanus hirsutus* from the Faroë Channel and *B. coralliformis* from near Kerguelen Island. Two more are now described from Bering Sea, greatly extending the range of the group.

In wanting radii these forms are more primitive than the typical *Balani*. The teeth of the mandible are longer and more slender than in most others of the genus. None of them are littoral barnacles.

Balanus hoekianus, new species. [Pl. XIII, fig. 3–7, pl. XV, fig. 1–2.]

Type no. 38666 U. S. National Museum.

Type locality: Albatross station 4778, Bering Sea, N. lat. 52° 12′, E. long. 179° 52′, in 43 fathoms, seated on a gastropod shell (*Buccinum*).

A species of the group G of Hoek; base excessively thin, partly membranous; plates of the wall solid, without pores; no radii.

The shell and opercular plates are white throughout. Shape shortly subcylindric, flaring outward at the large triangular ovate orifice. The parietes are slightly roughened but not distinctly ribbed or sulcate, with no chitinous cuticle and no hairs. The alæ are smooth, with extremely oblique upper margins, so that the peritreme is deeply serrate. Internally the walls have a long glossy sheath below which they are somewhat sulcate, chiefly at the base of attachment.

The rostrum (fig. 8, A, internal view) is much the largest plate. Externally, while it is finely indistinctly rugose longitudinally, there is no distinct costation, and no trace of radii. Inside the sheath is tripartite. The carina (fig. 8, B) is strongly concave. The rostro-lateral plate is wide, triangular, with a well-developed ala but no radius. The carino-lateral plate is narrow, recurved, with the ala wider than the parietal area. Inside the sheath is bipartite. The strongly recurved carina is V-shaped above, with wide alæ and smooth, undivided sheath (fig. 8, B, inside view).

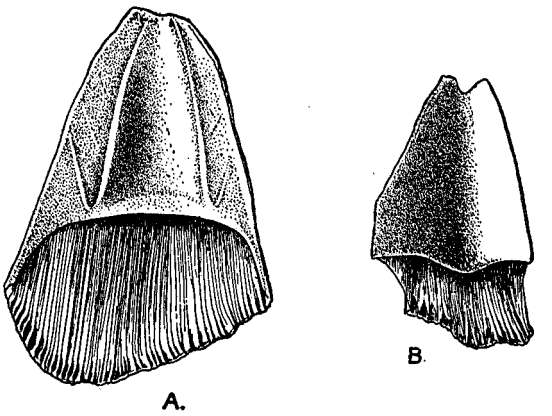


FIG. 8.—*Balanus hoekianus*. A, rostrum; B, carina. Internal views.

The base is an excessively thin transparent film, calcareous at the edges, membranous in the middle.

Height of the shell 8 mm.; diameter of the base 8 mm.

Mandible (fig. 9, B) has four principal teeth. The upper two are rather long and acute, the second one in the middle of the edge. The third and fourth teeth are blunt, and there are two denticles between them. The lower point is short and slightly bifid. The lower edge of the mandible is heavily bearded. The two mandibles are exactly similar.

Maxilla (fig. 9, C) has an even edge except for a notch below the upper two large spines. There are six or seven large spines and a few smaller ones below the notch. A band along the edge of the maxilla and below the lower angle is bristly, and there are a few hairs along the upper edge.

The first cirrus (fig. 9, A) has unequal rami of 9 and 13 segments. Those of the longer ramus protrude slightly, and all are densely hairy. The second cirrus has rami of 9 and 11 segments which are convex on the anterior side but do not protrude; third cirrus has unequal rami with 12 and 13 segments. The other cirri are longer, the sixth with 23 segments, each with three pairs of spines, the lower pair rather small. (Fig. 9, D, 10th and 11th segments of cirrus V.)

The scutum (pl. XIII, fig. 3, 4, 5) is moderately thick. It flares outward and is twisted toward the apex. Externally it is indistinctly marked with fine, weak growth-striae and rather widely spaced growth-arrest lines which are scarcely raised. Inside there is a short but well-developed articular ridge, about one-third the greatest length of the plate. The articular furrow is narrow and distinct though not deep. There is no adductor ridge, though a noticeable thickening extends downward from the lower end of the articular ridge, representing a vestigeal adductor ridge. A shallow oblong pit marks the insertion of the depressor muscle.

The tergum (pl. XIII, fig. 6, 7) is very thick for so small a plate, white, the scutal margin concave, carinal margin short, strongly convex. The spur is long and narrow, separated from the scutal margin

by nearly its own width. A smooth depressed band runs to it. The area on the scutal side of this band is marked with widely spaced, strongly arched, linear riblets. The wide area on the other side has very oblique linear riblets, and an interstitial sculpture of very weak, fine, longitudinal striae. There are some minute hairs on the cuticular riblets, along the scutal border, but none on the outer surface of the plate. Internally the upper or beak portion of the plate is transversely striated. The articular ridge is high and massive, arcuate; the articular furrow wide but not very deep. The crests for the depressor muscle are short and sharp.

This species is related to *B. corolliformis* Hoek and *B. hirsutus* Hoek, the former from southeast of Kerguelen Island, 150 fathoms, the latter from the Faroë Channel, in 516 fathoms. Both have a more or less hairy cuticle, while *B. hoekianus* has no noticeable cuticle on the walls. *B. corolliformis* has some resemblance in shape of the walls to *hoekianus*, but the sheath is shorter, only one-third the length of the plates, and the tergum is of quite different shape. In *B. hirsutus* the articular ridge of the tergum projects conspicuously beyond the scutal margin, in external view, being much larger than in *B. hoekianus*, and the spur is scarcely removed from the baso-scutal angle of the plate, whereas in *B. hoekianus*

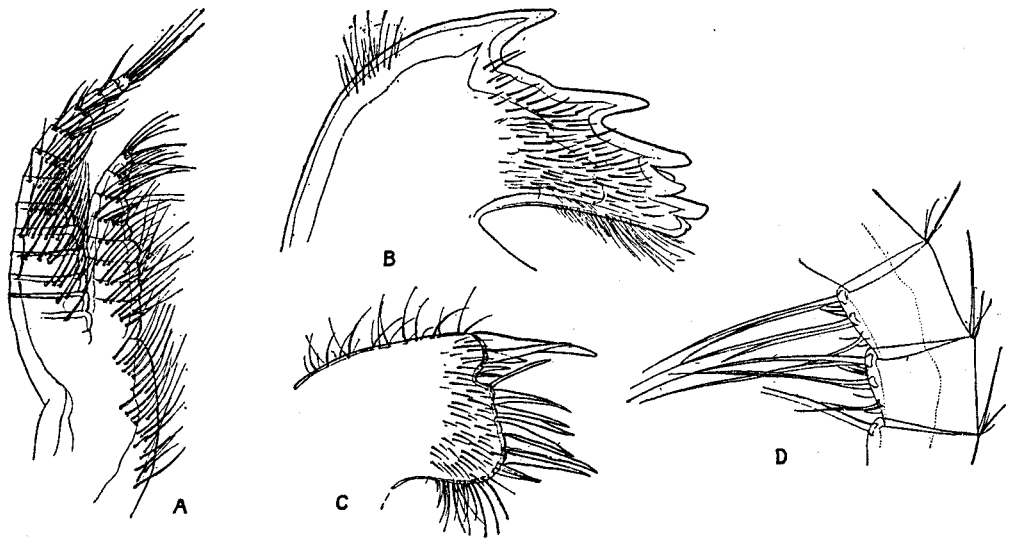


FIG. 9.—*Balanus hoekianus*. A, first cirrus; B, mandible; C, maxilla; D, 10th and 11th segments of cirrus V.

the baso-scutal angle is conspicuously produced, and the spur is separated from it by at least the basal width of the spur. The mandible of *B. hoekianus* has a smaller tuft of hairs on the upper margin, and the lower teeth are conspicuously obtuse, not acute as in *B. hirsutus*. This bluntness of the teeth is not the result of wear, since the unexposed teeth of the next moult, visible through the mandible, are equally obtuse. The maxillæ are also somewhat different in the two species. The number of spines on the segments of the posterior three pairs of cirri is smaller than usual.

B. hoekianus, named in honor of Dr. P. P. C. Hoek, is therefore quite distinct from its two antipodal relatives.

Balanus callistoderma, new species. [Pl. XII, fig. 5, pl. XV, fig. 3–7.]

Type no. 38690 U. S. National Museum.

Type locality: Albatross station 5068, Suruga Gulf, Japan, in 77 fathoms.

A species of Hoek's Section G. Base in large part membranous; parietes solid; no radii. The shell is in form a broadly truncated cone, the orifice rather large, ovate, with deeply toothed border. Parietes lemon yellow, fading to whitish near the orifice; alæ whitish. Under a lens the exterior is

seen to be marked with rather regularly spaced transverse darker lines, those near the base bearing fine shining bristles in a single close series. These bristles are largely lost on the older part of the wall, and some specimens lack them entirely.

The rostrum is the largest plate, triangular in shape. Its sheath is tripartite, as usual. The rostral latera are nearly as large. Like the carinal latera and carina, it has a well-developed, distinctly sunken ala. The carinal latera are very narrow. The carina is V-shaped in upper view.

The sheath occupies more than half the total height. It is closely ridged transversely, the ridges narrow, not hairy. Its lower edge is continuous with the surface below it, not in the least overhanging.

The base has a calcareous rim at the edge, sometimes as much as 6 mm. wide. The central part is membranous.

Altitude of cup about 32 mm. greatest diameter of base 30 mm.; of orifice 16 mm.

The scutum (pl. xv, fig. 5, 6, 7) is curved, the outer side concave, covered with a dense golden olive cuticle. It is sculptured with well-raised transverse thread-like ridges, each bearing a close

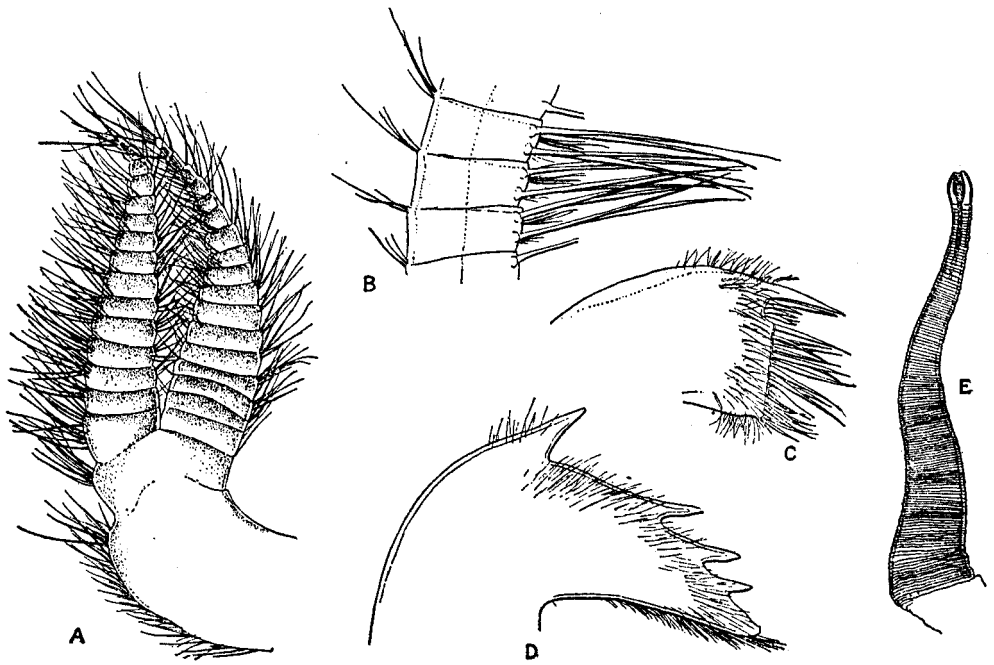


FIG. 10.—*Balanus callistoderma.* A, first cirrus; B, 32d to 34th segments of cirrus v; C, maxilla; D, mandible; E, penis.

row of minute shining spicules. Along the occludent edge there is a series of oblique nodes, formed by the enlarged extension of every alternate ridge of the outer surface (pl. xv, fig. 5). Internally there is a somewhat massive but low articular ridge extending along two-thirds of the scutal margin. The articular furrow is deep but very narrow. The adductor ridge is represented by a low callus only. The pit for the depressor muscle has several short but emphatic crests.

The tergum is covered with yellowish cuticle paler than that of the scutum. It has a concave scutal border, the adductor ridge not projecting beyond it. The convex carinal margin is equal in length to the basal margin. The spur is short, rather wide, and separated by about half its width from the baso-scutal angle. A slight depression, marked only with arcuate growth-lines, runs to the spur. On the scutal side of this band the surface has narrow arched thread-like riblets. The larger area on the carinal side of the spur-band has similar oblique riblets. There are no noticeable longitudinal striae. The articular ridge is arcuate, rather high; the articular furrow broad and shallow.

There are some acute crests at the insertion of the depressor muscle; and in old individuals the whole inner surface is slightly roughened. The spur is not thickened inside, but the scutal border, near the basal angle, is raised in a thin laminar flange (pl. VIII, fig. 3, 4). The inner faces of both scuta and terga are white.

The mandible (fig. 10, D) has four slender teeth and a lower point. The second tooth stands midway of the cutting edge. There is a copious beard along the lower margin, and there are some hairs near the cutting edge. The maxilla (fig. 10, C) has a notch at the upper angle and numerous larger and smaller spines; both upper and lower margins are bearded. The first cirrus (fig. 10, A) has subequal rami of 16 and 14 segments, which are rather densely spinose; and while convex at the sides, the segments do not protrude. The second cirrus has subequal rami of 18 and 22 segments, more copiously spinose than the first cirrus. Third cirrus, with 25 and 29 segments. The fourth to sixth cirri are longer and more slender, and are similar in armature. The fifth cirrus has rami of about 48 segments, several of the lower ones difficult to distinguish, as usual. Each segment is armed with two pairs of very long spines, with a group of quite small spines between and slightly below the large ones of each pair (fig. B, 32d to 34th segments of cirrus v). The posterior border of the cirri, in the basal half, is very minutely serrate or shortly spinulose. The penis (fig. 10, E) is remarkably short, only about 7 or 7.5 mm. long, very closely annulate, and wholly without hairs.

This handsome barnacle is readily distinguished from *B. corolliformis* and *B. hirsutus* by the shape of the tergum, which has a spur distinctly removed from the baso-scutal angle of the plate, and the articular ridge does not project beyond the regularly concave scutal margin of the plate. In these characters, *B. callistoderma* is more like *B. hoekianus*, in which, however, the cuticle of the opercular plates and walls is not hairy, the tergum is much narrower, and the smooth sheath has a free lower edge, as usual in *Balanus*. In *B. callistoderma* the sheath is transversely ridged and continuous below with the rest of the plate, with no overhanging ledge.

Genus ACASTA Leach.

Acasta spongites japonica, new subspecies. [Pl. XVI, fig. 1–9.]

Type no. 38681 U. S. National Museum.

Type locality: Albatross station 4936, off Kagoshima Gulf, in 103 fathoms.

A form more closely related to *A. spongites* than to any other described species. The deep basal cup is about half the height of the carina, broadly ovate in contour. Externally it has fine, uneven circular striæ and low, inconspicuous, narrow, longitudinal riblets, each terminating in a minute point on the upper margin. Inside there are no ribs and no teeth at the margin.

The plates of the wall are only loosely connected, and have a few calcareous points or spines. The radii are narrower than the parietes. The carina is decidedly larger than the rostrum, quite concave within. The carino-lateral plate has a narrow parietal area, its basal width contained 2 to 2.3 times in that of the rostro-lateral plate, thus being much wider than in *A. spongites*. The rostrum is the widest and shortest plate. Internally the plates of the wall show only the weakest traces of longitudinal ribs below the sheath, which is continuous with the surface below it and occupies more than half the length (pl. XVI, fig. 6, 7, 8, 9, interior views of rostrum, rostro-lateral, carino-lateral and carina). The sheath is glossy, and in the carina and carino-laterals is ridged across with smooth, thread-like riblets. The rostro-laterals are less strongly ridged, and in the rostrum the ridges are very weak and low.

The scutum (pl. XVI, fig. 4, 5) is concave outside, with sculpture of low transverse lamellæ and delicate radial striæ. The articular ridge is rather low and about half the length of the tergal margin. There is no adductor ridge.

The tergum (pl. XVI, fig. 1, 2) has a concave band from apex to the spur, and is sculptured elsewhere with transverse threads. The low articular ridge is continuous with a low ridge which continues upon the spur. The spur is united until near the end with the baso-scutal angle, in this respect being unlike *A. spongites*.

This form differs from *A. spongites* of the Mediterranean, etc., chiefly by the wider parietes of the carino-lateral plates, the absence of an adductor ridge in the scutum, and the different shape of

the spur of the tergum. It is apparently as distinct a form as several which are ranked as species, but without a large series the constancy of the differential characters can not be tested. I have therefore ranked the Japanese form temporarily as a subspecies. The type is a unique individual which had been wholly overgrown and filled up with the sponge-host, but with the walls and opercular plates complete and perfect.

Genus TETRACLITA Leach.

Tetraclita porosa (Gmelin).

Locality: Matsushima, on shore.

Genus PACHYLASMA Sowerby.

Pachylasma crinoidophilum, new species. [Pl. XVII, fig. 1–11.]

Cotypes no. 38675, U. S. National Museum.

Type locality: Albatross station 4934, off Kagoshima Gulf, in 152 fathoms.

A species somewhat related to *P. aurantiacum* Darwin. Base apparently membranous, walls solid, not porous. The basal contour is oblong, the ends elevated to conform to the shape of the supporting crinoid stem, on which the barnacle always sits lengthwise. The carina rises vertically, the other plates slope inward more or less. Rostrum and rostral latera white, carina, carinal latera and tips of the opercular plates pink tinted. All of the plates are thin and without radii. The parietes have a fine, indistinct sculpture of short, irregular impressions vertical to the faint lines of growth. The alæ have very oblique, wide-spaced grooves. The carina and the median latera are large plates, the others being much smaller.

The rostrum and rostral latera are narrowly triangular, united by linear sutures (pl. XVII, fig. 3, *r.*, *r. l.*). Internally the rostrum is glossy and slightly ridged transversely in the upper two-thirds (fig. 6). It has narrow alæ on both sides. The rostral latera are about as wide as the rostrum at their bases, and obliquely triangular, without alæ (pl. X, fig. 7, interior view). The median latera (pl. XVII, fig. 2, *m. l.*) are very large, with triangular parietes and an ala of irregular shape. Inside (pl. XVII, fig. 8) the apical portion of the plate is slightly ridged transversely, the ridges opaque-white; a radius is faintly indicated. The basal margin of the plate is sharp and smooth. The carinal latera (pl. XVII, fig. 2, *c. l.*) are quadrangular, about twice as long as wide, and externally are divided by a diagonal ridge into parietal and alar areas. Internally there is an obliquely ridged area near the beak (pl. XVII, fig. 9).

The carina (pl. XVII, fig. 2, *c.*) is recurved at the apex, V-shaped as viewed from above. Outside there is a rather narrow, triangular parietal area, and two much larger triangular alæ. Inside more than half of the plate is transversely ridged, the ridges white.

Length of base 9, width 6.2, height of carina 7 mm.

The scutum (pl. XVII, fig. 4, 5) is triangular, the width half of the length, marked externally with narrow, widely spaced transverse grooves. Inside the articular ridge is well developed, nearly as long as the tergal border of the plate. Articular furrow narrow but rather deep. The apical part of the plate is transversely ridged. The tergum (pl. XVII, fig. 10, 11) has a strong ridge along the scutal border, and is concave near it. The surface is marked with lines of growth and spaced grooves. Some radial lines are weakly sketched. Internally there is a very wide but short articular ridge and a deep articular furrow. There is a group of sharp crests for the depressor muscle, projecting as small teeth at the lower border of the plate. The tergum has a truncate shape at the apex, and is marked internally with arcuate ridges there.

The mandible (fig. 11, E) has three long, acute teeth and a blunter, multispinose lower point. It is somewhat profusely hairy, as shown in the figure, the hairs projecting below the lower point. There is also a patch of hairs on the upper margin.

The maxilla (fig. 11, B) has an irregular, step-like edge, with numerous spines, and is hairy on the upper and lower borders. The first cirrus (fig. 11, C) has short unequal rami of 9 segments, which are very profusely hairy on the inner face, much less so outside. The second cirrus is similar but larger. The rest of the cirri are quite long, with three pairs of long and one of very short spines on each segment, and a tuft of several spines at each suture posteriorly (fig. 11, A). Cirrus VI (fig. 11, F) has rami of 22

and 23 segments. The penis (fig. 11, F, *p.*) is very long, with indistinct traces of annulation. There is a pencil of hairs at the tip, and a few sparsely scattered elsewhere. Terminal appendages are very minute, about 1.25 mm. long, composed of 8 rather profusely bristly segments (fig. 11, D).

This species is known by seven individuals, all very similar. It is much smaller than *Pachylasma giganteum* (Philippi) of the Mediterranean and *P. aurantiacum* Darwin from New South Wales, the only species of the genus hitherto known, and differs from them in so many details that a comparison would be superfluous. The specimens had been removed from the crinoids before reaching me, and therefore the exact nature of the base could not be ascertained. From the thin, acute basal

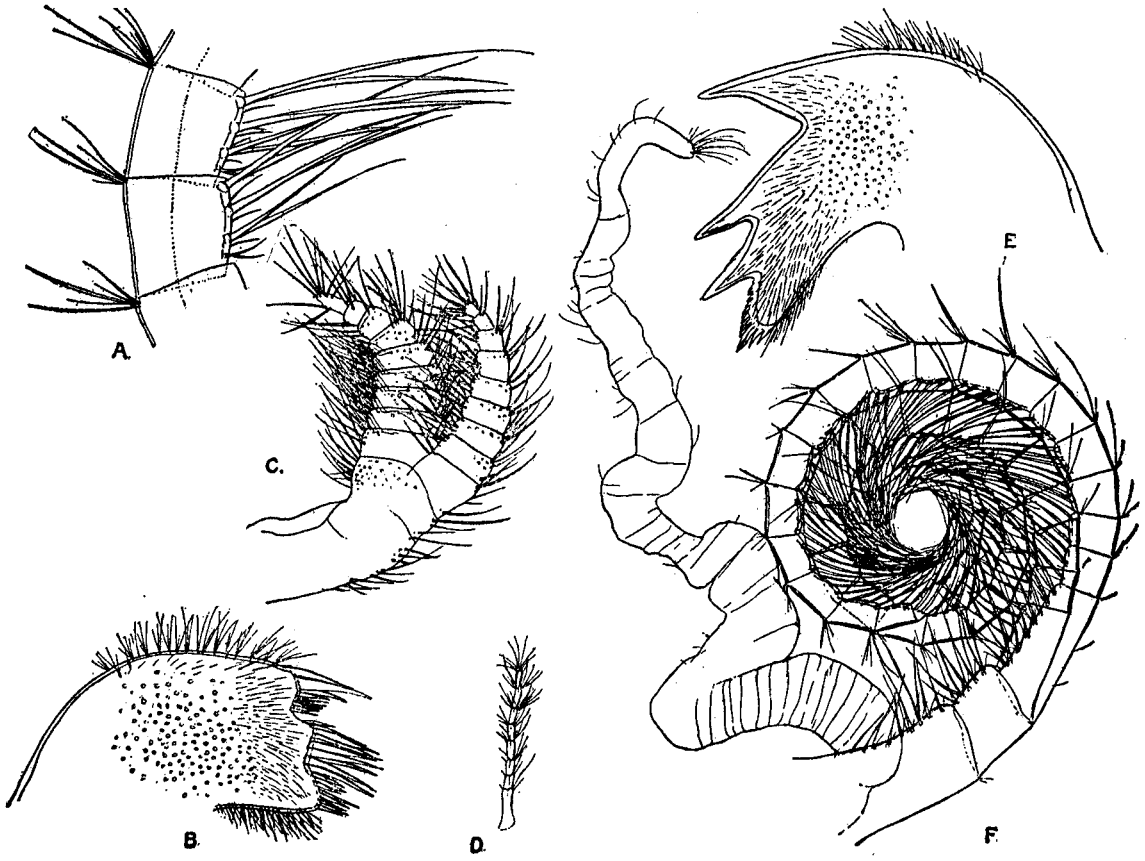


FIG. 11.—*Pachylasma crinoidophilum.* A, two segments of cirrus v; B, maxilla; C, 1st cirrus; D, terminal appendage; E, mandible; F, 6th cirrus and penis.

edges of the plates of the wall, and the nearly perfect condition of the soft parts, I presume that the base is wholly membranous. The base of the cup is hollowed to fit the stem of the crinoid, upon which all were seated in a longitudinal position.

Catophragmus (Chionelasmus) darwini Pilsbry.

1907. *Catophragmus darwini* Pilsbry; Bulletin of the Bureau of Fisheries, vol. XXVI, p. 188.

The Hawaiian barnacle described as *Catophragmus darwini* Pilsbry, and known by mutilated individuals only, has many points of resemblance to *Pachylasma crinoidophilum.* The mouth-parts, cirri, and penis are very similar, and the terga, scuta, and plates of the wall are alike in many respects. In

texture and finer sculpture the plates are similar; so that I can not doubt that the forms are related. Unfortunately the number of plates of the wall is not known in the Hawaiian species, since only fragmentary remains were preserved; yet so far as these go they indicate an octomerous wall, the median latera of which are still unknown. The development of an accessory basal whorl of plates in *C. darwini* indicates affinity to the genus *Catophragmus*. I am disposed to believe that when perfect individuals come to light, *C. darwini* will prove to belong to a distinct genus, or at least subgenus, intermediate between *Pachylasma* and *Catophragmus*, and distinguished from *Catophragmus* by the well-developed caudal appendages, the wall with a single series of accessory basal plates, part of them with alæ, and by the dense, porcellanous texture of all the plates. This group may be called *Chionelasmus*.

EXPLANATION OF PLATES.

PLATE VIII.

Fig. 1, 4. *Scalpellum rubrum* Hoek, lateral and dorsal views of an adult, no. 38680, U. S. National Museum, x 4.7.
Fig. 2. *Scalpellum rubrum*, rostrum and adjacent parts.
Fig. 3. *Scalpellum rubrum*, rostrum and adjacent latera seen from the inside.
Fig. 5–7. *Conchoderma auritum* Linnaeus, posterior, ventral and lateral views of living specimens from Plover Bay, Siberia. Drawn by Wm. H. Dall.

PLATE IX.

Fig. 1. *Scalpellum stearnsi* Pilsbry. Young individual, no. 38678, U. S. National Museum, x 6.
Fig. 2, 3. *Scalpellum gonionotum* Pilsbry. Lateral and dorsal views of the type, no. 38678, U. S. National Museum x 10.
Fig. 4. *Scalpellum gonionotum*. Rostrum and adjacent plates.
Fig. 5, 6. *Scalpellum weltnerianum* Pilsbry. Lateral and dorsal views of the type, no. 32679, U. S. National Museum, x 9.
Fig. 7. *Scalpellum weltnerianum*. Rostrum and adjacent plates.

PLATE X.

Scalpellum japonicum Hoek.

Fig. 1, 2. Lateral and dorsal views, no. 38684, U. S. National Museum, x 4.
Fig. 3. Rostrum of the same individual.
Fig. 4, 5. Lateral view and rostrum of another individual from the same station, x 4, no. 38685, U. S. National Museum.
Fig. 6, 7, 8. Ventral, dorsal, and lateral views of a very young *Scalpellum* of the *japonicum* type, x 12.7, no. 38688, U. S. National Museum.
Fig. 9. Outline figure of the type specimen of *S. japonicum*, x 5 ¼.

PLATE XI.

Fig. 1, 2. *Scalpellum japonicum biramosum* Pilsbry. Right and left lateral views of the type specimen, no. 38686, U. S. National Museum, x 3.
Fig. 3. Rostrum and adjacent parts of the same individual.
Fig. 4, 5 *Scalpellum molliculum* Pilsbry. Lateral view (x 3) and rostral detail of the type, no. 38687, U. S. National Museum.
Fig. 6, 7. *Octolasmis orthogonia* Darwin, no 38676, U. S. National Museum. Two varieties from off Kagoshima Gulf, x 8.6.
Fig. 8, 9. *Heteralepas* sp. undet. Ventral and lateral views, x 6, no. 38682, U. S. National Museum.

PLATE XII.

Fig. 1–3. *Heteralepas vetula* Pilsbry. Dorsal, lateral and ventral views of the type, no. 38689, U. S. National Museum.
Fig. 4. *Balanus rostratus apertus*, no. 38670, U. S. National Museum, natural size.
Fig. 5. *Balanus callistoderma* Pilsbry, walls of type, natural size.
Fig. 6. *Balanus rostratus* Hoek, Tokyo Harbor, Japan, no. 1814, Academy of Natural Sciences, Philadelphia, natural size.
Fig. 7. *Balanus rostratus apertus* Pilsbry, no. 38667, natural size.

PLATE XIII.

Fig. 1, 2. *Balanus rostratus apertus* Pilsbry. Scutum of no. 38667; U. S. National Museum.
Fig. 3, 4. *Balanus hoekianus* Pilsbry, scutum of type.
Fig. 5. *Balanus hoekianus* Pilsbry. Profile of scutum of type.
Fig. 6, 7. *Balanus hoekianus* Pilsbry, tergum of type.
Fig. 8, 9. *Balanus rostratus apertus* Pilsbry, tergum of no. 38667, U. S. National Museum.

PLATE XIV.

Fig. 1, 2. *Balanus crenatus* Bruguière. Top and lateral views of the walls of an individual of the solitary conic form.
Fig. 3. Tergum of the same individual.
Fig. 4. *Balanus crenatus*, columnar or colonial type. Profile of scutum. No. 38672, U. S. National Museum.
Fig. 5, 6. Tergum of same individual.
Fig. 7, 9. Scutum of same individual.
Fig. 8. Colony of the columnar type.

PLATE XV.

Fig. 1, 2. *Balanus hoekianus* Pilsbry. Lateral and top views of the walls of the type.
Fig. 3, 4. *Balanus callistoderma* Pilsbry. Tergum of the type, no. 38690, U. S. National Museum.
Fig. 5. Profile of scutum, occludent aspect, same individual.
Fig. 6, 7. Scutum of same example.

PLATE XVI.

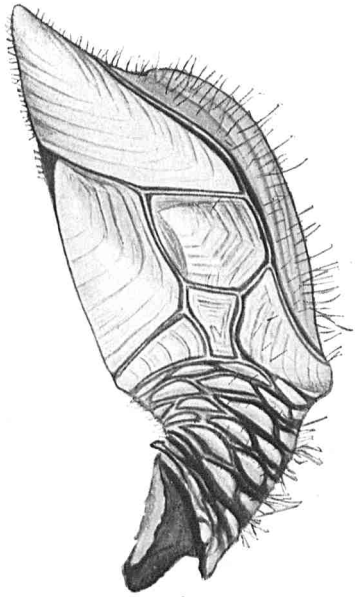
Acasta spongites japonica Pilsbry.

Fig. 1, 2. Tergum of the type, no. 38681, U. S. National Museum.
Fig. 3. Walls, lateral view.
Fig. 4, 5. Scutum.
Fig. 6–9. Plates of the wall, internal aspect. 6, rostrum; 7, rostral latus; 8, carinal latus; 9, carina.

PLATE XVII.

Pachylasma crinoidophilum Pilsbry.

Fig. 1–3. Top, lateral, and rostral views of the type.
Fig. 4, 5. Scutum of same individual.
Fig. 6–9. Plates of the wall. 6, rostrum; 7, rostral latus; 8, median latus; 9, carinal latus.
Fig. 10, 11. Tergum, same individual.



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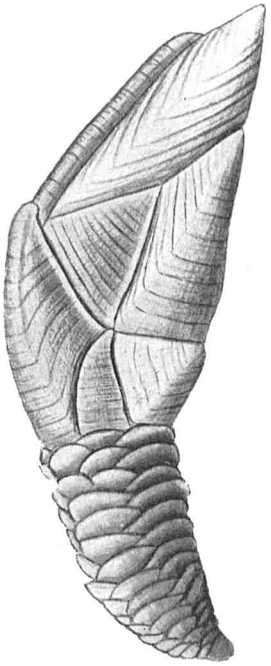

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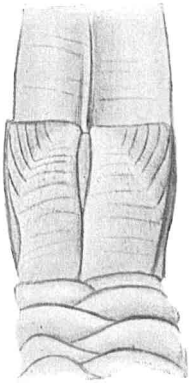

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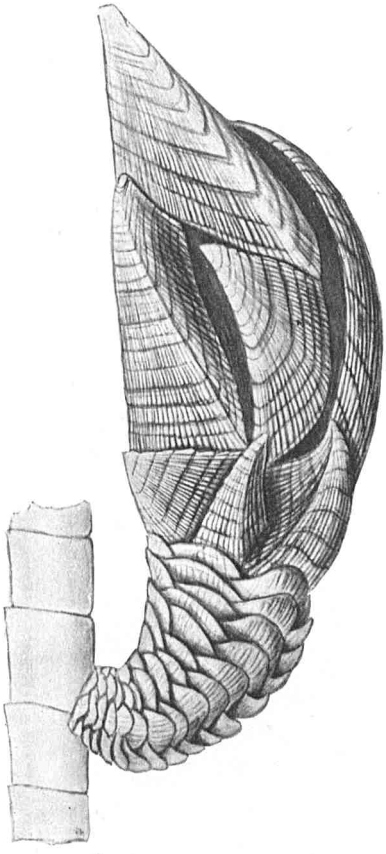

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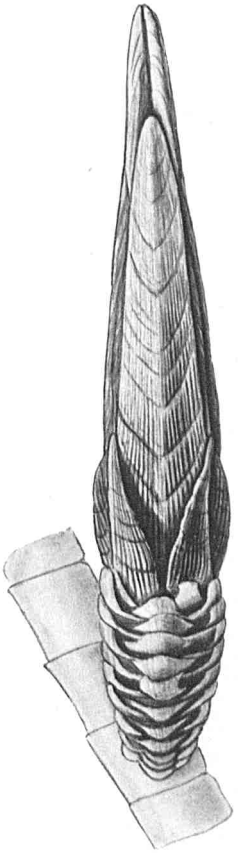

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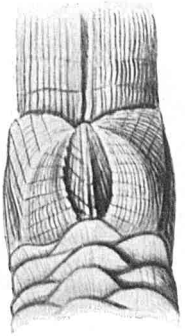

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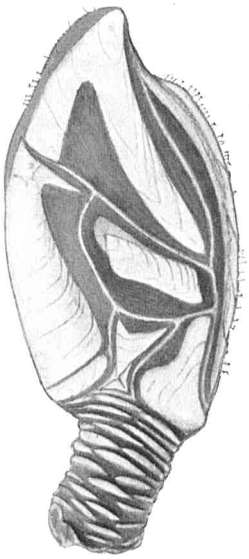

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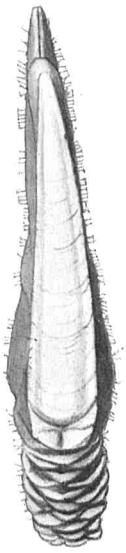

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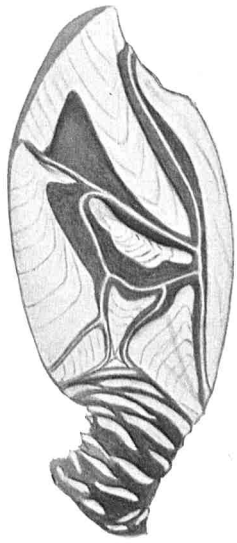

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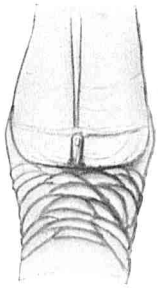

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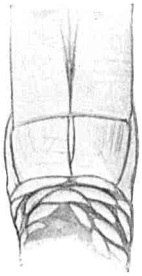

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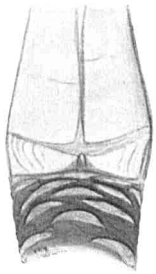

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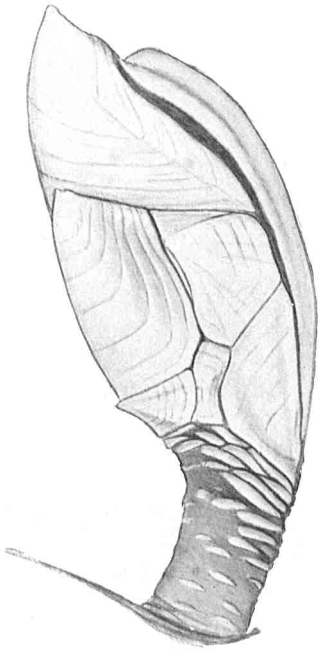

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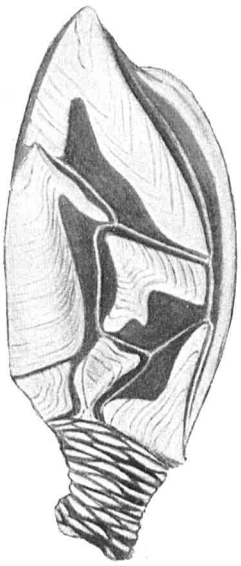

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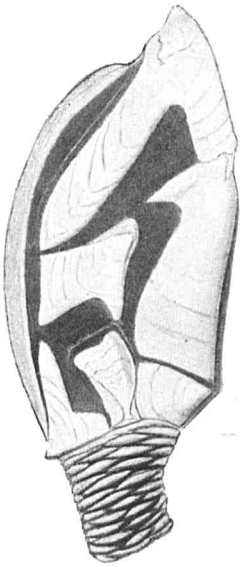

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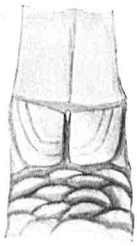

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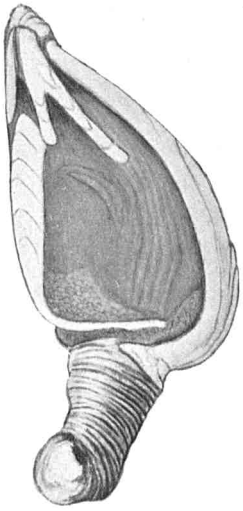

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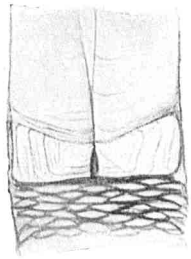

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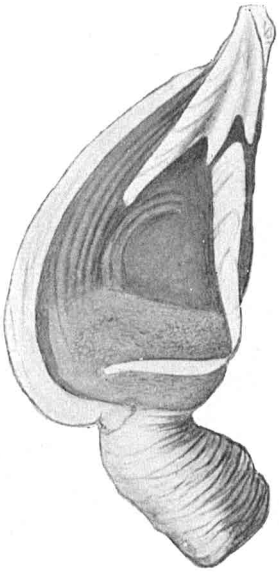

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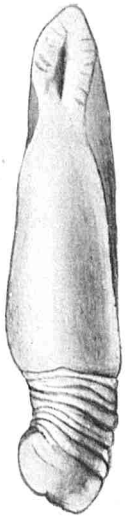

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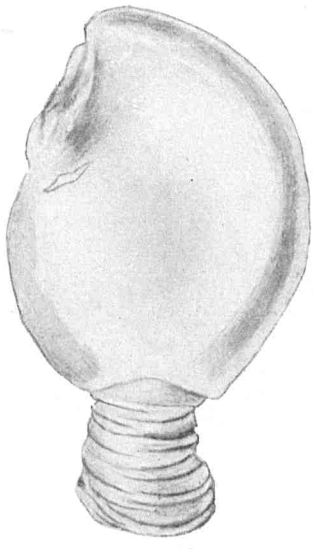

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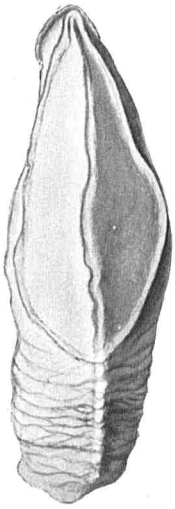

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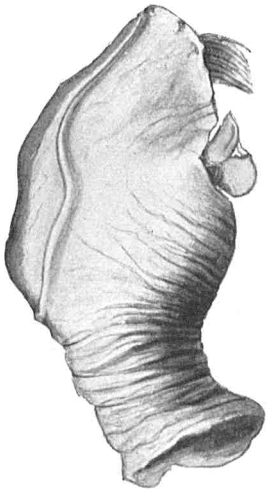

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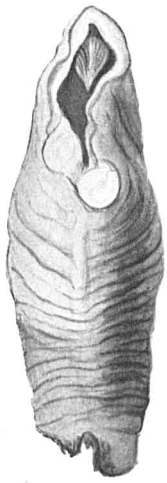

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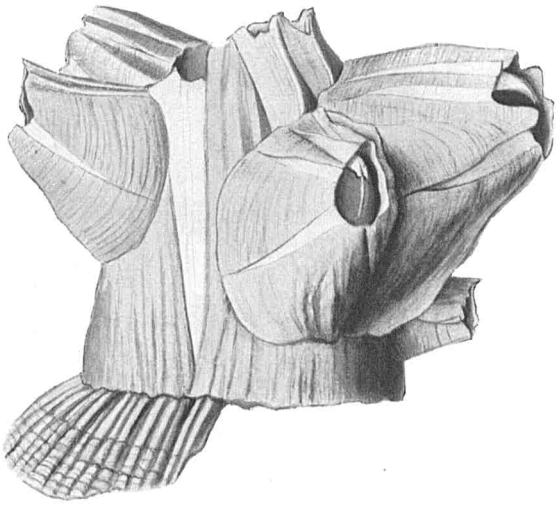

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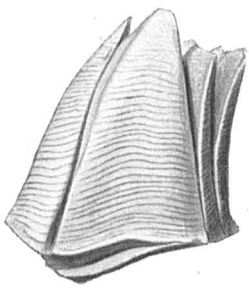

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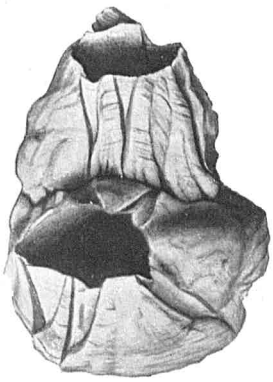

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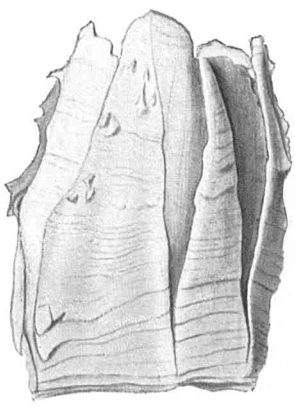

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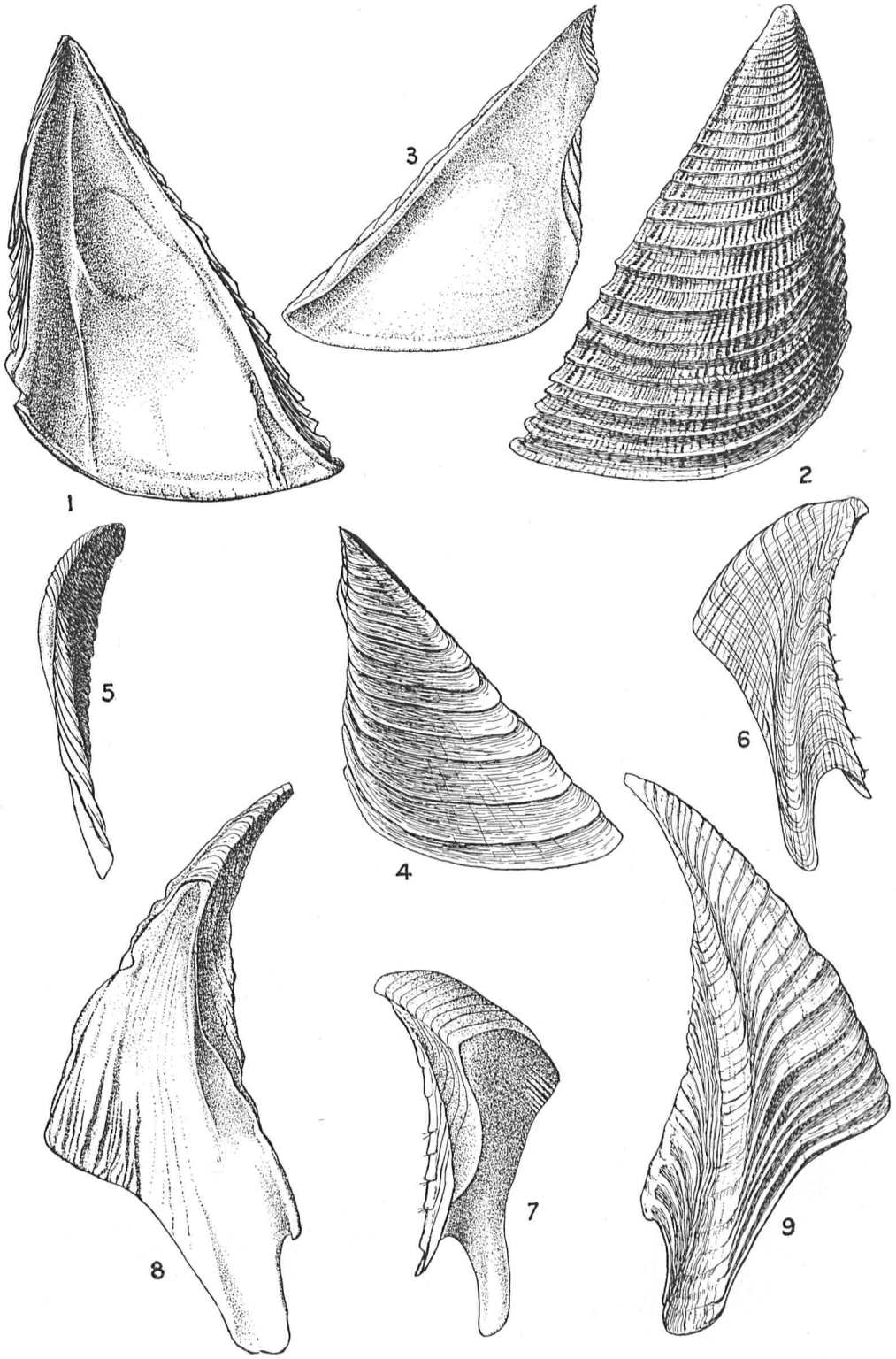
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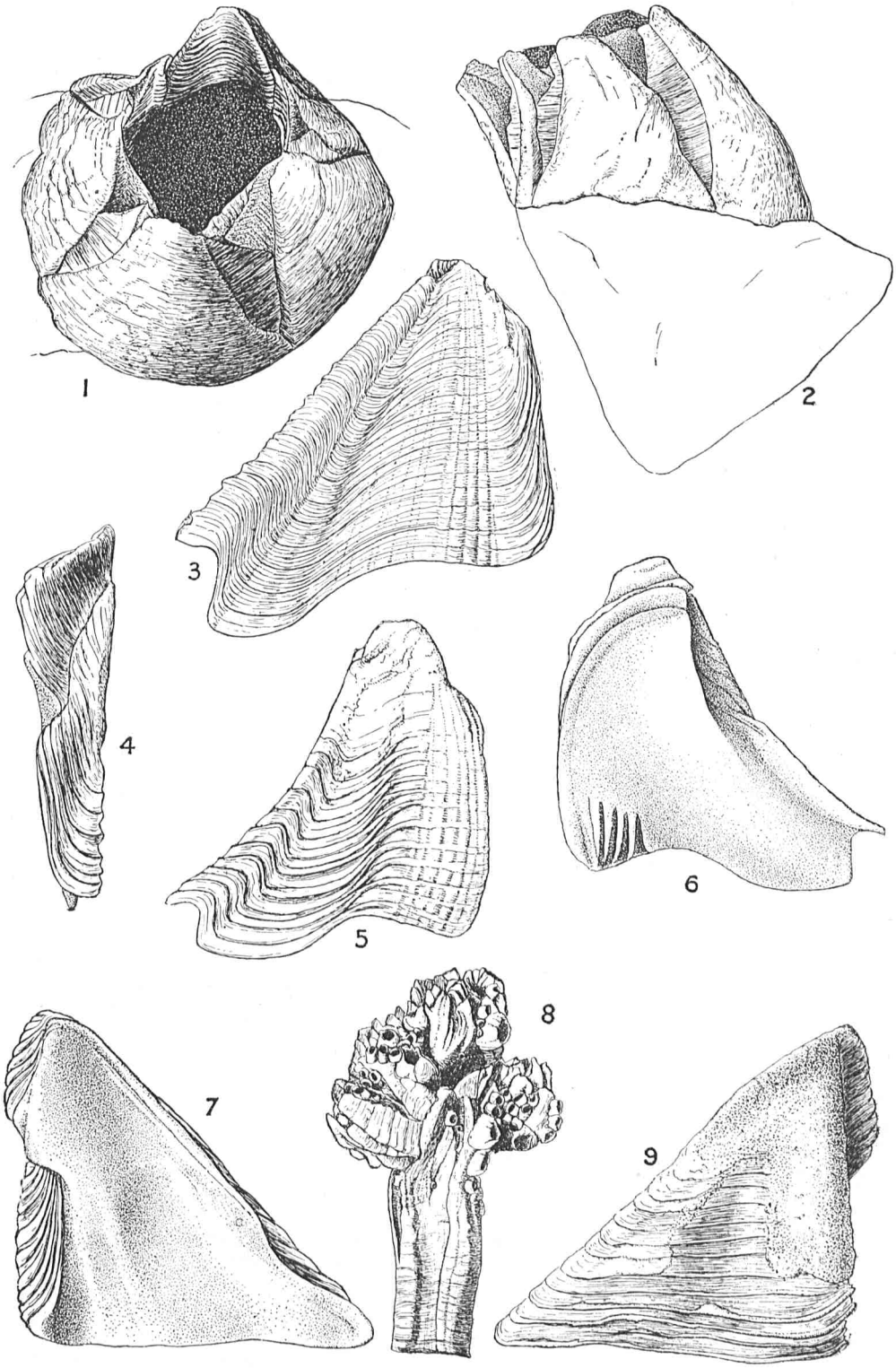
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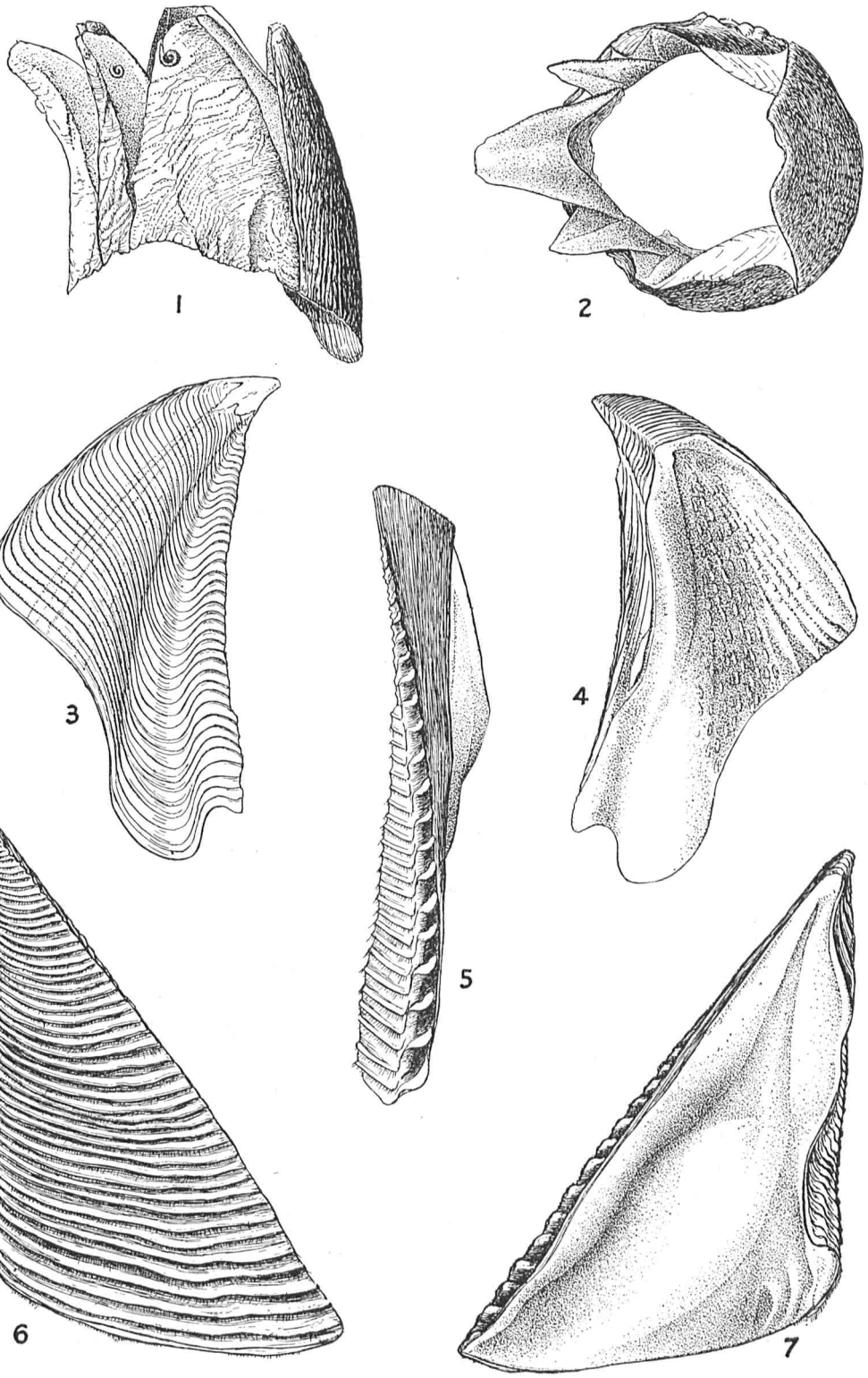
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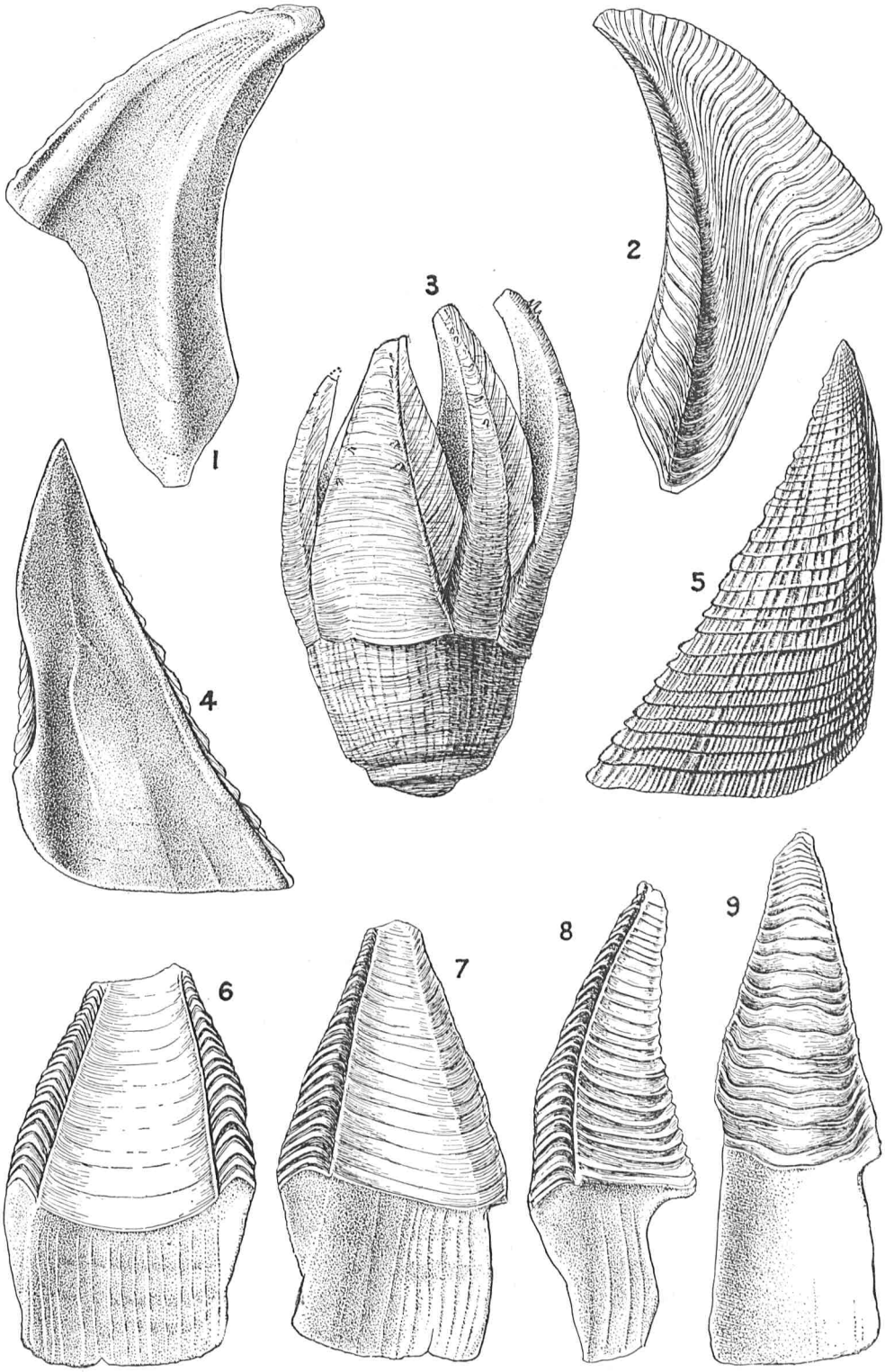
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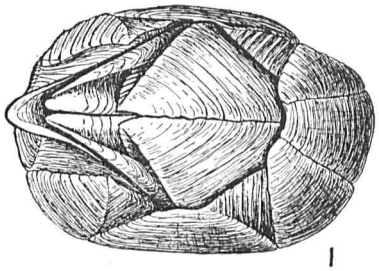

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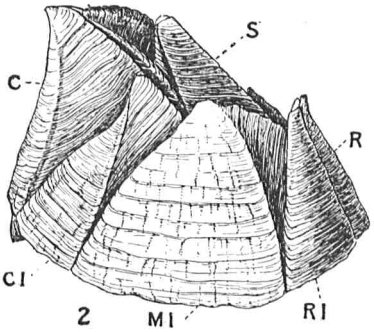

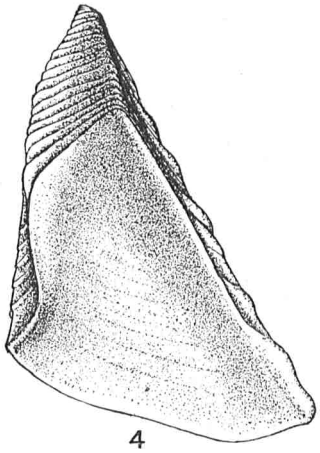

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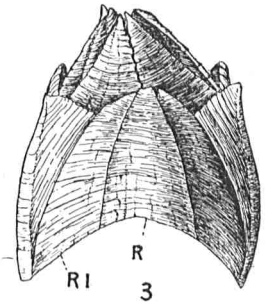

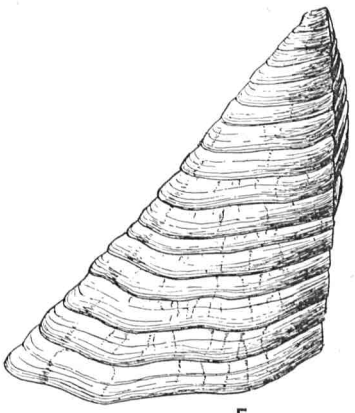

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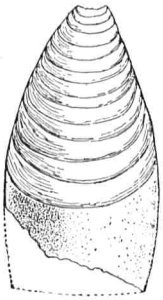

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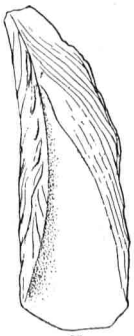

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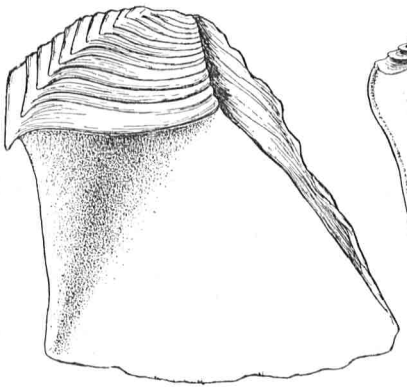

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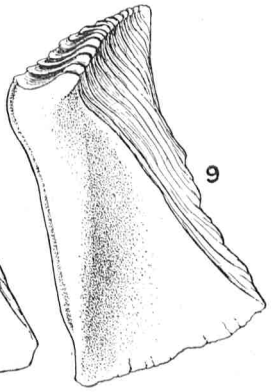

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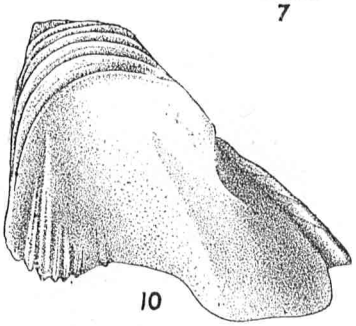

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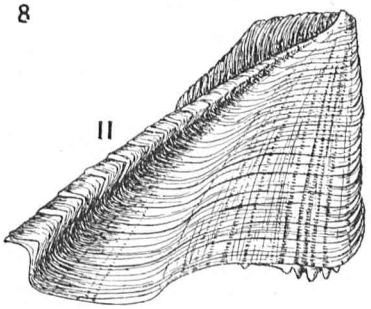

11

THE FOOD VALUE OF SEA MUSSELS

By Irving A. Field

U. S. Fisheries Laboratory, Woods Hole, Mass.

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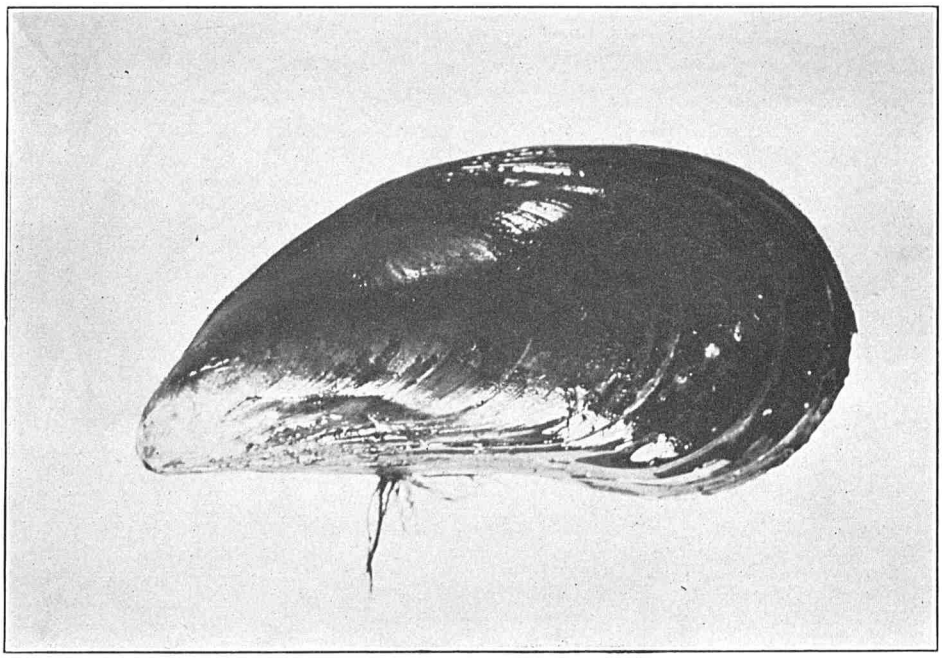

1.—The sea-mussel (*Mytilus edulis* Linnæus).

2.—A bed of sea-mussels 1 year old.

THE FOOD VALUE OF SEA MUSSELS.

By IRVING A. FIELD.
U. S. Fisheries Laboratory, Woods Hole, Mass.

INTRODUCTION.

The purpose of this report is to make known the character and food value of one of our abundant, nutritious, and palatable sea products which has been little utilized up to the present time. The substance of a previous paper on the subject [a] is here added to and amplified into a more complete, and, it is hoped, more useful discussion.

The sea mussel has been, so far as most of this country is concerned, in the category of many other unappreciated resources which have later become valuable. Familiar examples are the sturgeon and the eel. Finnan haddie, too, have only recently come into popular favor. The large snail, or abalone, of the California coast, at first eaten only by the Chinese, is now relished by the American palate. Raising frogs for market is now a profitable industry in various parts of the United States, although in 1903 a bill introduced into the Pennsylvania legislature for the protection of frogs was greeted with shouts of laughter. The mussel bids fair to become as valuable as any of these products, for its merits are unquestionable, once the groundless prejudice shall have given way.

The basis of this report is a series of investigations carried on during three summers for the United States Bureau of Fisheries at its laboratory at Woods Hole, Mass.

NATURAL HISTORY OF THE SEA MUSSEL.

FORM AND STRUCTURE.

The common sea mussel, *Mytilus edulis* (pl. XVIII, fig. 1), along with the oyster and clam, is a member of the class Lamellibranchia in the phylum Mollusca. In form it is triangular ovate. The umbo or beak is much pointed and is situated at the anterior end of the valves (pl. XIX, fig. 3). In size it measures from 2 to 4 inches in length and from 1 to 1½ inches in diameter. Occasionally specimens 4½ inches long are found. The color of the shell proper varies from violet to pale blue. Externally it is covered with a horny epidermis of shining blue-black. The sea mussel is most apt to be confused

[a] Field, I. A: Sea mussels and dogfish as food. Proceedings Fourth International Fishery Congress, Bulletin U. S Bureau of Fisheries, vol. XXVIII, 1908, p. 241–257.

with the horse mussel, *Modiola modiola*, which it most closely resembles. Close observation, however, will show that the umbo or beak of the horse mussel is not at the extreme end of the shell, but a short distance back near one margin, and that the epidermis is brown instead of blue.

Internally, the most conspicuous part of the body is the mantle (pl. XIX, fig. 3 and 4), which is made up of two lobes, each attached to and filling one of the two valves of the shell. Just before breeding, the mantles are thick and fleshy and assume a characteristic color by means of which it is possible, in a general way, to distinguish the two sexes. The males are white or pink, while the females vary from an orange to a brick red color. Another means of distinguishing the sexes is to note the surface character of the mantles, which in males shows closely aggregated follicles filled with spermatozoa (pl. XIX, fig. 1); in the females it presents a uniform granular appearance containing scattered groups of pigment cells (pl. XIX, fig. 2). During the quiescent period the mantles are thin and almost transparent.

The foot (pl. XIX, fig. 3), so well marked in the fresh-water mussel, is a muscular organ of small size in the sea mussel, tongue-like in form, with a longitudinal groove on the underside. Its hinder portion contains the byssus gland, which secretes the byssus or "beard" for the attachment of the mollusk (pl. XIX, fig. 3).

There are three important sets of muscles in addition to those in the foot. (1) The adductors (pl. XIX, fig. 3) are two in number. They extend across from one valve to the other and serve for closing the shell. The posterior adductor is the large muscle which it is necessary to cut before the shell is opened. The anterior adductor is inconspicuous and located, as its name implies, at the front end of the shell. (2) The retractors (pl. XIX, fig. 3), which are two in number and serve for withdrawing the foot, are long, narrow, paired muscles attached to the foot, from which one pair extends forward and the other backward to attach to the shell. (3) The pallial muscles (pl. XIX, fig. 3) are a row of delicate structures along the border of the mantle which serve to attach it to the shell.

The digestive tract has a complicated arrangement. It consists of a large mouth (pl. XIX, fig. 3) located at the anterior end just in front of the foot, a short gullet opening into a stomach which is surrounded by a large, dark-colored digestive gland, sometimes called the liver (pl. XIX, fig. 4). From the posterior end of the stomach the intestine passes backward to the posterior adductor muscle, where it turns forward in an oblique manner to the left side of the stomach. At this point it turns back again and passes through the ventricle of the heart and over the posterior adductor muscle to the anus, which is a short distance behind this muscle. The labial palps (pl. XIX, fig. 3), two pairs of loose flaps which lie just inside the edge of the mantle attached to the lower lip of the mouth, may be considered as accessory structures of the digestive system. They are covered with cilia and serve to direct food to the mouth.

The gills (pl. XIX, fig. 3) are a pair of filamentous structures extending along each side of the body from between the inner and outer palps to the posterior end of the animal. In cross section they present the form of a narrow W attached by the central part of the letter; the outer and inner arms remain free at their upper ends.

The kidneys, or so-called organ of Bojanus, consist of two symmetrical sacs on the ventral side of the body situated one on either side of the foot. Each extends backward to its opening, which is located on the inner side of the point of attachment of the gill just anterior to the posterior adductor muscle.

The circulatory system is well developed and completely closed as in all other mollusks. The heart lies in the mid-dorsal region in a pericardial chamber. From the heart a single large blood vessel is given off, which passes forward as the anterior aorta. It breaks up into a network of arteries that ramify all through the body. The blood is collected into a large, longitudinal vein on the ventral side of the body, from whence it passes through the kidneys to the gills and finally to the heart. The blood is colorless.

The nervous system, as in other lamellibranchs, is made up of three pairs of ganglionic centers connected one with the other and giving off nerves to supply the various surrounding organs. One pair is located in the head region with a ganglion on each side of the gullet, another in the foot, while the third, just ventral to the anterior edge of the posterior adductor muscle, supplies the digestive and reproductive organs, heart, gills, and posterior portion of the mantle.

The reproductive system is much more extensive than is found in most other mollusks. It is made up of a complicated branching network of canals which radiate throughout nearly the entire body. Internally each canal ends in a pocket or follicle. Externally the canals open out on either side of the body through a genital papilla which is at the inner point of attachment of the gills in front of the posterior adductor muscle and just in front of the kidney opening (pl. XIX, fig. 4). Since there is no definite organ which can be designated as an ovary or testis, it is impossible during the quiescent period to determine the sex of an individual. In mussels from Woods Hole, Mass., genital products were found developing in these canals during the early spring and summer months. (Compare fig. 1–4, pl. XXIII). According to Williamson (1907) the eggs arise from certain minute, brown-colored cells which he found present in the mantle of the female. My own observations are to the effect that the sexual products are formed by a process of budding from the cells lining the walls of the genital canals. At first the cells formed are extremely small and undergo rapid division. After a time division stops and the cells enter upon a period of growth. By the time the sperms and eggs are ripe they occupy almost the entire portion of the mantles, which are greatly distended by them. They fill the floor of the pericardial region, the wedge-shaped abdomen and cover to greater or less degree the outer walls of the digestive gland (pl. XIX, fig. 3).

REPRODUCTION.

With such an extensive genital system the mussel is capable of producing an enormous number of germ cells. For the past two summers between 200 and 300 mussels were kept in a shallow trough of running sea water where the process of egg laying and fertilization could be readily observed. The extrusion of the sexual elements on the part of two or three individuals began within an hour after bringing them in from the natural beds, and as time passed the number of spawning individuals

increased. After from twenty-four to thirty-six hours all the ripe mussels of a given lot were spawned out. It was observed that spawning started soonest among specimens which had been roughly handled before being placed in the trough. The duration of spawning varied with different individuals. Some would deposit practically all their products at one time, which required from twenty minutes to an hour. Others would spawn intermittently for short periods of several minutes each and finally stop altogether without having discharged half their genital products.

A male mussel discharges a stream of milt which will color the water for a distance of 10 or 12 feet before becoming too diffuse to be seen. In quiet water a female mussel will discharge her eggs so that they will fall in a heap. They can easily be removed by means of a pipette and measured in a graduate, a method which revealed the fact that mussels lay from 1 to 4 cubic centimeters of eggs at a single spawning. Knowing the average diameter of the eggs to be 0.07 mm., it is easy to calculate the number in a cubic centimeter, which approximates more than 3,000,000. On August 2, 1909, a mussel 3¼ inches long was seen to begin the deposition of eggs. A homeopathic vial of about 10 c. c. capacity was immediately placed in such a position as to receive the string of spawn as it was discharged. The egg laying proceeded at a remarkably rapid rate and continued for 15 minutes, when it suddenly stopped.

The mussel was watched for an hour longer and, when it was seen that no more eggs were to be laid, was removed from the trough and the shells opened to expose the mantle. The condition found is shown in figure 4 of plate XIX. All of the eggs except little patches here and there near the edge of the mantle had been discharged. Of course it was not known whether any of the eggs had been laid before this individual had come under my observation. The number of eggs laid measured 4 c. c., which means that this mussel liberated in round numbers about 12,000,000 eggs in 15 minutes. This is possibly more than the number usually produced. Three other mussels under my observation liberated from 6,000,000 to 9,000,000 each.

The period of reproduction varies for different regions and is influenced considerably by climatic conditions. It has been hard to determine when the mussel breeds on our northern Atlantic coast. Verrill and Smith (1873) and Goode (1887) say that the mussel breeds early in the spring. Ganong (1889), writing in Acadia, states that the height of the breeding season appears to be April and May. Mr. Charles H. Silverwood, of Pawtucket, R. I., who for years has been watching the habits of the mussels in Narragansett Bay, writes that the breeding season varies with the weather, beginning sometimes as early as the middle of June and lasting until late in August. Mr. George A. Carman, of Canarsie, N. Y., observes that the mussels in Long Island Sound spawn during April and May, while those in the open ocean do not spawn until about September 1. My own observations on the development of the sexual organs in mussels from Woods Hole, Mass., are in harmony with Silverwood's statement. Specimens of mussels were collected every month from February 7 until August 24. The mantles were sectioned and mounted for microscopical examination. The series of preparations show a gradual development of the sex cells during the whole period. No mature

sexual products were observed before July 3. On that date I found spermatozoa, which, when placed in sea water, were very active; they clustered about the eggs and by their active movements caused the eggs to slide gradually hither and thither across the microscopic field.

In England, on the Lancashire coast, Scott (1901) found that the mussels do not breed until midsummer. He kept the mussels in tanks under constant observation for a year and made frequent comparisons with those in natural beds. The sex organs developed at about the same rate in the two lots. The first eggs were discharged on May 6 by individuals in both the tanks and the beds. No spermatozoa, however, were observed until June 13 and the first developing eggs were found on June 14. The spawning season continued up to the middle of July. In France, where the water is much warmer than on our coast, the mussel spat appears in February and March. It is clear from the above evidence that the mussel breeds at various times between the months of February and September according to the temperature of the water in which it lives.

The ripe egg is a spherical body so small as to be hardly visible to the naked eye. It is surrounded by distinct membrane. On account of the great number of opaque yolk granules which fill the egg, none of its internal structures, such as the nucleus and nucleolus, are clearly visible under the microscope. The spermatozoa are pin shaped, with a conical protuberance upon the head. When liberated in the water they swim about actively and show great tenacity of life. Specimens placed in a bowl of sea water kept up active movements for more than six hours.

It has been an open question whether fertilization of the eggs takes place within the body of the female or not. M'Intosh (1885) and Wilson (1886) believe that it is accomplished outside of the female. That this is possibly so, Wilson has demonstrated by mixing ripe ova and spermatozoa in a beaker of sea water. He obtained the sexual products by mincing up portions of the mantle of the two sexes. Scott (1901), who studied the mussels kept in tanks, believes, on the other hand, that fertilization of the eggs takes place in the branchial chamber of the mother. He observed that "the embryos flow from the female in a slow, distinct stream." If the water is quiet, they settle on the bottom, forming a pinkish mass. In this position they continue to develop for from eight to twelve hours, finally becoming ciliated larvæ, which rise to the surface and swim about. At this time they are borne hither and thither by the tidal currents for about four days, so that eventually they reach almost every yard of our coast line within their range. At the end of this period the larvæ undergo important changes. They develop a shell and settle upon seaweeds, hydroids, or other convenient objects for attachment. At this stage they vary from $\frac{1}{11}$ to $\frac{1}{21}$ of an inch in diameter. The foot now becomes the chief organ of locomotion. By means of it they can creep from unfavorable situations over seaweeds and other objects to a more suitable position. In young forms the foot is capable of great extension and has the appearance of a long, white, flexible thread. By extending, attaching, and contracting this foot, the mussel readily draws itself forward. Of the myriads of brood mussels that appear shortly after the breeding season, only a small portion ever reach suitable places for growth, and of these only a few are destined to reach maturity.

GROWTH.

The rate of growth is dependent upon circumstances of situation, temperature, salinity of the water, and the amount of food available. Mussels in sheltered positions grow more rapidly than those exposed to the force of waves. The ideal location for the mussel is an estuary where food is supplied in great abundance, where the exposure to air between tides is not long, and where there is no deposition of silt. In such a place, if not too thickly crowded, they may grow to the average size of 2 or 3 inches in length in a single year. On the English coast, where they are cultivated by the bed system, it requires not less than two years and usually three years for them to reach a length of 2 inches. In France, where they are cultivated by the buchot method, that size is acquired in about a year and a half. On our Atlantic coast Charles H. Silverwood, of Pawtucket, R. I., says the mussels of Narragansett Bay reach marketable size, which I take to be not less than 2 inches, in from twenty-eight to thirty-four months.

Overcrowding is a very important factor affecting the growth of mussels. A single pair produces myriads of young, most of which are doomed to early death through lack of space and other conditions necessary to growth. After the free swimming stage is over, the young mussels often apply themselves in such close proximity to each other that no space is left for increase in size. In order to grow it is necessary for the stronger to smother out the weaker competitors. Sometimes the death rate from this cause is so high that the many disintegrating bodies apparently contaminate the closely applied living individuals and cause their destruction. This process may go on so far as practically to destroy what looks like a promising bed. Mussels on the margin of a thick cluster will almost always be found larger and in a more thrifty condition. Consequently, the healthiest individuals and specimens of largest size, other conditions being the same, are found in beds where the mussels do not lie in close contact with each other.

FOOD.

The food of the mussel is an important topic for study. A knowledge of the food and feeding habits of the marine animals which are utilized as food by man is of much greater importance than is ordinarily supposed. Especially is this true of forms like the mussel and oyster, which may be propagated by artificial means. The agriculturist who plants his grain regardless of the presence or absence of nitrates, phosphates, and sulphates in the soil is apt to reap very small crops. These chemical substances constitute an essential part of the food of plants, and the amount of the harvest's yield depends largely upon their presence in the ground on which it grows. The important relation of soil composition to crop production is well known and is receiving very serious investigation in every State of the Union.

The cultivation of marine products depends upon this same principle. The would-be oyster culturist who plants his seed oysters in any convenient spot, without knowledge of what constitutes their food or of its presence in the water, will be even less successful than

the farmer who ignores the first principles of agriculture. Up to the present time, however, very little study has been made of the food of marine animals or of the relative fertility of the waters in various parts of the sea. Such investigations as those of Peck (1894 and 1896) on the sources of marine food, and of Moore (1907) on the food of the oyster are of very great economic value.

My observations on the food of the mussel were necessarily limited. They were confined to the vicinity of Woods Hole and to the months of July and August. Lack of time did not permit a determination of the food value of the water over the mussel beds. During the summers of 1908 and 1909, however, a microscopic examination was made of the material found in the digestive tracts of 50 mussels.

Two methods were employed. The first was to extract the stomach contents by means of a pipette, which was thrust down the animal's gullet. The substance drawn out from the stomach was mixed with a few drops of water and a thin layer spread across the middle of a microscopic slide. The slide was then passed several times through the flame of an alcohol lamp, until the organisms were thoroughly fixed by the heat and the water almost evaporated to dryness. A drop of glycerin or of hot glycerin jelly was next applied and a cover glass pressed down upon it. Permanent mounts were later made from these preparations by cleaning the slides outside the boundary of the cover glass and ringing the mounts first with King's cement and, twenty-four hours later, ringing them again with asphaltum. This method proved best for preserving the animal forms, Protozoa, found in the stomach.

The second method was to place the mussels, immediately after removal from their natural beds, in small dishes of filtered sea water. After two or three hours' time the bottoms of the dishes were covered with intestinal discharges, which were removed by means of a pipette and transferred to a vial containing 95 per cent alcohol. After the sediment had completely settled the alcohol was drawn off and fresh alcohol added. The process was repeated, using absolute alcohol instead of the weaker grade. This was followed by a few minutes' treatment with xylol, and after removing most of the xylol three or four drops of a rather thin solution of Canada balsam were added. This mixture was allowed to stand for a few hours, until the xylol, sediment, and balsam were thoroughly mixed. Then, by means of a pipette, a large drop was transferred to a microscopic slide and on it was placed a cover glass. This method was found best for the preservation of the plant organisms which are known as diatoms. The diatoms, thus prepared, have had the pigments and coagulated protoplasm more or less completely removed, leaving a clear view of the striations and other markings on the skeleton.

The food of the mussel was found to consist of microscopic plants and animals which are carried by chance to the mollusk by water currents and are swept into the mouth by means of cilia on the gills and palps. The wall of the gullet is also lined with cilia, which direct the movement of the food material into the stomach. Not only food, but dirt and other indigestible substances are swept in. From the alimentary tracts of 50

mussels there were found 29 species of diatoms and 9 species of Protozoa.[a] The relative abundance of each species is indicated in the following list:

ORGANISMS CONSTITUTING THE FOOD OF THE MUSSEL.

DIATOMACEÆ. [Plates XX and XXI.]

Actinoptychus undulatus Ehrenberg (fig. 12)	Common.
Amphiprora lepidoptera Cleve	Very common.
Amphora proteus Gregory (fig. 2)	Frequent.
Biddulphia favus (Ehrenberg) H. V. H. (fig. 11)	Do.
Biddulphia rhombus (Ehrenberg) W. Smith (fig. 1)	Do.
Coscinodiscus excentricus Ehrenberg (fig. 25)	Do.
Grammatophora marina Kützing (fig. 16)	Do.
Hyalodiscus subtilis Bailey (fig. 23)	Very common.
Melosira sculpta Kützing (fig. 14)	Do.
Navicula didyma Ehrenberg (fig. 6)	Common.
Navicula lyra Ehrenberg (fig. 8)	Occasional.
Navicula lanceolata Kützing (fig. 7)	Frequent.
Navicula splendida var. puella Ad. Schmitz (fig. 10)	Occasional.
Nitzschia sigma Grunow (fig. 15)	Common.
Nitzschia sigma var. rigida Grunow	Do.
Nitzschia sigma var. sigmatella Grunow (fig. 13)	Do.
Pleurosigma affine Grunow	Frequent.
Pleurosigma angulatum W. Smith (fig. 24)	Do.
Pleurosigma balticum W. Smith (fig. 18)	Common.
Pleurosigma decorum W. Smith (fig. 20)	Do.
Pleurosigma elongatum W Smith (fig. 19)	Do.
Pleurosigma naviculaceum Brebisson	Very common.
Rhabdonema adriaticum Kützing (fig. 5)	Frequent.
Rhabdonema arcuatum Kützing (fig. 9)	Do.
Rhizoselenia setigera Brighter (fig. 17)	Very common
Stephanopyxis appendiculata Ehrenberg (fig. 21)	Occasional.
Surirella ovalis var. ovata Brebisson (fig. 4)	Common.
Synedra gallionii Ehrenberg (fig. 22)	Very common.
Tabellaria fenestrata Kützing (fig. 3)	Frequent.

PROTOZOA. [Plate XXII.]

Ceratium fusus Ehrenberg (fig. 3)	Frequent.
Distephanus speculum Stohr (fig. 4)	Common.
Exuviælla lima Ehrenberg (fig. 5)	Very common.
Exuviælla marina Cienkowsky (fig. 1)	Common.
Glenodinium compressa Calkins (fig. 2)	Do.
Peridinium divergens Ehrenberg (fig. 6)	Do.
Prorocentrum micans Ehrenberg (fig. 7)	Very common
Tintinnopsis beroidea Stein (fig. 9)	Do.
Tintinnopsis davidoffi Daday (fig. 8)	Common.

[a] The identifications were made by Mr. T. E. B. Pope, assistant of the Bureau of Fisheries.

The organisms included in this list are of the most primitive type, and, as Peck (1896) has demonstrated, are the ultimate source of food for all marine animals. The food of diatoms is the dissolved mineral matter removed from the soil and carried by rivers and the smaller streams down to the sea. It is absorbed through the surface of their bodies and transformed into living tissue. When their bodies have increased to a certain size, each individual divides into 2; as these grow they divide into 4, the 4 into 8, 8 into 16, etc., in geometric ratio. Under favorable conditions multiplication by this means is so rapid that millions may be produced in a day from a single individual. The Protozoa on which the mussel feeds multiply in much the same way, but in feeding habits differ from the diatoms in that they consume solid food, chiefly diatoms, in addition to absorbing soluble nourishment through the surface of the body. It is interesting to note, as Professor Brooks has pointed out, that these unicellular organisms are the means of bringing back to us in the form of food our mineral wealth which is continually being lost through the agency of erosion and solution.

ENEMIES AND PARASITES.

The enemies of the mussel are numerous. Killifish, cunners, and scup are very fond of the young mussels, greedily stripping them from the wharf piles, seaweeds, and other objects of attachment. The squeteague and tautog eat them from the beds. Among the mollusks the drill, *Urosalpinx cinereus*, destroys large numbers by boring a hole through the shell to the soft parts on which it feeds. On nearly every mussel bed numbers of shells may be found pierced with a hole about the size of a pin head which testify to the ravages of this voracious snail. Another snail, *Neverita duplicata*, is supposed to feed upon them in the same manner but the hole drilled is much larger. The so-called whelks, *Busycon canaliculata* and *B. carica*, also prey upon them to considerable extent. Perhaps the worst enemy is the starfish, which destroys them to as great a degree as it does the oyster. In England, Lebour (1907) reports that one whole bed of mussels at the mouth of the River Tyne was completely destroyed by this echinoderm. Crows and rats are said sometimes to eat mussels from the beds when they are exposed. Seaweeds like *Ulva* and eel grass (*Zostera marina*) are very injurious to the health and growth of mussels when they spread over the beds. Two of the largest beds near Woods Hole, Mass., have been practically ruined this year (1908) by a dense mass of eel grass which has sprung up over them. The weed by its growth not only gradually smothers the mussels, but causes the sand and mud to silt over them at such a rate that in a few months all signs of the bed are obliterated. The decaying bodies of the shellfish fertilize the soil and finally what was once a bed of mussels is a thrifty bed of eel grass.

The parasites of the mussel are few. The most common one is a little crab, *Pinnotheres maculatum*, which is very similar to the oyster crab but larger and with a tougher shell. It apparently works no injury to either the health or growth of the shellfish. Indeed, some observers believe the relation is symbiotic rather than parasitic. The

crab lives in the gill chamber, where it is protected from outside harm. In return for this protection it is said that the crab runs out and collects food which on returning it chews up in the gill chamber and shares with its host. From the examination of the stomach contents of several of these crabs, however, I found no evidence to support this belief. The only food material found consisted of diatoms and other microscopic organisms which probably would have been utilized by the mussel had not the parasite been present. Other hosts, such as the giant scallop and smooth scallop, are known to harbor this same species of crab. In describing it (Goode, 1884), Rathbun says:

> Another species of *Pinnotheres* (*P. maculatum*) frequently occurs in the shells of the common sea mussel (*Mytilus edulis*) and the smooth scallop (*Pecten tenuicostatus*), between the gills of the animal. It attains a size larger than the oyster crab, and, as in the case of the latter, the females alone are parasitic, the males only having been found swimming at the surface of the sea. We have never heard of this species being eaten, probably because neither the mussel nor the smooth scallop has ever been used as food in this country. In the summer of 1880, while dredging off Newport, R. I., the United States Fish Commission steamer *Fish Hawk* came upon extensive beds of the smooth scallop, from a bushel of which nearly a pint of these crabs were obtained. Again, in 1881, the same species was encountered in great abundance by the same party in Vineyard Sound, in *Mytilus edulis*. As an experiment, they were cooked along with the mussels and found to be very palatable, although their shell is, perhaps, somewhat harder than that of *Pinnotheres ostreum*.

In my own experience with mussels I have observed no other parasite, but in Europe Lebour (1907) found a boring annelid, *Polydora ciliata*, which attacks the Northumberland mussels. The worm burrows through the shell from the outside, making a hole about the size of a pin. It causes the mussel to grow pearly excresences, often to considerable extent, over the internal surface of the shell, which interfere with the muscular development of the animal and frequently almost destroys the posterior adductor muscle. If the pearly masses press upon the mantle, the reproductive lobes fail to develop in such places. Aside from injuring the mussel, the presence of the pearly excrescences gives the mussel an unsightly appearance and consequently renders it unfit for market.

Three larval trematodes are also found in the Northumberland mussels. The cercarias of the pearl trematode have been found in the mantle, the encysted cercarias of *Echinostomum secundum* in the foot, and a third unidentified species encysted in the liver. These trematodes, however, even when present in large numbers, work very little injury to their host.

Several species of mollusks are commonly found living with the sea mussel. Oysters are very often associated in the same beds with them and usually to the detriment of the oyster, if the mussels are present in large numbers. The mussels, having the power of free movement which the oysters do not possess, are able to acquire the more favorable positions for collecting food and thus deprive the oysters of much nourishment. The soft-shelled clam, *Mya arenaria*, and the hard-shelled clam, *Venus mercenaria*, are sometimes found growing among the mussels in good, healthy condition. Boat shells, *Crepidula fornicata* and *C. convexa*, are very common. Sometimes three or four individuals are attached to a single mussel, covering it almost completely, but apparently doing

no injury. Large numbers of periwinkles, *Littorina litorea*, are usually present on the beds, where, according to Allen and Todd (1902), by feeding upon the seaweed and thus keeping down the growing vegetation, they are a positive benefit to the mussel.

DISTRIBUTION AND HABITAT.

The sea mussel has a very wide distribution, occupying most of the coast line of the northern half of the Northern Hemisphere. It is circumpolar in range and extends down our eastern coast to North Carolina, down the Pacific coast to San Francisco, Cal., on the Asiatic coast to Japan, and on the European coast southward to the Mediterranean Sea. It is extremely abundant in the shallow, sheltered bays along the coasts of New Jersey, Long Island, Rhode Island, and Massachusetts.

The mussel seems to grow equally well in shallow and deep water. The bathymetrical range is from the littoral zone to about 100 fathoms. In the channel between Eastport, Me., and Deer Island, Verrill and Smith (1873) dredged them in from 40 to 50 fathoms and report that later their party dredged them in deeper water, but do not state from what depth. Some of the beds near Boston, Lynn, and Vineyard Sound lie in from 5 to 7 fathoms of water.

The favorite habitat of the mussel is where the water is slightly brackish, in shallow, protected bays and estuaries, on a bottom of mud rich in diatoms and covered more or less with stones or other solid objects to which it may attach by means of its byssal threads. The swift tideways of shallow inlets are also very good situations for the mussel. In these localities it is generally distributed from halfway between tide marks to a level several feet below low water. Other situations chosen by the animal are the piles and timbers of bridges, wharfs, and other objects, buoys, light-vessels, and rocks. But these locations are not so advantageous as the first ones mentioned, where mussels thrive in enormous beds, sometimes acres in extent, and where it is possible for a man to collect them daily by the ton.

PRESENT USES OF SEA MUSSELS.

The sea mussel, which is practically unknown as a food in the United States outside of New York City, has been utilized in other parts of the world for hundreds of years. According to Quatrefages (1854) the artificial culture of mussels for food began as early as the year 1035. Gould (1870) states that this shellfish is extensively used as a food in England, France, Norway, and Russia, and that it is more palatable than the common clam, *Mya arenaria*. Anderssen (1880) refers to it as a cheap and healthful food in America, France, Spain, and Portugal, where it is eaten raw with vinegar and pepper or boiled with milk. Goode (1884) writes that in Europe *Mytilus* holds an important place among the sea foods. Ganong (1889) says that as a food in Europe the mussel ranks second only to the oyster and takes the place of the soft-shelled clam, which is not eaten. This state of affairs we find at present reversed in America, where the soft-shelled clam is so popular that there is danger of the demand exceeding the supply, while the mussel, although exceedingly abundant, remains almost unutilized.

In the early colonial days, however, the settlers did eat mussels, as may be seen in Lescarbot's description of De Mont's settlement at St. Croix Island (Dochet Island of to-day), written in 1604. From this account Ganong (1889) makes the following quotation:

> There is a little chapel built after the fashion of the savages, at the foot of which there is such a store of mussels as is wonderful, which may be gathered at low tide, but they are small. I believe that Monsieur De Mont's people did not forget to choose and take the biggest and left there but the small ones to grow and increase.

Of how the change in attitude toward the mussel and clam came about Ganong (1889) offers a very plausible explanation. He attributes it to the influence of the Indians, who ate the soft-shelled clam to the almost total neglect of the mussel, which, without reason, they superstitiously avoided. He furthermore thinks that this was unfortunate for us, since the mussel is a superior article of food. Goode (1887) refers to the use of mussels on the northwest coast of America, where it is the chief molluscan food. The Indian women and children collect them from the rocks every day the year around. Mussels are also consumed by the white inhabitants of that region. The Russian name for them is "black shells" (chornie rakooshka). In Alaska the method of cooking is by boiling; on Vancouver Island they are more commonly roasted.

Aside from being useful as an article of food, the sea mussel is valuable for other purposes, the most important of which is bait. In England the mussel is valued as the best hook bait known. The quantity used in Great Britain for this purpose amounts to more than 100,000 tons annually. In this country, however, fishermen rank it second to the squid in bait value.

Next in importance the mussels are valuable for the production of fertilizer. The so-called mussel mud constitutes one of the best fertilizers known. It is formed in places where the mussel beds are exposed to constantly depositing silt, which slowly destroys the mollusks and buries them beneath their offspring. The slow accumulation and decay forms a mass of very rich fertilizer, enormous quantities of which are taken along the coasts of Long Island and New Jersey, where it is considered excellent for carrots and onions. Goode (1887) stated that for the last thirty years he had seen it applied to lands where onions had been grown with a product varying from 300 to 600 bushels per acre. At that time the mussel mud sold, delivered several miles from where it was dug, at $4 to $5 a cord. It is gathered during the winter, piled up and exposed to the frosts, and then distributed in amounts of from 4 to 8 cords to the acre. For bait and fertilizer the value of the mussel fishery to the United States is estimated at $37,500 annually.

Pearls of some value are sometimes found in mussels. Usually, however, although quite commonly present, they are small and of such poor color that the price they bring is low. In England they have been sold for from 1s. 6d. to 4s. per ounce.

The shells can be used by oyster planters for cultch upon which to catch oyster spat. When polished, they may be used in numerous ways. Artists use them as receptacles for gold or silver paint. They may be mounted on marble for paper weights

or made into pretty needle books and scent bottleholders, earrings, crosses, pins, and pin cushions. It is said that the American Indians and the natives of New Zealand used the mussel shells as tweezers for pulling out their beards.

SEA MUSSELS AS FOOD.

The fact that the sea mussel is so widely used as a food and yet is not utilized to any extent in the United States, where it grows prolifically in great beds, has led me to investigate its properties as a human food and to determine whether or not there is any reason for not making wide use of it in our diet. A food substance to be of value must measure up well to four standards. It must be palatable, digestible, nutritious, and economical.

By palatable I mean that the substance must have a flavor that will appeal to the average man's taste. To determine this quality, I found it necessary first to taste or eat the substance in question myself. If the flavor was agreeable and no evil results followed its use, I persuaded members of the Woods Hole scientific staff to follow my example and express their opinions concerning the dish. If they gave a favorable report, I had mussels served on certain tables of the Marine Biological Laboratory mess hall and to other persons who were interested enough to try them. The general opinion expressed was taken as an indication of the palatability of the food. By this method it was often possible, also, to obtain criticisms which would suggest new ways of preparing the substance to improve its flavor.

The second standard, digestibility, means several things. It relates to the proportion of the food that can be digested, to the ease or rapidity with which it can be digested, and to the degree in which the material agrees or disagrees with the user. Comparatively little is known concerning the relative rapidity of digestion of different foods within the body. Most of the current statements referring to this are apparently based on experiments carried on outside of the body, and it is certain that the processes in the two cases are not exactly the same. The artificial process takes much longer than the natural one, although the relative rates of digestion as regards different substances appear to be much the same. For example, under natural conditions, soft boiled eggs will digest more quickly than hard boiled ones. The same proportionate results are obtained by the artificial method. The artificial process serves merely to determine the rate of digestion of the substance compared with that of staple foods. How it agrees or disagrees with the user can only be determined by taking the article into one's own stomach and awaiting results.

The third standard, nutritive value, involves such questions as the ratio of edible portion to refuse and the chemical composition and proportion of nutriment that can be absorbed by the body under normal conditions.

The fourth standard, economy, means that a food of high nutritive value must be so abundant and easily obtained that it can be sold reasonably cheap. If it can be readily prepared in various ways so that it may be preserved for long periods, its value is still further increased. Any food that measures up well to these four standards ought to find a large and ready market.

PALATABILITY.

From the standpoint of palatability I have abundant testimony from scores of persons who have eaten mussels prepared in various ways (pickled, steamed, roasted, stewed, and fried) that in flavor and texture they are superior to the long clam and fully equal to the oyster. A few people were inclined to rank them not so high. On July 30, 1907, pickled mussels were served on three tables of the Marine Biological Laboratory mess hall. About 36 persons ate of them and all expressed their appreciation of the unfamiliar dish. The only adverse criticism that was made related to the tough, muscular part of the foot, which was difficult to masticate.

Two days later one of the residents of Woods Hole was given four dozen mussels, which he took home for family use. He had them steamed and served with salt, pepper, butter, and oil. They were pronounced "elegant and superior to clams."

On August 3, 1907, mussels dipped in egg and cracker crumbs were fried and served to about 25 persons at the Marine Biological Laboratory mess hall. They were declared to be equal to or better than fried oysters, and were so relished, in fact, that there was a general call for more. A few days later, in answer to this request, a large quantity was prepared and served to 40 persons. Enthusiastic comments were made as to the appetizing appearance, rich flavor, and delicate texture of the flesh.

On August 13 mussel chowder was served to the same 40 persons and called forth the same favorable comments, especially as to richness of flavor and tenderness of the meat. The tender quality of the flesh is a point decidedly in favor of the mussel when compared with the clam, the meat of which latter in chowder is so tough that few persons ever think of trying to masticate it.

Mussel fritters were next tried on the tables of the mess hall on August 27. They were eaten with relish and pronounced excellent.

The following year, 1908, the work of preparing mussels in various ways and serving them in the mess hall to friends and visitors of the Bureau's laboratory was continued, with the result that quite a general interest in the food value of this shellfish has been aroused and a local demand now exists. For some years past at certain points along the coast of Rhode Island, New York, and New Jersey a few people have been in the habit of collecting mussels for their own personal use. Some of the summer visitors also have learned to eat them. I have met several persons living in the vicinity of New York City who say they have always prized the sea mussel as a food and that it is their custom to pickle a number every summer for use during the winter.

For the benefit of those interested in making use of the mussel in their diet, a few recipes for cooking them will be given in another section of this paper. They have been tried repeatedly and have proved to make most palatable dishes.

DIGESTIBILITY.

Personal testimony in various instances is very favorable to mussels for their digestibility. Persons with weak stomachs say that they can eat them without suffering any inconvenience. Others have eaten them just before retiring and experienced no

discomfort. One man with whom meat does not ordinarily agree states that he can eat freely of mussels and digest them without difficulty. Many persons have declared that in their opinion mussels are more digestible than either clams or oysters, a fact due to the character and properties of the flesh which by cooking is rendered tender and mealy, whereas the oyster and clam become very tough.

But the problem of really determining the digestibility of a given food material is surrounded with great difficulties. It is an easy matter for one to eat the food and learn by experience how it agrees or disagrees with him; but to determine the rate of digestion and the proportion of nutriment which the body absorbs from a given quantity of the food involves a series of very complex chemical studies.

EXPERIMENTS TO SHOW AVAILABLE PROTEIN.

By artificial methods it is possible, however, to determine approximately the proportion of protein which is rendered soluble and absorbed by the animal body. Digestion experiments of this sort were made by Dr. C. L. Alsberg. His method and results are as follows:

Mussels, hard-boiled eggs (yolk and white together), and thoroughly boiled beef were each ground up in an ordinary kitchen sausage machine. Each chopped-up sample was thoroughly mixed to make it as uniform as possible. Then 5-gram samples were weighed out. Each sample was placed in a flask containing 100 c. c. of artificial gastric juice. This juice was prepared by dissolving 0.5 gram pepsin in 1 liter 0.15 per cent hydrochloric acid. All the flasks were placed in a thermostat at a temperature of 38° C. At stated intervals they were all shaken by hand. After two hours one-half the flasks were removed from the thermostat. The remainder were removed after four hours. Immediately after taking them out of the thermostat each flask was brought to a boil in order to destroy the enzymes. Each was then filtered through an ash-free quantitative filter, and when all the liquid had passed through the filter the undissolved residue was washed with 100 c. c. of distilled water. When all the wash water had passed through the filter, the amount of nitrogen was determined by the Kjeldahl method in the combined filtrate and wash water as well as in the undissolved residue. From the relative amounts of nitrogen in the filtrate and undissolved residue an opinion may be formed as to how much protein has been rendered soluble by the action of the gastric juice. This method is not accurate, but it is believed to be more accurate than the methods commonly employed, in which the various digestion products are precipitated out and weighed. The washing and drying of such proteins upon filters presents great difficulties. It is believed that the determination of the nitrogen rendered soluble gives a better index of the effect of the digestion. The figures obtained were multiplied by 6.25 to indicate the amount of protein corresponding to them. The resulting figures are given in the following table, each figure representing the average of several experiments:

TABLE 1.—RESULTS OF EXPERIMENTS TO SHOW AVAILABLE PROTEIN IN MUSSELS.

Substance.	Protein in filtrate.	Protein in residue.	Per cent dissolved.
	Grams.	*Gram.*	
For two hours' digestion:			
Mussels	0.5783	0.2012	74.1
Egg	.6168	.1866	76.0
Beef	1.1656	.2705	81.1
For four hours' digestion:			
Mussels	.6107	.1522	80.0
Egg	.7455	.2104	77.9
Beef	1.2930	.1450	96.7

It will be seen that under the conditions of these experiments there was no very great difference in the digestibility of the egg and the mussels, while the beef was considerably more digestible than either. It must, however, be pointed out that beef has more nitrogenous extractives than egg and that the greater digestibility of the beef may be accounted for in part by the fact that under the conditions of these experiments the nitrogenous extractives are calculated as protein. How much nonprotein nitrogenous extractives mussels contain is not known. It must be noted, however, that, judged by sight, the greater part of the mussels went into solution. The undissolved portions consisted mainly of the tough portions, such as the foot and posterior adductor muscle.

Finally, it should be pointed out that experiments such as these must be interpreted cautiously. Digestion *in vitro* is surely not so effective as digestion in the intestinal canal. It is even probable that in the intestinal canal all these three foodstuffs may be equally perfectly utilized. This can be determined by careful metabolism experiments.

METABOLISM EXPERIMENTS.

The metabolism experiments were made a special subject of research by Dr. Donald D. Van Slyke, assisted by Messrs. W. M. Clark and C. B. Bennett. In Doctor Van Slyke's report, which follows, the rate of digestion and proportion of nutriment absorbed from cooked mussels and squid is compared with that of beef as a standard:

The work outlined was undertaken to determine the comparative rapidity and completeness with which various sea foods are digested, absorbed, and utilized in the animal organism and the effects of different modes of preparation and preservation upon the food value. The substances were compared with beef as a standard. The experimental animal was a fox terrier bitch of 12½ pounds weight. While more valuable results, from a practical standpoint, might be obtained from experiments on men, the latter could not tolerate for a long time the simple diet used, nor be subject to regular catheterization. The experiments, furthermore, were for comparison of the behavior of different protein foods under the same conditions, and it is probable that the foods would rank in the same order when tested in dogs or in men, although the absolute completeness and rapidity of utilization varies with different species and individuals.

PRINCIPLES OF METHODS.

The daily rations were so proportioned, from analyzed foods, that the dog obtained just the amount of protein required to maintain nitrogenous equilibrium. Fats and carbohydrates were also kept constant. The amount of protein digested was calculated from analysis of the food and feces, the nitrogen in the latter being ascribed to undigested protein. The rate at which the protein is digested, absorbed, and utilized is measured by the rate at which its nitrogen is excreted in the urine.

METHODS IN DETAIL.

The dog was brought to nitrogenous equilibrium by feeding on a constant diet of cracker dust, lard, lean beef, and salt. In the experiments with fish flesh, the beef was replaced by an amount of steamed fish meat. The fish was cleaned and the flesh steamed immediately after the fish was caught, in order to prevent autolytic or bacterical changes. The remainder of the ration was the same as in the beef diet, except the amount of lard was reduced in proportion to the fat content of the fish flesh, so that the fat content of the ration was kept the same as in the standard beef diet. All foods were analyzed for nitrogen and fat. On alternate days animal charcoal was mixed with the ration, in order that the feces from food consumed on successive days might be separated by their colors. In case the entire daily ration was not consumed, the remainder was fed through a tube.

The animal was catheterized immediately before feeding the day's ration, and at three-hour intervals thereafter for twelve hours, then again at the end of twenty-four hours after feeding, the bladder being washed out with 0.6 per cent sodium chloride solution at each catheterization. The nitrogen excreted in the urine during each interval was determined by Kjeldahl analysis. The urine obtained at each catheterization, combined with the cage washings in case the dog had urinated during the interval, was acidified with sulphuric acid, diluted to 500 or 1,000 volumes, and one-twentieth taken for analysis.

The feces containing the undigested portions of each day's rations were collected and the nitrogen content determined. The animal charcoal in the alternate day's feces made a separation possible, and the 5 grams of bone ash fed daily insured a well-formed, solid stool.

It was found that analysis of both food and feces for nitrogen and fat could be made accurately without preliminary drying in a dessicator. For fat analysis about 10 grams of the fresh material were ground up with anhydrous copper sulphate until the mixture became a dry, homogeneous powder. This was extracted for about ten hours with carbon tetrachloride, ground again, and reextracted for a few hours. Representative samples of flesh for nitrogen determination were obtained by grinding the flesh as fine as possible in a meat grinder, and taking 2 grams or more for the sample.

The daily diet consisted of 25 grams of fat, 50 grams of cracker dust, and sufficient beef or fish flesh to bring the total nitrogen of the diet up to the amounts indicated in the table. About three-fourths of the protein ration was contained in the flesh, the other one-fourth in the cracker dust. To the lard, cracker dust, and meat were added 5 grams of sodium chloride and 5 grams of bone ash.

After being fed squid for two days, the dog refused to consume completely the rations offered and was partially starved for several days. During the feeding of raw beef and squid she consumed and excreted 2.5 grams of nitrogen daily, as indicated in the two lower curves of the figure.

The results are briefly indicated by the following tables and figure:

TABLE 2.—SHOWING RESULTS OF METABOLISM EXPERIMENTS.

	Ration containing—			
	Raw beef.	Steamed squid.	Steamed beef.	Steamed mussel.
Nitrogen in ration (grams)	2.497	2.505	2.085	2.131
Nitrogen excreted in feces	.423	.291	.285	.444
Nitrogen digested	2.074	2.214	1.800	1.687
Per cent nitrogen digested	83.1	88.4	86.3	79.1

	Ration containing—			
	Raw beef.	Steamed squid.	Steamed beef.	Steamed mussel.
Nitrogen in ration (grams)	2.497	2.505	2.085	2.131
Nitrogen in urine+feces	2.489	2.485	1.910	2.117
Nitrogen retained	+0.01	+0.02	+0.18	+0.01

CONCLUSION.

The above results indicate (table 2) that the protein of the ration containing steamed mussel was digested somewhat less completely (79.1 per cent) than that of raw beef (83.1 per cent), while the squid gave higher results (88.4 per cent) than the raw beef. The steamed-beef figures (in table, not in the figure) are of doubtful accuracy, as a portion of the feces may have been lost, causing the high figures for digestibility (exceeding those of raw beef, which is improbable) and for nitrogen retention The digestibility figures indicate only the relative digestibility of the meats fed. A considerable

proportion of the undigested (fecal) nitrogen is due to the cracker-dust protein, which is known to be less digestible than ordinary flesh proteins. Consequently, in order to determine the digestibility of the meat proteins alone, a correction must be applied for the undigested vegetable protein. Unfortunately, we lacked time to determine this correction.

The urine curves must be considered in pairs, because the amount of nitrogen given in the raw-beef and steamed-squid diets was greater than that given later in the steamed-beef and mussels ration. The beef and squid (upper) curves show that the beef protein was metabolized more rapidly, as the beef curve rises more rapidly after feeding. The difference is not great, however, and the total amount of squid nitrogen metabolized and excreted in the urine in twenty-four hours is slightly the greater, coinciding with the fact that less squid nitrogen was found in the feces. Apparently squid proteins are digested slightly less rapidly than those of beef, but more completely

The steamed-beef and *Mytilus* curves show a similar relation, the beef being metabolized more rapidly in the hours immediately following feeding, the *Mytilus* curve overtaking and passing the beef curve later, however.

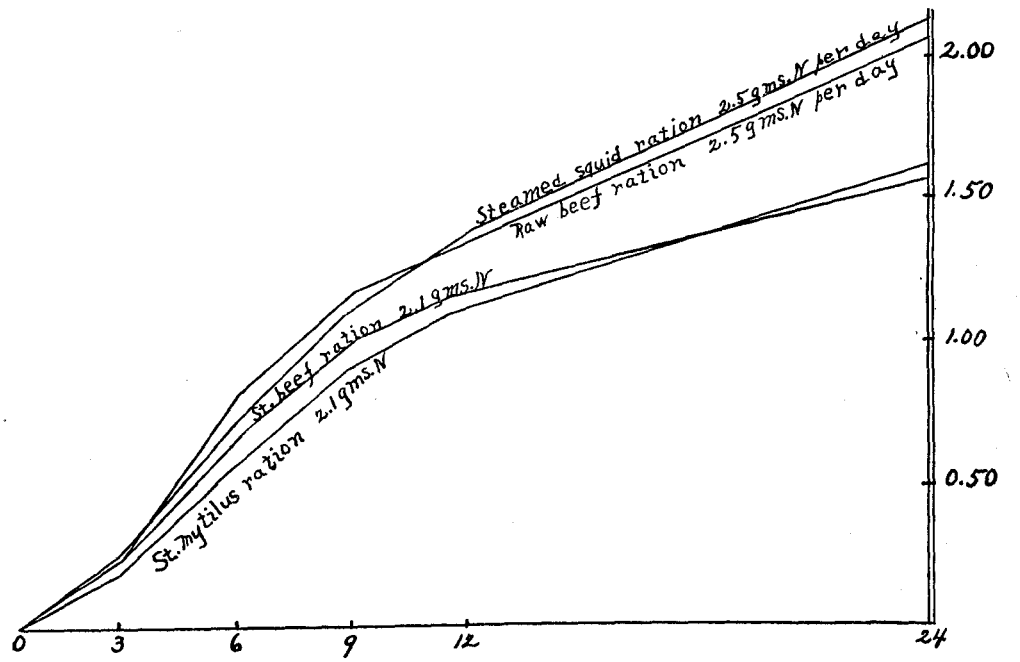

FIG. 1.—Curves showing results of metabolism experiments. Figures on base line indicate number of hours since feeding. Figures in vertical line at right show number of grams of nitrogen excreted in urine.

The raw-beef figures are taken from three successive days' results, the figures for the other meats from the results of two days' experiments each. The brief time (less than three weeks) available precluded longer tests, which would have been desirable, and limited the experiments to those above reported. They must be regarded as merely preliminaries to a thorough investigation of the problem.

It is clear, from the evidence just presented, that the mussel measures up well to the standard of digestibility. It agrees well with the consumer and the rate of digestion and proportion of nutrients supplied to the body approximate very nearly those of steamed beef.

COMPOSITION AND NUTRITIVE VALUE.

The function of food is to build up new tissues and repair them as they are worn out by use, to supply heat energy for keeping the body warm and muscular energy for doing work. The nutritive value or degree to which a food material is able to perform this function depends upon two factors, (1) the ratio of edible portion to refuse and (2) the relative amounts of nutrients contained in the edible portion. The first of these is determined by separating the flesh and liquor from the shells and byssus of the mussels, then weighing them separately and determining the percentage of each present. The second factor is determined by means of a chemical analysis of the edible portion.

The nutrients sought represent four classes of compounds: (1) Protein, which forms the nitrogenous basis of blood, muscle, connective tissue, etc.; (2) carbohydrates; (3) fats, which may be stored up as fat or consumed for fuel; and (4) mineral matters or ash, which are used chiefly in the formation of bone.

In studying the ratio of edible portion to refuse two sets of determinations were made. One was based on the examination of fresh or uncooked specimens and the other on mussels which had been cooked by steam. In the first case the mussels were weighed after being washed free from dirt. They were then quickly shucked and "bearded," the meats and liquor being preserved in separate dishes. What liquor adhered to the flesh was drained off and added to the other dish. The weights of the flesh and liquor were ascertained and recorded. The total weight of the mussels minus the combined weights of the flesh and liquor was considered the amount of refuse matter. This method, it will be observed, places the loss due to handling in the refuse column. The results obtained from the examination of five separate lots of mussels will be found in the following table:

TABLE 3.—SHOWING PROPORTION OF EDIBLE PARTS TO REFUSE IN THE SEA MUSSEL.

Determinations from fresh or uncooked material.

Date.	Number taken.	Total weight.	Average weight.	Flesh.	Liquids.	Total edible portion.	Refuse.	Flesh.	Liquids.	Total edible portion.	Refuse.
1908.		*Lbs. oz.*	*Ounces.*	*Lbs. oz.*	*Lbs. oz.*	*Lbs. oz.*	*Lbs. oz.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
July 10	50	5 4	1.68	1 8½	1 6½	2 14½	2 5½	28.87	26.78	55.65	44.35
July 13	100	9 13	1.57	2 13⅜	2 8	5 5⅜	4 7⅝	28.75	25.48	54.23	45.77
August 8	50	4 5½	1.39	1 1⅞	1 ½	2 1⅜	2 3⅛	25.35	23.74	49.09	50.91
August 26	20	2 3½	1.76	0 9⅜	0 10⅜	1 3⅞	0 15⅝	26.10	29.00	55.10	44.90
August 28	11	1 1⅜	1.68	0 5⅜	0 4⅜	0 9⅞	0 7⅜	30.80	25.00	55.80	44.20
Total	231	22 11⅜	1.57	6 5	5 13⅜	12 2⅜	10 8¾	27.79	25.75	53.54	46.46

In the second case the total weight, as above, was taken after washing the mussels free from dirt, but before removing the meats and liquor the shellfish were cooked by means of steam until the shells began to open. This treatment gives very different results from those obtained from the raw material, as may be seen in the following:

TABLE 4.—SHOWING PROPORTION OF EDIBLE PARTS TO REFUSE IN THE SEA MUSSEL.

Determinations from steamed material.

Date.	Number taken.	Total weight.	Average weight.	Flesh.	Liquids.	Total edible portion.	Refuse.	Flesh.	Liquids.	Total edible portion.	Refuse
1907.		*Lbs. oz.*	*Ounces.*	*Lbs. oz.*	*Lbs. oz.*	*Lbs. oz.*	*Lbs. oz.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
August 12	119	10 0	1.34	2 2½	1 8	3 10½	6 5½	21.56	15.00	36.56	63.44
Do	167	15 0	1.44	2 15	1 2	4 1	10 15	19.58	7.50	27.08	72.92
August 13	186	16 0	1.38	3 4	1 11	4 15	11 1	20.35	10.54	30.89	69.11
Do	192	16 0	1.33	3 3	1 14	5 1	10 15	19.92	11.71	31.63	68.37
August 14	204	17 0	1.33	3 8	2 2	5 10	11 6	20.58	12.50	33.08	66.92
August 15	213	18 0	1.35	3 13	2 6	6 3	11 14	21.18	13.19	34.37	65.63
August 26	180	16 0	1.42	3 1	1 12	4 13	11 3	19.14	10.97	30.11	69.89
August 27	330	25 0	1.21	5 9	2 10	8 3	16 13	22.25	10.50	32.75	67.25
August 28	88	9 0	1.63	1 9½	0 8	2 1½	6 14½	17.71	5.55	23.26	76.74
1908.											
July 9	91	9 1	1.60	1 13	0 10	2 7	6 10	20.00	6.89	26.89	73.11
July 12	218	23 3	1.70	4 1	1 14	5 15	17 4	17.52	8.09	25.61	74.39
July 15	106	12 0	1.81	2 6	0 15	3 5	8 11	19.79	7.81	27.60	72.40
July 16	356	36 0	1.61	6 9	2 12	9 5	26 11	20.34	7.63	27.97	72.03
July 30	356	31 8	1.44	5 7	2 10	8 1	23 7	17.26	8.33	25.59	74.41
August 8	287	32 5	1.80	4 12	1 15	6 11	25 10	14.70	5.99	20.69	79.31
August 10	212	20 3	1.52	2 15	0 15	3 14	16 5	14.55	4.64	19.19	80.81
August 11	180	18 0	1.60	2 5	0 12	3 1	14 15	12.84	4.16	17.00	83.00
August 14	744	74 12	1.60	15 12	9 3	24 15	49 13	21.15	12.29	33.44	66.56
Total	4,229	399 0	1.50	75 1	37 3	112 4	286 12	18.81	9.32	28.13	71.87

A comparison of the two tables reveals a wide difference in the ratios of edible parts to waste. In case of the raw material it is 53.54 per cent of meat and liquor to 46.46 per cent of refuse. With the cooked material it is 28.13 per cent to 71.87 per cent. This great dissimilarity of results is due to two facts. In the first place, cooking removes considerable water from the flesh and in the second place the opening of the shells of many of the mussels during the process of cooking causes considerable loss of the natural liquor. The loss of water and liquor is thus added to the refuse column and makes the difference between the useful and waste parts appear greater than it really is. These figures apparently indicate that much loss of food material results from cooking, but such is not the case. The loss in weight is due almost entirely to the extraction of water.

A comparison of the mussel with the oyster and long clam on the basis of the relative amounts of edible parts to refuse will help one to appreciate its real value as a food. The figures used for this purpose are taken from Atwater (1891) and incorporated in the following table:

TABLE 5.—SHOWING PERCENTAGE OF EDIBLE PARTS AND REFUSE IN THE MUSSEL, LONG CLAM, AND OYSTER.

Kinds of shellfish.	Number of specimens.	Edible portion.			Refuse (shells, etc.).
		Flesh.	Liquids.	Total.	
		Per cent.	*Per cent.*	*Per cent.*	*Per cent.*
Sea mussel	50	32.66	18.00	50.66	46.69
Long clam	441	34.77	21.78	56.55	41.77
Oyster	3,383	9.81	7.65	17.46	81.40

Measured by the above standard, the mussel contains about the same proportion of flesh and liquids as the long clam and about three times as much as the oyster. If

the flesh of each species contained the same amount of nutrients we might conclude that for equal weights of the shellfish the food value of the mussel is about equal to that of the long clam but three times that of the oyster. This obvious superiority over the oyster is due to the thin, light shell of the mussel, which stands in sharp contrast to the heavy, thick shell of the oyster. A consideration of the chemical composition of these forms, however, will show that the difference in food value between the mussel and oyster is even greater than is indicated by the above table.

The account which follows is taken from Doctor Alsberg's personal report to me. In view of the fact that the methods used in making the analyses differ in some important particulars from those employed by Atwater (1891), with whose results comparisons are made, it is necessary to describe them briefly.

In preparation of a sample a large quantity of the mussel meats was ground up in a meat chopper and the ground-up sample thoroughly mixed. Of this, a small sample of 50 grams was weighed out into a weighed glass dish. Enough sulphuric acid was added to make the reaction neutral. As the reaction of the juices of invertebrates is very alkaline, this is a most important matter. If it is neglected, much nitrogen is lost as ammonia. This precaution has apparently not been taken by Atwater or anyone else. Probably Atwater's figures for oysters are too low for this reason. Doctor Alsberg's high nitrogen values are probably in part due to this method. The glass dish containing the 50 grams of neutral material was then evaporated to dryness on the steam bath, with care that the reaction remained neutral. Atwater dried in a stream of hydrogen. There were no facilities for doing this in the present work, but it is thought that the results are unaffected, except to a slight extent for the fat determinations.

The material thus dried was very difficult to pulverize, partly because of the fat content, which made it greasy, and partly because invertebrates contain hygroscopic salts. Therefore the material was boiled out with 95 per cent alcohol until the latter was colorless. The alcoholic solution was made up to a known volume and analyzed by itself. The results were added to those obtained from the residue. The sum of the two gives the figures for the total. The residue from the alcohol was easily ground up and sampled in an agate mortar. The material for all the determinations was weighed out at the same time. In addition, about 1.50 grams were weighed in a weighing bottle and dried at 60° C. in vacuo over sulphuric acid in a Schmiedeberg drying apparatus. In this way the total quantity of water was determined and the determinations calculated accordingly. The water determinations are therefore more correct than those of Atwater.

The fat determinations were done by extracting with carbon tetrachloride (CCl_4) in a Soxhlet apparatus. It was not safe to use ether, as Atwater did, because of the danger of fire in a wooden building. As carbon tetrachloride is a better solvent than ether, the figures obtained are naturally a little higher than those of Atwater. Another reason why they are higher is that the material was not dried in hydrogen.

Nitrogen was determined by the Kjeldahl method, which had not been discovered in Atwater's time. He used the soda-lime method, which is probably as good.

Atwater made no determinations of carbohydrates. Inasmuch as the oyster contains much glycogen, an attempt was made to determine glycogen in the mussel. This

was done by Pflüger's method in its latest modification. One hundred grams of absolutely fresh material were used and the determination begun at once to prevent the hydrolysis by enzymes. The purified glycogen was determined in three ways: (1) It was filtered through a weighed Gooch crucible, dried, and weighed. It was then ashed and the crucible weighed again. The weight of the ash, which was always under 2 per cent, was then subtracted, and the resulting figures are those given in the table. (2) The glycogen was then hydrolyzed with dilute sulphuric acid and the sugar determined titrametrically with Fehling's solution. (3) The glycogen was hydrolyzed with dilute sulphuric acid and the resulting sugar determined in the polariscope.

The figures for flesh calculated on fresh substance do not quite total 100 per cent. This is probably not due to errors in methods or technique, but to errors of calculation. Thus the proteins are calculated arbitrarily. It is assumed that all nitrogen is present as protein, whereas as a matter of fact some is in the form of extractives and some in the form of fats (lipoids). It is assumed, further, that the proteins of mussels have the same nitrogen content as those of vertebrates. As they have not been investigated, this is an arbitrary assumption, and the factor 6.25 may be wrong. Moreover, as some of the nitrogen is in the fat (lipoids), this figures twice in the tables, once as protein and once as fat. The crude ash, too, does not quite correctly represent the inorganic substances of the mussel, because in the process of ashing some is volatilized, while new phosphoric acid and sulphuric acid are formed from the protein. All these, however, are errors inherent in all analyses of this nature.

The structure of the flesh of male and female mussels being very different (compare figs. 2 and 3, pl. XXIII), separate analyses were made of the two sexes. The distinction of the sexes was based on the color of the mantle, white flesh being called male and red flesh female. This method of separation is, however, not absolutely accurate. Microscopic examination revealed the fact that in about 2 per cent of the cases a red mussel might be a male and a white or cream-colored one a female. The results of the analyses are as follows:

TABLE 6.—SHOWING COMPOSITION OF MUSSELS CALCULATED FOR WATER-FREE SUBSTANCE.

[August 15, 1908.]

Ingredients.	White flesh (male).	Red flesh (female).	Average for white and red flesh.
In flesh:	*Per cent.*	*Per cent.*	*Per cent.*
Nitrogen	9.35	10.75	10.05
Protein (N×6.25)	58.44	68.18	63.31
Fat, CCl_4 Ext	8.51	12.01	10.26
Carbohydrate	13.61	9.41	11.51
Crude ash	6.74	6.03	6.38
In liquids:			
Nitrogen	.....	.....	3.62
Protein (N×6.25)	.....	.....	22.62
Fat, CCl_4 Ext	.....	.....	.28
Carbohydrate	.....	.....	Trace.
Crude ash	.....	.....	65.50
In total edible portion:			
Nitrogen	.....	.....	9.19
Protein (N×6.25)	.....	.....	57.43
Fat, CCl_4 Ext	.....	.....	8.93
Carbohydrate	.....	.....	9.97
Crude ash	.....	.....	14.27

TABLE 7.—SHOWING COMPOSITION OF MUSSELS CALCULATED FOR FRESH SUBSTANCE.

[August 15, 1908.]

Ingredients.	White flesh (male).	Red flesh (female).	Average for white and red flesh.
	Per cent.	*Per cent.*	*Per cent.*
In flesh:			
Water	76.62	76.18	76.40
Nitrogen	2.44	2.46	2.45
Protein (N×6.25)	15.25	15.38	15.31
Fat, CCl_4 Ext	1.98	3.10	2.54
Carbohydrate	3.19	2.24	2.71
Crude ash	1.58	1.44	1.51
In liquids:			
Water	.....	.....	95.64
Nitrogen	.....	.....	.16
Protein (N×6.25)	.....	.....	.99
Fat, CCl_4 Ext	.....	.....	.01
Carbohydrate	.....	.....	.....
Crude ash	.....	.....	2.86
In total edible portion:			
Water	.....	.....	83.27
Nitrogen	.....	.....	1.63
Protein (N×6.25)	.....	.....	10.18
Fat, CCl_4 Ext	.....	.....	1.64
Carbohydrate	.....	.....	1.74
Crude ash	.....	.....	1.99

The above figures indicate that, for a shellfish, the mussel contains a high percentage of each of the four classes of food materials and that the white-fleshed individuals (males) differ considerably in chemical composition from the red-fleshed ones (females), the latter containing a much higher percentage of protein and fat but less carbohydrate. This difference is accounted for by the fact that the whole body of the female, during the spring and summer, is distended with eggs which are rich in yolk material. It is during this season, therefore, that the mussels are at their best as a food.

A fair idea of the food value of the mussel may be obtained by comparing its fuel value with those of several standard food materials, e. g., oysters, long clams, and beef. Fuel value refers to the number of calories of heat equivalent to the energy which the body is supposed to obtain from 1 pound of a thoroughly digested food material. The fuel values of various food materials are calculated by using the factors of Rubner, which, in terms of the English system of weights, correspond to 1,860 calories of energy for every pound of protein or carbohydrate and 4,220 calories for each pound of fat.

TABLE 8.—SHOWING COMPARATIVE FUEL VALUES OF MUSSELS, OYSTERS, LONG CLAMS, AND LEAN BEEF.

Food materials.	Refuse.	Water.	Protein (N×6.25).	Fat.	Carbohydrate.	Ash.	Fuel value per pound.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Calories.*
Mussels, in shell	46.69	41.1	5.0	0.8	0.85	.....	140
Mussels, edible portion	.....	83.3	10.18	1.64	1.74	1.99	290
Oysters, in shell[a]	81.4	16.1	1.2	.2	.7	.4	45
Oysters, edible portion	.....	86.9	6.2	1.2	3.7	2.0	235
Long clams, in shell[a]	41.9	49.9	5.0	.6	1.1	1.5	140
Long clams, edible portion	.....	85.8	8.6	1.0	2.0	2.6	240
Beef, hind quarter as purchased[a]	16.6	55.3	16.7	11.2	.....	.8	785

[a] From calculations of Atwater and Bryant (1906).

A comparison of the fuel values of the mussel and oyster based on the total weight of waste and edible portions shows that the value of the mussel as a food is three times greater than that of the oyster. The ratio between the fuel values of the edible portions of these two shellfish is more nearly equal, but the mussel in this case is superior to the oyster by 65 calories per pound. The fuel values of the mussel and long clam are about the same. Compared with lean beef we might say that 5½ pounds of mussels in the shell, or 2¾ pounds of meats and liquor in their natural proportion, are equal in food value to 1 pound of beef.

As a food material, therefore, from the standpoint of chemical composition and nutritive value, the mussel is far superior to the oyster, is equal to the long clam, and has about one-third the value of lean beef.

MUSSELS A CHEAP FOOD.

Measured by the fourth standard, economy, we again find the mussel taking high rank among food materials. It is widely distributed, extremely abundant, and easily obtained. Mussels abound in the bays and estuaries of our Atlantic coast from North Carolina northward and on our Pacific coast from Alaska to San Francisco. They grow in great beds, often acres in extent, on the surface of mud or sand extending out from between tide marks to several fathoms of water. Plate XXIV, figure 1, is a view of an exposed mussel bed at Menemsha Pond, Marthas Vineyard, Mass. This bed is but two years old and represents hundreds of tons of valuable food. Mussels are also found growing in great abundance out in the deeper waters. On one occasion in Vineyard Sound, not far from Robinsons Hole, the steamer *Fish Hawk* dredged up a beam trawl full of them, a quantity approximating a ton or more. A resident of Pawtucket, R. I., writes that there are places in Narragansett Bay where a man could obtain 50 bushels a day for the whole season if he had a partner to receive and dispose of them. Under these conditions he considers 35 cents a bushel a reasonable price to ask. The total supply of New York City, which amounts to 75 barrels of mussels in the shell and 400 gallons of the pickled variety per day, is furnished chiefly from the bays bordering Long Island. The man who provides nearly this whole supply informed me that the quantity of mussels is far in excess of the demand.

As has already been shown, the mussel breeds at an almost inconceivable rate and grows very rapidly. Even if the demand should grow to exceed the supply from the natural beds it would be an easy matter to meet the increase by means of cultivation. The methods which may be utilized for this purpose are discussed in another chapter.

The question of real economic importance to the consumer of food is the ratio between the cost of a given food and the amount of nutriment it supplies. Milner (1903) groups food materials into three classes: (1) Cheap, those which furnish more than 1,900 calories energy for 10 cents at ordinary prices; (2) Medium, those which furnish 800 to 1,900 calories energy for 10 cents; and (3) Expensive, those furnishing less than 800 calories energy for 10 cents. A bushel of mussels weighs about 70 pounds.

At 35 cents a bushel the rate would be half a cent per pound, or 10 cents for 20 pounds. In table 8 we find the fuel value for each pound of mussels in the shell to equal 140 calories energy. $20 \times 140 = 2{,}800$ calories energy, the amount 10 cents would purchase at 35 cents per bushel. This, however, is calculated on the wholesale price. The retail cost would probably be double this amount. Consequently, our fuel value should be cut in half, making 1,400 calories energy the purchasing value of 10 cents at retail rates. Thus the calculation on wholesale prices places the mussel in the class of cheap foods. The calculation on retail prices puts it among the cheaper of the medium-priced foods, such as beef flank, neck and shank, milk, beans, and turnips.

To thousands of families who live near the coast, the mussels are to be had for the slight effort required to gather them, and yet up to the present time all this vast wealth of food has been ignored and wasted. This, too, where families in easy reach of a rich supply of the shellfish are facing poverty.

PRESERVATION METHODS.

At the present time there is great need for methods of preserving perishable foods in such a manner as not to injure their palatable flavor and nutritive qualities or greatly increase the price at which they may be sold to the consumer. Especially is this true for fishery products, which spoil very quickly after removal from the water. The decomposition which sets in so rapidly is caused by the presence of bacteria, which multiply with great rapidity, the rate of putrefaction progressing in direct proportion to their increase in number.

To preserve fishery products, then, it is necessary to keep them free from the action of bacteria, and this may be accomplished by eliminating one or more of the three conditions on which the life and growth of the organisms depend—namely, heat, moisture, and oxygen. Cold storage deprives the organisms of sufficient heat for growth, desiccation takes the needed moisture from them, and canning at high temperatures destroys the germs present and, furthermore, excludes the air required for growth. Antiseptics, such as salt, vinegar, and boracic acid, are employed to prevent the multiplication of bacteria. All of these methods are applicable to the mussel.

CANNING.

The sea mussel is of all the shellfish particularly adapted for canning. Unlike the oyster, it remains tender and retains its full flavor when subjected to the high temperatures necessary to prepare it in this way. The process which has been devised as most feasible is as follows:

The mussels when taken from the collecting boats are rapidly picked over by hand to eliminate any dead or unhealthy ones which may be present, as well as the coarse adhering débris. Then they are placed in a cleaning apparatus, such as is shown in figure 2. It consists of a rectangular box 2 by 2 by 3 feet, which revolves on its long axis. The ends of the box are of solid yellow pine and are firmly held in place by four pairs of braces 3 feet long, 2 inches wide, and ½ inch thick. Three sides of the box are

inclosed with ¾-inch mesh galvanized wire netting. The fourth side has a door 8 inches wide, running the length of the box. The door is clamped firmly in place by means of a lever, which is swung over it. The rest of the side is filled in with parallel strips of wood placed one-half inch apart. The projecting ends of the axis rest on the walls of a trough 1½ feet deep, in which there is running sea water. A crank at one end serves as a means to rotate the cage.

About 1 bushel of mussels is placed in this cleaning apparatus, which is set in rotation at the rate of 30 revolutions a minute for fifteen minutes. The treatment cleans off from the shells all clinging sea weeds, sand, and débris, besides breaking open the

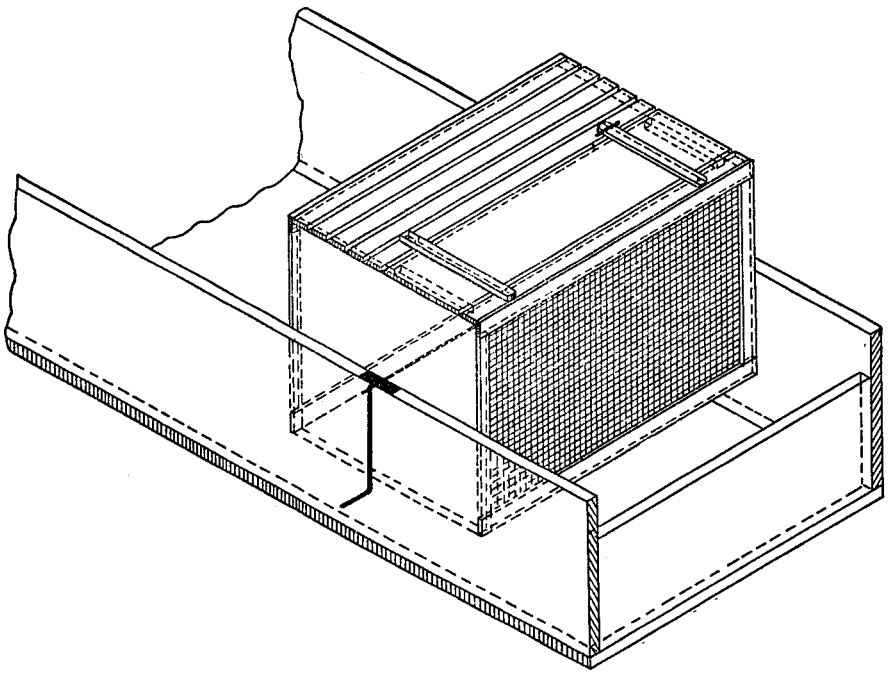

FIG. 2.—Apparatus for cleaning mussels preparatory to canning or other preservation process. (Drawn for the author by Prof. L. C. Harrington.)

shells of dead mussels and washing away the injurious substance contained within them. In the experimental work this method of cleaning mussels proved very effective. For cleaning on a commercial scale the device may easily be constructed on larger dimensions and operated by means of steam or water power.

After this treatment the mussels are removed and rinsed off with clean water. They are placed in a chest and subjected to live steam for from five to ten minutes, or until the shells begin to open. They are next emptied out into shallow pans to cool and the natural liquor which has escaped into the chest is preserved in a separate dish.

As soon as they are cool enough to be handled, the mussels are shucked and the horny "beard" removed, the meats and liquor being preserved in separate dishes.

While the liquor taken from the steam chest and that taken from the mussels during the process of shucking is filtering through a fine-meshed cloth, the mussel meats are packed in glass jars or bottles. The filtered liquor is brought to a boil and 2 ounces of salt are added for each gallon. The jars containing the meats are then filled with the boiling liquid and sealed. To insure complete sterilization, the sealed jars are placed in a steam chest and subjected to 5 pounds pressure for fifteen minutes. They are allowed to cool down slowly and when the temperature has fallen to about 100° F. they are removed and set aside for future use.

Persons wishing to can mussels for use in their own homes and who lack the facilities described in this process, may do so by modifying the method in the following way: After thoroughly cleaning the outsides of the mussels by means of a stiff-bristled brush, rinse them in clean water and place them in a large, closely-covered kettle with a little water covering the bottom—about one cup of water to each gallon of mussels. Place on the stove and bring to a boil, continuing the cooking for about fifteen minutes or until the top shells have opened. Pour out the liquor that has collected in the bottom of the kettle and preserve it in a separate dish from the mussels. Shuck the mussels, being careful to remove the byssus or horny tuft of threads growing out from the base of the foot. While the liquor is filtering through a fine-meshed cloth pack the meats in pint or half-pint glass jars of the ordinary household type. To each quart of the filtered liquor add one heaping teaspoonful of salt and bring it to a boil. Pour the boiling liquid over the mussel meats, filling the jars to the brim, and then quickly clamp or screw on the lids. The jars should next be placed in a large vessel, such as a wash boiler, containing boiling water, and left to boil for at least half an hour. At the end of this time the vessel with its contents should be removed to the back of the stove and allowed to cool. As soon as convenient the jars may be removed and the tops tested to see that they are sealed air tight. Treated in this manner, the mussels ought to keep for many months and preserve their natural flavor. When desired for use on the table they may be prepared according to almost any of the methods employed in preparing the fresh mussels for food.

PICKLING.

At the present time, in the United States, the pickling of mussels is the only form of preservation in use. As an article of trade they are known only to New York City and vicinity, one man supplying most of the demand with 400 gallons per day. They are eaten both by Americans and foreigners. The process for preservation by pickling involves the use of vinegar and spices in various proportions according to individual fancies. In my own experience I have found the following formula most satisfactory in results:

After thoroughly washing the mussel shells in the cleaning apparatus already described, the mussels are placed in a steam chest for about ten minutes, or until the shells have opened. They are then shucked, the liquor and meats being preserved in separate vessels. Care should be taken to see that the horny filament or "beard" is removed from the base of the foot. For each quart of natural liquor there is added 1 pint of vinegar, ½ ounce of allspice, ½ ounce of cinnamon, ¼ ounce of cloves, ¼ ounce of salt, and 1 small red pepper. The mixture is allowed to simmer upon the stove for fifteen minutes and is then poured over the meats. After standing about twenty-four hours the meats are removed from the spiced liquor and are neatly packed in bottles or fruit jars. The liquor after being filtered through a fine-meshed cloth, to remove the undissolved spices and sediment that is formed, is heated to boiling and poured over the meats until the jars are brimming full. The jars are sealed air tight and placed in a steam chest, where they are subjected to 5 pounds steam pressure for fifteen minutes.

After this treatment they will remain in a good state of preservation for about two years. If the pickled mussels are desired for immediate consumption, it is not necessary to seal them up in jars. They may be kept a week or more in open tubs without deteriorating. If kept much longer than this, they gradually turn dark and fall to pieces. A New York dealer told me that he was able to sell pickled mussels in the tub at 35 cents per gallon, but this gave him very little profit.

DRYING.

The preservation of mussels by means of desiccation is a problem to which I have devoted considerable attention. So far the efforts have been hardly successful enough to make mention of them in this report. A few words concerning the difficulties involved in the process, however, and some observations may be of value. The problem to solve in drying mussels for food is to regulate the process, so that the flavor of the meats is not impaired nor the appetizing odor lost.

The plan originally employed was to clean the mussels, steam and shuck them by the method already described, and transfer the meats to an artificial dryer, which consisted of a large chamber, 3 by 5 by 6 feet, tapering off at the top into a flue. Two drawers with galvanized wire bottoms extended into this chamber. A current of air was forced by means of a 24-inch fan over a hot radiator into the bottom of the chamber, from whence it passed upward through the meshed drawer bottoms and over the substance to be dried. The temperature of the air as it passed over the drying flesh was 50° C., or 122° F. Material subjected to this treatment dries very rapidly, even in the very humid atmosphere of Woods Hole, Mass. In from seven to twelve hours mussel flesh treated thus will lose 70 per cent of its weight. The accompanying table of 12 experiments indicates that after seven hours' drying most of the water which it is possible to extract by this method has been removed.

TABLE 9.—SHOWING LOSS OF WEIGHT IN MUSSELS DUE TO DRYING.

Date.	Weight of flesh.	Time in dryer.	Weight after drying.	Per cent of loss.	Per cent remaining.
1907.	*Ounces.*	*Hours.*	*Ounces.*		
August 28	10 5/8	13	3 1/4	69.4	30.60
August 29	25	15	5 1/8	79.5	20.50
August 30	60	7	17 1/2	70.83	29.17
1908.					
July 9	29	12	7 5/8	73.71	26.29
July 10	24 1/4	14	6 3/4	72.13	27.87
July 12	65	20	23 3/8	64.04	35.96
July 15	[a] 42	25	9 3/4	76.79	23.21
July 16	105	18	36 1/4	65.48	34.52
August 10	47	17	14 1/8	69.95	30.05
Do	37	19	11 3/4	68.24	31.76
August 26	24	20	6 3/4	71.84	28.16
August 28	30	22	7 1/2	75.00	25.00
Total	499 1/8	[b] 16 3/8	149 3/4	69.99	30.01

[a] Had been salted down 15 hours. [b] Average length of time in the dryer.

The product of this treatment is a brown brittle substance with an unappetizing look and odor. The appearance is greatly improved by passing the material through a sausage grinder, which breaks it up into a mass of brown granules. In this condition it looks well when put up in glass jars or fiber-ware packages. The only remaining objection to it is an offensive alkaline odor. In attempts to eliminate this disagreeable quality I have treated both the raw and cooked flesh with salt, with vinegar, and with hydrochloric acid in various proportions and for various periods of time preliminary to the drying, but without success. The purpose of using the acid, which was in very dilute solutions, was to neutralize the alkaline compounds as fast as they were formed. Dried mussels which had been soaked in a 0.2 per cent solution of hydrochloric acid for two hours before desiccation were rendered remarkably free from any bad odor. After being bottled up for a few weeks, however, they acquired the smell so characteristic of the dried material.

In spite of this offensive property the dried mussel can be used in preparing a very palatable soup or chowder. A better smelling variety will have to be produced, however, before there can be a possibility of attaching commercial importance to it.

The chief trouble with this process is that the drying is accomplished at a high temperature, where chemical changes within the food material are accelerated, causing the production in large quantities of undesirable substances. This difficulty is removed by means of an improved method of desiccation devised by Shackell (1909). Briefly, this consists in freezing the flesh, and drying it, while still in the frozen condition, in a vacuum. At this low temperature chemical changes practically cease and with the extraction of moisture a very stable substance is secured which will withstand all ordinary temperatures. Mussel flesh treated by this method shows remarkable properties. It retains the color and form of the fresh material; it is light and porous and can be easily crushed between the fingers. In air-tight bottles it may be preserved indefinitely.

A sample of mussel thus prepared, after having been kept a month, was placed in a small dish of water. The dried material rapidly absorbed moisture and at the same time the natural juices dissolved out into the water, giving it the characteristic opalescent color of fresh mussel liquor. The odor was that of perfectly fresh mussels, and when made into soup the aroma and flavor were those of cooked fresh material. This method of preservation is ideal but for one reason—the high cost forbids its use commercially. The inventor of the method is working to overcome this disadvantage.

COLD STORAGE.

The mussel is not well adapted to the method of preservation by means of cold storage. The writer wishes to make this statement with reserve, however, since his experiments in this respect have been very limited. Attempts to keep mussels fresh in an ice chest for more than twenty-four hours met with failure. They appeared to live no longer in the cold than in the open air. Decay did not seem to be retarded by the lower temperature of the ice box. This fact was a matter of complaint made by a New York dealer who wished to develop a market for mussels inland. I was informed that it would be possible to develop quite a trade in mussels if a method for preserving them in the fresh or living condition could be devised. At present I can only suggest a probable solution of the problem; that is to reduce them to a freezing temperature and ship them in a double walled carrier having a vacuum between the walls. The vacuum being a nonconductor of heat insures the continued low temperature of the mussels and does away with the surplus weight of ice usually employed in cold-storage transportation. The mussels preserved in this manner would have to be used almost immediately after removal from the carrier. Further mention of this method of preservation will be found in my conclusions and recommendations.

RECIPES FOR COOKING SEA MUSSELS.

CREAMED MUSSELS.

Thoroughly wash the mussels and place them in boiling water until the shells begin to open. Pour off the water quickly, take out the "beard" or byssus, and remove the meats from the shell, preserving the liquor in a separate dish. For each cupful of chopped meats make one cupful of cream sauce, which is prepared by melting in a saucepan one tablespoonful of butter and stirring with it one tablespoonful of flour; cook, being careful not to brown it; then stir in slowly one-half cupful of mussel liquor and one-half cupful of milk or cream and season with pepper and salt to taste. Continue to cook until it is thick and creamy, stirring all the time; add the mussels just before serving. Pour the mixture over small pieces of toast laid on the bottom of the dish.

FRIED MUSSELS.

After thoroughly cleaning the outsides of the mussels boil them until the shells begin to open. Take out the "beard" and remove the meats from the shell. Season with salt and pepper, then roll in cracker or bread crumbs, dip in egg beaten up in milk, and roll again in the crumbs; fry quickly in hot fat; drain on paper as fast as taken up. Serve hot, garnished with slices of lemon. Have them as free from grease as possible.

MUSSEL CAKES.

Clean and scald the mussels as directed above, beard, and remove the meats. To one pint of chopped mussel meats add two eggs, one-half cupful of milk, two teaspoonfuls of baking powder, and a pinch of salt. Stir in enough flour to make the mixture a little thicker than pancake batter and fry.

MUSSEL CHOWDER.

Clean and scald the mussels as directed above, take out the beard, and remove the meats, preserving the natural liquor in a separate dish. To a quart of the meats take a quarter pound of salt pork; cut it into small squares and fry to a brown in the bottom of the kettle. At the same time add three or four sliced onions and cook until the pork is well tried out; then add the mussel liquor, mixed with an equal quantity of water, and when it comes to a boil add six finely chopped or sliced potatoes and boil in a closely covered dish until the potatoes are done; then add the mussels with one quart of boiling milk, season with pepper and salt to taste, and serve.

MUSSEL CROQUETTES.

Clean and scald the mussels as directed above, beard, and remove the meats from the shell. Chop up one pint of meats, moisten with a thick cream sauce, add one teaspoonful of chopped parsley and bread or cracker crumbs sufficient to make the mixture firm enough to shape, season with salt and pepper. Let the mixture get cold, then shape into croquettes and fry in hot fat, in a frying basket if available; drain and serve on a hot napkin.

MUSSEL FRITTERS.

Two eggs, one tablespoonful of oil, one cupful of flour, one-half cupful of mussel liquor, pinch of pepper and salt, tablespoonful of lemon or vinegar, one cupful of chopped mussel. Have the mixture quite thick and drop from a tablespoon into hot fat and fry until an amber color.

MUSSEL PATTIES.

Cut one quart of scalded mussels into small pieces and stir into one cup of rich drawn butter based on milk, season to taste, cook five minutes, fill the patty cases, heat two minutes, and serve

MUSSEL SOUP.

Clean and scald the mussels as directed above, beard, and preserve the meats and liquor in separate dishes. To one pint of the liquor add an equal quantity of water; season with pepper, mace, and salt, and boil five minutes. Then put in the mussels, either whole or minced, and boil for five minutes with the vessel closely covered. Then add a pint of milk thickened with a little flour and butter or fine cracker crumbs. The addition of a little chopped celery and onion improves the flavor.

ROASTED MUSSELS.

Wash the shells thoroughly with a brush and cold water. Place them on a pan and bake in a hot oven until the shell opens. Remove the upper shell carefully, so as not to lose the liquor, and arrange them on plates. On each mussel place a piece of butter and a little pepper and salt. Do not roast too long.

STEAMED MUSSELS.

To a gallon of thoroughly washed mussels, add one cup of water and boil in a closely covered vessel for ten minutes or until the mussels on top are well opened. Then pour off the water and place the mussels in a large dish on the center of the table. Serve to each person some melted butter to which may be added vinegar and pepper to taste. The mussels may be removed from the shell, bearded, and, held by the foot, dipped into the butter and eaten.

The French people are noted for their excellent preparations of mussels for the table. The characteristic feature of nearly all their methods is to serve them on the half shell. From Audot's "La Cuisinĕre de la Ville et de la Campagne" I have taken the following recipes:

MUSSELS (ENTRÉES).

Choose mussels which are fresh, heavy, and of medium size, scrape and wash them through several waters. (In order that one may have no fear of them, it is necessary to cleanse them for five or six hours in water which is renewed several times. Not only are they able to reject the impurities within them, but they gain in quality. It is necessary to avoid using them from April to September, during which time they are apt to be unhealthy.)

A la marinière.—Having cleaned the mussels well, place them in a saucepan with some white wine, a glass to 4 quarts, or else a spoonful of vinegar, some slices of carrots, onion, and parsley chopped fine, thyme, clove of garlic, a little salt and pepper, 2 cloves, and a piece of butter the size of an egg. Place the saucepan on a good fire, keeping it covered from the first to make the shells open. Stew continuously until the shells have opened, when the mussels are done. From each remove one of the shells and take out the little crabs which are found in them, but which are not injurious in any way; they are found present principally during the months of the year which do not contain the letter "r." When the mussels have thus been opened, stew them a while (stirring or shaking to prevent them from sticking to the saucepan) and then turn them into a large, deep dish with a quart of their dressing strained clear. The remainder of this dressing makes a very agreeable onion soup.

A la poulette.—Take up quickly some of the prepared mussels (steamed and prepared on the half shell), as they are called, and make a sauce with a piece of butter, a pinch of flour, a little of their liquor, and the yolks of eggs, if these are desired. Turn this upon the mussels and serve.

A la béchamel.—Pour over the mussels a béchamel sauce in place of the sauce poulette.

BÉCHAMEL SAUCE.

Melt a piece of butter (about 1 ounce) and mix well with it a spoonful of flour and some salt and white pepper. Moisten it with a glass of milk, a little at a time with constant stirring; let it boil, being continually stirred. At the same time warm over that which you wish to serve with the sauce. To make it more elaborate, place in a saucepan some butter, slices of onion, a carrot, a bunch of parsley, some mushrooms, and place it on a fire. Moisten with some boiling milk, adding a little at a time with constant stirring; add some salt, white pepper, and nutmeg, and stir until it boils. Allow it to cook very slowly for three-quarters of an hour, then strain it through a colander. In a saucepan make a light-brown butter sauce with 3 spoonfuls of flour and turn into it the milk broth; let it boil three minutes.

Attention should be called to the fact that Audot's precaution to avoid eating mussels between the months of April and September does not apply to all parts of the world. On our northern Atlantic coast the months between April and September are the very months when the mussels are best for eating purposes, while during the fall and early winter they are unfit for use. The explanation of this is that the mussels of France breed in the early spring while these on our coast breed in the late summer and fall. After spawning the mussels become sickly and great numbers of them die. A more general way to state the precaution is: Avoid eating mussels from a given locality during the four months following their spawning. At the end of this period they again become fat and healthy.

CULTIVATION OF MUSSELS.

In Europe, where there is considerable demand for mussels as food and bait, it long ago became necessary to cultivate them artificially on a large scale. Two methods were devised. One may be termed the buchot system or French method, and the other the bed system or British method. The buchot system is apparently much the older and its history, although published in many French and English periodicals, is so interesting that it ought to be recorded again briefly at this point.

Strange as it may seem, this French system of culture was invented by an Irishman named Walton who was the sole survivor from a shipwreck in the Bay of Aiguillon near the village of Esnandes some seven or eight centuries ago. Authors disagree as to the exact date. Quatrefages (1854) states that it was in the year 1035, Bertram (1865) says 1135, while Coste (1883) puts it at the close of the year (1235). Walton was kindly received by the French fishermen, with whom he decided to make his home, although the prospects of making a good living were not very bright.

Up to the time of Walton's arrival the inhabitants of the coast had been unable to get much sustenance from the sea, but the newcomer was ingenious and was not long in originating a means for earning a livelihood from this source. His first step was to explore an immense lake of mud which was in the locality and there observing that large numbers of land and sea birds were in the habit of skimming over the water at twilight, he determined to catch them as an object of trade. For this purpose he devised a large net, the "alluret," which was between 330 and 430 yards long and 10 feet in height, fastened in a vertical position to stakes driven into the mud to a depth of 3 or 4 feet. Birds flying into its meshes were entangled and held securely. Shortly after beginning his bird-catching business, Walton discovered that young mussels in great numbers were collecting on the submerged stakes of his net. He also observed that mussels suspended for some distance over the mud grew to a larger size and were better flavored than those upon the mud. He experimented by putting down many more stakes, which in turn became covered with growing colonies of mussels. Continuing his experiments he was soon convinced that the young of native mussels could be easily gathered and profitably raised in artificial reservoirs.

The buchot system of mussel culture that was finally established by Walton is still followed and has proved a lasting reward and blessing to that locality, where at the present time buchots extend for miles along the coast and give support to several thousand inhabitants. In 1905 the village of Esnandes alone marketed 215,253 bushels of mussels, valued at $112,433. The total number of mussels cultivated on the French coast in 1905 is estimated at 425,492 bushels, valued at $222,439.

Walton's buchots, or wooden inclosures for the artificial rearing of mussels, were made V shaped, with the apex pointing out to the sea, the purpose of this arrangement being to protect the structure from the destroying action of the wind, waves, and ice. Each wing of the V consisted of a row of stakes placed about 2 feet apart and interlaced with a meshwork of flexible willow or chestnut branches some 12 to 18 feet long and

2 inches in diameter at the larger end. The stakes were trunks of trees, ½ to 1 foot in diameter and from 12 to 15 feet long, driven into the mud for about one-half their length. The meshwork covered the stakes to within 8 inches of the bottom, the space being left to allow free circulation of water, so as to prevent the deposition of mud at the base of the stakes. Each horizontal line of branches was tightly woven to the stakes to prevent slipping up or down. They were arranged about 20 or more inches apart, because, if brought together closer than that, they were apt to collect mud and cause deposits that would interfere with navigation and perhaps seriously injure the apparatus itself.

The length of wings to a buchot at any particular place depended, as now, on the nature of the bottom on which they were constructed. At present they occupy about one-fourth of the distance between the extreme limits reached by the water at high and low tides. In the Bay of Aiguillon they are now constructed about 250 yards long, and according to Herdman (1894), who has made an extensive study of this region, are no longer arranged in the V form, but in parallel rows about 30 yards apart at right angles to the shore. The buchots are practically made up of two divisions, one for collecting spat and the other for the growth and fattening of the mussels.

Five series of buchots may be included in these two divisions: (1) Buchots d'aval, (2) buchots batisse, (3) buchots du bas, (4) buchots batards, and (5) buchots d'amont.

The buchots d'aval are out in the deep water, sometimes 3 miles from high-water mark, and are exposed only at the lowest tides. They are composed merely of solitary stakes placed about 1 foot apart. They serve to catch the spat and constitute a most favorable place for the early growth of the mussels, since it is necessary for the young to be protected from long exposure to the sunlight or extreme cold. The spat collects on these stakes during February and March. By July the young mussels have attained the size of a haricot bean.

At this time the seed mussels are scraped off the piles by means of hooks fastened in a handle, are collected in baskets, and transferred to the next zone of weirs, the buchots batisse, toward shore and ordinarily uncovered after high tides. The parcels of young mussels are fastened by means of old netting to the branches, where, before the netting decays away, they become firmly attached by their byssal threads. When the mussels have grown so large as to be crowded on the wickerwork, they are thinned out by removing the larger ones to the next higher buchots, and so on from one section to the other, each time transferring the mussels nearer the shore. The mussels are attached by the same operation already described, but are not wrapped so carefully since their size is such as to enable them to be more securely fastened without help of the netting. The work of transferring from one buchot to another goes on day and night whenever low tide permits it.

After about one year's treatment under these conditions the mussels attain marketable size, which is between 1¾ and 2 inches in length. Before being offered for sale, those that have reached the desired size are transplanted to the highest row of buchots, the buchots d'amont. In this location, although left dry twice each day, they thrive well and can be easily handled when desired for market. The mussels on these upper rows become inured to exposure and consequently keep longer and fresher than those from

the lower rows. The poorest of cultivated mussels are considered superior to the best mussels grown under natural conditions.

To traverse the soft mud from one buchot to the other Walton devised the "acon," a characteristic mudboat still used by the bucholeurs. Herdman (1894) describes it as follows:

> The "acon" is composed of a plank forming the bottom and bent up in front to make a flat prow. The sides and stern are each made of one piece of wood, sometimes the sides are of two planks each. The size is 9 or 10 feet in length, from 2 feet to 2 feet 6 inches wide, and about 1 foot 6 inches deep. There is a shelf at the stern, a narrow thwart close to the bow, and a small wooden stool in the middle of the floor; these with a wooden paddle and a short pole complete the equipment. The boatman in using the "acon" faces the bow, grasps the sides about the middle firmly with both hands, rests his left knee on the floor of the boat, and putting his right leg (encased in a long sea boot) over the side, he plunges it into the mud and pushes it onward. He is able to propel it at a great rate over the soft mud, and when he gets to a channel of water where the "acon" floats he works with paddle or pole until he again reaches mud and is able to use his foot.

The British method of mussel culture, briefly, is to collect young mussels from salt water and transfer them to artificial beds in favorable localities. These are generally situated in estuaries where the water is brackish and where they are not exposed at low tide, both of which conditions are supposed by many to favor growth and fattening. Others believe that the presence of fresh water is injurious to the young shellfish and of no advantage to the full-grown individuals. To support their views they point to the large beds of healthy, uniform-sized individuals in regions far removed from the influence of fresh water. Harding (1883) believes that the spat will not mature in anything but pure sea water, but that for fattening full-grown mussels brackish water of the density 1.014 is most suitable. It has been estimated that the average yearly yield of an acre of such mussel beds is 108 tons, worth at least $262.

Careful cultivators observe several rules in planting mussels. They may be planted on almost any natural bottom, but rich estuarine flats where there is plenty of sand and gravel covered with mud rich in diatoms, infusoria, and spores of algæ is considered the ideal situation. They are placed in positions where they are not exposed to dangers from floods, gales, shifting sands, or frost. The beds are so placed that they will not be uncovered long at low tide nor where silt is likely to deposit upon them. Should this evil be discovered the bed is immediately transplanted to a better situation. In planting the beds care is taken not to place the individuals so close together that one will come to lie on another and thus cause a too crowded condition.

For collecting the mussels a rake or dredge is used, the former instrument being considered better than the latter for the reason that it does not crush the shells nor cause sand to shift over the bed. In size it has a breadth of about 18 inches, with the teeth 1 inch apart. It is fixed to a pole 20 to 25 feet long and has a wire net bag behind it for holding the catch. The large and small mussels are separated by means of a riddle, which is an instrument having a 1-inch iron mesh. The bunches of various size mussels are first separated by hand and then sifted, or riddled. The large and small mussels thus divided are then placed in separate beds or the large ones utilized for bait.

Other methods of myticulture are followed in certain localities. Goode (1887), describing some of the European methods, says:

> In the North Sea these [spat collectors] consist of large numbers of trees, from which the smaller branches have been cut, and which are planted in the bottom of the sea at such a distance from the shore that their upper portion is partially laid bare at low water. After four or five years they are raised, stripped, and replaced by others. In the Bay of Kiel, Germany, alone about 1,000 of these trees are annually planted and about 1,000 tons of mussels are brought on the market. Bad seasons occur, however, both with respect to quality and quantity, owing to various causes. In the Adriatic the mussels are-raised on ropes extended between poles rammed into the ground. The ropes are raised and stripped once in eighteen months.

The question now arises, Which is the better method for artificially propagating mussels on our coast? This depends on two factors; (1) the quality of mussels produced, and (2) the actual expense of propagation as compared with the financial return. Though I unfortunately can not answer this question now, I can throw a little light on it from the experience of others. In France, where labor is cheap, the buchot system is most profitable, while in England, where the cost of labor is much higher and where favorable localities for buchot culture are few, the bed system has to be employed. That the buchot method of culture is not practicable for the Scottish coast is very evident from the extensive report of Fullarton (1891), whose conclusion I quote:

> The buchot experiment, therefore, does not promise to yield in Scotland the same good results as in France. This is due to the character of the mud along our shore, to the climatal conditions of our Scottish waters, and the influence of these on animal life. But the financial aspect of the question, as shown above, is absolutely fatal to the system. I can not conceive what modifications of the buchot system would be likely to yield results which would benefit the fishermen of Scotland, nor mitigate in any important degree the mussel famine; while the bed system only requires to be developed in suitable localities in order that fishermen may obtain an ample supply of bait at a cheap rate and on sound financial principles.

Calderwood (1895) states that the buchot system of culture has been tried on a small scale at five different places in Scotland, and in every case was a failure. At Little Ferry the mussels were washed from the structures by gales; at Tain one buchot was covered with shifting sand, while another erected in an unfortunate position yielded little return. At Inverness the cost of handling the mussels was found prohibitive and at Montrose the system was found unsatisfactory because the mussels fell from the laths, which were used instead of branches. Where the cost of building material and labor are high, the buchot system will be found unprofitable.

Herdman (1894) believes that mussels grown on buchots are no better than those grown on beds, and thinks the buchot system is necessary only in localities where the mud is soft and so constantly depositing as to prohibit a bed of mussels from being established. Lebour (1907), describing the mussel beds of Northumberland, believes that the bed system is the only suitable method of cultivation on the coast and that the buchot system is not a practical one to apply even at Budle Bay and Holy Island, which regions are best adapted for their use.

In view of the facts just stated, and especially in consideration of the high cost of building material and of labor in the United States, the prospects are very poor for

successfully cultivating mussels by the buchot method on our shores. No serious objections having yet been found to the bed system, we are left to utilize that method with better hopes of success, unless in the meantime a better method is devised.

POISONOUS MUSSELS.

Mussels, like oysters, clams, and other shellfish, are subject to contamination from parasites, bacteria, and the ptomaines generated by these, which render them a dangerous food unless selected with proper care. Cases of serious illness from eating poisonous mussels are known and a number of persons have died from the effects. The same is true of oysters and clams, and inasmuch as the symptoms in all the cases are similar, there is nothing here to indicate that the mussels are not just as safe a food as the other shellfish when gathered with the same precautions. If they are collected from pure water and eaten in a fresh condition, they are a wholesome food. It sometimes happens, however, that the individual is peculiarly susceptible to poisoning from shellfish, and such persons I would advise to abstain from eating them.

The most common cases of poisoning from mussels and other shellfish are due to ptomaines, which are poisonous substances resulting from the action of micro-organisms upon the animal tissues. Their formation usually, although not always, accompanies putrefaction and they are said to be most abundant in its early stages. It is therefore safest to prepare for the table only shellfish that are in a healthy, living condition. Dead mussels should never be purchased. Good specimens are free from any stale odor and do not remain with the shells open after being slightly irritated. They defy all efforts to open their shells until the muscle which holds them shut is cut.

Dangerous intestinal troubles, followed by eruptions on the skin, have been known to result from eating apparently fresh mussels. Various explanations have been offered to account for these effects. Goode (1887) states that the Alaskan Indians, recognizing this fact, eliminated it by removing the byssus or beard whenever it had a greenish color, which was a sign that the animal had been feeding upon poisonous material. Better evidence, however, shows that these evil effects come rather from mussels which grow in impure waters, and that the injurious qualities lie in the liver rather than the byssus.

In the year 1885, at Wilhelmshaven, Germany, a large number of people were taken seriously ill after eating the sea mussel, *Mytilus edulis*, gathered from the harbor of that place. Several died from the effects. The symptoms of the poisoning were of three kinds, (1) a swelling in the head and abdomen, with the appearance of red spots on the body; (2) diarrhea, cramps, and prostration; and (3) paralysis.

A careful study of the conditions revealed that the water from which the mussels were taken was stagnant because of the inclosing breakwater, which cut off the effects of the tides. Although no sewage emptied into the harbor and ships were forbidden from dumping refuse into the water, the stagnated water was so impure that its effect upon animal life was highly injurious. Fishes that found their way in through the sluice gates soon became so sluggish that they could easily be caught by hand. Eels were

observed to lose almost all their vitality during the summer. Mussels from these waters, when cooked and fed to rabbits, acted as a most virulent poison, killing them in from two to ten minutes. If the mussels were transferred to places where currents of pure water could flow over them they lost all their poisonous properties; and, on the other hand, if harmless mussels were transferred from outside waters to the harbor they acquired poisonous qualities in less than two weeks.

Virchow (1886) and Wolff (1886) affirm that the poison was not the result of any decomposition and that the mussels had no external signs of disease. Wolff's experiments indicate that the liver is the sole source of the poison. Inoculations from that organ into rabbits and guinea pigs were fatal in every case in from two to twenty minutes, while inoculations from other parts were without effect. He believes that the poison originated in the liver and was not due to the absorption of copper salts, as popularly believed.

Another record of a serious case of poisoning from the eating of mussels by a party of Alaskan Indians is briefly mentioned by Dall (1870) and Petroff (1884). In response to a request for further details of the incident Doctor Dall wrote me the following story, which is amplified somewhat from notes gleaned from the references just cited: The Sitkan natives, being able to get better prices from the Hudson Bay Company, refused to trade with Baranoff, the Russian director of Alaska. Baranoff therefore resorted to importing, on a sailing vessel from Unalaska and Kodiak, a large number of Aleut hunters with their skin canoes, to take sea otter in the islands of the Sitkan Archipelago. In the year 1799 a party of about 200 camped on the shores of the strait separating Baranoff from Chichagof Island, where the tides are great and at low water expose great numbers of mussels. Being accustomed to eat them at home, the Aleuts gathered a quantity of mussels and feasted upon them. In a few hours they were taken violently ill, and 150 died within a day or two. This incident gave rise to the name Peril (in Russian, Pogibshi) Strait, which name it bears to this day. Mussel poisoning in this region is known to have occurred on other occasions and is supposed to be due to the ptomaines developed in the liquor of the mussels exposed to the sun. Doctor Dall was informed by the Aleuts that specimens not actually out of water were always safe.

In Audot's "La Cuisinĕre de la Ville et de la Campagne," page 677, a paragraph is devoted to the symptoms and treatment of mussel poisoning. A free translation of it is as follows:

> The true cause of the poisoning produced by mussels is not yet known, but it is a mistake to attribute it to the presence of the small crabs which are found in their shells. The opinion more generally accepted to-day is that the mussels, by attaching themselves to the bottoms of ships sheathed with copper, absorb a certain quantity of verdigris, which produces the poison causing indigestion. Whether this is so or not, the use of these mollusks sometimes leads to symptoms of very serious poisoning, of which the more common are: A sharp pain in the region of the stomach, violent cramps, severe contractions of the chest, an alternating quick and slow pulse, a redness and swelling of the face, an eruption of little red spots upon the skin, cold sweats, and oftentimes convulsive movements and delirium.
>
> When these symptoms manifest themselves it is necessary to combat them promptly by employing an emetic (2 grains of emetic in a glass of tepid water taken several times at six-minute intervals), and

when a sufficiently long time has elapsed since the ingestion of the mussels, follow the emetic with a purgative such as 60 grams of caster oil in a cup of light bouillon. If the symptoms continue in spite of these means, give the patient some mucilaginous drink and call a doctor.

The foregoing account would probably frighten the average person from ever attempting to use mussels as an article of food. Careful inspection, however, will reveal the fact that the mussels which have caused serious illness came either from impure waters or had been exposed to the heat of the sun so long that ptomaines had time to form in the liquor within their shells. Mussels taken from pure water which has free circulation have never been known to produce injurious effects when eaten. A New York dealer who has been selling mussels for years has never known of a case of poisoning from them. Nevertheless, too much emphasis can not be given to the fact that care must be exercised in choosing proper localities for the cultivation and collection of mussels for market. They must be sold to the consumer in a perfectly fresh condition or serious results will be likely to follow.

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS.

1. The sea mussel, *Mytilus edulis* Linnæus, is not utilized as a food to any extent in the United States outside of the vicinity of New York City.

2. As a food material it is superior to many articles which are commonly eaten. Scores of persons have pronounced it to be equal in flavor, or even superior, to the oyster; it is easily digested, has high nutritive value, and is exceedingly abundant and general in its range. Especially for persons living on the coast it is an excellent cheap food.

3. Along most of our eastern coast the mussel is in season for food purposes when the oyster is out of season.

4. The mussel is well adapted to preservation. When canned or pickled it will retain its natural flavor for months.

5. The mussel breeds at a prolific rate, it develops rapidly, requires less special conditions for growth than the oyster, and may therefore be easily cultivated.

6. The only difficulty in the marketing of mussels for food purposes is that they spoil quickly after being removed from the water. It is necessary to use them within twenty-four hours after they are collected or ptomaine poisoning may result. To insure one's self against illness from eating them, the mussels must be taken from water that is pure and subject to the constant circulation of tidal currents.

7. Other important ways for utilizing mussels are as bait for the fisheries and as fertilizer for soil on which onions and carrots are to be raised.

In view of these facts it is clear that the mussel beds of our eastern and western coasts constitute a valuable food resource of the nation which so far has not been developed. The natural beds alone are capable of supplying wholesome food to thousands of persons at the expense of a little trouble to collect the mussels and to hundreds of thousands more people, through the markets, at a moderate price. It is possible to develop an industry in the marketing of mussels which may surpass even that of the oyster and at the same time have no injurious effect upon the oyster trade. The success

with which mussels may be canned and pickled promises a good future for such a branch of the business.

The author recommends (1) that the facts set forth in this paper be made known to the packers of marine food products and widely advertised among the fishing population of our northern Atlantic and Pacific coasts; (2) that investigations be instituted to determine a method for preserving mussels in a fresh living condition long enough to permit their being readily shipped and sold at the inland markets, and the further investigations on methods for preserving mussels by canning, pickling, etc., which will make it possible to transport to long distances without being broken or otherwise injured should be continued; and (3) that a detailed study of the life history of the mussel be made as of the oyster. The solution of these problems, it is believed, will help to develop a new and profitable branch of fisheries industry.

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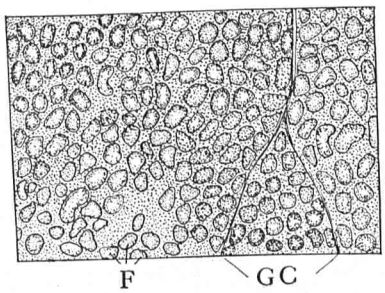

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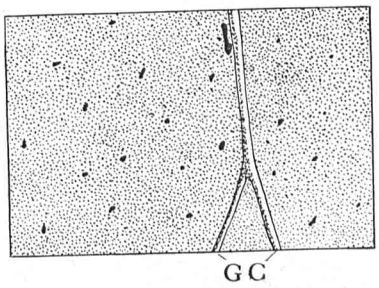

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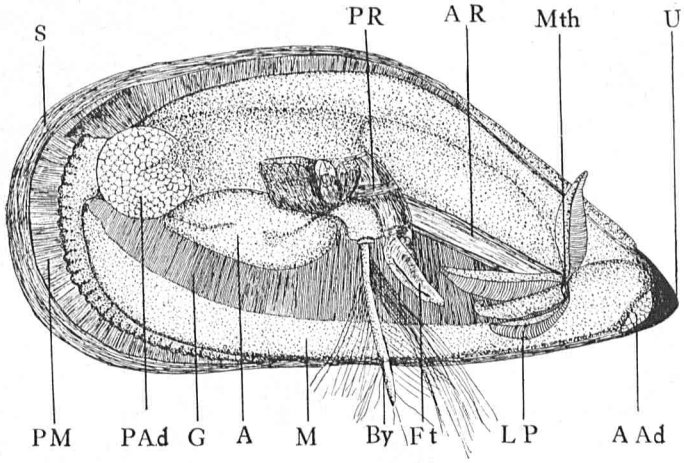

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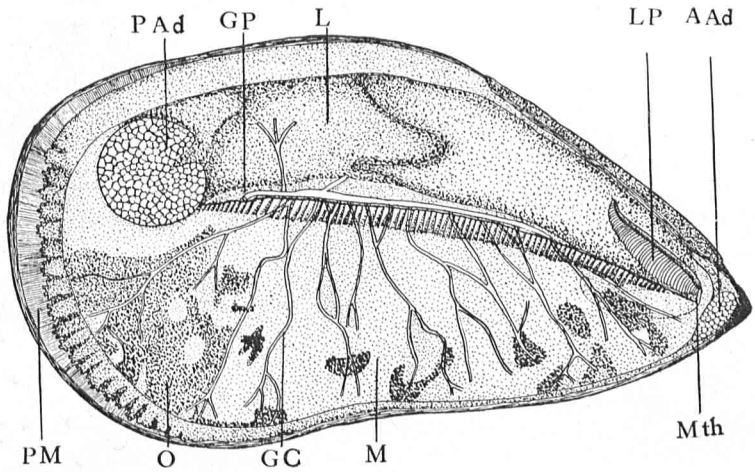
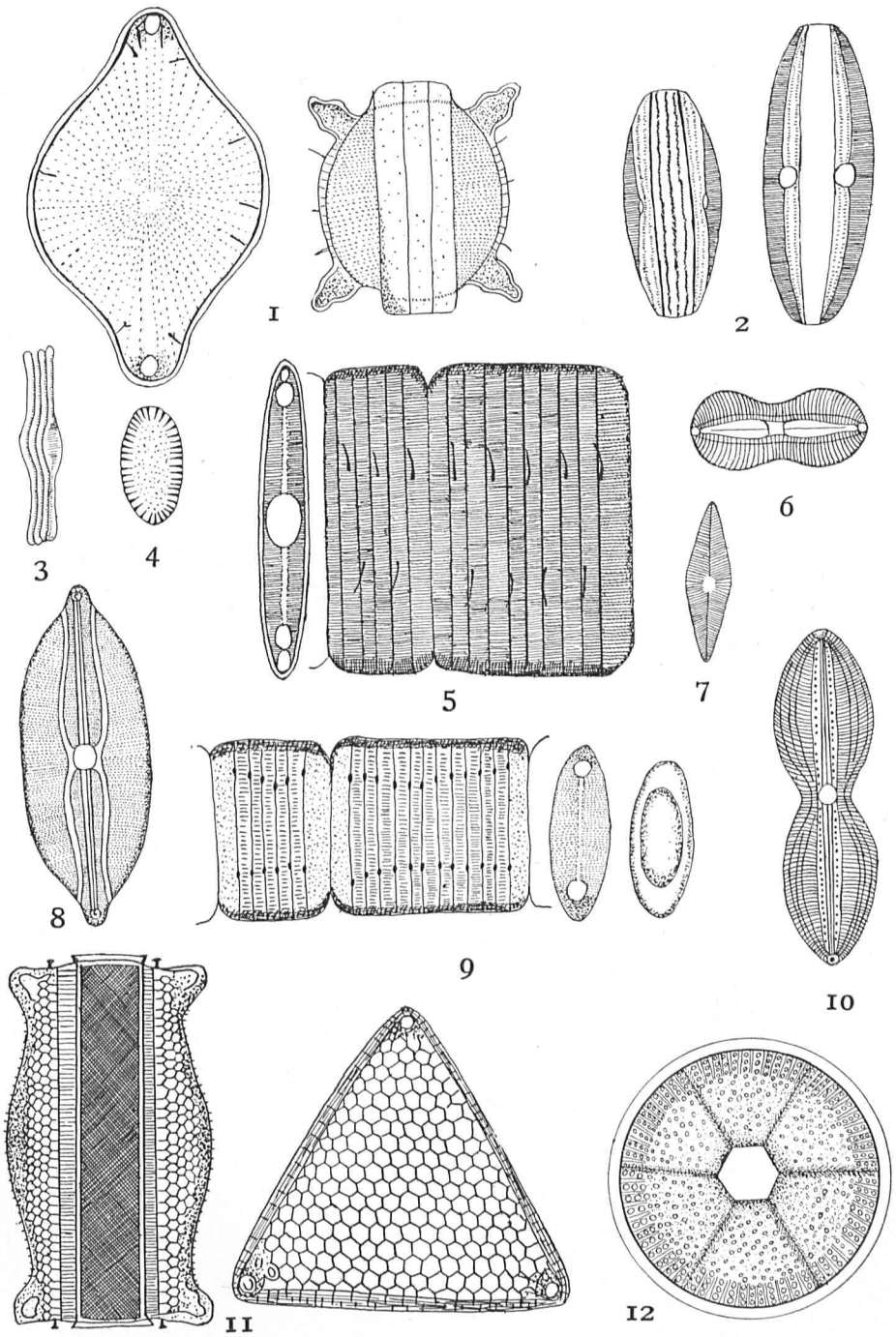


4

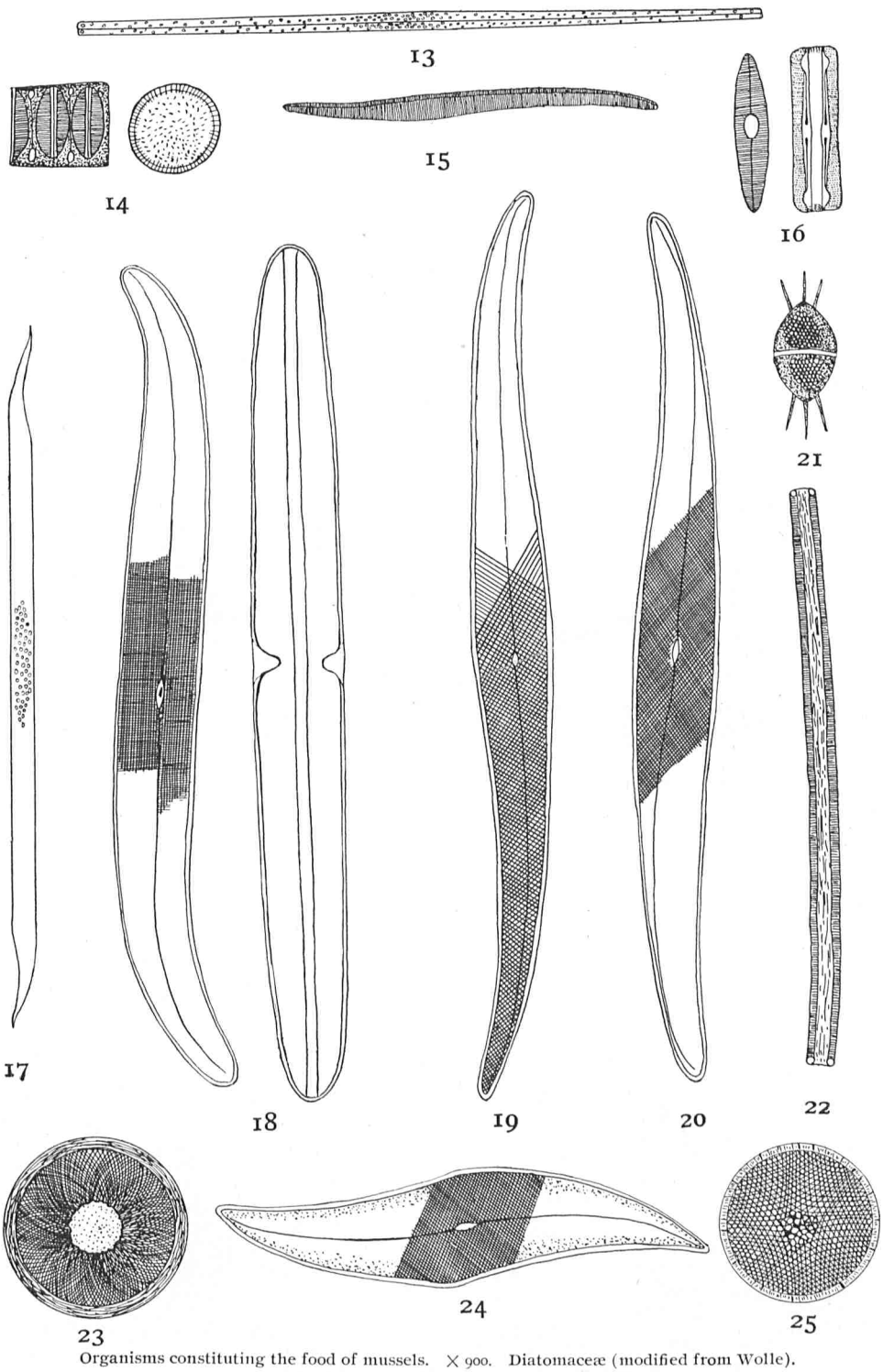
1.—Interior surface view of the mantle of a male mussel. × 10.
2.—Interior surface view of the mantle of a female mussel. × 10.
3.—Lateral view of a mussel with the shell and mantle of one side removed. Slightly enlarged.
4.—Lateral view of a female mussel with the shell and mantle of one side and the foot, gills, and abdomen removed to show the main canals of the genital system. Slightly enlarged.

Abbreviations: A, abdomen; AAd, anterior adductor muscle; AR, anterior retractor muscle; By, byssus; F, follicle containing male genital products; Ft, foot; G, gills; GC, genital canals; GP, genital papilla; L, liver or digestive gland; LP, labial palps; M, mantle; Mth, mouth; O, ova remaining in the mantle after spawning (4 cc); PAd, posterior adductor muscle; PM, pallial muscles; PR, posterior retractor muscles; S, shell; U, umbo.



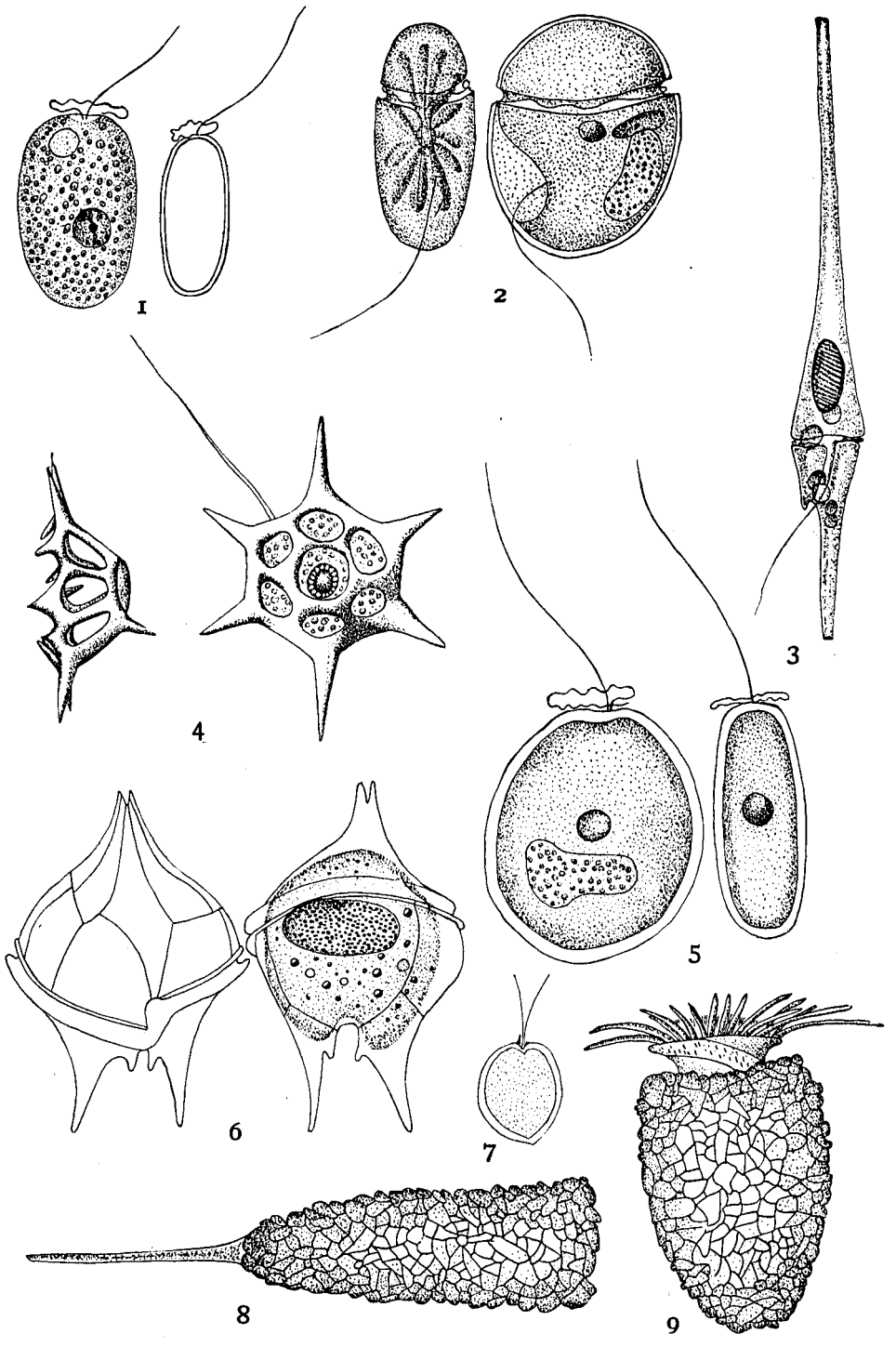
Organisms constituting the food of mussels. × 1,000. Diatomaceæ (modified from Wolle).

1. Biddulphia rhombus (Ehrenberg) W. Smith.
2. Amphora proteus Gregory.
3. Tabellaria fenestrata Kützing.
4. Surirella ovalis var. ovata Brebisson.
5. Rhabdonema adriaticum Kützing.
6. Navicula didyma Ehrenberg.
7. Navicula lanceolata Kützing.
8. Navicula lyra Ehrenberg.
9. Rhabdonema arcuatum Kützing.
10. Navicula splendida var. puella Ad. Schmitz.
11. Biddulphia favus (Ehrenberg) H. V. H.
12. Actinoptychus undulatus Ehrenberg.



Organisms constituting the food of mussels. × 900. Diatomaceæ (modified from Wolle).

13. Nitzschia sigma var. sigmatella Grunow. × 114.
14. Melosira sculpta Kützing.
15. Nitzschia sigma Grunow.
16. Grammatophora marina Kützing.
17. Rhizoselenia setigera Brighter. × 38.
18. Pleurosigma balticum W. Smith.
19. Pleurosigma elongatum W. Smith.
20. Pleurosigma decorum W. Smith.
21. Stephanopyxis appendiculata Ehrenberg.
22. Synedra gallionii Ehrenberg.
23. Hyalodiscus subtilis Bailey.
24. Pleurosigma angulatum W. Smith.
25. Coscinodiscus excentricus Ehrenberg.



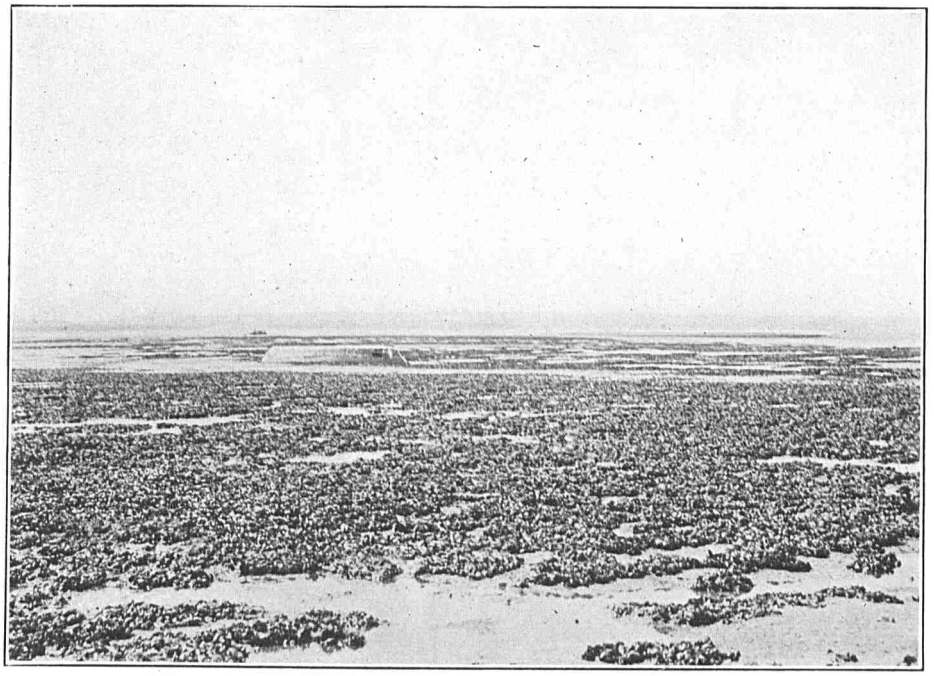
Organisms constituting the food of mussels. Protozoa. (All figures except 7 after Calkins.)

1. Exuviæella marina Cienkowsky. × 780.
2. Glenodinium compressa Calkins. × 822.
3. Ceratium fusus Ehrenberg. × 315.
4. Distephanus speculum Stohr. × 960.
5. Exuviæella lima Ehrenberg. × 780.
6. Peridinium divergens Ehrenberg. × 636.
7. Prorocentrum micans Ehrenberg. × 375.
8. Tintinnopsis davidoffi Daday. × 354.
9. Tintinnopsis beroidea Stein. × 900.

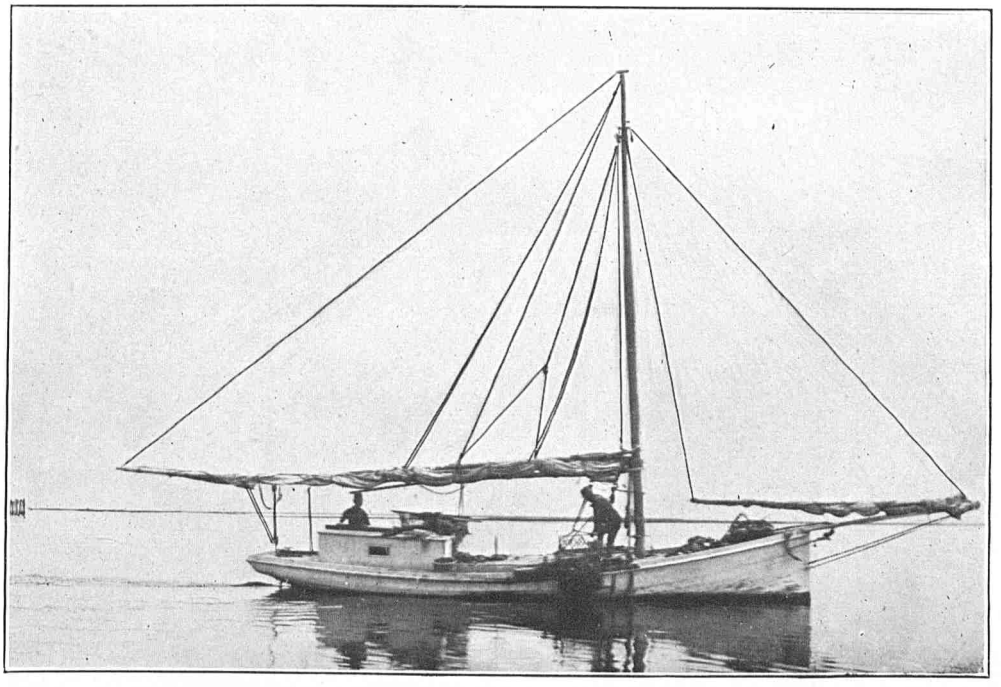
2

4

1. Cross section of the mantle of a female sea-mussel, March 3, 1908; fixed in Flemming's fluid and stained with Mayer's hæmalum. × 150.
2. Cross section of the mantle of a female sea-mussel, August 20, 1907; fixed in sublimate-acetic fluid and stained with Heidenhain's iron hæmatoxylin. × 100.
3. Cross section of the mantle of a male sea-mussel, June 27, 1908; fixed in Flemming's fluid and stained with Mayer's hæmalum. × 105.
4. Cross section of the mantle of a spent female sea-mussel, August 16, 1908; fixed in Flemming's fluid and stained with Mayer's hæmalum. × 105.

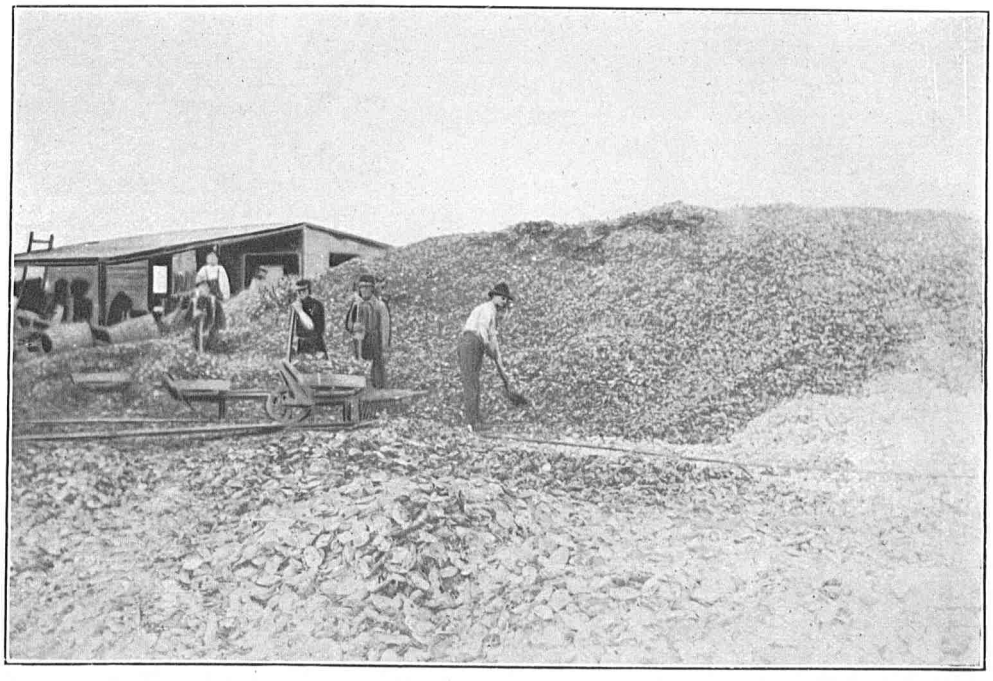


1.—A mussel bed at Menemsha Pond, Marthas Vineyard, Massachusetts, exposed at low tide. (Photographed by Dr. R. W. Miner.)



2.—Dredging for mussels. This vessel operates on the ocean and bays from Princes Bay to Fire Island, and gathers from 200 to 250 bushels a day. (Photograph by courtesy of Mr. George A. Carman.)

1.—A heap of mussel shells, the result of a few days' work. (Photograph by courtesy of Mr. George A. Carman.)



2.—A heap of shells from mussels which have been pickled for the New York market. The shells are used as cultch for seed oysters. (Photograph by courtesy of Mr. George A. Carman.)

THE MIGRATION OF SALMON IN THE COLUMBIA RIVER

By Charles W. Greene, Ph. D.

Professor of Physiology and Pharmacology, University of Missouri

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THE MIGRATION OF SALMON IN THE COLUMBIA RIVER.

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ESTABLISHED FACTS AND THE UNSOLVED PROBLEMS.

The life history of the anadromous fishes is one of the most interesting subjects in biology. The detail of facts surrounding the migration of the young from the fresh water to the sea and the migration of the adults to fresh water for spawning purposes are indeed little enough known of themselves. How much more shrouded in obscurity, therefore, must be the causes operating during these migrations. The United States Bureau of Fisheries has never ceased in its efforts to untangle this thread of piscatorial history.

In the instance of the Pacific coast salmon of the genus *Oncorhynchus*, thanks to the labors of Evermann, Gilbert, Meek, Rutter, Chamberlain, and others, the following general facts are now established within a reasonable degree of certainty:

1. The young of the species of *Oncorhynchus*, which have been hatched in the fresh-water streams, migrate to the sea, where they can secure an abundance of food during their developmental period. Evermann [a] in 1894 and 1895 observed many young *O. tschawytscha* and *O. nerka* in the Salmon River headwaters in Idaho. He says: "We are not yet able to say just when the young salmon leave the waters where they were hatched and begin their journey to the sea, but it undoubtedly occurs between September of the first and July of the second year following that in which they were spawned. Later Rutter [b] followed the downward migration of young salmon in the Sacramento River, California. He found that young salmon fry "begin their down-stream migration as soon as they are able to swim." They reach the estuary in large numbers in from ninety to one hundred days or more. He found also that many young salmon "summer

[a] Evermann, B. W.: A preliminary report upon salmon investigations in Idaho in 1894. Bulletin U. S. Fish Commission, vol. xv, 1895, p. 253, 1896; and A report upon salmon investigations in the headwaters of the Columbia River in the State of Idaho in 1895, together with notes upon the fishes observed in that State in 1894 and 1895. Bulletin U. S. Fish Commission, vol. xvi, 1896, p. 184.

[b] Rutter, Cloudsley: Natural history of the quinnat salmon. Bulletin U. S. Bureau of Fisheries, vol. xxii, 1902, p. 102.

residents" remained in the headwaters of the Sacramento until the first winter rains, when they all went out.

2. The salmon feed in the ocean for a period of years. For the chinook salmon this period is believed to be from three to five years, though the evidence is not entirely conclusive. The feeding period continues until maturity is reached.

3. At the end of the feeding and maturing period the salmon migrate up the Pacific coast rivers to spawning grounds, which are sometimes only a few miles from the sea and scarcely beyond brackish water, but often for hundreds of miles, apparently always into cold fresh waters of the streams fed by springs, lakes, and mountain snow fields.

4. It has long been known in a general way that the migration of *O. tschawytscha* to the spawning grounds is made wholly without food.

5. The most striking and least expected climax to this interesting life cycle was discovered in 1894 by Evermann[a] for the species *O. tschawytscha* and *O. nerka*, namely, the fact that death invariably follows the spawning act. Evermann states, on page 260 of his preliminary report upon the 1904 expedition, that on September 13th he counted 72 dead salmon in a three-mile stretch of Salmon River and a mile or more of the lower portion of Alturas Creek in Idaho. Only one live salmon was noted on this date. He quotes numerous observations and conclusions of local men of the region tending to confirm the deduction expressed on page 153 of his final report as follows: "The chinook salmon which come to these waters die after spawning."

This brief salmon history is repeated here for the reason that it is the most effective way of presenting the setting for the problems that appeal to the physiologist. Of these problems I have in a previous paper[b] attacked the question of the acclimatization of the chinook salmon to fresh water after its life in the sea. That study was based on an examination of the blood and other body fluids. The special interest attaches to the osmotic changes during the passage of the fish through the various degrees of brackish water in the journey from the salt water of the sea to the fresh water of the rivers. The further osmotic change during the run up the river was also studied.

The changes in the blood and body fluids are relatively slight and are carried on very slowly and gradually. The osmotic changes in the body fluids give little or no intimation of the length of time consumed by the fish in the transition from salt to fresh water. Neither do the osmotic changes give any measure of the duration of the sojourn in fresh water. In order to arrive at any adequate explanation of the profound changes in the tissues and organs during the migration it becomes almost a necessity that the rapidity of change in the environment and the total duration of the period be determined. The time element in this change is indeed the most important factor, yet an almost wholly unknown one.

The present paper gives the results of a preliminary experiment designed to secure more tangible evidence as to the time element in the migration, especially on the Columbia

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[a] Evermann, B. W., op. cit., vol. XVI, p. 151.

[b] Greene, C. W.: Physiological studies of the chinook salmon. Bulletin U. S. Bureau of Fisheries, vol. XXIV, 1904, p. 429.

River.[a] The question can be better understood when analyzed into the following points or questions:

1. How long do salmon remain in brackish water? Or, stated more fully, how rapidly do salmon pass from salt water through the various degrees of brackish water at the mouths of the rivers?

2. What evidence is there that salmon swim back and forth with the ebb and flood of the tide during the migration through brackish water?

3. When once quite within the fresh water of the rivers, how rapidly and how continuously do salmon travel on their course up the rivers to the spawning grounds?

4. What evidences do salmon give of special responses to unusual conditions, such as obstruction to their course, individual injury, etc.?

PRINCIPLE AND METHOD OF EXPERIMENT.

This experiment is based on the principle that an understanding of the details of the migration phenomena can only be had by a study of the movements of individual fishes. The information derived from the movements of large schools of fishes, while often of extreme value as corroborative evidence, can never be taken as conclusive evidence of the movements of individuals. Even if it were safe to assume that the movements of a given school of salmon represent the average of the movements of the component individuals, yet it is quite impossible to identify certainly any given school at different points along the river.

In order to subject the above questions to a preliminary test, I arranged a salmon marking experiment on the lower Columbia River. The experiment was accessory to a physiological investigation under my immediate direction during the summer of 1908. Fifty-nine fish were marked with individual tags and liberated in the Columbia River at the head of Sand Island, which is just within the mouth of the Columbia. The point at which the fish were liberated was about eight miles up the river above the Canby light-house on Cape Disappointment. This experiment was launched on August 14, 1908.

Superintendent Nicholay Hansen, of the Chinook (Wash.) fish hatching station, contributed the catch of the Washington state fish trap. He also generously furnished transportation to the trap and granted me the assistance of the hatchery foreman and crew. I was assisted also by one of the staff of the United States Bureau of Fisheries. On the above date the trap contained a two-days catch. We reached the trap at about 9 o'clock in the morning, just before extreme low tide, and the net was lifted soon afterwards. The fish were run from the net into a special live car used by the Chinook hatchery crew to transport fish from the trap to the retaining grounds. The fish were later dipped from the car with a large dip net, lifted out of the net by hand, and quickly measured for total length. The marking tag was next inserted and the fish turned loose into the current. It goes without saying that the utmost

[a] A briefer paper based on this experiment is published under the title, "An experimental determination of the speed of migration of salmon in the Columbia River," in the Brooks Memorial Volume of the Journal of Experimental Zoölogy, vol. 9, 1910.

dispatch was used to prevent asphyxiation and care taken to avoid injury during the necessary handling.

MARKING TAGS AND TOOLS.

The tags used to mark the salmon in this experiment were made of aluminum and were extremely light and very strong. The entire tag or button weighed 2.6 grams ($\frac{1}{12}$ ounce). The tag was made of two pieces on the general principle of a Yankee button (fig. 1). The piece *B* consisted of a circular disk, 1 mm. thick by 19 mm. in diameter, which was forged to a hollow shaft, 7 mm. long by 7 mm. in diameter. The shaft had a hole through its length some 4 mm. in diameter. A serial number was stamped on the face of the disk (fig. 1, *D*). Piece *A* was a disk similar to *B* but forged to a solid rivet, 4 mm. in diameter by 9 mm. long. On this face was stamped the words "U. S. Fish," as shown in *E*. When the rivet of piece *A* is inserted into the shaft of *B* (fig. 1, *C*), the rivet projects 2 mm., which gives ample length for securing. When the two pieces are adjusted and the rivet compressed, the soft aluminum fills the shaft and the end is mashed down so that the two pieces can not be torn apart (fig. 1, *D*).

The marking pliers (fig. 2) used in this experiment were supplied by the manufacturer of the marking buttons. They were of cast iron, quite large, and rather heavy for quick work. The pliers were 28 centimeters long and weighed 670 grams. Between the handles there was inserted a hollow punch that cut a hole 7 mm. in diameter. The width of the pliers was adjustable to the length of the button, the adjustment being made by threading in one jaw. It was not necessary to use this adjusting device in the salmon experiments, since the thickness of the salmon fin was never so great but that the pieces of the button could be completely thrust home with the fingers without the aid of the pliers.

CONDITIONS AND DETAILS OF MARKING PROCESS.

When a salmon is caught up in a dip net he struggles vigorously to get away. One should use a relatively large dip net with a wide flat bottom (i. e., not the usual round or kettle-shaped bottom). With such a net it is very easy to manage a fish through the struggling stage so that it does no injury to itself. It is not necessary that scales should be lost, even in such loose-scaled fish as the silver salmon.

In this experiment when a fish was caught it was held with the bottom of the net just deep enough in the water for the fish to struggle against the resistance of the water. While this method resulted in a goodly quantity of water being thrown over the operator, it had the very desirable effect of quickly producing a temporary fatigue of the salmon. As a result of this fatigue, the fish remained quiet for a number of seconds.

The instant a fish stopped struggling it was lifted out of the water, seized by the tail with a strong grip of the hand, swung free of the net, and over the free arm of the operator. The next instant it was quickly but gently laid out on the measuring platform and its length read off. The measuring platform consisted of a broad board with an upright at one end. A meter stick was tacked to the board with its zero against the upright. Loose folds of burlap were laid over the board and over the meter stick for

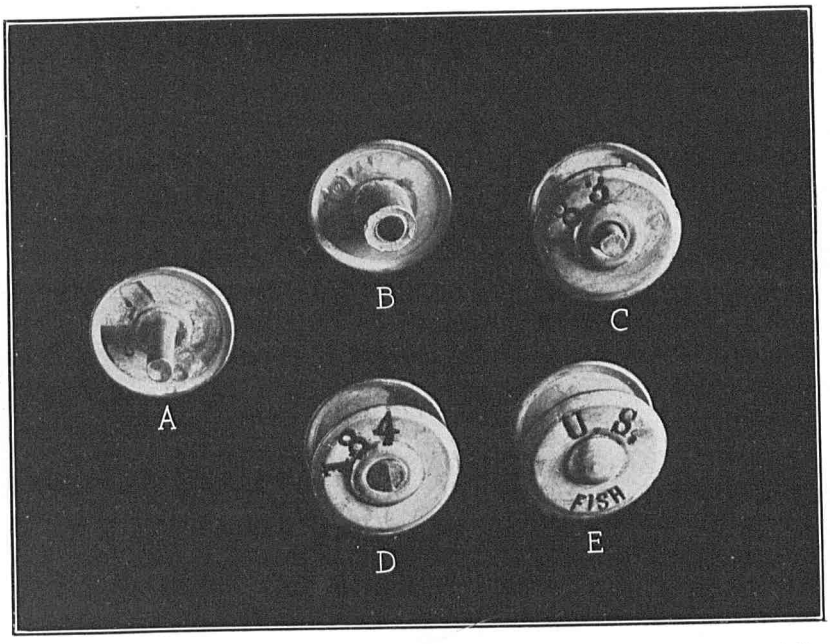

FIG. 1.—The two pieces of the marking button are shown in A and B, the former especially arranged to show the rivet, the latter to show the shaft. In C the two pieces are shown put together but not riveted. In D the parts are riveted together, and in E the converse side is figured.

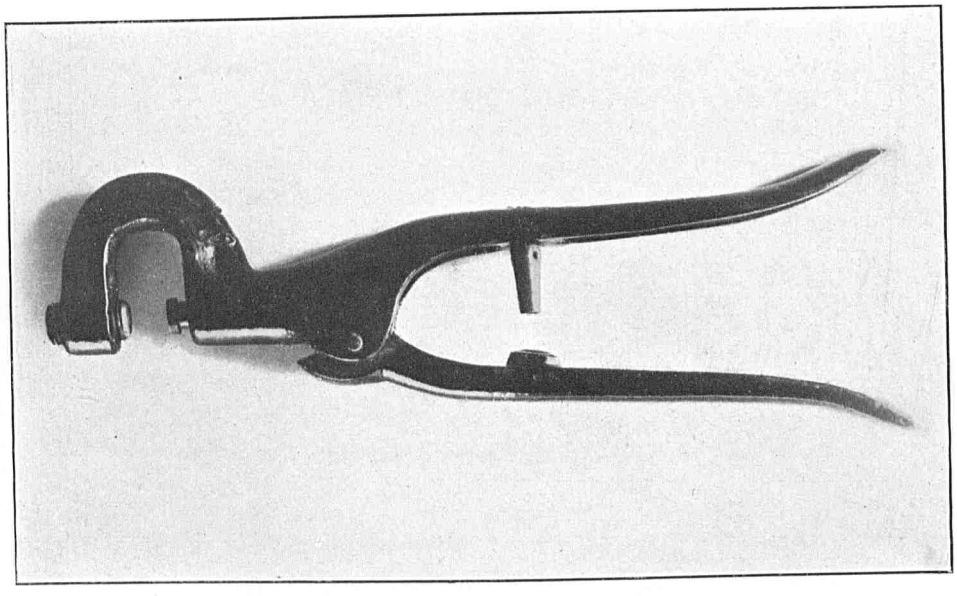

FIG. 2.—Pliers used in attaching the marking buttons.

the greater portion of its length. A fold of the burlap was so arranged that it could be quickly thrown over the middle portion of the body of the salmon whenever desirable, i. e., occasionally with the largest specimens.

When a fish was laid out on the measuring platform the tip of its nose was allowed just to touch the vertical piece and its tail was extended to full length. The total length was then read off by the measurer and announced to the recorder. The tail was, however, never released from the grasp of the operator during this move; a struggle is apt to begin at any moment, and if the fish struggles it must be swung free into the air to prevent pounding on the board and injury to itself. If the length was not caught by the measurer before struggling occurred, the process, of course, had to be repeated. Lifting a salmon from the water, taking it from the net, and reading its length on the measuring board really consumed only a very few seconds—not so long a time as required to describe the process.

After the length was read the next step was the insertion of the marking button. This was done by the person who did the measuring. The buttons in this experiment were all inserted in the caudal fin. The upper lobe was used except in a few cases where a cleft was present, in which case the lower lobe was used for the button. The inserting tool, previously described, although intended for use on the domestic animals, was reasonably workable on salmon. Its chief deficiency was in the fact that its use required two very different movements. The first movement was to slip the handle over the lobe of the fin in order to punch the hole for the button (see fig. 2). The second act was for the purpose of compressing the button and riveting it securely in place. If the fish began to struggle at the instant the button was being compressed, the button had to be released instantly lest it be torn from the fin. In cases where the tail was released, the unriveted button was usually thrown out and had to be reinserted. A special tool is being devised for future work that will punch the hole, insert the button, and rivet it home in one continuous movement. Such a tool will materially increase the rapidity of the work.

The salmon that came through the marking process in good condition were immediately released overboard in the direction of the open water. If there was any questionable degree of asphyxia, the fishes were released into the car and turned overboard only when fully recovered. In two fishes that were markedly asphyxiated it was necessary to use artificial respiration for a short time. Both were strong and active when ultimately released from the live car. The fishes took the water readily and quickly swam away. My previous experience in handling live salmon enables me to state that the present handling was well within the limits of treatment which salmon endure without danger or risk.

The weight of the fishes was estimated by Foreman Borkman, who has a reputation for skill in the accuracy of his judgments. Mr. Borkman's estimates have come very close to the actual weights of certain of the fish retaken. In at least one of the largest fish the actual weight tallied exactly. The judgments of the weight were arrived at during the handling of the fish in the net and on the measuring board. These estimates

are only of relative value, however, as indeed are the measurements of length in this preliminary test, and no calculations are to be based on either set of measurements.

DISCUSSION OF TECHNIQUE.

It should be remembered that the procedure related here was done on the first and only attempt to tag fish in the migration run up the Columbia River. The details are given rather fully for the guidance of those who may in the future try this or similar experiments. The technique in handling can be improved as regards two factors; first in the convenience of arrangements for increasing the speed of dipping, measuring, and tagging the fish; second, in the skill which comes with continued handling which will reduce the chances of local injury and of asphyxiation of the fish.

The fishes suffer no physical injury up to the point where the hole is punched in the tail to receive the button. Careless or inexperienced handling, however, may lead to some injury. For example, if the meshes of the dip net are too large it requires care lest the fins be split or a gill torn in removing the fish from it. These injuries can be reduced by care and skill, as has just been stated. Silver salmon will also lose scales in struggling unless they are swung free of the operator's body. For example, if a silver salmon should begin to struggle just as it is swung into the arms of the operator and the operator should undertake to hold it firmly, a number of scales would almost invariably be lost. But if the fish be quickly swung by the tail free of the operator's body until the struggles cease no injury will be done.

Other fins, such as the dorsal or pectorals, might better have been tagged than the tail fin. The objection can be legitimately raised that, since the tail is the most active organ, it would be better to run no risk of its injury, even though the injury were slight, as in this experiment. On the whole, I am of the opinion that this is a well-founded objection. If the button is inserted a little too near the base of the tail, there will be some delay in the healing of the wound. Most of my fish were reported as retaken in fine condition, but some that were taken at The Dalles, Oreg., and had therefore made the longest runs, were reported to have buttons that had become very loose.[a] The holes for the insertion of the buttons had not healed—in fact, had grown larger. The dorsal fin, or even the adipose fin, are possible points that might prove more advantageous for the insertion of the marker. The possibility of tearing out the button in gill nets and the like must always be given consideration in making a choice of points for marking.

As for the tag or marker itself, various criticisms have or may be offered regarding it—that it is too large, that it is too heavy, that it may frighten the fish, since it is bright and shining, that "it may act to the fish like the proverbial tin can to a dog's tail." All of these have little basis in fact and reason. Considered in relation to the size and

[a] "[On August the 25] a 35-pound chinook salmon, in the very best of condition, button snugly in place without any sign of sore, was caught by seine about 15 miles upstream (from the state trap) in the Columbia River, in the main ship channel opposite Altoona, Wash."—Wm. H. Bailey, of the Miller's Sands Fishing Company, of Altoona, Wash.

"We got a steelhead to-day, No. 98. * * * This button wears a big hole in the tail, large enough almost to drop out."—Frank A. Seufert, The Dalles, Oreg., under date of October 5, 1908.

"I inclose herewith serial tag No. 87, taken from a 10-pound silver salmon on the 10th of October, caught by Mr. Ed. Le Roy in a trap at the head of Cottonwood Island. Mr. Le Roy states that the fish was in first-class condition when taken."—H. C. McAllister, master fish warden of Oregon.

weight of the fish, I regard this particular aluminum button as almost ideally light and strong and conspicuous for use in tagging salmon in fresh water. It is probably not visible to the fish that wears it, so can not frighten him, and the possible effects on other individuals are of little importance. As for the "tin can" comparison, this point makes a very good joke, but has no basis in fact. I have marked numerous salmon on the spawning grounds and find that the marked fish come and go with the unmarked fish without any disturbing behavior to distinguish them from the other fish of the schools.

For sea-run fish, where the sojourn in salt water lasts for a year or more, aluminum will not do. Salt water corrodes aluminum and the disk will probably drop off within a year. The corroding property of aluminum in salt water is, however, very valuable as an accessory check on salmon that are making the journey through tide water. (See figs. 3 and 4.) The degree of corrosion of the aluminum button indicates the relative immersion in salt water, although from this fact alone one can not distinguish between the corrosion due to a relatively short immersion in concentrated and that produced by a longer immersion in more dilute sea water.

LITTLE INJURY TO FISH IN HANDLING.

The necessary physical injury to salmon while marking them by the methods used in this test are two, or at most three. The first of these is the degree of asphyxiation produced by the handling of fish out of water. The second injury is that of cutting the 7 mm. hole through the caudal fin. The third is the physical effects of the handling.

By asphyxiation is meant the condition which results from the inability of the salmon to secure the usual quantity of oxygen and to get rid of the carbon dioxide rapidly enough. With fishes this exchange of oxygen and carbon dioxide takes place between the blood in the gills and the water flowing through the mouth and over the gills, the oxygen being absorbed from the water into the gills and the carbon dioxide exchanged at the same time passing in the opposite direction. If a fish is taken from the water and air is allowed to pass freely over the gills, the conditions for the gaseous interchange between the air and the blood through the gills is for a time as good, or even better, than with water. The trouble comes when the gill covers are tightly closed down and when the gill filaments, no longer supported by water, adhere together in a mass. These conditions sharply reduce the respiratory efficiency, and asphyxiation results. This is slight at first, but is more intense and more rapidly developed later. One who gives attention to the fact can not but be impressed by the degree with which salmon withstand asphyxiation and the ease with which asphyxiation can be overcome by artificial respiration. In the above experiments only two salmon required the artificial respiration. One of these was a fish weakened by old injuries that were quite severe. I do not consider ordinary mild asphyxiation of any particular injury to the fish unless it be so pronounced that the irritability of the respiratory center in the medulla is lowered enough to stop completely all respiratory movements.

The injury to the fish from cutting the small hole in the tail for the button is very trifling indeed. This cut is for the fish about like making a pin prick in the skin of the

hand to a man. It gives a stimulation that produces physiological reflexes for the moment, and that is small. If the button is carelessly inserted, it might tend to further stimulate the skin during the succeeding two or three hours, but the effects even in this instance would be so slight that it seems to me there would be no very noticeable influence on the fish. Scarcely a fish is caught in the upriver fish wheels where I have worked but that shows physical injuries greater than this.

There still remains the general effect of the handling. No doubt a certain amount of fright and stampeding must have resulted from the handling of these fish, just as it would have resulted if the same fish had been turned loose directly by the lifting of the trap or from a seine. This effect will be discussed more fully in the next chapter.

EFFECTS OF MARKING ON MIGRATION.

The question that naturally presents itself is, What effect will all this have on the migration and on the manifestations of the migratory instinct of the salmon? In my opinion, it will have little or none, and the following pages will reveal my reasons.

First of all, one must divest himself of the customary attitude toward reactions of such complex animals as man and the domestic animals. These are far too complex for comparison with salmon. The reactions of a form so low as the salmon must be considered in the light of its biological development.[a] For example, the salmon brain is very simple in its type and low in its development. The cerebral lobes are relatively small and the so-called cortex layer consists of little more than a single and simple layer of nerve cells. That it possesses anything beyond the very simplest of association fibers is improbable. With such a low form of brain the salmon can not carry out very complex reactions; it has no machinery for such reactions.

The simplicity of the salmon's brain when compared with that of a bird or of a mammal is like the mechanical simplicity of the spiral screw in the ordinary cannery soldering device when compared to the most complicated intricacies of the vacuum solderless heading machines. This salmon brain is complicated enough to coordinate certain particular functions; for example, the circulation, respiration, muscular motions, etc. That the salmon may carry out consecutive nerve reactions such as psychic deductions is impossible. To illustrate, when the hole is punched in the tail in the tagging process, there are slight muscular movements in the region of the tail—local motor reflexes. Sometimes, but by no means always, there may be general motor reactions and the fish struggles to free itself. There are also momentary inhibitions of respiration involving one or two respiratory movements, and, judging by other experiments conducted to determine the fact, there are reactions on the circulatory apparatus. All these are of the simpler reflexes and are comparatively slight, and disappear within a few minutes at most. The mechanical stimulus of inserting the marking button furnishes an occasion for the repetition of the whole series of the above reactions, but in a milder degree. If one can rely on the observations made on sharks, which are not far removed from the salmon in their development, one must conclude that mutilations much more severe

[a] Edinger, L.: Ueber das Hören der Fische und anderer niederer Vertebraten. Zentralblatt für Physiologie, bd. XXII, 1908, p. 1.

will be ignored by the fish within a very short time—a time probably measured by minutes.

The chief objection one can raise here is to assume that the button when once inserted acts as a continuous source of stimulation to the individual fish, thus driving it into panic. One may assume that the button is not where the fish can see it and that it makes no sound which the salmon can hear, granting the questionable fact that the fish recognizes unusual sounds. The only other possibility is that the button is a continuous source of cutaneous sensory stimulation. This last seems plausible, but the fact is that either the wound will heal and adapt the surface to contact with the button or the injured surface will begin to degenerate, in which process the local nerve endings will soon lose their function and become insensitive.

Those conditions which lead to the migration of the salmon are the chief directive stimuli for the salmon at this phase of its existence. They overshadow all others. In comparison with this series of reactions, the so-called migratory instinct, small physical injuries are as nothing. If it were not so, the numerous fish that are injured by seals or sea lions, that are torn by hooks and the rocks, that are even more profoundly injured in the escape from the gill nets, would not appear in such vast numbers on the upper fishing grounds of the river. By my own count on different occasions net-injured fish in the catch of some of the wheels during the summer of 1908 amounted to from 25 to 60 per cent of the total, and I am reliably informed that at certain times the per cent may run to 80 or 90. My observations indicate that some of the salmon recover from these bruises received from the gill nets, though what per cent of recovery occurs I can not say. Salmon are, however, frequently taken on the Celilo fishing grounds with injuries so profound that one wonders how they could have survived so long, yet these severely injured fish are forging ahead toward the spawning grounds. The migratory stimuli overshadow even these most profound injuries and continue to do so until death ends the struggle, and death must inevitably end the struggle of these unfortunates long before the spawning act is consummated.

DETAILED RESULTS OF EXPERIMENT.

The location chosen for the marking of the salmon of this experiment is the Washington state fish trap, a few hundred yards above the head of Sand Island. The point is some 7 or 8 miles within the mouth of the Columbia, on the Washington side, and 10 or 12 miles below Astoria. The border of the channel above the island is bounded by a line which represents the legal limits regulating the setting of fish traps by the fishermen. The state trap is located just outside these limits, permission having been secured for the location by the Washington fisheries authorities from the United States engineers in order to catch fish for the Chinook hatchery. The point also marks the limits on the north to the area over which gill-net fishermen drift their nets. In fact, gill netters occasionally have their nets caught by the cross currents and thrown on this trap. Standing, as it does, just on the border of the north channel on the line that separates the gill netters' field on the one hand from the set traps on the other, this trap is especially well located for this experiment. It is in the area of brackish water,

yet it is several miles upriver from the lower fishing limits, and therefore gives a chance to test whether the marked fish ever run toward salt water.

Of the 59 fish marked and liberated on August 14, there were 25 chinook salmon (*Oncorhynchus tschawytscha*), 16 silver salmon (*O. kisutch*), and 18 steelheads (*Salmo gairdneri*). These fish ranged in total length from 41 to 103 cm. for the chinooks, 47 to 78 cm. for the silvers, and 71 to 90 cm. for the steelheads. The largest chinook weighed 35 pounds. The fish, while few in number, were well distributed as regards size.

Information as to the import of the experiment was given out to the fishery interests on the Columbia. Fishermen were requested to record the place and details of the catch of any marked fish, to note any injuries or other facts of interest, and to report the same to me. Fishermen were also requested to send in the marking buttons with the tails of the fish. The various salmon-packing firms were especially helpful in reporting catches and in forwarding the marking buttons.[a]

Seventeen out of the 59 fish marked were retaken and reported to me. This number retaken represents 29 per cent of the fish liberated, a very favorable proportion considering the 12 to 15 days of closed season following the 25th of August. Of these fish 6 were chinooks, 6 were silver salmon, and 5 were steelheads. The time of the retaking extended from the date of the marking, August 14, to October 10, a total of 57 days. The general record of all the fish retaken is presented in table 1.

TABLE I.—DISTRIBUTION, TIME, AND OTHER FACTS CONCERNING THE 17 SALMON AND STEELHEADS RETAKEN OUT OF THE 59 MARKED AND LIBERATED AT THE WASHINGTON STATE TRAP, COLUMBIA RIVER, AUGUST 14, 1908.

Species, number, and sex.	Weight.	Length.	Date retaken.	Days out.	Place taken.
CHINOOK.					
	Pounds.	*Cm.*			
80♂	35	103	Aug. 25	11	Ship channel opposite Altoona.
109♂	5	54	Aug. 15	1	Chinook, Wash.
110♂	10	68	Aug. 15	1	Do.
113♀	15	82	Aug. 20	6	Republic spit.
115♂	1.5	45	Aug. 15	1	Chinook, Wash.
123♂	14	76	Sept. 14	31	Opposite Brookfield.
SILVER.					
75♂	9.5	69	Sept. 12	29	Celilo rapids.
76♂	14.5	78	Sept. 11	28	Do.
79♂	5	62	Sept. 16	33	Do.
87♀	9	67	Oct. 10	57	Cottonwood Island.
89♂	8	66	Sept. 13	30	Celilo rapids.
97♀	9	67	Sept. 16	33	Do.
STEELHEAD.					
98	14	81	Oct. 5	52	Celilo rapids.
116	12	81	Aug. 14	0	Republic spit.
124	11	78	Sept. 18	35	Celilo rapids.
125	16	86	Bet. Sept. 14 and 20	31–36	Cottonwood Island.
?	.....	.....	Aug. 21	7	Chinook, Wash.

[a] Marked fish were caught by or reported to me by the following persons and firms: P. S. McGowan & Sons, McGowan, Wash.; N. Futrup, Chinook, Wash.; W. and M. McIrvin, Chinook, Wash.; Wm. Graham, Ilwaco, Wash.; Pillar Rock Packing Company, Pillar Rock, Wash.; Wm. B. Bailey, of the Millers Sands Fishing Company, Altoona, Wash.; "Sunderland Trap," Brookfield, Wash.; Ed Le Roy, Cottonwood Island; Seufert Brothers, The Dalles, Oreg.; B. Soderlund, Chinook, Wash.

TABLE I.—DISTRIBUTION, TIME, AND OTHER FACTS CONCERNING THE 17 SALMON AND STEELHEADS RETAKEN OUT OF THE 59 MARKED AND LIBERATED AT THE WASHINGTON STATE TRAP, COLUMBIA RIVER, AUGUST 14, 1908—Continued.

Species, number, and sex.	Distance from state trap.	How taken.	By whom taken or reported.
CHINOOK.	*Miles.*		
80♂	15	Seine	Millers Sands Fishing Co., reported by Wm. B. Bailey.
109♂	0	Trap	W. N. Futrup.
110♂	0	....do	W. & M. McIrvin.
113♀	[a] 4	Purse seine	W. Graham.
115♂	0	Trap	W. & M. McIrvin.
123♂	15	....do	Sunderland's trap, reported by H. C McAllister.
SILVER.			
75♂	210	Seine	Seufert Brothers Company.
76♂	210	....do	Do.
79♂	210	....do	Do.
87?	70	Trap	Ed Le Roy.
89♂	210	Seine	Seufert Brothers Company.
97♀	210	....do	Do.
STEELHEAD.			
98	210	Seine	Seufert Brothers Company.
116	[a] 4	Purse seine	Pillar Rock Packing Company.
124	210	Seine	Seufert Brothers Company.
125	70	Pound net	Ed Le Roy.
?	½	Trap	B. Soderlund.

[a] Downstream.

The fact that aluminum is corroded by immersion in salt water has in a degree served to indicate the career of the marked fish after they were turned back into the Columbia. The degree of corrosion does not enable one to distinguish as between a relatively short time in concentrated salt water and a longer time in relatively dilute brackish water, but where corrosion occurs extensively in a short period of time, as in fish number 80, which was out only 11 days, it is pretty safe to assume that the fish spent most of the time in relatively concentrated sea water. Tables and figures are presented below for the purpose of showing the degree of corrosion of the marking buttons.[a] An examination of these tables and figures will show that each group of fishes of the three species liberated had certain individuals that had gone into sea water long enough to produce corrosion of the marking buttons.

TABLE II.—MARKED CHINOOK SALMON RETAKEN, SHOWING THE EXTENT OF CORROSION OF THE MARKING BUTTONS BY SOJOURN IN SALT WATER.

Number.	Time out in days.	Distance from state trap.	Corrosion of marking button.	
			"U. S. Fish" surface.	Numbered surface.
		Miles.		
80♂	11	15	Very light corrosion in groove around head of rivet.	Corrosion over four-fifths of raised rim of shaft and around rivet.
109♂	1	0	Smooth	Smooth.
110♂	1	0	....do	Do.
113♀	6	[a] 4	....do	Do.
115♂	1	0	....do	Do.
123♂	31	15	Blackened and slight corrosion around head of rivet.	Deeply etched about rivet where it emerges from shaft, and on inner margin of shaft.

[a] Downstream.

CAREERS OF INDIVIDUAL SALMON RETAKEN.

CHINOOK SALMON.

Of the chinook salmon, three, numbers 109, 110, and 115, were retaken in traps in the immediate vicinity of the point where they were liberated. They were taken at the next lift of those traps on August 15 and may have entered the traps at any time during the interval of a little less than 24 hours following their liberation. These three salmon are the only fish of the marked series reported retaken by the traps of the vicinity. They are of interest chiefly as showing that the great majority of the fish took to the main channel in the direction in which they were liberated. The currents at the time of liberation were toward the trap field. On the theory that salmon stem the currents in the tide waters as well as in fresh water, it is obvious that the liberated fish would be directed away from the trap field. These observations are in the main in harmony with this theory.

Chinook number 113 was caught 6 days after liberation and by a purse seine operating near Republic spit. Republic spit is a point marked by the wreckage of a vessel which obstructs the channel off the south shore of Sand Island. It is located about 4 miles down the river from the state trap. The aluminum marking button of this salmon is quite smooth. Had the fish gone out into the pure sea water it might have shown some slight signs of corrosion. Six days in brackish water would scarcely lead to corrosion of the aluminum. It is probable, therefore, that this salmon had spent the time swimming back and forth in the tide water of the vicinity in the process of acclimatization. Whether or not it swam long distances, either upriver or out to sea, does not appear, but judging by the results of the comparison with specimen number 80 it is probable that the time of number 113 was spent in the relatively fresh water in the neighborhood of Sand Island.

Number 80 was taken 15 miles up the river from the state trap and on the eleventh day after liberation. The time required by a straightaway swim for the salmon to travel 15 miles could not be over one or two days (three of the silvers averaged over 7 miles a day, see numbers 75, 76, and 89); hence this fish had about 9 days in which its movements are not accounted for. The corrosion of its tag is slight on one side but quite extensive on the other. So much corrosion in the short time of 11 days can only be accounted for on the theory that the fish was in relatively salt water. My guess would be that this fish went well out toward the jetty or even beyond during its 11 days' stay, and that the average of its time was spent in water as salt as in the vicinity of lower Sand Island or of Canby light.

Chinook number 123 was out 31 days, yet this salmon had traveled upriver only 15 miles when taken near Brookfield. Its button was the second deepest etched of the series recaptured. The corrosion indicates a sojourn in salt water or in relatively concentrated brackish water. The evidence given by the corrosion of this button is to my mind conclusive evidence that its bearer had spent considerable time well below the point where it was liberated, probably at or beyond the lower end of Sand Island. I would

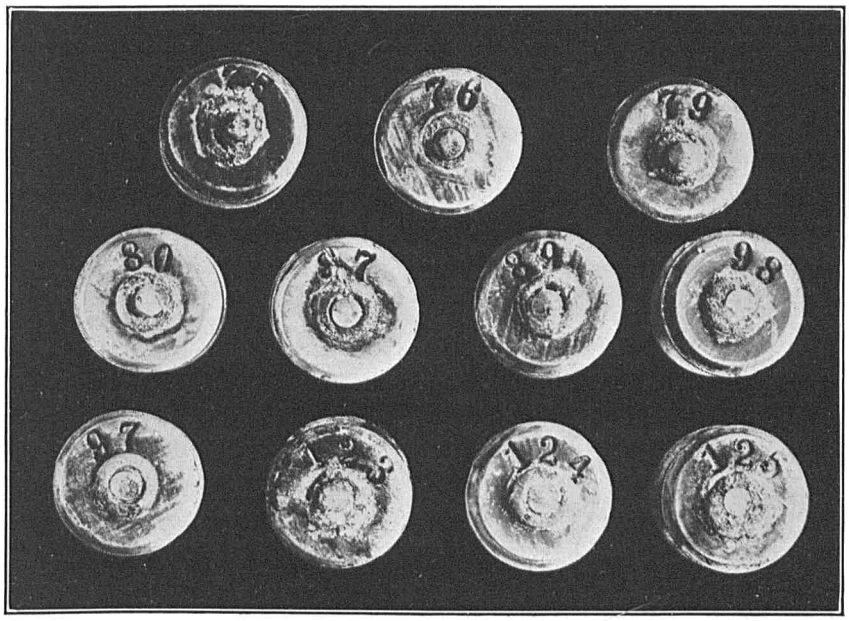

FIG. 3.—Photograph of eleven of the marking buttons after they were recovered from the marked fishes. This and the next figure show the corrosion of aluminum on the exposed surfaces. The buttons are shown natural size.

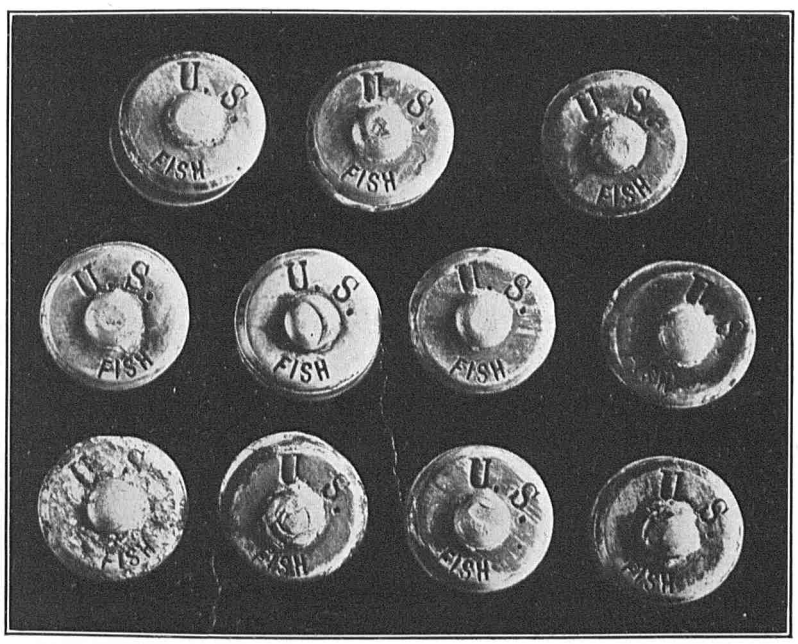

FIG. 4.—Photograph of the converse faces of the eleven marking buttons shown in figure 3. The buttons have the same relative positions in the two photographs. Reading from left to right the numbers of the top row are 75, 76, and 79; of the middle row 80, 87, 89, and 98: and of the bottom row 97, 123, 124, and 125. Buttons photographed natural size.

value this evidence second only to actually capturing the salmon out toward the sea from the state trap.

Marked chinooks were not recaptured above Millers Sands. Whether they got through during the closed season from August 25 to September 12, or from what other reason they were not retaken, is wholly a matter of conjecture. Sharp lookout was kept for them all along the river at the United States hatcheries, and especially at the Ontario (Oreg.) state hatchery, where I collected in early September. No marked fish appeared at the Ontario station up to the close of the fishing about November 1, and none were taken at the government stations.

SILVER SALMON.

The silver salmon, with a single exception, were all retaken by Seufert Brothers Company on the Celilo rapids at the Tumwater seining grounds. One, number 87, was taken at Cottonwood Island, by Mr. Ed Le Roy. This last fish was out the longest of all the fish retaken—57 days.

An examination of table III and of figures 3 and 4 will show that great diversity exists as to the degree of etching by corrosion shown by the buttons of these silver salmon. The button of number 79 was smooth and clean on both sides. This salmon was out 33 days, but evidently did not spend much if any of its time in brackish water after it was marked.

TABLE III.—MARKED SILVER SALMON RETAKEN AND EXTENT OF CORROSION OF MARKING BUTTONS BY SOJOURN IN SALT WATER.

Number.	Time out in days.	Distance from state trap.	Corrosion of marking buttons.	
			"U. S. Fish" surface.	Numbered surface.
		Miles.		
75	29	210	Smooth	Slightly corroded about rivet.
73	28	210	Slightly corroded about head of rivet	Deeply corroded on head of shaft and about rivet.
79	33	210	Smooth	Smooth.
87	57	70	do	Corroded over surface of head of shaft and about rivet, but not deeply pitted.
89	30	210	Slightly corroded about one-half the head of rivet.	Corroded over entire head of shaft, and deeply pitted about rivet and on inside of end of shaft.
97	33	210	Deeply corroded and pitted over this surface of the button except head of rivet; most corroded of all the buttons.	Corroded on one-third the head of shaft and slightly on end of rivet.

Number 97, which was out the same length of time and retaken at the same place as 79, had the most deeply corroded and pitted button of the entire series. It was even more corroded than chinook button number 123 which was out 31 days and was retaken only 15 miles up the river. Number 89 was also a deeply corroded button. These two fish, 89 and 97, bear evidence of a considerable sojourn in salt or strongly brackish water after they were tagged. The buttons of the 3 remaining silvers grade between the extremes just discussed, number 75 being almost smooth and 79 considerably corroded.

Yet it will be noted that these 5 fish were retaken by Seufert Brothers within the period of 5 days from September 12 to 16. Silver salmon number 87 is a decided exception in this list. It was retaken only 70 miles up the river and was out the longest time of all the marked fish, namely, 57 days. Its button, however, does not present a history of long contact with salt water. It is etched to some degree on one surface, but not more than would be possible by a long career in slightly brackish water.

STEELHEADS.

Of the 18 steelheads marked, only 5 were retaken. One of these, number 116, was caught down the river 4 miles below where it was liberated and between four and five hours after liberation. As already stated, the fishes were liberated on a strong flood tide and it is evident that this particular fish at once made about a mile an hour speed toward sea. It was taken by purse seine in the channel near Republic spit in the same locality where chinook number 123 was captured 6 days later. These two fishes give absolute proof of downstream movements of salmon. The fishing annals of the lower Columbia have many instances of similar outward movements of schools of salmon.

TABLE IV.—EXTENT OF CORROSION OF THE ALUMINUM MARKING BUTTONS OF THE STEELHEADS RETAKEN.

Number.	Time out in days.	Distance from state trap.	Corrosion of marking surface.	
			"U. S. Fish" surface.	Numbered surface.
		Miles.		
98.....	52	210	Slightly corroded about head of rivet...	Markedly corroded over head of shaft and around rivet within the shaft.
116.....	0	[a] 4	Smooth.....	Smooth.
124.....	33	210	.....do.....	Slightly corroded about rivet.
125.....	30–35	70	Corroded about head of rivet.....	Deeply corroded about rivet and slightly pitted.
.....	7	½	Button not preserved.....	Button not preserved.

[a] Downstream.

It is said that at certain times, following a period of stormy weather or when for other reasons the gill nets have not been operating on the lower river, the seines on lower Sand Island capture fish with definite marks received from fishing gear—marks that can be accounted for only on the theory that the fishes have moved seaward after receiving the marks.

One steelhead was reported captured in a trap only about one-half mile upriver from the state trap where it was liberated. This fish was out 7 days, but as its button number was not taken and since the button itself was not sent to me, no record could be made of the character and extent of its corrosion.

Of the two steelheads retaken by Seufert Brothers, number 124, out 33 days, shows slight corrosion, but number 98, out 52 days, shows marked corrosion. Evidently the former spent little time in tide water, while the corrosion of the button of the latter indicates considerable contact with salt water.

The steelhead number 125, which was caught only 70 miles up, shows a salt-water history similar to that of number 98, which had gone 210 miles up the river.

MIGRATION SPEED.

The speed of the total migration is unquestionably divided into two periods, first, the migration through the various stages of tide water, and, second, the migration up the river when once quite within fresh water. This preliminary experiment was launched in the tide-water zone, hence can not directly solve either speed period. In discussing the three groups of fishes a number of instances have been given to show that these fishes spent much time in brackish water after their marking. One may assume the broad working hypothesis that salmon travel at an average speed that is apparently uniform for different individuals under similar conditions. Table v shows the days out, total distance traveled, and the average speed made for the time. A glance at the table suffices to show either that the hypothesis is unsatisfactory or that a number of the salmon have not made direct runs upstream.

TABLE V.—MARKED FISH ARRANGED IN THE ORDER OF THE AVERAGE TIME TAKEN TO TRAVEL THE DISTANCE COVERED BEFORE RECAPTURE.

Species.	Tag number.	Days out.	Distance traveled.	Average speed per day.
			Miles.	*Miles.*
Silver	76	28	210	7.50
Do	75	29	210	7.24
Do	89	30	210	7.00
Do	79	33	210	6.36
Do	97	33	210	6.36
Steelhead	124	33	210	6.36
Do	98	52	210	3.85
Do	125	±35	70	±2.00
Chinook	80	11	15	1.36
Silver	87	57	70	1.23
Chinook	123	31	15	.48
Do	113	6	[a] 4	.66
Steelhead	116	0	[a] 4	24.00

[a] Downstream.

Rutter[a] branded a number of salmon on the Sacramento River in September, 1900, at Rio Vista, which is above the salt-water tides of the river. Three of these fish were retaken, two at the Mill Creek hatchery and one at Battle Creek. They covered the distance in an average speed of 4 to 5 miles per day. This speed was exceeded by six of the marked fish in the present experiment, these six making an average individual speed of from 6.36 to 7.50 miles a day with a general average of 6.8 miles.

The observations of the commercial fishermen on the Columbia River make it quite probable that the highest speed shown in table v is low for the migration rate of Columbia River salmon under favorable conditions of the river.[b] The statistics of the

[a] Rutter, Cloudsley, op. cit., p. 124.

[b] Mr. Frank A. Seufert writes me as follows: "Usually it is from 7 to 9 days from the time a run is reported entering the river in July or August when we get the effects of it here." Seufert Brothers' fishery is 210 miles up the river, which would give a speed of 23 to 30 miles a day for a heavy run.

commercial fisheries would indicate a maximal speed of three or four times that given by my highest rates. It is very probable, therefore, that the lack of uniformity in speed shown in the table is due to days consumed in ways not accounted for by the direct run through fresh water in the course up the river.

An interesting side light is thrown on these observations if the speed for all is computed on the basis of the average speed made by number 76, the highest on the list.[a] Table VI presents the results of this recomputation.

TABLE VI.—RESULTS OF COMPUTING TIME ACTUALLY TAKEN IN RUN, ON BASIS OF AVERAGE SPEED OF 7.5 MILES A DAY.

Species and number.	Distance traveled in miles from point of liberation.	Days out.	Days required to cover distance at an average speed of 7.5 miles a day.	Days unaccounted for.
Silver, 75	210	29	28	1
Silver, 89	210	30	28	2
Silver, 79	210	33	28	5
Silver, 97	210	33	28	5
Steelhead, 124	210	33	28	5
Chinook, 80	15	11	2	9
Steelhead, 98	210	52	28	24
Steelhead, 125	70	35	9	26
Chinook, 123	15	±31	2	29
Silver, 87	70	57	9	48
Chinook, 113	[a] 4	6	0	[b] 6

[a] Downstream.

[b] Had not yet left tide water.

I fully recognize that table VI is based on an assumption. Nevertheless, it can not at present be displaced by observed facts, and serves better than any other method devised to illustrate the great discrepancy in the time consumed by numbers 80, 87, 98, 123, and 125. The last column of the table shows that these particular fishes must have played around in the lower waters of the Columbia. Certain of them have not gone beyond tide water—for example, 80 and 123. This last fish has taken a whole month to go only 15 miles up the river. By the computation there are three others that have about the same time available for playing around or resting quietly somewhere, and the history of number 123 renders it quite probable that they all spent this extra time in tide water.

We have, therefore, from this experiment two series of facts that throw light on the life history of salmon in tide water, namely, the etching or corrosion of the aluminum marking buttons and the probable time consumed by the salmon after they were marked at the state trap before they began the strictly fresh-water journey. Both observations show an unexpectedly long time in tide water, i. e., as long as 30 days (chinook number 80) or even 48 days (silver number 87).

Rutter[b] has advanced the theory that salmon make the journey through tide water by running up during the ebb and down during the flood tide, stemming the current each

[a] It is evident from the slight corrosion of the button of this fish that it spent some time in brackish or salt water. It made, therefore, a really higher average speed during the time in fresh water.

[b] Rutter, Cloudsley, op. cit., p. 122.

way. He applied this principle in his studies of the chinook salmon of the Sacramento River. Following the variations in the catch of the fisheries at the different towns along the bay and lower Sacramento, he estimated that a school of salmon made its way from Vallejo, on the lower bay, to Sacramento, on the river, in 4 days for the spring run when the river is relatively high. In the summer and fall they move more slowly. This he explains by the fact that the river is low and the tides in the bay therefore more nearly equal in time, thus requiring more time for the salmon to pass through the bay.

My fish were marked in August, hence are to be compared with the movements of fall fish as described by Rutter. I accept Rutter's hypothesis as partially explaining the movements of salmon in tide water. Undoubtedly currents in the rivers are directive on the movements of the migratory fishes. In tidal waters this factor is still active. In the tidal area at the mouth of a river the relative time of the flood and ebb currents rapidly changes toward the upper tidal limits, where the former entirely disappears. If salmon were directed by currents alone they would make the journey more and more continuously as they come within the brackish area. Figured on the basis of the difference of the duration of the flow of the flood and ebb currents as against the observed speed of salmon, it is obvious that the fish would pass through the tidal area in a much shorter time than these observations indicate. Other factors are operative, for currents alone are not sufficient to account for the movements. I believe that a much more influential factor is the condition of the water as regards its amount of salt. Salmon are sharply responsive to the stimulus that comes from variation in the degree of admixture of sea water and river water in the tidal area, a stimulus that is doubtless in the nature of a negative chemotaxis. Attention has already been called to the changes in the osmotic equivalents of the blood in fresh-water salmon as compared with those in sea water. These changes, though slight, are due in large measure to the transition from a sea-water environment to one of fresh water. Such physiological adaptations require a relatively long time. If a salmon entering the mouth of the Columbia should swim into an area of water relatively fresh before his gills and other epithelial tissues were sufficiently adapted to it, chemotactic reaction would stimulate him to increased activity, which, by the law of such reactions, would lead him in the end toward salt water. These journeys into areas now relatively fresh, now relatively salt, but in the balance ever toward fresh water, will continue until the epithelial tissues of the individual fish have become adapted to life in fresh water. The rate at which this adaptive process takes place determines the total time required for the passage through the tidal area. The observations recorded in this experiment indicate a very much longer time spent in tide water by the salmon on the Columbia River than allowed by Rutter for salmon on the Sacramento. While not numerous enough and not sufficiently varied to make the deductions absolutely conclusive, yet these experiments strongly indicate that salmon spend not less than from 30 to 40 days in passing the tidal area of the lower Columbia.

SUMMARY OF CONCLUSIONS.

Remembering that this experiment is preliminary and that the observations are entirely too few to make the deductions conclusive beyond question, still the following tentative answers may be given to the questions announced in the beginning of this paper.

1. Salmon may take from 30 to 40 days to pass through the brackish water within the limits of the fishing waters at the mouth of the Columbia River.

2. That salmon spend considerable time swimming back and forth in tide water during the acclimatization to fresh water is indicated (*a*) by the fact that two fishes were taken below the point at which they were marked, (*b*) by the corrosion of the aluminum marking buttons by salt water, and (*c*) by the long time spent by certain fishes in reaching the lower limits of fresh water.

3. When wholly within fresh water, the silver salmon and the steelhead make the migratory journey at an average speed of from 6 to 7½ miles a day and probably more.

4. There is little evidence that the process of marking or that the partial obstruction of the course by fishing gear does more than produce a temporary checking of the migratory journey.

NATURAL HISTORY OF THE AMERICAN LOBSTER

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INTRODUCTION.

The present work when originally undertaken in 1903 was designed to form the zoological part of a history of the lobster in both America and Europe, but subsequent events led to a modification of this plan, and when it was decided to issue this section separately, its character and scope were somewhat changed.

Dr. Hugh M. Smith, of the United States Bureau of Fisheries, had planned to deal with the lobster fishery and the economic questions which this great industry has raised, in a comprehensive manner, and hope is entertained that this design may still be carried out.

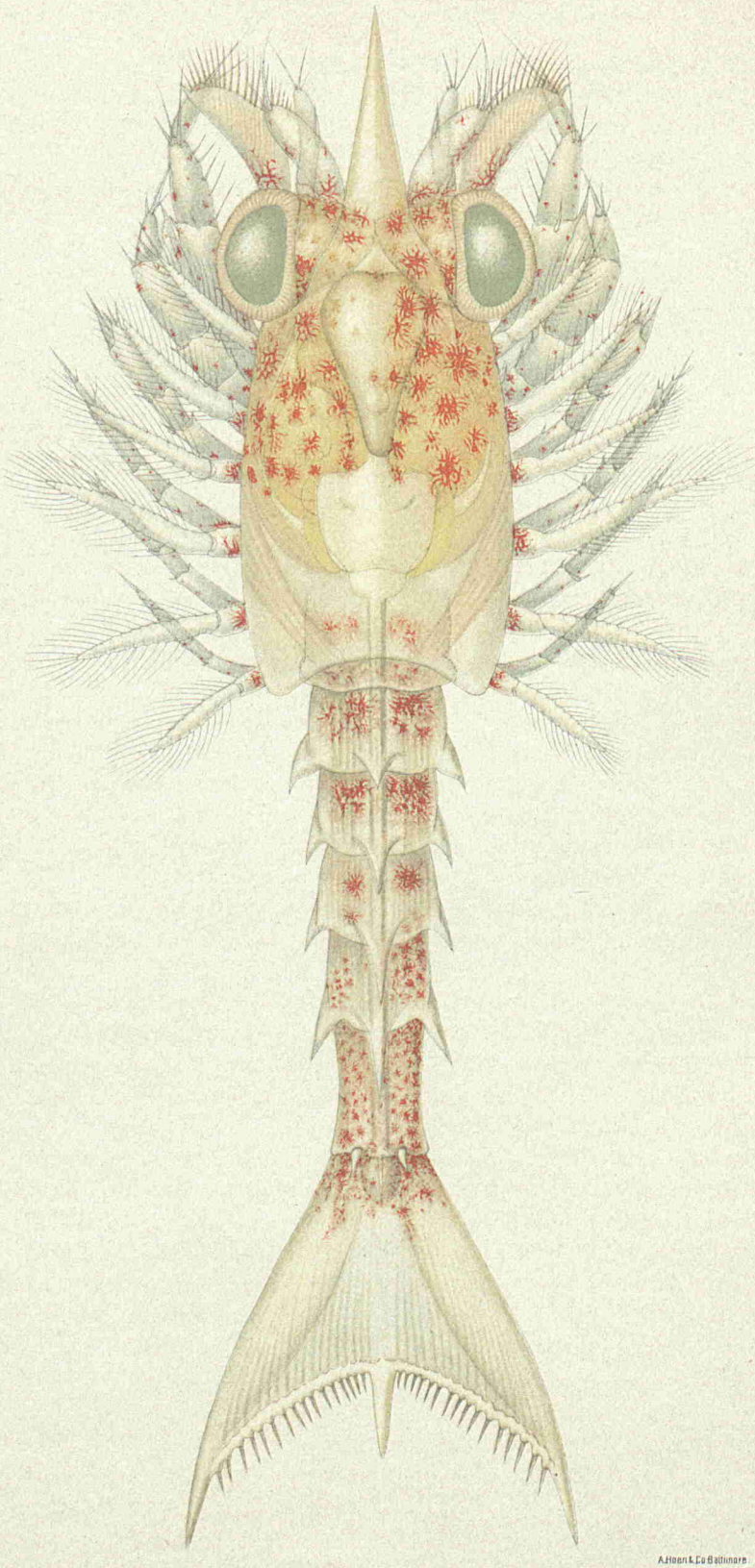
Though essentially a distinct work, this is in a measure both a revision and an extension of my earlier report upon The American Lobster, published by the United States Commission of Fish and Fisheries in its bulletin for 1895. But little from the latter, however, has been incorporated directly, and this only when newer or better research has failed to give us more light upon the subject. Six drawings of the young lobsters, three of which are in colors, have been reproduced, after slight revisions, from my former report; all of the rest are new and deal chiefly with the anatomy of the body and appendages, especially with torsion, reflex amputation, and the developmental history of the toothed and cracker claws, the sexual organs, and the germ cells. I have depended mainly upon the store of materials collected in former years, but have received accessions from the United States Bureau of Fisheries, for which as well as for many courtesies, now extending over a long period, I wish to offer my sincere thanks. The Bureau has generously given me the privilege of a free lance, and all critical sections of this paper should be read in the light of individual opinion only, directed, it is true, in a friendly spirit, and as we believe from the standpoint of science.

Our knowledge of the lobster has increased to such an extent during the past fifteen years that in all probability there is no marine invertebrate in the world which is now better known. This result is due to the suggestive ideas or elaborate researches of a large body of naturalists in both America and Europe, and to their labors the reader will find abundant reference in the pages which follow. As a result of this advance in the biological field, a signal success has been achieved in the artificial propagation or culture of the lobster, and particularly in rearing the delicate young to the bottom-seeking stage, a success from which this fishery should not be slow to profit, and which it owes to experiments begun under the auspices of the United States Fish Commission at Woods Hole, Mass., and afterwards carried to a high degree of perfection by the Commission of Inland Fisheries of Rhode Island, under the direction of Prof. Albert D. Mead, at Wickford. Through the aid of such a practical method there is ground for hope, not only of restoring our depleted fisheries on the Atlantic coast, but of establishing new ones on the Pacific, as well as in other parts of the world.

While many dark puzzles have been solved, and many questions, raised fifteen years or more ago, can now be answered with assurance, no enterprising or resourceful worker need be told that the field is still fertile for fuller or more exact researches in many directions. We hope that some of these subjects will be suggested by the imperfections of the present work when attention is not called to them directly.

F. H. HERRICK.

CLEVELAND, OHIO.



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FIRST LARVAL OR

NATURAL HISTORY OF THE AMERICAN LOBSTER.

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Chapter I.—THE LOBSTERS AND ALLIED CRUSTACEA; THEIR ZOOLOGICAL RELATIONS, HABITS, DEVELOPMENT, AND USE AS FOOD.

NATURAL HISTORY OF THE CRUSTACEA.

Nature works according to definite principles, and with a degree of uniformity which for most of our purposes is practically absolute. Accordingly we find that whenever an animal or plant has been successfully domesticated or whenever the young of any form have been successfully reared by the artificial impregnation and subsequent care of the eggs, as in the case of the oyster or the whitefish, this has been accomplished by acting, whether intelligently or not, in accordance with the principles of nature. The mollusk or the vertebrate is made to yield to experiments which a knowledge of its habits and structure would suggest. In the lobster we have to deal with another and distinct type, for although this animal swims in the sea, it is not a fish, but an arthropod, and a knowledge of the ways of fishes and mollusks will help but little in the study of its habits or in the propagation of its race.

The following paragraphs on the general characteristics of the arthropods will be of little or no use to professional zoologists, but may help to set our subject in a clearer light for other readers.

Of the eight or more animal types recognized by naturalists the arthropods are distinguished for their complicated structure and wonderful diversity of form, for the wide range and specialization of their instincts, their almost unparalleled fertility and corresponding activity. In the latter respect, at least, some of the insects are not surpassed by birds, the most active vertebrates.

The body of the arthropod is composed of a series of successive segments, the somites or metameres, which in conformity to vertebrate anatomy are divided into three groups, pertaining to the head, thorax, and abdomen. (Pl. XXXIII, and table 4.) Theoretically, each somite at one time possessed a pair of jointed limbs, and many of the segments still retain them. In the living adult state, the body is normally maintained in a definite upright position, which is often one of unstable equilibrium, whether the animal is in motion or at rest. These characteristics are shared in some degree by the annelid

worms, their nearest allies, as well as by the vertebrates. The arthropod possesses in addition a dorsal brain, united by a ring-commissure about the esophagus, to a ventral chain or "ladder" of paired ganglia, a character also shared by the higher worms; the heart is dorsal and overlies the food canal; the cuticle, which encases the body and lines every inward fold, is secreted by the outer layer of the skin, the epidermis or hypodermis, and is chitinous—that is, contains chitin, a complex nitrogenous substance, by some chemists regarded as analogous to cellulose and lignin, which occur typically in plants and form the basis of all their woody tissues. This cuticle of the Crustacea is often reinforced by thick deposits of lime and other minerals, thus forming a hard external skeleton, to which every peripheral muscle is directly or indirectly attached, and by which every soft and delicate organ in the entire body is protected. No other animals possess all the several characteristics just enumerated. Since the arthropods embrace the insects, with their hundreds of thousands of species, it is not surprising that according to some estimates they include three-fourths of all the known species of living animals.

Of the five commonly recognized classes of arthropods the Crustacea are the lowest and most primitive. They fall into two principal subclasses: (*a*) The Entomostraca, embracing all the simpler, more primitive and generally smaller forms, such as water fleas, copepods, and barnacles, and (*b*) the Malacostraca, to which pertain the larger and the most highly organized of living Crustacea, such as lobsters, shrimps and crabs. The ancient name of the class served the older zoologists to distinguish those animals which possessed a "crust," or a shell flexible at certain joints, from the Testacea, or animals like the oyster and clam in which the shelly covering was a hard and unyielding "test."

Eight orders of Malacostraca[a] have been recognized, of which the more important, in view of their size, numbers, economic and general zoological interest, are the Amphipoda and Isopoda, which embrace the beach fleas on the one hand and terrestrial wood lice on the other; the primitive Stomatopoda, of which the edible mantis or "praying" shrimp are well known representatives, the small Schizopoda, or cleft-feet, and the ten-footed and stalk-eyed Decapoda, which mainly interest us.

In both the isopods and amphipods the eggs are carried in a brood chamber on the underside of the thorax, formed by membranous plate-like outgrowths from the thoracic legs in the female; the schizopods also carry their eggs in a similar way.

The breeding habits of the stomatopods are highly peculiar; although celebrated for their widely dispersed pelagic larvæ, and although it was understood that they dwelt in mud burrows under water, and did not carry their eggs attached to the body as in decapods, little was known of their early life history until the studies of Professor Brooks upon *Gonodactylus chiragra* of the Bahama Islands appeared in 1893, when he gave the first full account of their habits, and the first record of the rearing of a young stomatopod from the egg. Fortunately this animal does not deposit its ova deep in the mud, but in a burrow, apparently of its own making, in the soft coral rock; they are glued together by a viscous cement and molded to fit the convex form of the mother's

[a] In the classification briefly outlined in this chapter we shall follow mainly the excellent work on Crustacea by Geoffrey Smith, in vol. IV of the Cambridge Natural History. London, 1909.

body. With its egg cluster on its back *Gonodactylus* stands or sits on guard at the mouth of the burrow, awaiting its prey, and meantime keeping its eggs aerated by the fanning movements of the swimmerets. Says Professor Brooks:

> When the burrow is broken open she quickly rolls the eggs into a ball, folds them under her body in a big armful, between the large joints of her raptorial claws, and endeavors to escape with them to a place of safety. The promptness with which this action is performed would seem to indicate that it is an instinct which has been acquired to meet some danger which frequently presents itself.

The decapods have the general characteristics given for the lobster in chapter VI. All glue their eggs to their swimmerets and carry them thus attached, protecting and aerating them for a period of weeks or months with unerring instinct until they hatch. After pairing, the sexes frequently separate, as is possibly the case with lobsters (see p. 302), or they remain together, swimming side by side, and receiving mutual aid as in *Stenopus*, for as long at least as the period of fosterage lasts. The young, upon hatching, usually either swarm together for a time, or are immediately dispersed, as in the lobster. A long and perilous metamorphosis awaits the young of most of the decapods, during which they are pelagic or free surface swimmers, but every degree of abbreviation of this development exists, and in the crayfishes and certain other species, both fluviatile and marine, the young resemble the parent at birth, and a complex family life, which will receive attention later, may be developed.

The decapods are divisible into three intergrading suborders: (1) The Macrura, or long-tailed Crustacea like the shrimp and true lobsters; (2) the Anomura or hermit lobsters and hermit crabs, and (3) the Brachyura or true crabs, the most highly specialized of the entire class, in which the tail is not only very short but is even rudimentary in the male.

To follow out the Macrura only and in brief, they embrace numerous families possessing both zoological interest and economic value, of which the most important are (1) the Nephropsidæ (Astacidæ of many authors) or true lobsters; (2) the fresh-water crayfishes of the world, or Astacidæ of North America and Europe, and the Parastacidæ of the Southern Hemisphere; (3) the other decapods known collectively as prawns or shrimps, including the Peneidæ, Alpheidæ, Pandalidæ, Crangonidæ, and Palæmonidæ; (4) the Palinuridæ, variously known as spiny, thorny, or rock lobsters, and (5) the Scyllaridæ, which are sometimes classed with the Galatheidæ, and are known as warty lobsters. Representatives of some of these families will now be briefly considered, before dealing more fully with the special subjects of this work embraced in the family of Nephropsidæ.

The crayfish (of the family Astacidæ) has become a favorite subject in zoology, and very few invertebrates have received the degree of attention which naturalists have paid to every phase of its history. It is well known that the common crayfish, *Astacus fluviatilis*, has been used for centuries as food all over the continent of Europe, while in France the farming of crayfish in order to increase the natural supply of this crustacean has been successfully practiced for some time. For many years also crayfish have found their way to the markets of American cities which possess large populations of foreign birth, as New York, New Orleans, Chicago, Milwaukee, and San Francisco; but many persons would probably be surprised to learn the present status of the cray-

fish industry in this country, where vast numbers are not only eaten but used to supply classes in zoology or some phase of nature study in nearly every State of the Union.

Professor Andrews,[a] from whose paper the following statistics are taken, thinks that the demand for the fluviatile crayfish is likely to grow steadily, and may help to counterbalance the waning supplies of marine food, especially in the form of lobsters and crabs.

The crayfish of the eastern central regions belong to the genus *Cambarus*, the Potomac supplying *C. affinis;* Chicago, *C. virilis;* New Orleans, *C. blandingii;* and Montreal, *C. bartoni.* A considerable fishery for the large and handsome American species of *Astacus*, a counterpart of the European form, has been developed on the Pacific coast. This centers in Portland, Oreg., where, in 1899, the product reached 117,696 pounds, valued at $19,556.

Andrews has shown that the common *Cambarus affinis* not only breeds annually, but that its young reared from spring eggs may in turn lay eggs the spring following, when under a year old, while at the age of 3¼ years they attain the average market size of 4 inches. It is further suggested that the large 6-inch Oregon *Astacus*, which is more lobster-like in appearance, could doubtless be successfully introduced into Eastern waters, and, with a growing demand, profitably reared, since there is no reason to suppose that climatic changes would offer any obstacle to its development.

The prawns and shrimps distributed among the various families enumerated are undoubtedly the most active and most graceful, as well as the most plentiful of all the decapod Crustacea. Many species are highly valued as food, and are netted and sent to market in vast numbers over a large part of the world. The most important shrimp fisheries of the United States center in the Coast States of the Gulf of Mexico and Pacific Ocean.

Among the best-known species in North America are the edible shrimp of the South (*Penæus setiferus* and *P. brasiliensis*), the still more abundant common shrimp (*Crangon vulgaris*), found on both coasts and closely related to the common European shrimp The California shrimp (*Crangon franciscorum*), the largest and most important of the edible species on the western coast, attains a length of 3½ inches. It not only supplies abundantly the local markets, but occupies an important place in the export trade of San Francisco, being boiled, dried, and shipped to China in large quantities.

Prawns are extremely abundant in the East Indies from Japan to Australia, and, commercially considered, are the most important crustacea of the Orient. Thirteen species of the genus *Penæus* alone are taken in Japanese waters. "They are highly prized and extensively used as food and bait, and dried prawns annually exported to China amount to about 900,000 kilograms in weight and to about 200,000 yen ($131,000) in value. The dried prawns belong almost exclusively to the genus *Penæus.*"[b]

Closely allied to prawns, though placed in a distinct family, are the Alpheidæ, of which over 100 species of snapping shrimps belonging to the genus *Alpheus* and *Synalpheus* alone have been described. They are essentially tropical, and abound in

[a] Andrews, E. A.: The future of the crayfish industry. Science, n. s., vol. XXIII, 1906, p. 983-986. New York.

[b] Kishinouye, K.: Japanese species of the genus Penæus. Journal of the Fisheries Bureau, Tokyo, vol. VIII, 1900, no. 1, p. 1-29.

the coral seas of both hemispheres. The Alpheidæ have no commercial value, but are of great biological interest, on account of their wide variation in form, coloring, and development, as well as for their remarkable instincts and habits.

The large and handsome spiny or thorny lobsters (family Palinuridæ) are represented chiefly by the single genus *Palinurus*. The langouste of the French, which has been celebrated from antiquity, is noted for its great size, brilliant coloring, and formidable appearance, though claws are lacking, as well as for its small and numerous eggs and grotesque transparent larvæ. Its flesh, which is mainly confined to the thorax and tail, is considered by many quite as delicate as that of the true lobsters. From 13 to 16 species have been described from the temperate and tropical seas of the world. According to Spence Bate,[a] this genus is represented in the South Indian Ocean by *Palinurus edwardsii*, the range of which extends from the Cape of Good Hope to New Zealand, by *Palinurus trigonus* and allied forms in Japan, by *Palinurus frontalis* on the coast of South America, and by *Palinurus longimanus* and related species in the West Indies. The common spiny or rock lobster (*Palinurus vulgaris*) of southern and western Europe is an important article of marine food, particularly in France and on the coasts of the Mediterranean Sea and its islands. It is commonly seen in the markets and restaurants of London, where it commands a good price.

According to Ritchie,[b] *Palinurus vulgaris* occurs on all the shores of the British Isles except a part of the east coast to the north of Flamborough Head. It is most abundant in the southwest, and scarcer northward, but is frequently debarred from entering traps on account of its stout, unyielding antennæ. *Palinurus* in the adult state is unknown in the North Atlantic Ocean north of the Bermuda Islands, but its pelagic larvæ are undoubtedly borne far to the northward by the Gulf stream. It is represented on the western coast of North America by *Palinurus interruptus*.

The carapace of the langouste is not "buttoned" to the tail so effectively as in the common lobster; all the thoracic legs end in long dactyls with indurated tips, which are studded with dense bunches of stiff setæ. The first two pairs of legs are greatly elongated, and the tactile setæ of their dactyls, which resemble bottle brushes, exhibit an extraordinary development.

The largest of the scaly or warty lobsters is represented by *Scyllarus*, which occurs both in the Mediterranean and the North Atlantic Ocean, and is said to attain a length of 18 inches and to excel all other lobsters in the quality of its flesh. Their quadrangular, flattened shell and small, slender legs give them a singular appearance, but specially remarkable are the short, scale-like antennæ, which are possibly used as shovels or scoops in burrowing. Their small and widely separated eyes are completely embedded in the carapace, which is studded all over with wart-like tubercles, thus giving it a granulated and leathery texture, while on the inside it has the appearance of a fine sieve of uniform pattern. Each hole gives passage to a bundle of tactile setæ, which spread in the upper layers of the shell and issue through minute pores

[a] Bate, Spence: Report on the Crustacea Macrura; Scientific results of the voyage H. M. S. Challenger; Zoology, vol. XXIV. London, 1888.

[b] Ritchie, James: Distribution of Palinurus in British waters. Proceedings of Royal Physical Society of Edinburgh, vol. XXIII, p. 68–71. Edinburgh, 1910.

upon the tubercles or around their margins. The last pair of thoracic legs, in the females only, bear claws, which led to the fanciful notion that they were used by the mother in rupturing the eggs and liberating the young. The eggs are very small, and, as in *Palinurus*, the young issue in the peculiar transparent larva known as phyllosoma.

The whole front of *Palinurus guttatus* is armed with stout spines culminating in a pair of rostral horns, which in large specimens rise vertically to the height of an inch or more in parallel planes, thus shielding the eyes and presenting one of the most effective types of protective armature to be seen in an adult crustacean. The antennules are extremely long and slender, while the antennæ have very stout basal stalks, and long stiff flagella, encircled at intervals with sharp teeth, like the war mace of a South Sea Islander.

The second segment of the antenna bears a notable structure, usually described as a stridulating organ. The inner surface of this division is free, and carries a pad and flap which, with the movements of the antenna, plays backward and forward over a smooth ridge or track on the somite. The sound, which it is said may be heard in or out of water and may be produced artificially after death, is evidently caused by friction of the hard chitinous surface of the pad on the track over which it slides. (See p. 240.)

The California spiny lobster, according to Rathbun, may attain a length of 14 inches, and an average weight of 3⅓ pounds, the greatest weight recorded being 11½ pounds. The usual length of *Palinurus vulgaris*, as given by Bell (*20*)[a] in 1853, was about a foot, but 18 inches was sometimes reached. His description was from a male of the latter size, which weighed 5 pounds. "I can not but think," said Bell, "that Dr. Milne Edwards is greatly mistaken in attributing to individuals of that size a weight of from 12 to 15 pounds." The Californian langouste is most abundant on the southern part of the coast. It is often trapped in great numbers, but even twenty years ago we are told by Rathbun that the species was in danger of extermination from overfishing.

Artificial propagation of the Japanese spiny lobster, *Palinurus japonicus* Gray, was undertaken by the fisheries institute, near Tokyo, previous to 1899, and a report of progress was published in that year. Great difficulty was experienced in handling the larvæ, on account of their minute size and long metamorphosis. The spawning and hatching periods of this lobster, as I am informed by Tasute Hattori, who conducted the experiments, extend from late April to late September. The larvæ were easily hatched, but gradually died off after the fifteenth or sixteenth day. No success had been attained in 1901, since which time no further information has been received.

The Nephropsidæ, the best known of the Crustacea, on account of their high commercial value as food, are represented by three species, the Norwegian lobster, *Nephrops norvegicus* Linnæus, the common lobster of Europe, *Homarus gammarus* Linnæus, and the common lobster of America, *Homarus americanus* Milne Edwards.

The technical names for the lobsters adopted in a former work (*149*) are here retained, pending a decision upon the question by the International Committee on Nomenclature of the International Zoological Congress, which met in Boston in 1907.

[a] Italic figures in parentheses refer to works enumerated in the bibliography at the end of this paper.

The question of the validity of Latreille's types in his "Considérations Générales . . ." of 1810, has been raised by Stebbing, who would restore the terminology of Leach, designating *Astacus Potamobius* and *Homarus Astacus*.[a]

Aside from the merits of this controversy, it may be well to point out again that Latreille and others who have followed him were wrong in asserting that Aristotle makes no mention of the river crayfish (*149*). On the contrary, the Father of Zoology uses the term *ἀστακός* to designate both crayfish and lobster, and so far as antiquity is concerned neither has the claim of priority.[b]

The Norwegian lobster is common not only to Norway but to the coasts of Scotland and Ireland. While essentially a northern form, it is found as far south as the Mediterranean but in much less abundance. It attains a length of from 7 to 8 inches, and in life is of a delicate flesh tint, boldly marked with light brown in symmetrical pattern over the abdomen and tail fan. Its slender form suggests the shrimp type, and its large kidney-shaped eyes remind one of *Penæus*, and of the adolescent lobster (*Homarus*) when from 1 to 3 inches long. The claws of the first pair of thoracic legs are slender, of nearly equal size and keeled above, below, and at the sides, each keel having a single, or at the sides a double row of spines. Bell, writing at the middle of the last century, said of this species that it was frequently on sale in the Edinburgh markets, and was occasionally seen in London.

The European lobster is found on the shores of the British Islands, and on the western coast of Europe from Norway to the Mediterranean. The southwestern coast of Norway appears to be the central point of its distribution and still supports the largest of the European fisheries, but the species is found northward as far at least as Tromsö, or to about 69°–70° north latitude. (See *306*.) It is very rare, if present at all, in Iceland. It does not appear to enter the Baltic, and is not common in the Mediterranean, being limited in its eastern range by the Adriatic Sea. In Great Britain it is chiefly confined to certain districts on the west and north coasts.

Of the three kinds of lobsters already described for the Atlantic and its tributaries, the Norwegian and common lobsters are typical northerly forms, while the langouste or *Palinurus* abounds only in the south. The best fishing grounds for the common lobster in the Scottish seas are said to be the Orkney and Outer Hebrides islands.

The common lobster of Europe resembles the American lobster so closely in every structural detail that the two might at first sight be considered as geographical varieties of the same stock rather than as distinct species. It has been pointed out that the under side of the beak or rostrum is smooth in the *Homarus gammarus*, while in the American form it is armed with a spine, a rather trivial distinction in view of the variable character

[a] This commission reported to the Congress, which met at Graz, August, 1910, in favor of accepting Latreille's type designations. The term *Astacus* should therefore be restricted to the crayfishes, and the names stand as designated in the text. See opinions rendered by the International Commission on Zoological Nomenclature. Publication No. 1938, Smithsonian Institution, Washington, 1910.

[b] Those interested in discussions of this character are referred to no. 225 and no. 260 of the bibliography at the end of this work, and also to the following: Rathbun, Mary J., List of the decapod Crustacea of Jamaica, Annals of the Institute of Jamaica, vol. 1, no. 1, 46 p. Jamaica, 1897; Faxon, Walter, Observations on the Astacidæ in the U. S. National Museum and in the Museum of Comparative Zoology, with descriptions of new species, Proceedings U. S. National Museum, vol. xx, p. 643–694, Washington, 1898; Stebbing, Thomas R. R., The late lamented Latreille, Natural Science, vol. xii, p. 239–244. London, 1899.

of such structures. In fact, either one, two, or three spines of inconstant size may be present in the American lobster, though this is a condition which in some cases might be attributable to an injury and its imperfect repair. In the slight differences observed in the development of the American form, however, there are more valid reasons for maintaining the specific names.

It has been the accepted belief that the American lobster attains a greater size than its European counterpart, but it is possible that in early days the maximum size was essentially the same. The fishing of lobsters in Europe is of great antiquity, and the average size of the adults taken has been reduced in consequence, while the industry in this country has been mainly developed during the last hundred years. The same gradual falling off in size, due to the same cause, has nevertheless been experienced on the New England coast and in the maritime provinces. It seems certain, however, that the American lobster has larger claws, and, length for length, it will weigh more than the European form. (See chapter III, p. 195.)

The slight differences in the development of the two forms, already referred to, are seen in the young at the moment of hatching. The abridgement of the larval period has been carried a step farther in the common lobster of Europe, so that its young issue from their eggs in a stage nearly comparable to the second larva of the American lobster.

DEVELOPMENT OF THE CRUSTACEA.

All the decapod Crustacea are developed from eggs which in the Macrura are fertilized outside of the body and are generally carried until hatched on the under side of the tail or abdomen of the female, where they are glued to certain hairs of the swimmerets. The sperm cells are vesiculate and often "rayed." The eggs vary in number from less than a dozen, as found in small species of *Synalpheus* with abbreviated development, to several millions, as in *Callinectes* and *Palinurus*, and from nearly $\frac{1}{6}$ inch, in certain deep sea shrimp, to less than $\frac{1}{100}$ inch in diameter.

The time of fertilization, so far as known, always coincides with that of oviposition and attachment. By means of a liquid cement the eggs are fixed, in a way to be later discussed, often to one another and always to the swimmerets under the abdomen. In life the swimmerets beat rhythmically backward and forward, whether the animal is in motion or at rest, and the attached eggs are thus constantly cleaned and aerated under natural conditions.

The ova are delicate and soon die if cut loose and left to themselves. In order to rear them successfully under such conditions, artificial aeration of some kind must be resorted to and conditions devised to prevent the accumulation of sediment or parasitic growths over the surfaces of the eggs. The best "brooder" of any decapod's eggs is undoubtedly the mother, whether lobster, shrimp, or crab.

The period of fosterage varies from a few days or weeks in some of the smaller tropical decapod crustacea to nearly a year in the lobsters. There is a similar variation in the frequency of spawning; certain Alpheidæ of the Bahama Islands apparently have a succession of broods the year round, while others may lay their eggs twice or once only each year. In the American lobster the breeding period is biennial, but it is possible

that successive annual broods are occasionally produced, as has been known to occur in *Homarus gammarus* on the English coast, and after transplantation to New Zealand.

In many of the prawns the eggs all hatch in the course of a few hours, and at night or very early in the morning, as I have observed in *Pontonia*, *Stenopus*, and *Synalpheus*. The adult *Pontonia* lives in the mantle chamber of *Pinna*, a large bivalve mollusk. For a day or two its young move about in a dense cluster like a swarm of gnats.

The young in most crustacea are hatched in an immature state, and in most species they cut loose from the parent at once, proceed to the surface, and as pelagic larvæ lead an independent existence for days or weeks. Though as adults they may be sedentary and chained to the bottom, as larvæ they are usually most active, and it is during this period of free swimming that they undergo their metamorphosis, or series of changes by which most of their proper adult characters are acquired.

So remarkable are some of these larval changes, and so great is the difference of degree in which they are expressed, even in forms so near akin as lobster, crayfish, and prawn, that the fact when first affirmed was denied as incredible. The credit for the discovery of the metamorphosis in Crustacea, which has proved to be a most fruitful generalization in zoology, belongs primarily to a Dutch naturalist, who has not always received his just dues, and secondarily to an Irish zoologist, for the old observations of Martin Slabber,[a] made June 24–28, 1768, and published with excellent drawings in 1778, were not followed up and fully understood until J. Vaughan Thompson confirmed and completed them by studies began in 1822, continued for many years, and published at various times from 1828 to 1843. The sea-waterflea or *Taurus* of Stier, which Slabber figured and distinctly described as passing by metamorphosis to a different and higher form, was afterwards regarded as representing an independent genus of animals and renamed *Zoé* or *Zoëa* by Bosc[b] in 1802.

Bell, who has given a very fair account of this subject in the introduction to his work already referred to, thought that the zoëa which Slabber had under observation was the larva of the common ditch prawn *Palæmon varians*, later described by Du Cane.

Very shortly Thompson obtained in abundance larvæ resembling the *Zoëa taurus* of Bosc by rearing the eggs of the common English crab, *Cancer pagurus*. Again in 1835, by extending his studies to the common green crab, *Carcinus mœnas*, he showed that it not only was hatched as a zoëa, but passed from this larval state into a megalopa before acquiring the true crab-like form and characteristics, proving that this mythical genus which had been proposed by Leach was, like the zoëa, only a passing phase in the metamorphosis of the crab. Then it was shown that in the course of its development from the egg the crab passed through two consecutive stages which were so unlike each other and so unlike the adult form that former naturalists had placed them not only in different genera but in different families.

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[a] Slabber, Martinus. Natuurkundige Verlustigingen behelzende Microscopise Waarneemingen van In-en Uitlandse Water- en Land-Dieren. Waarneeming van een Zee-Watervloo, genaamd Taurus of Stier, v. stukje, 5 plaat, p. I–XII, 1–166, pl. 1–18. Haarlem, 1769–1778.

[b] Bosc et Desmarest, Manuel de l'histoire naturelle des Crustacés, t. II, p. 237. Paris, 1830.

Few general laws are without exceptions, and the fact that metamorphosis, which is even more common in crustacea than in insects, is sometimes scamped or wanting altogether, led at once to confused and contradictory ideas. The abbreviated larval history of the crayfish which had been worked out with great care by Rathke in 1829 and that of the European lobster first announced by Thompson (*262*) in 1831, and confirmed by Brightwell in 1835, as well as that of the West Indian shore crab, *Gegarcinus ruricola*, determined at the same time by Westwood, led to temporary difficulties, which were eventually cleared away when the development of many kinds of both macruran and brachyuran crustacea had been studied with sufficient care.

It thus appears that the term "zoëa" was first applied to the larva of a prawn and crab, in which the swimming appendages are three pairs of claw feet or maxillipeds, the thoracic legs being rudimentary buds when represented at all. The abdomen is segmented, but bears no appendages and ends in a forked telson. There is a long depressed rostrum and a very long and sharp dorsal spine which springs from the middle of the carapace, both of which seem to be admirably adapted for protection. Though many variations occur in the larvæ of closely related genera and it is difficult to make general terms fit the varying degrees of modification which larvæ have undergone, it seems best to preserve the historical usage of the word zoëa as far as possible. For this reason we speak of the young lobster when hatched with its thoracic appendages well formed and using both its great maxillipeds and following thoracic legs for swimming simply as a larva rather than as a zoëa, however modified.

Most true crabs and prawns hatch as zoëas from minute eggs, and are commonly translucent and flecked with brilliant red and yellow pigment cells. They molt frequently during the first few weeks of life, passing in the case of crabs through a megalops stage, and then gradually assuming the structure and habits of the adult animal.

Entomostraca generally, and exceptionally certain of the Malacostraca, such as the decapod *Penæus* and the schizopod *Euphasia*, hatch from eggs still more minute and in a much simpler larval form called the nauplius. It is unsegmented, possesses but three pairs of appendages, representing the antennulæ, antennæ, and mandibles of the adult, and has a single median "nauplius" or "Cyclopean" eye. Upon the theory of recapitulation, the nauplius has been regarded as the representative of a primitive or ancestral form, but it seems more probable that existing larvæ of this type have become modified to meet the present conditions of their environment.

In every metamorphosis individuality is preserved from egg to adult, and development proceeds according to this simple formula: Egg = embryo = larva 1, 2, 3+ = adolescent stage 1, 2, 3+ = adult stage 1, 2, 3+ $\begin{cases}\text{eggs, or}\\ \text{sperm.}\end{cases}$

A long metamorphosis which entails a long pelagic life near the surface means greater risk and greater destruction than one of short duration. Consequently it is not surprising to find a general tendency to shorten this larval period, reducing the metamorphosis by shifting it to the egg, or, more exactly, by lengthening the period of egg development. In this case the supply of food yolk is increased to support a longer life within the egg membranes, and the larvæ or young issue in a more advanced state, and as a rule have

a shorter pelagic period. The size of the individual egg is increased, but the number of eggs is diminished. The alternative lies between two extremes as follows:

a { Eggs small, but many of them.
Long metamorphosis.
Less chance for individual survival, but more individual chances.

b { Eggs large, but few in number.
Metamorphosis shortened.
Greater chance for the individual, but fewer individuals to take it.

Between these two types of adjustment many compromises have been made. The principal larval stages or types in decapods which have received definite names, being the survivals in some cases of a period when crustacean larvæ were considered adult forms, are the following:

(1) Nauplius and metanauplius. The shrimp *Penæus* is hatched as a nauplius and passes through the metanauplius, first and second protozoëa, first and second zoëa, and mysis stages, before attaining the adult form. *Lucifer* hatches as a nauplius, molts into a metanauplius stage, with buds of three more appendages present; then passes successively through the protozoëa, zoëa, schizopod or mysis, and mastigopus stages, and finally to the adult.

(2) Protozoëa, zoëa, and metazoëa. The shrimps *Sergestes* and *Stenopus* hatch as protozoëas, and pass the successive stages as given for *Lucifer*.

In the protozoëas the antennæ are large and are often used in swimming; the carapace is formed, and the abdomen is unsegmented or but incompletely marked off into somites. The telson is forked and garnished with plumose setæ.

A protozoëan stage has been assigned to the lobster, but erroneously, as will be later explained.

The zoëa characteristic of the crabs has seven pairs of appendages and a segmented abdomen. The last two pairs—first and second maxillipeds (*Callinectes*)—are swimming feet, which in the adult are converted into mouth parts. Many shrimp are hatched as modified zoëas with three pairs of locomotor maxillipeds, and the abbreviation is carried a step farther in some species of *Synalpheus* (*S. minus*) where buds of three pairs of thoracic limbs appear behind the maxillipeds, and still farther in others (*S. brevicarpus*), where the first young to appear are in a "mysis" stage similar to the second larva of the lobster.

(3) Megalopa. The changes which follow in the early development in the crab zoëa lead first to the metazoëa, with rudimentary thoracic limbs and pleopods, and then by a sudden leap to the megalopa, a form comparable to the fourth stage of the lobster. The megalopa has large, free, stalked eyes, large claws, and functional walking legs. The swimming exopodites or outer branches of the maxillipeds have atrophied and disappeared, and like a lobster from the fourth stage onward, it has a segmented abdomen with functional swimmerets. It has also well-developed statocysts or balancing organs and no longer reels in its motion through the water by day, but maintains a definite, upright position. In the course of succeeding molts the abdomen becomes reduced and modified, while the animal acquires the peculiar structure and habits of

the adult crab. The development is abbreviated in the *Gegarcinus ruricola*, the gaily colored terrestrial crab of the West Indies, the large eggs and young of which were a puzzle to the early observers.

(4) Mysis or schizopod stage. The biramous condition of the thoracic legs characteristic of this stage is transitory in the larvæ of the higher Crustacea, but permanent in the lower order of schizopods. The oar-like exopods of the larval thoracic appendages persist in the lobster until the fourth molt, when they are suddenly reduced to rudiments, and after the fifth stage no vestige of them remains.

(5) Larval period reduced in various degrees, and metamorphosis in some cases practically absent. In addition to the crayfishes, lobsters, and other illustrations of abbreviated development already given, we may mention *Synalpheus longicarpus* of the West Indies as a striking example, in addition to certain fluviatile and many deep-sea forms.

Like other animals, the Crustacea tend to recapitulate in some degree the history of their ancestors in the course of their own development, and to become modified in structure and instincts to fit them for a temporary pelagic life which is totally unlike that assumed when adult. Their history is further complicated, as has just been seen, by the tendency to abridge the larval period or lengthen the time spent in the egg.

Shortening the path of development is not a peculiarity of arthropods, but is common with both vertebrates and invertebrates. It depends in a large degree upon the relative amount of food yolk and protoplasm of the egg cell, both of which are derived from the parent, and primarily upon the unknown variations and conditions which have led to this result. The size of the egg is proportional to the amount of yolk which it contains, not the size of the animal producing it. Thus the egg of a snapping shrimp 1 to 2 inches long may be many times larger than that of the lobster, while the egg of the latter is hundreds of times larger than that of the blue crab. When the amount of yolk is small, as in the egg of the starfish or spiny lobster, the young hatch in an immature condition; at the other extreme, when the egg is relatively large, as in the crayfish or domestic fowl, the whole period of early development is passed at the expense of the egg substance, and within its envelopes. The chick hatches in the form and with many of the instincts of an adult bird, ripe for the experience of bird life and capable of using it with profit.

The yolk retards the progress of development up to the time of hatching, but greatly shortens the adolescent period. The chick of the domestic fowl spends 21 days in the egg, but in the hands of the poultry breeder it may later attain the weight of 1½ pounds in 3 months, when it is ready for market.

On the other hand, the egg of the starfish or sea urchin, which is unencumbered by a great mass of yolk, and very small in consequence, measuring about $\frac{1}{200}$ inch in diameter, hatches at ordinary temperatures in 24 hours. It must, however, lead a long life as a larva, make its own living, run the gauntlet of enemies, and keep up the struggle for months. Thus the handicap at the start may count for little in the end. The advantage gained by the fowl in having a few very large eggs is offset by that of a vast number of almost microscopical ova in the echinoderm.

In the lobster the conditions of development are intermediate between such extremes, but in weighing them the structure and habits of the animals at every stage, the environment, and their adjustment to it must be considered. The whole period of development is long, followed by a long period of adolescence, but the relative duration of the swimming life, which is about 3 weeks, is shorter than in the starfish or in *Palinurus* (see p. 160). This is a fortunate circumstance in view of the possibilities of artificial propagation, as will be later seen.

While the abbreviation of the metamorphosis is attended by an accumulation of yolk in the egg, it is impossible to explain either how this has been effected or why in any case such a course should have been followed to secure greater harmony or fitness to the environment.

In fresh-water forms and in deep-sea species the shortening of the metamorphosis may be more uniform and the advantage derived more apparent. In all cases, however, it is a question of the survival of the young, but no one can say why in *Palinurus* the problem has been solved by increasing the number of individual chances and in the lobster by lengthening the period of fosterage and reducing that of the larva. In any case the tax on the parent, when no parental instinct is involved, is essentially the same, though the items are changed, since the total amount of food yolk manufactured in the ovaries of a crab, which lays millions of eggs, is probably not relatively greater than that produced in the organs of the lobster, whose eggs are counted only by tens of thousands. The greater the size of the egg, however, the longer is the tax issue upon the energy of the young deferred and the greater the reduction of its rate.

The adjustment represented by either extreme is certainly advantageous in the long run, but probably neither is the best under all circumstances.

FAMILY LIFE IN CRAYFISH.

The crayfishes, which are now all inhabitants of fresh water or burrowers in soil where moisture is available, are undoubtedly descended from marine lobster-like ancestors, and, as we have seen, for reasons not fully understood have undergone a still greater reduction in larval development. They have, further, acquired an interesting family life, which was noticed by Rösel von Rosenhof over one hundred and fifty years ago. An adequate account of this relation has finally been given by Andrews,[a] and in concluding this chapter we shall give a résumé of one phase of it, based upon his work.

Metamorphosis has been curtailed to such an extent in *Astacus* and *Cambarus* that they are hatched in a form which suggests the fourth stage of the lobster. In reality the young crayfish presents a curious compound of embryonic, larval, and adult characters. The peculiar family relation which serves to tide the young over a helpless period of infancy to complete independence endures, according to Andrews, for about a fortnight, or until after the second molt in *Astacus* and after the third in *Cambarus*.

[a] Andrews, E. A. The young of the crayfishes Astacus and Cambarus. Smithsonian Contributions to Knowledge, vol. XXXV, no. 17, 18, p. 1–80; pl. 1–X. Washington, 1907.

It is dependent upon a complicated chain of events, which suggests the story of the old woman who went to market to buy a pig. Thus if the egg stalk in *Astacus* does not adhere to a "hair" of the parental swimmeret or to another egg; if the two egg shells are not themselves adherent; if a certain delicate thread, which is spun, as it were, from an embryonic cuticle shed at hatching time, does not itself stick on the one hand to the telson of the young and on the other to the inside of the inner egg shell, and thus tether the little one to its mother; if again, a little later, when its leading string has broken, this young one has not been enterprising enough to hook on to some part of the egg glue with its great forceps, the tips of which have been bent into fishhook form, it comes to certain grief. The result is fatal at whatever point the chain weakens and snaps.

A few hours after hatching, the helpless little crayfishes, still dangling from the "telson threads" which secure each to the parent, begin to flap their abdomens and to open and close their big, hooked claws. In this way they manage to seize the old stalk of the egg and, with hooks embedded in its tough chitinous "glue," they hold on, literally for dear life, often grasping the same stalk with both chelæ.

At the second molt this crayfish is for the first time free, and soon begins to descend the parental pleopod, climbs over its mother's body, and makes short excursions in the neighborhood, returning again and again to the alma mater and the family brood. Hitherto it has been sustained solely by the generous amount of yolk inherited from its egg state, but since the egg stalks and cases, as well as the cast-off skins, which were attached to the mother, disappear at this time, it is thought that they are eaten by the young and constitute the first direct food they receive before beginning to forage for themselves.

In *Astacus* the "telson thread," according to Andrews, represents an embryonic molt or cuticle, and the abdominal part is turned inside out at the time of hatching and drawn out into the thread, the cuticle sticking on certain of the median marginal spines of the telson. The newly hatched *Cambarus* is tethered to its mother in a somewhat similar way by means of the partially inverted and telescoped "lost larval cuticle," which is shed at hatching and is in this instance an "anal thread," since it sticks at two points only—on the side of the mother to the egg membranes, which are adherent to her, and on that of the young *Cambarus* to a portion of the intestine where its cuticular lining is at first set free. As a result of the tension this embryonic molt is stretched and crumpled, with a tendency to turn the abdominal part inside out. This telescoping and partial inversion of the discarded cuticle is checked only by the molted plate of the telson, with the resultant production of a narrow creased ribbon, the "anal thread," which is firmly fastened to the intestinal wall.

Chapter II.—THE AMERICAN LOBSTER: ITS ECONOMIC IMPORTANCE AND GENERAL HABITS.

White men caught lobsters in Massachusetts Bay for the first time early in the seventeenth century. The Pilgrims and Englishmen who began to flock into the bay colony about the year 1630 were well acquainted with the products of the sea in their old home, and the coast of New England supplied their tables with essentially the same kinds, only in far greater abundance. It is said, indeed, that the Pilgrims began at once to pay their debts, due in England, out of the products of their fisheries.

In the chronicles of those early days the lobster is honored with frequent mention, and the early colonists must have enjoyed to the full both the new and the familiar kinds of American fish, lobsters, crabs, and clams, so big, so palatable, so abundant, and so cheap everywhere along that coast. Indeed, one would think there was no need of starvation, with lobsters and the other forms of sea food to be had on every shore. To quote from Mrs. Earle (*80*), the minister, Higginson, writing of Salem lobsters, said that many weighed 25 pounds apiece, and that "the least boy in the plantation may catch and eat what he will of them." Again, in 1623, when the ship *Anne* brought over many of the families of the earlier Pilgrims, the only feast of welcome which the latter had to offer was "a lobster, or a piece of fish, without bread or anything else but a cup of spring water."

The Pilgrim lobsters "five or six feet long," ascribed to New York Bay, take us back one hundred years further, to the time of Olaus Magnus. In a tabulated list of some fourteen of the biggest lobsters ever captured on the Atlantic coast (no. 9, table 1, p. 195) for which authentic weights or measurements have been preserved, the giant among them all weighed 34 pounds, and measured exactly 23¾ inches from spine to tail. No doubt the Pilgrims would measure a lobster as some fishermen do now, with the big claws stretched to their fullest extent in front of the head. In this condition the actual length of the animal is about doubled, so that the length of the New Jersey record breaker, when distended in this way, would reach nearly 4 feet, and the Pilgrim 6-foot lobsters have probably been stretched nearly a yard. (Compare fig. 1.)

In an account of marketing in Boston in 1740, "oysters and lobsters" are mentioned, "in course the latter in large size at 3 half-pence each," and this abundance continued for over one hundred years.

To revert at once to modern times, many no doubt remember when lobsters were sold by the piece, and at a few pennies at that. Five years ago, with a market price of 25 cents per pound, a lobster weighing 3 pounds 9¼ ounces, at an inland market in New Hampshire, cost 90 cents. The clear meat of the claws and tail of this animal, which had a fairly hard shell, were found to constitute but 27 per cent of the whole. (See table 3, p. 214) This would bring the cost of such meat to 90 cents per pound.

Even when every edible part of this animal was saved, which is seldom or never done, the total waste was found to be 45 per cent, and the cost of all edible parts 45 cents per pound. At the present retail prices of from 30 to 35 cents per pound, these estimates would have to be considerably increased.

GEOGRAPHICAL RANGE OF THE AMERICAN LOBSTER.

The American lobster (*Homarus americanus*) is found only on the eastern coast of North America. Its geographical range covers about twenty degrees of north latitude, from the thirty-fifth to the fifty-second parallel, and embraces a strip of the North Atlantic Ocean 1,300 miles long and 30 to 50 miles wide, and according to one estimate 7,000 miles in length when measured along the curves of the shore. Its vertical distribution varies from 1 to over 100 fathoms. The most northern point at which its capture has been recorded is Henley Harbor, Labrador (*209*); the most southern point, the coast of North Carolina.[a] Since the fishery was begun on the southern New England coast and was gradually extended northward, it is not surprising to find the lobster at the present time not only more abundant but attaining the greatest average size in the northerly parts of its range—in eastern Maine and the Maritime Provinces. It should be noted, however, that three of the largest lobsters captured in recent years are from New Jersey. (See fig. 1 and table 1, p. 195.)

HISTORY AND IMPORTANCE OF THE LOBSTER FISHERIES IN BRIEF.

According to Dr. Richard Rathbun (*227*), who was the first to give us a history of the American lobster fisheries, this fishery as a separate industry began toward the close of the eighteenth or the beginning of the nineteenth century, and was first developed on the coast of Massachusetts and in the region of Cape Cod and Boston, some fishing being "done as early as 1810 among the Elizabeth Islands and on the coast of Connecticut." "Strangely enough, this industry was not extended to the coast of Maine, where it subsequently attained its greatest proportions, until about 1840."

The early white men learned many lessons in fishing from the Indians, and those living upon the coast in the course of time began to supply settlers more remote, until the Cape Cod region, having become famous, attracted fishermen with their smacks from Connecticut and from other states, and furnished most of the lobsters consumed both in Boston and New York for fifty years, or until the middle of the nineteenth century. In 1812, as Dr. Rathbun remarks, the citizens of Provincetown, realizing the danger of exhausting their fishing grounds, succeeded in having a protective law enacted through the state legislature, apparently the first but not the last of its kind, for legal restrictions, including this statute, have been in force ever since. But this measure was designed to protect the fishermen rather than the lobster, for it was merely declared

[a] So far as known, the lobster has been taken but four times on the North Carolina coast during the past forty years, namely: One lobster in 1870 at Beaufort; one dredged by the *Albatross* in 1884 off Cape Hatteras in 30 fathoms; one said to have measured 18 inches, caught in a gill net at Nags Head in 1903 and exhibited for some time as a curiosity at Elizabeth, Virginia; and another, as noted by J. N. Cobb, was caught by a fisherman at Oregon Inlet, presumably not far from the latter date. For the last two notices I am indebted to Dr. H. M. Smith of the U. S. Bureau of Fisheries.

illegal for anyone not a resident of the Commonwealth to take lobsters from Provincetown without a permit. The laws later enacted proved of little or no avail; by 1880 the period of prosperity had long passed, and few lobsters were then taken from the Cape. Only eight decrepit men were then engaged in the business, and were earning about $60 apiece. This great local fishery was thus rapidly exhausted by overfishing, and it has never recuperated.

The history at Cape Cod has been repeated on one and another section of the coast, from Delaware to Maine, and is already well advanced in the greatest lobster fishing grounds of the world, the ocean and gulf coasts of the British Maritime Provinces of Canada, especially of New Brunswick and Nova Scotia, and in Newfoundland.

Every local fishery has either passed, or is now passing, through the following stages:

1. Period of plenty: Lobsters large, abundant, cheap; traps and fishermen few.

2. Period of rapid extension: Beginning in Canada about 1870, and much earlier in the older fishing regions of New England; greater supplies each year to meet a growing demand; lobsters in fair size and of moderate price.

3. Period of real decline, though often interpreted as one of increase: Fluctuating yield, with tendency to decline, to prevent which we find a rapid extension of areas fished, multiplication of fishermen and traps and fishing gear or apparatus of all kinds; decrease in size of all lobsters caught, and consequently of those bearing eggs; steadily increasing prices.

4. General decrease all along the line, except in price to the consumer, and possibly in that paid the fisherman.

The official statistics for the State of Massachusetts and for Canada afford pertinent illustrations of the older and newer phases of this history. Thus, in Massachusetts in 1890, 373 fishermen, working 19,554 traps, caught 1,612,129 lobsters of legal size and 70,909 egg-bearing females, with an average catch per pot of 82. Fifteen years later it required 287 fishermen, using 13,829 traps, to produce about one-quarter of this number, or 426,471, and less than one-seventh the number of egg-lobsters, or 9,865; while the catch per trap had diminished by nearly two-thirds, and was only 31. No substantial increase followed until 1907, when the legal length was reduced to 9 inches, and this was undoubtedly due to the large number of small lobsters caught.

The total product of the lobster fisheries in the United States for 1892 was 23,724,525 pounds, about three-fifths of which were furnished by Maine, and valued at $1,062,392. It is significant to notice that thirteen years later, in 1905, the total yield, according to Dr. Smith (*325*), had fallen to 11,898,136 pounds, with a value of $1,364,721; in other words, during this comparatively short interval, the supply was practically cut in two, but the value greatly enhanced.

The lobster fisheries of Canada, which next to those of the codfish and salmon are most valuable to the Dominion, have yielded, from 1869 to 1906, inclusive, a period of thirty-seven years, a grand total of $83,291,553. In 1897 the produce of this fishery was 23,721,554 pounds, valued at $3,485,265. Ten years later, in 1906, the yield had dropped to 10,132,000 pounds, but, though less than one-half as great, it had nearly the

same estimated value, namely, $3,422,927. Notwithstanding the increased cost to the consumer, even in Canada the total value of the fishery has begun to fall, the product for 1906 being less by half a million dollars than that of 1905.

The lobster grounds of the Atlantic coast were the finest the world has ever produced. In Canada alone 100,000,000 lobsters have been captured in a single year. If properly dealt with, it would seem as if this vast natural preserve should have yielded lobsters in abundance and in fair size for generations and even centuries to come. But instead, lean and still leaner years soon followed those of plenty, first in the older and more accessible regions of the fishery, until the decline, which has been watched for more than three decades, has extended to practically every part of this vast area.

The lobster fisheries of the old world, and especially the more important industries of Norway and Great Britain, when they came to be pursued with the system and energy characteristic of modern conditions, have experienced a similar decline, and upon the whole attempts have been made to meet it in a similar way and with the same result. The treatment has been of the symptomatic kind, and the real cause of the difficulty has not been reached. Sweden, indeed, is said to have felt the need of protective measures two hundred years ago, and to have framed the first laws regulating her lobster fishery in 1686. In 1865 the export of lobsters from Norway, to England chiefly, reached nearly 2,000,000 in numbers. Already as early as 1838 protective measures were being vigorously discussed, and it was proposed to establish a gauge limit of 8 inches; but this was rejected, and a close season (July 15 to September 30, and later extended from July to November) adopted instead. From 1883 to 1887 about 1,000,000 lobsters were captured on the Norwegian coast yearly, having a value of 640,000 francs ($128,000), a large part of the product being consumed in the interior and the rest exported alive. While this small fishery has maintained itself better than most others, it has suffered still greater reduction in recent years.

The product and value of the lobster fisheries of Norway from 1815 to 1907 are given by Boeck (*24*), and Appellôf (*305*), the latter from official returns. According to these data the best single year in its history was 1865, with a catch of 1,956,276 lobsters, and the best periods from 1821 to 1830, with numbers ranging from 784,511 (1823) to 1,609,051 (1825), and 1860 to 1886, with numbers varying from 987,370 (1877) to the greatest record as given above. Since 1886 the annual catch has not touched the million mark, and the numbers have varied from 549,446 (1892) to 992,761 (1907). It is further interesting to note the steady rise in value of the produce of this fishery. Thus the catch of 1883, namely, 1,255,790 lobsters, though greater than that of 1907 by 263,039, had only about one-half its value, or 423,083 crowns ($114,232), as compared with 835,002 crowns ($225,450). Expressed in another way the average price of lobsters had increased from 28.50 crowns per 100 in 1878 to 92.41 crowns in 1905, or over 300 per cent.

Herbst (*136*) writing about 1790, thus speaks of the importance of the lobster fishery Norway at that time:

> In the Stavanger district this trade brings every year more than 10,000 Reichsthaler into the country. Yet many maintain that it is detrimental to Norway, since owing to the extensive fishing of lobsters, other fish have left the Norwegian coast . . . The inhabitants of Zirkson, Holland, were the first to under-

take this trade, and through it they have become very rich. Up to the present time also the English have brought many lobsters from Hittland. From 39 to 40 lobster vessels come each year from Amsterdam and London to Norway, and each carries from 10,000 to 12,000 lobsters . . . When a load is safely landed it is very profitable, since a lobster which is bought in Norway for 2 Danish shillings is sold in England for a crown. This is the fixed price for a lobster, 8 inches or over in length, the legalized gauge. If a lobster lacks a claw, it is then sold for only a shilling . . . The females are considered the best eating.

The lobster fisheries of Denmark, Holland, Belgium, France, Portugal, and Spain are relatively of minor importance at the present time, and in most cases wholly insufficient to supply the home markets. Roché, in 1898 (*237*) placed the total annual value of the French fisheries of the lobster and langouste at 3,114,317 francs ($622,863), of which 1,425,572 francs ($285,114) was represented by the lobster (*Homarus gammarus*).

The yield of the lobster fisheries in the British Islands has in some years reached a total of 3,000,000 lobsters, and complaints of a diminishing supply have been loud and frequent. This would be a little over a third more than the returns of the Massachusetts fishery in 1888, with its higher gauge of 10½ inches at that time. Prince maintains that lobsters are so dear in England that only one person in 15 has one to eat in the course of the year. (See p. 368 footnote.)

Restrictive measures of some sort have been in force in England for a long period. Thus, R. Brookes in "The Art of Angling,"[a] under "necessary cautions," is careful to state that "Lobsters must not be sold under Eight Inches from the Peak of the Nose to the End of the Middle Fin of the Tail; the Forfeiture is One Shilling for each Lobster." He remarks that "Lobsters are taken in Pots as they are call'd, made of Wicker-Work," baited and set in 6 to 10 fathoms of water, or deeper, and adds: "Their Flesh is sweet, restorative and very innocent."

A review of the measures which have been taken to propagate the lobster and to check the decrease in its fishery in recent times is given in chapter XII.

THE CAPTURE, TRANSPORTATION, AND ACCLIMATIZATION OF THE LOBSTER.

The principle of the modern lobster trap is that of the old-fashined rat trap adapted for taking an aquatic animal with as keen a scent as the rodent, but with far duller wits. The device is undoubtedly of great antiquity, but as modified and applied for the lobster it is apparently not over 200 years old. It was introduced to this country from Europe, where, as Boeck (*24*) plausibly suggests, it was first applied in this way by the Dutch in 1713, and was adapted from the eelpot then in use.

Primitively lobsters were speared, gaffed, or hooked, and for a long time on the coast of Norway were taken with wooden tongs about 12 feet long and adapted for use in shallow water only; lobster tongs had not wholly disappeared at the middle of the nineteenth century. All animals taken by such means were injured more or less severely and were unfit for transportation. The gaffing of lobsters from small boats was a common practice in the early history of the American fishery, and a fisherman in Maine once

[a] 2d edition, London, 1740.

told me that in the period of plenty, from 1855 to 1860, he had taken 150 in this way in a single morning.

Then followed the hoop net or bag, sometimes called "plumpers" in England, or "Fallenkörbe" (basket traps) in Germany, which were in extensive use at the middle of the eighteenth and locally to the middle of the nineteenth century, or even later. This was a simple iron hoop with bag net attached and often with crossed and arched half hoops over its mouth. When baited and sunk it had to be watched and pulled at frequent intervals in order to secure the lobsters before they could crawl out. About the year 1858 a giant male lobster, said to have weighed from 25 to 30 pounds, was taken in one of these hoop nets in Golden Cove, Vinal Haven, Me.

Travis (*264*) describes the use of hoops at Scarborough, England, in 1768, but Pennant a few years later remarked that lobsters were sometimes—

> taken by the hand, but in greater quantity in pots, a sort of trap formed of twigs and baited with garbage; they are formed like a wire mousetrap, so when the lobster enters there is no return. They are fastened to a cord sunk in the sea, and the place marked by a buoy.

This English lobster trap undoubtedly came, as Boeck suggests, from the Norwegian "Tejner," or baskets, which were the Dutch adaptation of the eelpot, the Scandinavian name being derived from "tün," the long tough roots of the juniper tree (*24*). After 1713 they were made of plaited willow twigs. Linnæus saw similar baskets in 1746 in use on the coast of Bohuslän. Herbst (*136*), writing in 1790, says that lobsters were then caught in "Tüner," "Teiner," or lobster baskets ("Hummertienen" or "Hummerkörbe") made of birch twigs.

The tines in later use among the fiords of the Norwegian coast were sometimes made of slats or rods nailed to small hoops, and at considerable intervals, which were filled in with interwoven cords of hemp. There were entrance funnels at either end, a door at the top, and a flat stone lashed to the bottom for weight, while in the center of the trap was suspended a peg for attaching the bait. (See *309*, p. 733.) When a lobster was taken from the tine, his claws were securely bound with pack thread, and thus held until he was delivered to the submerged box or car to await final transportation to market.

Essentially this old-style trap has been retained in Europe, where it is to be seen at the present day. Those examined at St. Andrews, Scotland, where they are called "lobster creels," in July, 1896, were small cylinders, made of a wooden frame covered with netting, and were anchored by means of a flat stone tied to the bottom. A fisherman with whom I conversed on the beach had 40 of these creels, and was going to haul them at 5 o'clock that evening, but with no expectation of taking any lobsters, for, as he expressed it, the sea was too calm; rough weather brought better luck. The "tiner" of the Helgoland fishermen, according to Ehrenbaum (*84*), are birdcagelike, cylindrical or four sided, with the bottom weighted with stones, covered with netting or wirework, and with funnel-shaped ends, like eelpots. Each is sunk to the bottom with attached cord which is floated with corks. In Norway hemispherical wicker traps, with funnel at the top, were occasionally used.

The American lobster trap of the present time is simply a larger and more efficient modification of the old wicker "basket," but made of laths with netted heads or ends in the form of a funnel with entrance ring. On the outer islands and coast of Maine the half-cylinder form is preferred. They are 2½ to 4 feet long, 2 feet wide, and 18 inches high, the smaller sizes being now commonly used. A trap of this type which I measured on Great Duck Island in 1902 was 3 feet 9 inches in length and 25 inches in both height and width. The frame was of scantling, from which were sprung three arches or "bows" of spruce, and to these were nailed laths at intervals of 2 inches, one side being provided with a hinged door. The "heads" are made of netted cotton, or, preferably, of manila cord, tarred and strung to a "funnel bow" or entrance ring of spruce, 6 inches in diameter, and often, as in this case, set obliquely to the long axis of the trap, the whole head being drawn inward to form an upwardly directed funnel. The lobster, in order to get to the bait, must therefore climb up the funnel and pass through the entrance ring; when once a prisoner it is liable to crawl over the ring rather than through it to liberty. The spindle for holding the bait is an iron spike securely attached to the center of the floor. Flat stones or bricks are used as weights, and the trap is secured to a 6-strand manila warp, which serves to lower and raise it, as well as to mark its position. This cord, the length of which is determined by the depth of the water, is fastened by one end to a corner of the frame or "sill" of the trap and by the other to a wooden float or buoy, which bears the owner's color or mark. Traps are commonly set on single warps, but in summer are sometimes strung to an anchored ground line or trawl, to the number of 8 to 25 or more units and at intervals of about 30 feet, according to the depth, so that when one trap is hauled to the boat the next in line will be at the bottom. In this case the position of the anchor at either end of the trawl is marked by a buoy. Trawls were sometimes set across currents so that fine particles coming from the bait would be widely diffused, but the practice has been mostly given up. Fishermen tend from 50 to 125 traps, according to conditions, and some have two sets, the winter relay being left on the beach to dry out in summer. The "counters," or lobsters of legal size, are temporarily stored in floating cars until gathered up by well boats, which carry them to the large markets or to the numerous pounds along the coast, where they are stocked for the winter and summer trade.

The traps are baited with small herring, halibut, hake, or codfish heads or with fresh or salted fish of any kind. The fishermen try to follow the movements of the lobsters and in summer fish closer to the shores, ordinarily in from 1 to 10 fathoms, but in winter they often go out 5 or 6 miles and set their traps in 20 to 50 fathoms of water. The traps are pulled as often as possible, once or twice daily in summer, but in winter weather a week or even a fortnight may elapse before the traps can be visited, and many are destroyed by storms.

The fish commission of Massachusetts, in recommending the adoption of a double legal gauge for lobsters of 9 to 11 inches, inclusive, proposed a standard trap which should have an entrance ring not to exceed 3½ inches, with slats not less than 1½ inches

apart, to work automatically to the extent of not permitting lobsters above legal size to enter and of allowing the undersized to escape.

Lobsters destined for inland markets are successfully transported with or without plugging the claws, packed in wet seaweed, and with ice at the bottom. For a long time nearly the entire product of the Norwegian lobster fishery (see p. 172) has been sold in England, the animals, usually with claws bound with cord, being carefully packed in small fish boxes, in heather wet with sea water, and in summer with ice at the bottom; care is taken not only to shield them from the drip, for they can not stand fresh water, but also by means of paper linings to protect them from excessive cold; always with the precaution of leaving suitable openings at top and bottom to allow the air to enter and the water to pass out.

Early in the nineteenth century, according to Prince (*219*), several barrels of lobsters were sent from Nova Scotia, as a present to King George III of England. Again in 1862 several tubs of lobsters in sea water were forwarded from the coast of Maine to the Emperor Napoleon III of France. The longest sea journey yet made by the living lobster was accomplished some time previous to 1896, when the Otago Acclimatization Society of New Zealand succeeded in transplanting 9 lobsters from England, 3 only having died on a voyage of 54 days, covering a distance of 12,000 miles through the Tropics, where water not artificially cooled reaches a temperature of 84° F. The experiment was repeated in 1906, and up to May 30, 1909, four shipments had been made from Plymouth, England, to Portobello (Dunedin), for the fish hatchery and biological station there. The last of these proved most successful, 31 out of 34 lobsters being delivered alive. Each of the animals was given a separate compartment in the wooden shipping tank, and was supplied with clean, well-aerated and cooled water, and was fed during the voyage.

From 1874 to 1889 five attempts to acclimatize the American lobster on the Pacific coast were made by the United States Fish Commission, when 590 animals of both sexes, and some with external eggs, were successfully transported across the continent and distributed at different points from Monterey Bay to Puget Sound. Accounts of these early experiments have been given by Perrin (*319*), Rathbun (*228*), and Smith (*253, a*).

> No positive results having appeared [says Dr. Smith], the experiment was renewed in the fall of 1906, when a special carload of brood lobsters, numbering more than all the previous plants combined, was dispatched to Puget Sound, and in 1907 a still more extensive plant, aggregating about 1,000 adult lobsters, was made in the same water. Further consignments will be made until the lobster is removed from the list of failures and recorded as a great financial as well as a gastronomic success (*325*, p. 1406).

We believe that the Bureau has taken a most commendable step, and in the right direction, the initial attempt being to find a water where the Atlantic lobster will thrive. When this primary question has been settled, further importations to that point, supplemented in time by artificial propagation, promise well for the eventual establishment of new and remote fisheries which, for all that is now known to the contrary, may at some future day enjoy a greater prosperity even than those nearer home.

HABITS AND INSTINCTS OF THE ADULT LOBSTER.

At this point we shall examine certain facts in the general natural history of the lobster, leaving, however, such important subjects as reproduction, growth, and development for special consideration.

The sea bottom is the natural abode of the lobster, as it is of all the large and heavy Crustacea, the source of its food and the scene of all its activities, from the close of free pelagic life to old age. Its external world is the ocean floor, to which it reacts, and it knows no other. While its powers of locomotion are considerable, it never forsakes the water of its own accord or leaves the bottom, to which nature has consigned it by giving it a heavy body and a sedentary disposition. Lobsters wander close to the shore and out to depths of over a hundred fathoms, and the nature of the bottom, or more directly the supply of food, as well as the physiological condition of the animals, especially in respect to their molting periods, determine their abundance within these limits in any locality.

The supply of food, the temperature of the water, and in general the physical conditions of the environment vary greatly throughout the range of this animal, as one might infer from a study of the coast line. From Labrador to Maine the coast is very rugged, deeply indented with bays, and studded with islands, some of which present perpendicular walls to the sea. The coast of Maine, particularly in its eastern and middle sections, is essentially bold, rocky, and diversified to an extraordinary degree by deep channels, extensive bays, and inlets of all kinds, and these are studded with rock-ribbed, spruce-clad islands. The geological formation is pre-Cambrian, the rocks being mainly granites. From 10 to 30 miles from the shore we find large and important islands standing alone or closely related, as Monhegan Island and the Vinal Haven and Matinicus groups. All are essentially masses of granite, which in some cases have been cut by glacial forces into archipelagoes; they abound in basins and channels of various kinds, into which fresh sea water is driven with every tide, and thus form admirable breeding grounds for food fishes, the lobster, and a host of invertebrates. The Cape Cod region is distinguished for its extensive sand shoals, which resemble those of North Carolina. The northern part of the Massachusetts shore is rocky, while the southerly portions are very diversified, abounding in submerged ledges, sandy and weedy bottoms, a great variety of bays and channels, as in Vineyard Sound and neighboring waters. Here lobsters were once exceedingly abundant, until they were nearly exterminated by the fishermen.

Under the variety of conditions indicated we should expect not only to find lobsters larger and more abundant in some localities than elsewhere, a condition greatly influenced by the number and persistence of the fishermen, but also to meet with variations in the time of egg laying and hatching, of molting, and in the rate of growth.

This animal spends most of its time in the search for food and in reproducing its kind. Its instincts are constantly leading it to secure protection through concealment, and we find it burrowing in the mud or sand, or hiding under stones, whether to await its prey or to pass in greater security the crises of its successive molts.

In traveling over the bottom in search of prey the lobster walks nimbly upon the tips of its slender legs, which are provided with brushes of sensitive hairs. The large claws are directed forward, a position which offers the least resistance to the water, or when at rest are held somewhat obliquely, their tips touching the bottom, while the long sensitive "feelers," or antennæ, sweep back and forth continually to give warning of a foe or of objects which its other sense organs fail to detect. In exploring its feeding grounds the movement of the body is chiefly maintained by the swimmerets, or pleopods, which spring from beneath the tail in the form of a double bank of paddles on either side. The swimmeret consists of a short stalk and two flexible blades, which beat rythmically with a backward stroke, and thus impel the animal forward even without the aid of the ambulatory legs. Each blade is further garnished with a fringe of long and strong hairs or setæ, which add to its efficiency as a rowing organ, and certain of which in the female catch and hold the egg glue by which her progeny, in the form of thousands of eggs, are tethered to her body.

The most primitive sense of animals being that of touch, it is not surprising to find tactile organs widely distributed over the body of this crustacean. As will be seen later, they occur by thousands in the form of tufts and fringes of hair-like setæ on the legs and free margins of the shell, and in any part subject to frequent contact either with the body itself, with its food, or the ocean floor. It will also appear that instead of being incased in a solid, impenetrable armor, the crustacean can receive stimuli and impressions from without as readily as if it possessed a soft and delicate skin.

When an enemy appears, or the lobster is suddenly surprised and cornered, it will immediately strike an attitude of defense. Raising itself on the tips of its walking legs, it lifts its powerful claws over its head, after the manner of a boxer, and, striking the offending object, endeavors to crush and tear it to pieces.

When transferred from sea to land the lobster can only crawl in its vain attempts to walk, owing to the great weight of its body, which the slender legs are unable to sustain. If turned on its back its discomfort is immediately shown by attempts to right itself, which are usually successful. When taken directly from the water and left to its own devices on the beach, I have seen it strike out by the nearest path to the sea with as keen a sense of direction as a turtle shows on land. It should be stated, however, that this experiment was tried only within short distances from the water.

By far the most powerful organ of locomotion in the lobster is its "tail," called also the "abdomen" (terms borrowed from vertebrate anatomy), and the "pleon." By the rapid flexion of this muscular tail, aided by its terminal fan, the lobster shoots backward through the water with astonishing rapidity, going, according to one observer, 25 feet in less than a second. If tossed into the water, the animal quickly rights itself, and with one or two vigorous flexions of the tail makes quickly for the bottom as if sliding down an inclined plane.

On calm summer evenings toward sundown lobsters are often seen close to shore, lying on little patches of sand or in eel grass, awaiting their chance to seize a passing fish or crab. When alarmed, they assume the defensive attitude; but press them close,

or try to pin them down with an oar, and they will dart backward toward deeper water; if still pursued they flee in other directions, zigzagging their way over the bottom until safety is found at still greater depths.

Lobsters kept in aquaria of sufficient size and provided with running water often thrive, and if they receive proper care will live for a long period. If the tank is provided with a pile of stones, the lobster will examine this carefully until the most attractive holes are discovered. When several individuals are placed in the same aquarium, each soon selects a hole or corner, for the possession of which it is always ready to fight. This is true of the "lobsterlings" as well as the adults, showing that the power of association or of the formation of habits, which is the mark of intelligence, is well developed. When the occupants of the same aquarium are of equal size and show no weakness, they usually live in peace; but should one become disabled, as by the loss of a claw, it is quickly attacked by the strong and forthwith destroyed.

As the lobster lies in its corner of the aquarium, usually with the tail folded, and always so if a female in "berry," it slowly sweeps the water with its long, sensitive antennæ, which are now held erect, now lowered, until they lie horizontal and extend directly forward in front of the body. The smaller antennæ are elevated, while the stouter outer branch of each beats with a rythmical up-and-down movement; this branch carries the delicate hairs or setæ, which are regarded as the organs of smell. One often sees the animal deliberately lower the whip-like branches of the first pair of antennæ and clean them by drawing them through the brushes of the large maxillipeds; the great claws when not extended and ready for immediate use are turned obliquely inward and downward, with their tips touching the bottom.

All animals that play the part of scavengers must have strong powers of scent or keen eyes to guide them to their prey, and lobsters are no exception to this rule. The turkey buzzard sees, but, according to Audubon and Bachman, can not scent its prey, while the lobster, though dull of sight, has a keen chemical or "olfactory" sense. This is illustrated by the way in which it can be enticed into the traps. It is asserted that when traps are set on a trawl placed across the tide, the catch is greater than when the trawl is set in the direction of the current, since in the former case the chemical substances, or fine particles coming from the bait, are more widely diffused. Lobsters are sometimes wary and shy of entering a trap, and have been seen to crawl about it several times and examine it cautiously on all sides before, too weak or too hungry to resist temptation, they finally enter. When the pots are hauled, lobsters sometimes escape by darting backward through the narrow opening of one of the funnels, but this seldom happens and may be set down to accident.

Sluggish as the lobster may appear when out of the water and partially exhausted, it is quite a different animal, as we have just seen, when free to move at will in its natural abode on the bottom of the sea. In the water it is agile, wary, pugnacious, capable of defending itself against enemies often larger and more powerful than itself, and on occasion of exhibiting a high degree of speed. It often captures its prey by stealth and with concealed weapons. Lying hidden in a bunch of seaweeds, in a rock

crevice, or in its burrow in the mud, it waits until the victim is within reach of its claws. Though far less active and keen witted than many of the higher crabs, and sedentary in the sense of being restricted in its range, it is sluggish only at the period of the molt or in very cold weather. The sense of hearing is probably absent and that of sight far from acute, but this animal possesses a keen sense of touch and smell, possibly a sense of taste, and is quite sensitive to changes of temperature and light (see p. 184).

MIGRATORY INSTINCTS.

Adult lobsters never migrate up and down the coast at definite periods or in considerable numbers in any degree comparable to the semiannual movements of many fishes and birds; in April and May, however, they come in toward the shore, and again in fall retire to deeper water. Such migratory instincts as they possess are of a very diffuse type and are far from being generally displayed. The abundance of food and periodic necessity of molting and laying eggs, and the temperature of the water, may one and all enter with more or less force into bringing about local and restricted movements. When the question of food is paramount, lobsters will pass the winter in considerable numbers in the shallow waters of harbors, but usually only on a rocky bottom where food is to be found. The extent of their journeys is influenced by the slope of the bottom and the depth of water, as well as by the nature of the bottom itself, and varies in different sections of the coast as well as at the same point in different seasons.

Movements of tagged lobsters.—In order to test the extent and rapidity of the adult lobster's movements along the coast, as well as to and from deep water, some interesting experiments in tagging lobsters have been made by Bumpus (*43*) at Woods Hole, Mass., Mead and Williams (*195*) at Wickford, R. I., and by Meek (*316*) and Appellöf (*305*) in Europe.

In the summer of 1898 Bumpus tagged 479 lobsters from which eggs had been removed, and liberated them at various points about Woods Hole. Seventy-six of these were recaptured and the tags returned for identification. The valuable data thus obtained showed a great variation in the "migratory" impulse and remarkable rapidity of movement in individual cases. Some had not strayed far after gaining their freedom for from 3 to 4 weeks, being recaptured near the points where they had been set free, while others had moved at the daily rate of a mile for a period of 10 to 12 days. One of them which had been freed at Woods Hole on July 2 entered a trap at Cuttyhunk Island, 12 miles to the southwest, on July 13, having covered this distance in 11 days. It does not seem probable that such sporadic movements are determined by the search for more abundant food, or for more favorable conditions as regards the temperature and depth of the water or character of the bottom, but are to be set down to individual initiative and general restlessness of behavior. In this connection it would be interesting to learn whether the more sedentary or the more active individuals had showed any evidences of preparation for the molt, which is due in female lobsters shortly after the hatching of the eggs (middle May to middle July at Woods Hole).

Tagging experiments were undertaken by Mead in the summer of 1902 and 1903 at Wickford. Of the 16 released in the first season, the most enterprising traveler had

covered 10 miles in less than 8 days. Out of 385 lobsters tagged and set free in 1903, 30 were later reported, most of them having taken a southerly or southwesterly course down the Narraganset Bay. Eight which had been free from 9 to 31 days had traveled only a mile when captured, June 11 to July 3; 6 had wandered from 10 to 12 miles in the course of 22 to 58 days, having been liberated June 24 to July 26. Further systematic experiments in this interesting subject have been carried on at the Wickford station, and are recorded by Barnes (*15* and *16*, *a*). One of the fastest travelers made 4 miles in a single day.

Movements off Cape Cod and at Woods Hole.—If there were any considerable coastwise migration, it is evident that regions once depleted could be restored under favoring conditions by accessions from neighboring parts. Apparently this does not occur, and, as Rathbun has observed, we may regard each geographical section of the coast as inhabited by a more or less distinct colony, which tends to hold its ground fairly constantly, so that if its numbers be once seriously depleted, recovery under nature must needs be a slow process at best. The history of the Provincetown region on Cape Cod, already referred to, seems to support this idea.

The region about Woods Hole, Mass., including the western end of Vineyard Sound, No Man's Land, and the Elizabeth Islands, was studied for a period of 5 years, from 1890 to 1894, with reference to the general natural history of the lobster, and the following conclusions were then reached regarding its migratory habits: The general movement of lobsters toward the shore in the spring is modified by reason of females with old eggs finding it advantageous to remain on rocky ledges until their young are hatched, while the males press onward to shallower water. After hatching is over, the females make their appearance in large numbers in the sound toward the last of June or 1st of July, and form a large part of what fishermen call "school lobsters" or "buckle shells." Their appearance is probably not as sudden as it often seems. Fishermen as a rule work only one set of traps, setting them now here, now there. In order to follow the movements of these animals systematically, it would be necessary to set traps simultaneously in different places and on different bottoms, and to record the catch for a considerable time.

Some females with old eggs come into the sound before the young are hatched, but the majority do not. It must also be borne in mind that many lobsters remain in the sound and harbors the year round, and that these observations refer only to the movements of the larger number. Toward the latter part of August the pendulum begins to swing the other way, and the lobsters move into deeper water or to a rocky bottom. This outbound movement is continued during the months of September and October, but, as already remarked, it is by no means general and may be more pronounced in cold than in mild seasons.

Aside from their in and off shore movements, the lobsters must be regarded as essentially sedentary or stationary animals. Yet their occasional sudden appearance in great numbers, and often at points where a previous scarcity had been noted, creeping toward the shores in veritable swarms of thousands of individuals, as already reported by Sars (*244*), Appellöf (*305*), and myself (*149*, p. 21), indicate that at certain times and

under certain conditions not at present completely understood, movements of a somewhat different character may take place. The "traveling lobsters" of Sars probably belong to this category, and my former suggestion that they might represent "some large species of surface-feeding shrimp" (*149*, p. 19), may be an error, as Appellöf asserts. Sars's account, if correctly translated, is somewhat ambiguous; it is as follows: "The hard-shell and ponderous lobster must always make an extra exertion in moving about, and its movements can therefore not be of long duration. People certainly talk of the 'traveling lobsters' ('Faerd-hummer') which are said to come from the open sea in large schools, and some even say that they have seen such schools many miles from the coasts moving about rapidly near the surface of the sea. If this is really so, I consider it as absolutely certain that these schools come from no very great distance, possibly from some of the elevated bottoms off the coast." (No. *244*, p. 675.) We consider it highly probable that the "swarms" referred to represent only more concentrated movements of the usual inshore character, the animals coming from elevated areas not hitherto discovered and fished.

In general we conclude that since lobsters as a rule spawn in warming water the migratory impulse must be regarded as primarily correlated with the development of the reproductive organs, which periodically respond to a rising temperature. Incidentally the carriage of eggs, the abundance of food, and molting which occurs in the female shortly after the eggs are hatched, tend to disturb the regularity of these movements.

OPTIMUM TEMPERATURE.

While the question of food supply must be of paramount importance to all bottom-feeding animals like the lobster, the temperature of the water can hardly fail to exert some influence upon their movements. Whether there is a direct reflex response in the lobster to the warming waters of the shores in spring or not, it is a fact that it shows a marked tendency, as we have seen, to move shoreward at this time. Further, without any doubt, there is a certain optimum temperature, under the influence of which, when other conditions are favorable, growth is most rapid, and those dependent processes of reproduction and exuviation most accelerated. The data available, however, do not enable us to determine this point with much accuracy.

The physical conditions of Woods Hole region have been made the subject of special study by Sumner,[a] from whose account the following facts have been gathered. The temperature of sea water at Woods Hole for May ranges from 50° to 60° F. The warmest period extends from approximately July 12 to August 24 (which corresponds with the height of the spawning period of the lobster at this point), with a temperature of 70° to 71°. The September range of 69° to 65° is about the same as that for the first half of July. In the latter part of October the water cools to about the same temperature it had reached during the first half of May. The lowest daily temperature, of about 30°, is recorded for mid-February. The bottom temperature at the western end of Vineyard Sound, at the period of maximum summer heat, was found by Sumner to be 60.2°,

[a] Sumner, Francis B. An intensive study of the fauna and flora of a restricted area of sea bottom. Proceedings of the Fourth International Fishery Congress, Bulletin of the Bureau of Fisheries, vol. XXVIII, p. 1223–1264. Washington, 1910.

or about 10° lower than the average at Woods Hole at a corresponding period. A station in that part of the sound which showed in August a bottom temperature of 55° (60.3° at surface) gave in March 36.7° (at the surface 37.4°).

The temperature of the surface water of Winter Quarter Shoal, Virginia, ranges from 35° to 76° F.; at Five Fathom Bank, New Jersey, the range is 37° to 76°. Delaware Breakwater, which at one time was practically the southern limit of the lobster, is situated between the lightships anchored upon these two shoals. In the Gulf of Maine the mean annual range is approximately 32° to 62°, while at some points the maximum is only 54°. (*228.*)

The average temperature on the north shore of Prince Edward Island has been given as 56.56° in June, 63.40° in July, and 62.27° in August, the bottom temperature in 6 to 8 fathoms being estimated at 55°.

The temperature of the sea on the Labrador coast is said not to exceed 46.05° F. on the warmest summer days. The lobster thus seems to be debarred from this coast east of the straits of Belle Isle by the Arctic current and the lingering ice.

From the facts given above we may infer that the optimum temperature of the lobster lies between 50° and 60° F. When the temperature of the sea water marks from 50° to 55° in spring large numbers of these animals have already begun to creep nearer the shores into shallower and warmer places, and again in fall, when the temperature has fallen to this point, many have already been impelled to recede to greater depths. Many lobsters, however, remain in the relatively shallow water of harbors all winter, a fact already emphasized; so it is certain that temperature is not the only influence at work in directing these semiannual movements. The question of food or nature of the bottom may at times be of equal or of even greater importance.

The lobster, like many other marine invertebrates, is very sensitive to the extremes of heat and cold. If exposed to direct sunlight out of the water, or to the nipping air of a winter's day, it weakens or succumbs in a short time. On the other hand, if packed in seaweed with ice it will live for days or weeks, a fact daily illustrated in the transportation of this crustacean alive to inland markets far from the coast. (See p. 176.)

Lobsters which pass the winter in relatively shallow water often seek protection by burrowing in the mud, as usually happens when they are confined in pounds. In such cases a long period of severe cold may prove fatal. On March 10, 1882, a number of lobsters were taken through the ice by the scoop of a mud-digging machine off the coast of Prince Edward Island. They were said to be sluggish but not torpid.

INFLUENCE OF LIGHT AND NOCTURNAL HABITS.

The lobster is essentially an animal of the twilight, and in its semiadult and adult condition explores the bottom in quest of food mainly after sundown or at night, when it is generally far more active than by day. This may be proved by anyone who watches its behavior when confined in either lobster cars or pounds. These animals it is true on occasion move about by day, but at night they become exceptionally restless. It is probable that the eggs are laid and that pairing takes place as a rule under

the cover of darkness, either at night or in early morning. Such indeed is known to be the common habit of crayfish, shrimp, and many other Crustacea.

While the lobster is very sensitive to light throughout every stage of its existence, its reactions to this stimulus are of a complex character, especially during its free swimming career, as will be seen in a later chapter. It will appear that the young shun or avoid light of a greater intensity or move toward or away from a source of light and in the direction of its incident rays as a result of the varying state of the animal itself and of its environment. There seems to be ever a struggle among competing impulses, now one set of reactions winning the day, now another. In general the young seem to seek the light, as their swimming habits might lead us to expect, and are usually captured in the day time, but they are sometimes caught at night.

After the discovery of the bottom has been made, through all their later adolescent and adult stages they practice concealment, and prefer the twilight of their rock caves or tangles of weed amid the sand. Yet, under exceptional conditions, the adult may expose itself to stronger light.

According to Forel, light can not penetrate the ocean below a depth of 400 meters of tolerably clear water, but even in fifty fathoms off the Atlantic coast the difference between day and night can not be very considerable. This is not the case in shallow bays or sounds with sandy bottoms, which lobsters frequent in summer, and where we may expect to find the greatest difference between their diurnal and nocturnal habits.

The large floating cars in which lobsters are generally stored in readiness for market are always kept closed. When they are particularly shallow and the lobsters are exposed to the glare of the sun they are sure to suffer, and sometimes die in consequence. The majority of lobsters probably spend the greater part of the year at depths where the effect of sunlight is but slight, and during the course of its evolution the eye of this animal has become sensitive to a minimum quantity of light. For this reason alone we should expect that adults would tend to avoid intense sunlight.

BURROWING HABITS.

The lobster not only digs up the sea bottom in its search for shellfish and covers itself with mud in cold weather, but burrows under some conditions as extensively as the muskrat. Impounded lobsters will sometimes burrow during both summer and winter, and this habit is no doubt freely practiced when they roam at will.

The burrowing habit was typically shown in one of the pounds at Southport, Me., where the lobster holes were driven horizontally into a mud bank for a distance of from 1 to 5 feet. When we did not see the feelers and claws of a lobster projecting from its hole, the occupant could usually be felt by inserting the end of an oar, and it would sometimes grip the blade and allow itself to be dragged out clear.

The holes had an opening of from 8 to 10 inches in diameter, which allowed of their being readily probed and measured with an oar blade. I did not observe that they ever had an upward or downward curve, but they sometimes swerved to the right or left, which might be due to the presence of some obstacle in the path. In

some cases the burrows were under rocks, and the entrance was often much larger than that described, possibly owing to the union of the mouths of two originally distinct burrows. The pile of dirt and the broken clam shells which are sometimes seen near the hole of the lobster recall the excavations of the muskrat. It was exceptional to see a lobster with his tail projecting from the burrow, and when disturbed in this position they were quick in disappearing.

In digging, lobsters probably make use of their large claws and walking legs, and possibly the tail fan may be brought into service as a scoop or shovel, but we have no observation in support of the latter supposition. Yet, in some cases we have noticed the underside of the tail fan to be scratched and scarified, and the marginal fringe of hairs worn down in a way to suggest the probability of such use.

Mead (*193*) found that the young lobster sometimes burrows in its fourth or lobsterling stage, and this instinct is very pronounced in all its later phases. It removes bits of gravel presumably with its claws and deposits them short distances away, thus digging to a depth of 2 or 3 inches. Young lobsters, like the old ones, hide in their holes, and issue stealthily in search of prey. Indeed, it may be said that such commanding instincts of the adult as preying, concealment, and fear, are manifested suddenly and for the first time in the fourth stage.

The burrowing habits of certain species of crayfish are well known, while those of the stomatopods (see chap. 1) are equally characteristic. We meet with the same habit in many snapping shrimps, expressed in a greater or less degree in terrestrial crabs, and in a great number of the lower Crustacea.

FOOD AND PREYING HABITS.

The food of the adult lobster consists principally of fish, alive or dead, and of invertebrates which inhabit the bottom and come within its reach. It is not unusual to find bits of algæ or common eel grass in its stomach, and at times in such quantities as to suggest that it may not be an accidental occurrence. Vegetable matter, however, forms at most but a small and casual part of its diet. Fragments of dead shells, coarse sand, and gravel stones as large as duck shot are also swallowed. The former yield lime, which is in some measure absorbed; the latter are not needed in grinding the food as in the gizzard of the domestic fowl, since the lobster's stomach has, as is well known, a mill admirably adapted for this purpose, and their occurrence is probably accidental.

I have dissected soft lobsters, with fragile papery shells, from 3½ to 4½ inches long, in which the stomach was literally crammed with water-worn calcareous fragments of the dead shells of crustaceans and mollusks such as one can gather on the beach, besides other shells of mollusks which had undoubtedly been eaten alive. This suggested the possibility that the supply of lime for hardening the new shell might at times be obtained in this way (see *149;* p. 89–90) for it seemed hardly probable that they would be swallowed to be immediately regurgitated. The lobster undoubtedly regurgitates the insoluble and indigestible parts of its food, as is the known habit of crayfish. Some such outlet for waste matter is absolutely necessary in an animal

where the fluid or finely divided and digestible parts of the food only can pass to the delicate intestine. The hard parts of fish, mollusks, and crustaceans, however, appear to be retained until they have given up a good deal of their lime, thus contributing to the calcareous supply of the exoskeleton.

An analysis of the stomach contents of lobsters captured at Woods Hole from December to June revealed the following organisms, which are named in the order of their relative abundance: Fish (procured independently of the traps); crustaceans, embracing chiefly isopods and decapods; mollusks, consisting largely of small univalves; algæ, echinoderms, and hydroids. The bones of the fish eaten belonged as a rule to small individuals or species. Among the crustacean remains parts of small mud-crabs, *Panopæus* (*P. sayi* and *P. depressus*, the common species in Vineyard Sound), were almost invariably recognized, and it was not unusual to find parts of the skeletons of small lobsters. The isopod *Civolana concharum* is frequently eaten by the lobster, and often in large numbers. It is a scavenger, and devours the bait used in the traps, a fact which explains its common occurrence in the stomachs of lobsters newly caught. In the case of a female, captured in January, the stomach was filled with fresh lobster eggs in an advanced stage of development. These eggs were not stolen from any lobsters in the trap, but under what circumstances they were obtained one can easily conjecture. The egg-lobster is undoubtedly a shining mark, not only for predaceous fishes but even for members of its own species. The larger mollusks are eaten by crushing the shells and picking out the soft parts, while many of the smaller kinds are swallowed entire, and presumably pulverized in the gastric mill. Echinoderms probably enter largely into the diet of the lobster wherever they abound. Parts of the common starfish (*Asterias forbesii*) and rarely a few spines of the sea urchin (*Arbacia punctulata*) were detected, but it might be that the latter were swallowed together with other calcareous fragments. Very little change in the food was noticed during the winter and spring months, and there was little evidence that the appetites of these animals sensibly abated during cold weather, yet it is probable that food if not less abundant is less necessary in winter.

That lobsters catch fish alive there is no doubt, but few observers have ever seen the feat performed. Fish that inhabit the bottom, like the flounder, would naturally fall an easy prey to the powerful claws of the lobster, which is said to catch the sculpin; and I have known a lobster when confined in an aquarium to seize and devour a sea robin (*Prionotus evolans*).

While lobsters are great scavengers, it is probable that they always prefer fresh food to stale. Some fishermen maintain that there is no better bait than fresh herring. Fresh codfish heads, flatfish, sculpins, sea robins, menhaden, and haddock are also used, as well as salted fish. The flesh of sharks was occasionally used by the Gay Head fishermen on account of its firmness and lasting qualities. Nothing could be more offensive to the human nostril than the netted balls of slack-salted, semi-decomposed herring, which are commonly used as bait on the coast and islands of Maine, but by the wonderful chemical processes which are continually going on in the

laboratory of its body, the lobster is able to transmute such products of organic decay into the most delicate and palatable flesh.

Lobsters are very fond of clams, as they are of mollusks of all kinds, and when kept in pounds are constantly scoring and digging up the bottom in search for these shellfish. In a large lobster pound at the Vinal Haven Islands I have seen the muddy bottom scored in all directions, the work of lobsters in their search for clams. One was reminded of a pasture in which the soil had been rooted up by pigs. As a fisherman remarked, if you put lobsters in a pound and do not feed them they will soon turn over the bottom as effectively as it could be done with a plow. Some of the holes which the lobsters had made in digging clams were 2 feet in diameter and 6 inches or more in depth. Here they had dug up the eel grass, or loosened it so that it had floated to the surface, and cartloads had been cast ashore. We have already seen that the lobsters sometimes eat parts of this plant, but they had plainly rooted it up in this case with another object in view. The broken and often comminuted shells of the long-necked clam (*Mya arenaria*) could be seen strewn everywhere about their excavations.

The lobster probably attacks such large and powerful mollusks as the conchs, which live upon hard bottom in deep water, and devours their soft parts. An illustration of this was afforded in an aquarium at Woods Hole in the summer of 1892, when a conch (*Sycotypus canaliculatus*) was placed in the same tank with a female lobster which was nearly 10 inches long and which had been in captivity about eight weeks. The conch, which was of the average size, was not molested for several days, but at last, when hard pressed by hunger, the lobster attacked it, broke off its shell, piece by piece, and made quick work of the soft meat.

If a lobster that has fasted for a number of hours is fed with a little fresh meat, such as a piece of clam or fish, the process of feeding will be found to be one of no little interest. The lobster eagerly seizes a piece of food with the chelæ of the third and fourth pairs of walking legs, and passes it up to the third pair of maxillipeds, which are held close together, each being bent at the fifth joint and folded on itself. With the third maxillipeds thus pressing against the mouth, the food is kept in contact with the other mouth parts, all of which are in motion, and their action is thus brought to bear upon it. By means of the cutting spines of the appendages external to the mandibles—chiefly the maxillæ and second pairs of maxillipeds—the meat is as finely divided as in a sausage machine, and a stream of fine particles is passed on toward the mouth, to be finally subjected to the cutting and crushing action of the mandibles before entering it.

If one wishes to watch the movements of the complicated mouth parts more closely, one has only to take a lobster out of the water, place the animal upon its back, and when it has become sufficiently quiet stimulate the mandibles or the broad plates of the second pair of maxillipeds with the juice of a clam or the vapor of ammonia, which can be squirted with a pipette. Masticatory movements are immediately set up in the appendages, those belonging to the side stimulated usually working independ-

ently. The two small chelate legs are also drawn up rapidly to the mouth, as if to hand up pieces of food.

When stimulated in this way, the plates of the first pair of maxillæ come together over the lower posterior half of the mandibles. The movements of the masticatory parts of the second maxillæ are synchronous with the beating of the scaphognathite. These leaf-like plates project somewhat obliquely over the convex surfaces of the jaws, and are directed inward and slightly upward. The large plates of the first maxillipeds work up and down and at the same time inward toward the middle line, describing an ellipse. The second pair of maxillipeds move alternately or together, inward and outward, with slight up-and-down movement. The large maxillipeds move together, the toothed margins meeting like the jaws of a nutcracker, while the three terminal joints are bent inward and somewhat downward, as in the case of the second maxillipeds, so as to meet on the middle line below and hold the food up to the mouth. (For full analysis of the mouth parts, see ch. vi, p. 227.)

CANNIBALISM.

Lobsters are cannibals from birth, owing, primarily, to their strong instinct of pugnacity. The small, as well as the large, are ever ready to prey upon those still smaller or weaker than themselves. This is certainly true of all the lobsters which have been kept under observation in the restricted space of hatching jars or aquaria and where suitable food in suspension was either lacking or insufficient. In their natural environment in the sea, however, where the young are quickly and widely dispersed, opportunities for the display of this tendency could seldom arise. In the early stages, at least, it is questionable whether cannibalism would occur under any conditions, provided the larvæ were properly fed.

When crowded in cars or pounds, lobsters play the rôle of cannibals at a great rate. As Mr. F. W. Collins remarked to me in 1902, persons not understanding this will lose 20 per cent of their stock in a very few days. He usually counted on a loss in crowded cars of 5 per cent in the course of three days, the larger feasting on the smaller, even when the precautions of supplying them with food and separating the "soft shells" had been duly taken.

REVIEW OF THE INSTINCTS AND INTELLIGENCE OF THE ADULT LOBSTER.

The instincts of fear and of concealment by burrowing or hiding in seaweed or under stones; the restless activity of the lobster in exploring the bottom for food, feeling its course by whipping the water with its long antennæ, and testing all objects with both these and its sensitive feet, or smelling its way to food by beating its antennules, even seeming at times to stalk and approach its prey by stealth; storing up food or, at least, dragging dead prey into its burrows or sometimes burying it, to be afterwards exhumed, thus recalling a well-known trait of the dog; the fighting instinct so often displayed between members of its own race and not confined to captives, which brings into play all its caution and characteristic attitudes in attack and defense; its

incessant activity at night whether in search of prey or not; its irregular migratory movements to secure, it may be, a rocky bottom where food and better places of concealment abound, deeper or warmer water, or, in a word, those conditions which for the time suit better certain individuals of one or the other sex for feeding, spawning, or shedding the shell—these may all be observed in either free or captive animals.

In every movement the lobster is guided chiefly by the chemical sense and that of touch, and, least of all, by its eyes. Thus vision, which is never keen, is probably almost nil in bright lights. This explains its nocturnal activity and its frequent retreat from light to shadow.

Of the habits of the European lobster, Williamson (*282*) remarks that it has the sense of light and shade, that it will test a strong shadow with its antennæ, and will even jump at it with outstretched and snapping claws. It is guided mainly by its antennæ, with them finding and exploring every cavern, and with them searching its depths before entering or inserting a claw. As I shall point out elsewhere, the wary lobster, "tiptoeing" over the bottom, feels its way at every step. If food is thrown to the captive, no appeal is made to its sense of sight. The bait remains unnoticed unless it happens to touch one of the antennæ or legs; but a lively whipping of the antennules seems to announce the awakening of the chemical sense. The lobster immediately takes notice and begins to explore the water with its long "feelers," at first without leaving its hole. The antennules begin to whip in the direction of the food and explorations become more active. The lobster cautiously leaves its hole, goes straight for the bait, feeling its way. The food is usually picked up and handed to the mouth parts by the second pair of legs.

Meanwhile, says Williamson, the expected feast has by association stimulated the maxillipeds, which are actively working as if they were already masticating the food. Once this is seized it is conveyed to the maxillipeds and the lobster retreats to its hole, there to enjoy its meal. Two lobsters were noticed to have stored up in one case some mussels and in the other a dead sand eel (*Ammodytes tobianus*) in the inner recesses of their caves.

In regard to the interesting question of storing food, we give the account of a lobster which was kept at the Rothsay aquarium in England (*302*):

A flounder was unintentionally left in one of the aquaria, in which three lobsters were living. The largest animal immediately appropriated the fish, which was then dead, and buried it beneath a heap of shingle, over which it mounted guard. Five times within 2 hours was the fish unearthed, and as often did the lobster shovel the gravel over it with his huge claws, each time ascending the pile and turning his bold defensive front to his companions.

To this catalogue of instincts we must add the parental instinct of the mother lobster in protecting her cargo of eggs during the long period of fosterage. The parental instincts of birds are, as a rule, far keener than in the invertebrates; but it should be added that in many of our commonest birds they endure for a time which is only an eighth or a tenth as long. Through her inbred caution the mother lobster saves not only herself but her progeny from many a strong and clever adversary. Barring the fisherman's trap, she will run the gauntlet of daily life, escape a thousand perils,

and after 330 days or more of successful fosterage deliver her young to the teeming and merciless sea. She shows this parental instinct not only by keeping to cover but by folding her tail in emergencies, so that the inquisitive cunner and insidious eel and other troublesome neighbors can not pick off her eggs or pull them out of her brood pocket. Further, by the incessant beating of the egg-laden swimmerets, the lodgment of destructive parasites is discouraged. The lobster also instinctively cleans her antennæ by drawing their whips through the brushes of the great maxillipeds and applies the "broom," the tips of the last pair of slender legs, to the swimmerets and under side of the tail when ready to deposit a new batch of eggs.[a] Sexual union is largely, if not wholly, indiscriminate, and it is possible that the males "try" every lobster which they meet, or at least every female, whatever her condition (see p. 303).

Lobsters about to molt, and possibly after the shell is cast, often conceal themselves in sand or seaweed, and the soft lobster will instinctively eat its own cast or swallow a miscellaneous mass of calcareous fragments, presumably for the purpose of obtaining an immediate and abundant supply of lime for the hardening of its new shell (see p. 185).

Most important to the welfare of the lobster race no doubt is the instinct of fear upon which all their characteristic actions of burrowing, hiding, and what we have described as "stealth" and "caution" depend. Moreover, it is as important for the life of the young as of the adult, for this instinct manifests itself with comparative suddenness, as in birds, at the close of the larval swimming life, in the fourth-stage lobster, when, as if by magic, the lobsterling casts aside its larval habits, together with its characteristic larval organs, and appears in a new rôle, with new armor to suit the part which it is to play. It betrays fear and caution, and now goes to the bottom, digs burrows, and hides. The possession of the instinct of fear gives ground for the hope that the method of rearing the young to the fourth or fifth stage before liberation, which has met with complete success, may yet furnish a means of restocking our coastal waters, and of thus reviving the decayed lobster fisheries of the northern Atlantic States.

The intelligence of the lobster is shown in its power of associating things with actions or of forming habits in the technical sense; in other words, in a power, however limited, of profiting by experience. Thus the lobster habitually returns to its burrow or place of hiding, which it recognizes and claims as its own, being ready to fight for its possession. There can be little doubt that it finds its way back by the same process that the fox returns to its hole or the bird to its nest, through the power of association, though not necessarily through the mediation of the same sense.

But this rudimentary power of using experience as guide does not carry the lobster very far any more than it does many of the fishes and lower vertebrates generally. It does not enable it to escape from a trap or to avoid this engine of destruction in the future when once set free.

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[a] It may be noted further that Coste, who made some remarkable statements about the European lobster which are not confirmed by later observers, says that "In order to favor incubation the brood lobsters can expose at will their eggs to the light or keep them in shadow, according as they bend or straighten their tails; when assuming the latter attitude they will now bring their eggs to rest, or now wash them by gently moving the swimmerets." (55, p. 204.)

COLOR IN THE ADULT LOBSTER.

The color of the adult lobster is due primarily to the presence of pigments, either in a state of solution in the blood or in the form of granules in the protoplasm of certain cells, particularly the chromatoblasts, which lie beneath the cuticular epithelium. The chromatoblasts are richly supplied with blood, which flows in a system of irregular sinuses through the spongy tissues underlying the epidermis.

In the adult lobster the hard shell is an opaque lifeless substance, and the pigments to which it owes its characteristic coloring are excreted by the chromatoblasts of the soft underlying skin. These are immediately exposed upon removing the shell. The delicate skin is seen to be flecked or mottled with scarlet, and with the aid of a simple magnifying glass it is readily perceived that its color is due to branching pigment cells, groups of which correspond to the blotches of color on the shell itself. The excreted pigments undergo physical and possibly chemical changes in the hard cuticular shell and may thus come to differ markedly in color from the parent chromatoblasts. Since the colors of the lobster reside in a lifeless body, the pigment layer of the shell, it is evident that no changes of a vital nature can take place after this is definitely formed.

The coloration of the lobster is fairly uniform in plan, but extremely variable in details, even more so than we find in the case of the color patterns of many insects. The brilliancy and purity of the shell pigments depend largely upon the age of the shell or upon its condition with respect to the molting period. These pigments are usually most brilliant just after the molt, when the cuticle is thin and translucent, and dullest before ecdysis begins, when the old shell still encumbers the body.

The pigment cells themselves, as we have seen, reside in the soft skin, and when the shell is once hardened the color of the animal is more or less fixed and permanent. It is certain, however, that under the action of light and possibly from other natural causes the shell pigments undergo molecular or chemical changes. Men who handle lobsters have frequently observed that when they are exposed in shallow cars to unusually intense light they become decidedly bluer in color.

According to MacMunn (*185*) the coloring of the skin of the lobster is due to the presence of chromogens, which may be converted on slight provocation, as by dehydration, oxidation, or some molecular change, into a red lipochrome resembling rhodophan. Everyone is familiar with the wonderful change in color which the living lobster undergoes when boiled, and according to the same writer the beautiful pigment of the larval lobster is converted by alcohol into a true lipochrome.

Alcohol quickly converts the chromogens in the lobster's shell into lipochromes and dissolves them at the same time. This is seen when a recently molted lobster with brilliant coloring is placed in alcohol for preservation. The soft shell is first reddened, and then in a short time completely bleached, while a hard lobster treated in the same way will retain much of its shell pigment for years, if not indefinitely.

Lipochromogens are found in a natural state in the gastric glands, blood, soft skin (as the blue prismatic cyano-crystals, which are reddened by alcohol or by boiling),

and in the exoskeletons of crustaceans generally. MacMunn is of the opinion that they are "built up in the digestive gland and carried in the blood current to be deposited in other parts of the body." If this is true, it would not be remarkable if the color of the animal were affected by the nature of its food, yet this does not seem to be often the case.

Following the classification of Bateson (*19*) we distinguish between (*a*) variations in colors themselves, and (*b*) variations in color patterns. The variation in colors, which Bateson calls "substantive variations," may be the result of a physical or chemical change, and has no vital significance. The different colors themselves are further liable to different discontinuous variations, as when crustaceans occasionally lay bright, golden-yellow eggs, while the normal color is dark green.

The following substantive variations have been met with: (1) Blue lobsters, in which the prevailing color is blue; (2) red lobsters, which are pure red or reddish yellow; (3) cream-colored lobsters, characterized by the almost entire absence of color; and we should also add (4) black lobsters, to include possible cases of melanism, where the colors are extremely dark. A specimen of this kind was reported to me at Beal Island, near West Jonesport, Me., where a fisherman recently captured, in 3 fathoms of water among the eelgrass, a lobster about 6 or 7 inches long with moderately hard shell and almost jet black. He supposed at first that it was covered with coal tar. It did not appear to be preparing to molt. Malard speaks of meeting with cases of melanism in crabs, where in consequence of a lesion of the skin the animal becomes entirely black.

Changes in color pattern are more elusive. There are (1) the normal variety, in which the upper part of the body is mottled with green, blue, and cream color; (2) spotted or "calico" lobsters, the coloration of which is a bold pattern of green and light-yellowish or cream-colored spots; (3) pied or parti-colored varieties, in which the contrast of tints is abnormally pronounced. This may perhaps be better classed under substantive variation. The changes are due apparently to vital or physiological causes, which have at least no adaptational significance.[a]

There is no sexual color variation in the lobster, and such substantive variations as the eggs undergo are not of an adaptive character. The freshly laid egg is dark green, sometimes almost black, due to the presence of dissolved lipochromogens. Occasionally the ova are nearly pea-green, grayish-green, or greenish-straw color, but the golden-yellow variation, so striking in some of the snapping shrimps, has never been observed in the lobster.

If the eggs are treated with hot water, alcohol, or other killing reagents, the green lipochromogen is quickly converted into red lipochrome. When the water is heated gradually, the red color appears slowly, and it is interesting to observe that if these red eggs are now plunged into cold water the green color is restored. This change may be somewhat analogous to the breaking up and reconstruction of the blue compound of of starch and iodine upon the successive application of heat and cold, and to the variation in color which sometimes appears in the living animal at the time of the molt.

[a] For fuller account of red living lobsters and other color variations, with illustrations, see *149*.

Soon after the water has been brought to the boiling point the red color becomes permanent.

The colors of deep-sea animals that live in total obscurity can not be of any utility to the animal as a source of protection. The color may be very brilliant, red, scarlet, orange, rose color, purple, violet, and blue, which is less frequently reported, but they appear to be developed quite independently of the light. It has been shown by experiment with sensitive photographic plates that luminous rays do not penetrate ordinary sea water to a greater depth than 400 meters, as noted above. In depths of 50 fathoms or more there might be an appreciable amount of light on clear days, but even then, when the water was loaded with sediment and the bottom composed of dark materials, it seems hardly probable that colors would have any protective value whatever.

The normal colors of the lobster, which are spread like a mantle over the whole upper surface, tend undoubtedly to obliterate it and to screen its movements while crawling over a weedy or rocky bottom. The absence of all color or a more generous display of bright pigment would make it a more conspicuous object, especially upon sandy bottoms in shallow water, which it is usually careful to avoid in the daytime. The vivid red of the claws appears to be overlaid by a darker pigment in spots, particularly on the upper surface. The underside of the pleon, which rests upon the bottom when the tail is not folded, is very meagerly supplied with pigment, as is usually the case with marine animals which inhabit the bottom.

Chapter III.—GIANT LOBSTERS.

Stories of gigantic lobsters made their appearance at a very early period, and one could probably gather as many exaggerated accounts of this animal now as in the days of Olaus Magnus. Time, however, has narrowed the bounds of credulity, even among the ignorant, and we no longer hear some of the interesting legends which the old writers have carefully handed down. Thus Olaus Magnus tells us in his description of northern lands and seas,[a] published in 1555, that between the Orkneys and Hebrides there lived lobsters so huge that they could catch a strong swimmer and squeeze him to death in their claws. His curious figures were copied by Gesner, who has many others equal to any which are described in the old mythologies.

Giants are met with in all the higher groups of animals. They interest us not only on account of their actual size, but also in showing to what degree individuals may surpass the mean average of the race. It may be a question whether lobsters weighing from 20 to 30 pounds or more are to be regarded as giants in the technical sense, or simply as sound and vigorous individuals on whose side fortune has always fought in the struggle for life. I am inclined to the latter view, and look upon the mammoth lobster simply as a favorite of nature, who is larger than his fellows because he is their senior; good luck never deserted him until he was stranded on the beach or became entangled in some fisherman's gear.

Gesner gives a poor likeness of a lobster, but an excellent drawing of the large crusher claw of one which he had preserved in his collection on account of its great size. The length of this claw was 8¾ inches, and its breadth at the junction of the dactyl about 4 inches, so that it was borne by a lobster which weighed not far from 8 pounds.

The European lobster of to-day seldom or never attains so great size as the American species, as already remarked, and its average weight is considerably less. Buckland gives an account of large lobsters from the British Islands, in which the greatest weight recorded was 14 pounds, and European lobsters of this size are undoubtedly now very rare. The Academy of Natural Sciences of Philadelphia possesses a skeleton of *Homarus gammarus*[b] which, judging from its measurements, must have weighed from 23 to 25

[a] Historia de Gentibus Septentrionalibus, Rome. 1555.

[b] It is possible that a mistake has been made in attributing the Philadelphia specimen to the European species The determination was made by Prof. John R. Ryder, who evidently relied upon the character of the rostrum (see p. 161) in basing his opinion. Regarding this specimen, Professor Ryder wrote under date of March 10, 1894, as follows: "It turns out to be European instead of American. I send the data obtainable. The catalogue does not give weight or locality. At one time there was a label stating the weight; now that has also disappeared." Again on March 15, he wrote: "There is no doubt of the large lobster being *H. vulgaris*. I found no spines on the under side of the rostrum of the large specimen; perfectly smooth, as was also another smaller specimen of the same species. I made a very careful examination to-day and can assure you that the facts are as I state." He further added that the large skeleton "is also perfectly symmetrical and must have been a beautiful specimen originally, as it now is."

pounds. (Table 1, no. 15.) There may also be seen in the museum of Bergen, Norway, a lobster which Prof. S. O. Sars in 1878 described as an "immense specimen," the living weight of which could not have been much over 12 pounds.

Though it has been an accepted belief that the American lobster attains a greater size than its European counterpart, it is possible, in view of comparison of no. 10 and no. 16 of table 1, that the maximum size of each species is nearly the same. The data are not at hand for determining the question with certainty. It seems certain, however, that American lobsters of average or medium size are considerably stockier and have larger claws than the European, and that length for length, such animals will weigh more. The lobster fishery of Europe, though pursued for ages by primitive methods, is still very much older than that of America, and it is probable that the larger lobsters have been more effectually weeded out there than here. At the time Sars's paper was written (*244*) it would not have occurred to one familiar with the American species to speak of a 10 or 12 pound lobster as in any way remarkable, yet at present few of this size find their way to our markets. In fact the same gradual falling off, due evidently to the same cause, has been experienced for many years in Maine and Canada.

TABLE 1.—RECORD OF GIANT LOBSTERS.

[No. 1–14 refer to *Homarus americanus*, No. 15–16 to *H. gammarus*.]

No.	Sex.	Place of capture.	Date.	Length.	Length of carapace.	Crushing claw.		Toothed claw.		Where preserved.	Living weight.
						Length.	Girth.	Length.	Girth.		
				Inches.	*Inches.*	*Inches.*	*Inches.*	*Inches.*	*Inches.*		*Pounds.*
1	.....	Gloucester, Mass.	1840	.....	.....	13	17.50	.....	.....	Peabody Academy of Science, Salem, Mass.	[a] 28
2	♂	Salem, Mass.....	1850	21.75	9.94	12.50	15	12.37	.....	.....do.....	[a] 23–25
3	♂	Boothbay, Me...	1868	20.25	9.37	12.50	15.25	13.25	11.12	Land Office, Boothbay Harbor, Me.	[a] 24
4	.....	Small Point, Me.	.....	.....	.....	12.50	15.50	.....	.....	Portland, Me.....	[a] 24
5	♂	Delaware, Conn..	.....	.....	.....	13.12	16.12	12.87	8.50	Smithsonian Institution, Washington.	[a] 25
6	♂	Belfast, Me.....	1891	20+1	9+1	13.75	16.87	13.87	12.50	Adelbert College, Cleveland, Ohio.	[b] 28
7	♂	Lubec, Me.....	1892	20.62	9.25	12	15	11.50	11	Campobello Island, New Brunswick.	[a] 23
8	♂	Provincetown, Mass.	1894	20–21	.....	12–13	.....	.....	.....	Formerly at St. Nicholas Hotel, Boston, Mass.	[a] 23–25
9	♂	Atlantic Highlands, N. J.	1897	23.75	12.24	15	20.50	15.50	15.25	American Museum of Natural History, New York.	34
10	♂	Newport, R. I.[c]	1898	19.50	.....	11.75	.....	11.87	.....	Rhode Island Commission Inland Fisheries, Providence, R. I.	19
11	♂	Atlantic Highlands, N. J.	1899	22.50	10.28	14.66	17.68	14.40	13.54	American Museum of Natural History, New York.	31
12	♂	Monhegan Island, Me.[d]	1899	23–24	.....	.....	.....	.....	.....	.....	[a] 32+
13	♂	.....	.....	19.80	.....	12.33	15.60	12.40	11	American Museum of Natural History, New York.	[a] 24
14	♂	Near Bayonne, N. J.	1898	20.37	.....	14	16	13.50	11.50	.....	[a] 25–28
15	♂	Europe.....	.....	19.40	9.29	13.10	16.80	12.40	10.15	Museum of University of Pennsylvania, Philadelphia.	[a] 23–25
16	♂	Coast of Norway.	1850(?)	18.73	8.58	10.23	10.62	10.03	8.07	Bergen Museum, Norway.	[a] 12+

[a] Living weight estimated. [b] Living weight estimated from weight when boiled. [c] After Hadley. [d] Body length estimated.

The large Belfast lobster (no. 6, table 1), which came into my possession in 1893, was captured in Penobscot Bay, near Belfast, Me., in 1891. (For full account with photographs see *149*.) Its total length, had the rostrum been perfect, would have been 21 inches. The body seems surprisingly short for so powerful an animal, and it is indeed in the large claws that the greater part of the weight and strength resides. This may possibly be explained by the fact that as age advances the increase in length at each molt becomes less, while there is a corresponding gain in the volume of the body and of the claws. Thus Ehrenbaum mentions a lobster 42.2 cm. long, which showed an increase in length of scarcely 1 mm. on molting. The length of the crushing claw of the Belfast giant is 13.75 inches, and its greatest girth 16.87 inches.

GREATEST SIZE ATTAINED BY THE LOBSTER.

It is difficult to obtain exact data regarding the true weights and measurements of all big animals, and the lobster seems to be particularly deceitful in this respect. Remembering the decision of the judge that "affidavits are not lobsters," I endeavored to take a conservative position on this subject, when writing in 1895 (see *149*, chapter v). Fortunately since that time two specimens of the mammoth class have been added to the collections of the American Museum of Natural History in New York. Through the kind offices of the museum I have been able to obtain data and to present a sketch of one of the biggest known lobsters in the world. The larger (no. 9, table 1), when received in the fresh state, weighed, according to Whitfield (*278*), "about 34 pounds;" the weight of the smaller (no. 11 of table) is given as "about 31 pounds." Both were taken alive by fishermen off the Atlantic Highlands in New Jersey in the spring of 1897. The larger animal was exhibited in one of the tanks at the Castle Garden Aquarium, but neither lived more than a few days in captivity. Both specimens have been remounted at the museum, the smaller to show the upper (fig. 1) and the larger the under side.

The most important measurements upon which we can rely for exact comparisons are: (1) The length of the carapace from the tip of rostrum to hinder border, (2) the length of each of the big claws, taken with callipers from the short spur near the proximal end of the larger division of the claw to its apex,[a] and (3) the greatest girth of the propodus, measured in a line at right angles to the last. These values should be fairly constant by whomsoever made, and in whatever form the skeleton is mounted.

Knowing the measurements in the American Museum specimens to be correct, and assuming that the weights as given by Whitfield are correct also, I have taken these data as a new basis for estimating the weights of other large lobsters recorded in table 1, and believe them to be a closer approximation to the facts in each case than I was able to make in 1895. The former estimates were founded on the measurements and supposed weight of the Belfast lobster (no. 6, table 1), the largest specimen known at the time. I was assured that this animal weighed 23 pounds after it had been boiled, and allowing a shrinkage of 40 per cent in the process, its living weight was estimated at 28 pounds. Notwithstanding the doubts cast upon this statement at the time, com-

[a] Or from the spur near the proximal articulation to apex of propodus, the last measurement being somewhat less. Where big claws are chopped off for preservation, the joint is apt to be defective.

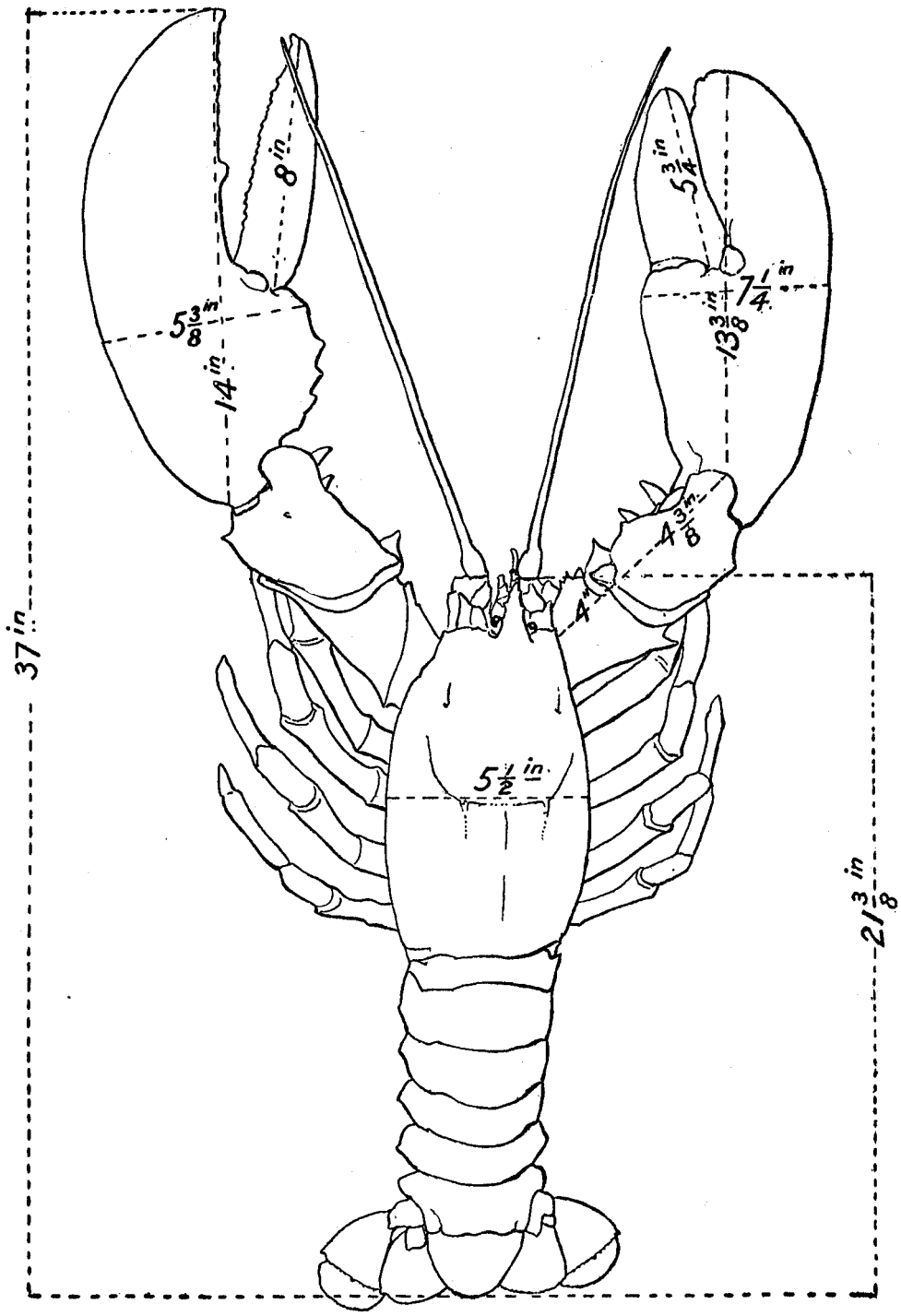

FIG. 1.—Giant lobster from New Jersey; living weight, 31 pounds. (See table 1, no. 11.) Outline after photograph, and reproduced through courtesy of the American Museum of Natural History, New York. General measurements of skeleton as mounted, indicated in inches. About one-fifth natural size.

parison with the measurements of lobsters 9 and 11 shows that it must have been substantially correct. It will be seen that this animal approaches closely the 31-pounder from New Jersey, the lengths for the carapace being 10 inches (allowing for 1 inch of the rostrum missing) and 10.28 inches, respectively, and the girth of the crusher claw 16.87, as opposed to 17.68 inches.

After taking account of the facts so far as ascertainable at present, my former statements regarding the weights of giant lobsters are revised to the following effect; the greatest known living weight of the American lobster is 34 pounds and that of the European lobster about 25 pounds. (See note, p. 194.) Altogether six or seven individuals of the American species weighing 25 pounds or more are known to have been caught on the Atlantic coast during the last 70 years.

The lobster (no. 12, table 1) which was seen by Cobb at Peak Island, Maine, in 1899, is said to have measured 44 inches with claws extended in front of the head. It was caught off Monhegan Island, Maine, and exhibited about the country by fishermen of that region. If this measure was correct, it would correspond to a body length of 23 to 24 inches and a corresponding weight of upward of 32 pounds, thus being one of the largest lobsters on record. The ratio of body length to the total length with extended claws varies greatly in small and large lobsters, being as high as 72 per cent in a female of 3 inches and 38 per cent in a male of 10.37 inches, while in the big Belfast lobster (no. 6) this ratio is somewhat under 55 per cent. On the other hand the ratio of carapace length to total body length for the average 10.5-inch lobster, as applied in the gauge law adopted in Maine, is 45 per cent (see chapter IV, p. 212).

In addition to the lobsters given in table 1, Cobb (*52*) has noticed a male said to have measured 25 inches and to have weighed 25 pounds. It was caught in a hake trawl off the Matinicus light, Maine, at a depth of 60 fathoms, in 1898. The given length in this case does not accord with the given weight, and is probably much too great. Another lobster is mentioned by Hadley (*126*) as having a length of 22.5 inches, but weighing only 19.5 pounds; the same kind of difficulty is presented here, the length calling for a much heavier individual. Waite (*274*) has also recorded the measurements of a large male lobster, which was captured at Block Island April 10, 1896, measured 21 inches and weighed when alive slightly over 22 pounds. The length and girth of the cracker and toothed claws were 13.25 and 16.5 inches, and 12.75 and 12.25 inches, respectively.

In June, 1898, Dr. H. M. Smith called my attention to a large lobster which had been recently captured in New Jersey and which was reported to have measured 23 inches in total length and to have weighed 36.5 pounds. Through the kindly aid of the late E. G. Blackford of the Fulton Market, New York, we were able to obtain a reliable account of this interesting specimen, together with the necessary measurements, which are given in table 1. This lobster was caught on June 21, 1898, by a fisherman in New York Bay, off East Forty-sixth street, near Bayonne, N. J., and was taken alive to the Bayswater Hotel, where it was on exhibition in a tank for several days. The man who was sent by Mr. Blackford to take the required measurements found that the animal

was then dead and partly dried out, the owner claiming that it had shrunk 2.62 inches in consequence. It is hardly necessary to show that this was impossible, since the body of a lobster can be distended at only one point, namely, at the articulation of the carapace and the tail, and there only to the limit of the articular membrane, which is inelastic. Drying would tend rather to contract this membrane and to give more accurately the true length, but the difference would not in any case be very great. The measurements taken from the dead shell show that this animal probably did not weigh over 25 to 28 pounds. In his letter to Dr. Smith Mr. Blackford remarked that the owner asked the modest sum of $250 for the specimen. We do not know what finally became of it.

In August, 1891, according to Mr. F. W. Collins, a lobster of undetermined sex was caught at Blue Hill Falls, Maine, which weighed 18.5 pounds, and in November, 1892, a perfect female lobster weighing 18 pounds was taken at Green Island, Maine. This outer island has long been noted for its fine lobster fishing. Mr. Collins stated that in August, 1891, he had 50 lobsters at one time in his establishment which would weigh from 10 to 18.5 pounds. About half of these came from Castine and the remainder from Blue Hill Falls. All of them were "new shell lobsters," or those which had shed in the year, probably in July.

After the lobster has attained a length of 20 inches and a corresponding weight of 23 to 25 pounds or more, we may be certain that the stage periods, or intervals between each molt, are long, and probably several years apart, and that this interval is gradually increased with advancing years. The relative increase in length seems to slow up with increasing age, but volumetric increase still goes on, and the animal becomes stockier and its big claws more powerful. There is no fixed limit to age, growth, or molting power, but the practical limit is probably not far from that of the largest animal on record. Whether giant or pigmy, the fighting strength is apparently renewed at each molt, when a brand new suit of armor is acquired.

The shell of the crusher claw of the Salem lobster (for full-sized drawing, see *149*, pl. 15) weighed but a trifle over a pound, and the living weight of this animal is now estimated at about 28 pounds. The skeleton of the crusher of a 12 to 15 pound lobster with very dense shell weighed 8.25 ounces. The Salem lobster had probably molted within less than 3 months from the time it was caught. The Lubec lobster (no. 7) had a clean shell, which indicated that not over 6 months had intervened between the time of its capture and the last molt. It was light for its length and the most perfectly proportioned large specimen I have seen.

In general it is undoubtedly true that the older the adult lobster the longer its stage periods and the less the increase at each molt. Yet it is almost equally certain that both may vary greatly in the giant as in the pigmy. At present our data regarding the molting of large lobsters is insufficient to enable us to estimate their age. Giants weighing from 25 to 35 pounds have possibly weathered the storms of life for half a century or more.

Chapter IV.—MOLTING.

Molting is an incident and expression of growth. The crustacean does not "grow by molting," as is sometimes said, but it molts because it has grown. It has outgrown its inelastic shell, which is cast off in one piece, normally without a break in any of its hard parts. Other animals molt or shed a part of their cuticle and its products, but nowhere is the process so striking, so abrupt, or so critical as in the higher crustacea. In these animals the span of life from infancy to old age and death may be divided into a series of stages, varying in length, each stage-period of life culminating in a molt.

Any influence which retards growth or unduly taxes the vital energies prolongs this period, and conversely the more vigorous and the more rapid the growth the shorter the interval between molts. Shortly after molting the body increases in size, probably in part through the absorption of water, but this expansion should be distinguished from the change that has already taken place, which is due to cellular growth, and is the primary cause of the molt. Thus in molting the animal parts with its old shell or epidermic exoskeleton at one stroke, and presently attains to greater size.

Molting begins on the second day after hatching and lasts throughout life or at least as long as there is any growth. The first three molts are passed in from 12 to 15 days. From first to last the cuticle is cast as one piece (excepting only the gastroliths), the animal escaping through a rent of the membrane between the tail and back. In healthy young animals molting lasts but a few minutes, but at all times the process is critical and it is frequently fatal. It often leads to the distortion or the loss of limbs and to a variety of deformities such as duplications of a limb or of its parts.

It is difficult to avoid repetition in dealing with the molting process since it has modified the habits of the animal at so many points, but we shall now consider the subject in regard to the adult animal as a whole. In order to understand the process it will be necessary to examine the structure of the shell and of the soft skin, of which the former is a product.

THE SKIN AND SHELL.

The skin as a whole is composed of the soft dermis, the soft epidermis, and the shell or cuticle which the latter secretes. The epidermis is typically composed of a single stratum of chitin-producing cells, and often rests upon a thin basement membrane, which then forms a distinct boundary between the two layers and like the outer shell is a cuticular product. The dermis is composed of connective tissue cells, which are often attached to the basement membrane, blood vessels, nerve fibers, pigment cells, and glands, which are apparently of epidermic origin. Wherever muscles are attached to the shell, the epithelium is greatly modified or reduced (see ch. VI, p. 241). The shell in sectional view shows four layers, namely, (1) a thin outermost stratum, which is structureless, called the enamel layer; (2) an underlying and lamellated pigment

layer, transversed by vertical canaliculi, abounding in pigment and impregnated with mineral salts; (3) the calcified layer proper, devoid of pigment, but otherwise like the last, and forming the greater part of the shell substance; and (4) a noncalcified inner stratum composed of very thin lamellæ.

The chitinogenous epithelium may be compared to the Malpighian layer of the epidermis of the vertebrate, while the layers of chitin represent its horny cuticle, though formed in a different manner. The vertical canaliculi of certain decapods, according to Vitzou (*272*), correspond to the boundaries of the epidermic cells, but this is not the case in the lobster, where they are close together and very numerous.

During the molting period the cells of the chitinogenous epithelium undergoes a great change, its cells being extended vertically into very long and slender rods (pl. XLVI, fig. 2). The epithelium developed over the surface of a budding limb is of a similar character. The chitinous layers of the new shell are formed by discontinuous thickenings of what, according to Vitzou, may be regarded as the upper wall of the epithelial cell. Thus are formed parallel lamellæ of varying density, which fuse with those of adjoining cells and make a continuous shelly crust.

At the time the shell is ready to be cast the tegumentary coverings consist of (1) the old shell, (2) the new shell, (3) an intermediate structureless membrane, besides the chitinogenous epithelium, and (4) the dermis. The new carapace, according to Vitzou, is composed of the enamel and pigment layers only. The calcified layer is not formed until after the molt.

Certain peculiar cells which have been referred to as connective tissue become very conspicuous at the molting period, particularly in the dermis, and experimental evidence seems to show that they secrete glycogen which is used in the production of the new shell, but no exact knowledge concerning these structures is available at present. The enamel layer is the first formed, and when once laid down can not be removed except by the shedding of the entire shell. However, it is worn away by abrasion, as seen in the old hard-shelled animals, and its function is purely protective.

The surface of the shell has a punctate appearance, due to hair-pores, which mark the points where hairs or setæ now pierce the shell or where they were present at an earlier stage of development. In the adult lobster the setæ of the carapace have disappeared more or less completely except upon its margins and in the orbital region.

The dense shell of this animal is in reality a veritable strainer, being perforated by hundreds of thousands of minute passages, which lead from the surface to the parts below it—to the tegumental glands on the one hand or to the sensory cells which lie at the roots of the hairs on the other.

PERIODS, CONDITIONS, AND SIGNIFICANCE OF MOLTING.

The hard-shell lobster is heaviest, has the firmest flesh, stands transportation best, and is therefore most valuable for the market. A large percentage of all lobsters taken during the fall and winter months are of this character, and nearly all lobsters caught in March, April, and May belong also to this class. Shedders and soft-shell lobsters are taken in greater or less abundance from June to October, varying somewhat with

the season and surrounding conditions, such as the nature of the sea bottom and the temperature of the water. By far the greater number of lobsters cast their shells during the months of July, August, and September. The time of shedding, however, varies considerably on different parts of the coast, being from 4 to 6 weeks earlier in some seasons in western Maine than in the extreme eastern section. Shedders are not fit for the market, being lean and watery, and soft lobsters are in a similar condition and will not bear much handling or transportation. Until the shell becomes tolerably hard the soft lobster is easily wounded and killed. Lobsters with very soft shells and those that have been mutilated are often kept in the lobster preserves or pounds until the shell is hardened or the injury repaired.

Traps set by Mr. Vinal Edwards at fixed points on the rocky bottom in the harbor of Woods Hole, Mass., for a period of 7 months, from December 1, 1893, to June 30, 1894, were daily hauled and the conditions of the shell of each lobster noted. The significant data thus obtained were as follows:

TABLE 2.—DATA FOR LOBSTERS EXAMINED AT WOODS HOLE, MASS., WITH REFERENCE TO MOLTING CONDITION.

Number of lobsters caught.		Lobsters recently molted or preparing to molt.	Shell hard and dull.	Shell soft.
Males	1,313	77	33	44
Females	1,344	33	7	26
Total	2,657	110	40	70

Of the entire catch, 110 lobsters had either recently molted or were preparing to molt; 77 of these were males and 33 females. The total number of males was smaller, yet the number of soft shells among them was nearly twice as great as in the other sex. This fact implies that the males molt oftener than the females, which would be an *a priori* deduction from the greater size which the male attains, or that they molt more frequently during this period, assuming that the distribution of these animals was uniform for the time and place.

In the fullest sense the molting process consists of two distinct phenomena: (1) The formation of a new shell and (2) the rejection of the old. When once formed the shell admits of no increase in size, since it is a dead structure, excreted by the soft skin below it, and when it is outgrown it must be cast off and give way to a new and larger covering. The new shell is gradually secreted under the old one, and when the latter is discarded the new cuticle is soft and flexible, so that it is easily distended to meet the requirements of growth. The growth of the lobster, as of every arthropod, is thus measured by a series of stages characterized by the growth of a new shell under the old, by the shedding of the outgrown old shell, a sudden expansion in size, and the gradual hardening of the shell newly formed.

Not only is the external shell cast off in the molt, along with the linings of the masticatory stomach, the esophagus, and the intestine, but also the internal linkwork of hard tendons described in chapter VI. The sloughing of the latter is rendered possible, first by the presence of absorption areas and secondly from the fact that the inner skeleton is in origin an infolded part of the cuticle; in molting the lobster withdraws its soft body from the mold of its old and hardened skeleton. It is thus easy to see why the molting act is a continually recurring crisis in the life of the decapod crustacean, for it is both dangerous and expensive, not only calling for a considerable excess of energy, but demanding that a long series of preparatory changes, to be later considered, must be exactly executed. Since it is dependent upon the condition of the individual, which is subject to wide variation, the molt does not take place at any stated time, but may occur in any month of the year. In general, molting in either sex is rare in winter and spring and most frequent in summer. Warmer weather, a more active life, a greater abundance of food, and a more vigorous appetite, which are characteristic of the lobster or its environment during the warmest part of the year, are most favorable to the renewal of the shell. The lobster, though a carnivorous animal, feeds less in winter, when its habits are relatively sluggish. Broken limbs and injuries to the shell are then but slowly repaired, and there is less energy to be drawn upon in molting.

As a rule, the adult female that lays her eggs in August of any given year carries them for 10 or 11 months, until they hatch in the succeeding June. Since the spawning periods are 2 years apart, Hadley (*126*) infers that the molting periods can not oftener occur and that the rate of growth in the female is consequently diminished. In average cases this rule may hold, but exceptions occur. Thus, I have recorded two cases (*149*) where soft-shelled lobsters with eggs were taken in which the molt could not have preceded ovulation by more than two or three weeks; still further, in exceptional cases, a second molt may possibly take place in late autumn or in the early winter, following the hatching of a brood.

It is several weeks before the new envelope becomes as hard as the one rejected, so that the lobster is, for a large part of its life, either preparing for a molt or recovering from one. Therefore it is not remarkable that lobsters have acquired many popular names among fishermen, such as "hard shell" or "old shell" lobster, "shedder," black shell," or "crack shell" (lobster preparing to molt), "soft shell," "new shell," "shadow," "rubber shell," "paper shell," "buckle shell" lobsters, etc. (animals which have recently molted).

Shedders can be readily distinguished by the dark, dull colors of the old shell, hence the common name of "black lobster," and by the deep reddish tint of the membranes at the joints, where the flesh is seen through the old and new cuticulæ. The lobster is now naturally sluggish and takes but little food, but it can not be said that the shedder never breaks its fast. It is not a very unusual experience for the fisherman to take both the soft lobster and its cast from his traps. When in this condition lobsters commonly haunt shallow water, with a sandy, muddy, or weedy bottom, and

at low tide have been taken out of bunches of eelgrass at a depth of a few inches only. They frequently dig a shallow hole in the mud under stones, where they can await the coming change with greater security from enemies. Fishermen have frequently seen a cast shell lying on the bottom and have found a soft lobster near by, protected by a rock or bunch of kelp.

Many of the prawns habitually molt in the early morning while it is yet dark, but lobsters which we have kept in aquaria have cast both by day and at night. Considering the nocturnal habits of the lobsters, we should expect to find the latter practice the commoner in a state of nature. In those captives which Brook (*37*) observed with great care, the shells were cast off in the night time and partially buried.

Anderton (*5*) found that the lobsters transported from England to New Zealand molted mostly at night, their cast shells being usually seen lying upside down on the bottom. The shedders retired to some secluded spot where the water was shallow, and appeared vicious upon the approach of intruders. On the 3d of September, says Anderton, "a male lobster was seen to be behaving in a very peculiar manner in the shallow end of the pond. It would walk alongside the concrete dividing wall for a distance of about 5 feet, halt, and then turning round would retrace its steps the same distance in the opposite direction. In this manner a rut several inches deep was formed in the gravel and at one end of this the lobster scooped out a hole about 4 inches deep and 12 inches in diameter." The water had to be temporarily withdrawn from the pond, but as soon as permitted to do so this lobster resumed its peculiar walk, and continued it through the night and the following day. Molting began at 4.30 p. m. of that day and lasted 35 minutes. The lobster at first lay on its side, with its large claws extended in a direct line with its body, and later turned on its back when the tail, the last part to be withdrawn, was released. The habit of scooping a hole in the gravel was noted on several occasions, when the soft lobster was found lying beside its "shadow." As noted in chapter IX, molting in the females was almost immediately followed by copulation, whenever a male was available, and the interval between this act and the laying of the eggs was in two cases observed—65 days. Molts in both sexes were recorded from November 18 to March 3, but rather more frequently in the warm months of November and December.

THE MOLTING ACT.

A male "shedder" was caught in the harbor of Woods Hole July 13 and placed in an aquarium. At exactly 2.48 p. m. this lobster began to molt and in 6 minutes was out of its shell.

When the lobster is approaching the critical point the carapace or shell of the back gapes away a quarter of an inch or more from the tail. Through the wide chink thus formed the flesh can be seen glistening through the old and new cuticle, giving it a decidedly pinkish tinge. Take the lobster up in the hand now and the tail drops down as in death, the strong muscles which bind the pleon to the carapace being completely relaxed. When this stage is reached the time of exuviation is at hand and the process becomes purely automatic, the animal having no control over its own movements.

The period of uneasiness, which foreshadowed the molt and was very marked, ended in this lobster by its rolling over on its side, briskly moving its legs, and bending its body in the shape of the letter V, the angle of the V corresponding to the gaping chink between the dorsal shield and tail. Presently the old cuticle, holding these parts together, began to stretch, the wall of the body pressing against it with considerable force, and the hinder end of the shield being slowly lifted up, while its anterior part remained attached to the rest of the skeleton. The slow but sure pressure of the parts within cause an increasing tension in the yielding cuticular membrane, which finally bursts, revealing the brilliant colors of the new shell. The legs and other appendages are occasionally moved, but no marked convulsive movements are to be seen. The carapace has now become raised to an elevation of perhaps 2 inches in its hinder part, in consequence of which, the anterior end being fixed, the rostrum is bent downward and the animal presents a very singular appearance.

When this stage has been reached the lobster becomes quiet for a few seconds and then resumes its task with renewed vigor. From this time on until free its muscles work intermittently. The doubled-up fore part of the body, with each effort of the animal, is more and more withdrawn from the old shell, and this implies the separation of the skin from the intricate linkwork of the internal skeleton, and particularly in its release, together with a part of the nerve cord, from the closed archway of this structure, as well as the freeing of the 28 separate appendages from their old cases and tendons, for the accomplishment of which special adjustments are made in advance. The cuticular sheath of every ectodermic structure is stripped off. The exoskeleton folded to fit so complicated a mold is virtually a continuous structure, and from the method of its regeneration the sloughing of one part necessitates the shedding of the whole.

The carapace is now elevated to such an extent from behind that the rostrum is directed obliquely downward and backward. The lobster is still lying in comparative quiet upon its side, but the muscles of all its appendages are undergoing violent contraction as the animal tugs and wrestles violently as if to free itself from ropes which bind it down firmly on every side. The carapace is unbroken, yet the two halves bend as upon a hinge along the median line, where the lime of the shell has been absorbed. Presently the pressed-down bases of the antennæ, the eyestalks, and the bent-down rostrum of the new shell can be clearly seen. No part of the covering of the large claws or of any of the legs have been split or cracked. The muscular masses of the powerful claws have been withdrawn through their narrow openings without a rent. Finally a few kicks free the entire forward half of the body, the antennæ, chelipeds, and varous other parts, which now lie above or to one side of the old covering. The tail has been gradually breaking away from its old case, and as soon as the forward part of the body is withdrawn the lobster gives one or two final switches and is free.

The newly molted lobster has a very sleek and fresh appearance, and its colors were never brighter or more attractive. Try to take it up in the hand, after some time has elapsed, and it feels as limp as wet paper; but immediately after casting the shell the muscles of the crustacean are hard and tense, probably from being in a state of cramp or tetanus. Every part of the old shell down to a microscopic hair has been

reproduced in the new one, but in the latter the fringes of stiff setæ are as soft as silk, the stony ends of the claws, the rostrum, and every spine of the body so soft as easily to bend beneath the finger. Possibly the hardest parts of the newly molted lobster are the horny surfaces of the teeth of the stomach sac. The large claws are considerably distorted, as well as some of the other parts, being compressed and drawn out to an unnatural length. After getting clear of the old shell the animal is not inclined to activity. It soon orients itself, however, resting in the usual way, and is capable of moving about with some degree of agility by the flexure of the tail. Fishermen who have had lobsters shed in their cars or traps have often been surprised by the ease with which they sometimes slip through their fingers.

The length of the cast shell of this lobster was 11.25 inches, and shortly after the molt the animal measured 12 inches from tip to tip. On July 17, four days after molting, the length was a little short of 12.5 inches. The increase in length was thus very nearly 1.25 inches. Very soon after molting the lobster is ready to take food, the body plumps out to its natural shape, and no further increase in volume can take place until another molt.

The increase in length of body at each molt in lobsters between 5.5 and 11.5 inches is between 11 and 12 per cent. Increase in length diminishes beyond this period, yet the volumetric increase of the entire body, especially the big claws, may be as great or even greater. Beyond the twenty-second stage, according to Hadley, the male grows more rapidly than the female.

WITHDRAWAL OF THE BIG CLAWS.

The shell of the large claw is molted entire without a rupture in any part. This means that the great mass of muscles which fill its terminal joints must undergo distention and compression to an extraordinary degree, since it is all drawn through the constricted base of the limb as wire is pulled through the holes of a drawplate. What this implies will be best appreciated when it is realized that the cross sectional area of the biggest part of the cheliped is more than four times greater than that at its narrowest point, in the second joint.

The lobster is aided in accomplishing this feat by the elasticity of the muscles and other tissues and by the removal of blood from the fine meat of the claw (pl. XL, and fig. 3, pl. XLVI), as well as by the development of absorption areas in the shell of the third and fourth segments of the cheliped. (Pl. XXXVII, fig. 2, *abs. a.*) The muscles of the big claw, which are pulled out like a stick of candy, are at first quite tense. Very soon, however, they relax and, filling with blood and presumably taking up some water, they assume their natural form, with proportional increase in size. The absorption areas, from which mineral matter is removed preparatory to the molt, are easily distinguished in the hard-shell lobster, though less clearly defined. The shell of the basal joint becomes a slender ring, but does not break.

At the time of the casting of the shell the large claws must be practically free from blood, since, as Vitzou has pointed out, if the claw were to be increased in size it would

be next to impossible for it to be withdrawn without rupture. The older naturalists used to explain the withdrawal of the large claws by a wasting of the tissues. The lobster was supposed to become sick and emaciated, which was, of course, an error. The most significant fact in this process is the displacement of the liquids which normally belong to these appendages. The terminal soft tissues of the claw are essentially a sponge work of involuntary muscle fibers, to which the returning blood stream has free access.

The changes in the armature of the lock forceps, which attend each molt in both young and adult, are discussed in chapter VII.

MOLTING OF THE "HAMMER" CLAW IN THE SNAPPING SHRIMP, ALPHEUS.

It would be erroneous to infer that all relatives of the lobster in molting withdraw the flesh of their big claws through the "drawplates" of the basal segments of the limb. This is not true of certain species of the snapping shrimp, in which the great "hammer" claws are proportionately larger than in the lobster.

On November 13, 1896, while at the zoological station at Naples, a large male of *Alpheus dentipes* molted in a small aquarium at 3 o'clock in the afternoon. Preparations for this act had been going on for several hours, and were probably begun in the early morning. In this case the muscular mass of the claw was withdrawn through a crack, which extended along the outer margin of the propodus. This cleft was continuous, with a similar fissure involving the proximal segments of the cheliped and extending through the basal ring. The great muscular mass of the hammer claw was thus withdrawn without distortion. This fissure was assumed to correspond to a linear absorption area, but I have not been able to repeat the observation.

CHANGES IN THE SKELETON PREPARATORY TO MOLTING.

At the time of the molt there is an intermediate membrane which makes its appearance between the new and old shells. It is noncellular, has a gelatinous appearance, is very transparent, and may be found adherent to the old shell after the molt is past. It bears the impress of a mosaic of cells, which can be none other than the cells of the chitinogenous epithelium. Vitzou is thus in error in supposing that this substance is a secretion of chitinogenous epithelium underlying the new carapace, which it traverses by endomosis. It must be either the first secreted product of the new shell or the innermost layer of the old shell modified by absorption, if not derived from tegumental glands.

In this cuticular membrane the parts which correspond to the cell boundaries of the chitinogenous epithelium have the form of elevated ridges on the under side, and in the center of each polygonal area there is a slight thickening. Réaumur [a] had in view a similar structure in the crayfish when he spoke of a glairy matter "as transparent as water, which separated the parts which the crayfish was soon to cast off from the rest

[a] Additions aux observations sur la mue des écrevisses, Mémoires de l'Académie Royale des Sciences, p. 263–274, 1 pl. Paris, 1719

of the body, and which allowed these to glide smoothly over one another." The old shell becomes brittle, owing to the absorption of organic matter previous to molting, and if the carapace is pressed between the fingers it will sometimes split down the back in the longitudinal median furrow, but in most cases the shell does not crack in this plane unless artificially compressed. In the course of the preparation for the molt the lime salts of the shell are absorbed along the middle line of the carapace, leaving a narrow, perfectly straight gutter extending from the spine or rostrum to the posterior margin of the shield. The chitinous portion of the cuticle still remains, forming an elastic hinge, on which the lateral halves of the carapace bend without breaking asunder. In the molted shell there is also a linear membranous area on either side of the rostrum. Absorption of the hard matter of the shell at these points tends to give greater latitude to the movements of the two halves of the carapace. If you examine a hard-shell lobster, you will find in place of the median furrow a blue line, drawn as if with pen and rule. Below this line the epidermic cells of the skin become so modified as to bring about the total absorption of the lime salts of the cuticle.

Other areas of absorption besides those of the great chelipeds, already described, include the wide lateral margins of the gill covers or branchiostegites, which in life are colored light blue, parts of the endophragmal skeleton, especially the roof of the passageway, in which are lodged the sternal blood sinus and part of the nerve cord, and the endotergites, three small teethlike projections from the under side of the carapace, on which the posterior gastric muscles are partly inserted. Rupture in the rostral regions is further provided against by the narrow absorption areas on each side of it, while the softening of the margins of the carapace makes the lifting of this from the body an easy matter during the molt. The softening of the endotergites and apodemes of the internal skeleton is also necessary to prevent injury to the soft tissues and to permit their release.

The lobster, as we have seen, leaves its old envelope by drawing the anterior part of its body backward and the abdomen forward through a rent in the soft membrane between carapace and tail. The cuticular lining of the masticatory stomach and esophagus comes out by way of the mouth, while whatever is molted from the intestine is withdrawn from the anus. The intestinal molt of the larva is apparently much more extensive than that of the adult. When the discarded carapace falls back into its natural position we might, as Réaumur says of the crayfish, mistake the empty shell for another animal.

THE GASTROLITHS, OR "STOMACH STONES."

The gastroliths of Crustacea are found only in the lobster and crayfish, and according to Patrick Browne, as noticed by Stebbing (*259*), in certain land crabs of the island of Jamaica. Having been first discovered in the common river crayfishes of Europe, they figured in the old pharmacopœias as *oculi seu lapides cancrorum*, and have excited the interest of naturalists from early times. Owing to their transitory character, they are not commonly seen in the lobster.

If the shell of the lobster which is nearly ready to molt is removed, there will be seen two glistening snow-white masses, one on either side of the stomach. A gastrolith taken from a lobster 11 inches in length was an inch long, three-quarters of an inch wide, and a quarter of an inch thick. Its outer convex side was applied to the sac in which it lay, while its concave side was separated from the cavity of the stomach by the old cuticular lining of this organ. When the stomach is raised the gastroliths almost break through its delicate outer wall by their own weight. They lie between the old cuticular lining of the stomach, which may be stripped off, and its delicate outer wall, next to the body cavity. The impression of the gastrolithic plate (pl. XXXIII) is seen on the new cuticular lining only. If the sacs in which they are formed are cut open, each mass separates into hundreds of small ossicles or columns, the majority of which are slender truncated prisms of irregular shapes and about one-fifth of an inch long. Each ossicle resembles a piece of milk-white glass, with transparent edges, and is faintly marked with transverse and longitudinal striations, like those seen in the cuticle.

The gastroliths, though a part of the cuticle, are not regularly cast off during the molt, but are retained in the stomach; when the old lining of this organ is withdrawn, they are soon set free, and breaking up into their constituent parts are speedily dissolved. Consequently it has been supposed that they served the function of providing a supply of lime for hardening the new shell. Messrs. Irvine and Woodward (*165*), however, have proved that the amount of calcareous matter obtained in this way is only about one one-hundred-and-eighty-sixth part of that of the entire skeleton, and therefore too insignificant to be of any practical value. Lime, moreover, is at hand in abundance in the form of the shells and skeletal fragments of mollusks and other animals, which lobsters make free use of at the time of the molt.

We have suggested that the gastrolithic plates or sacs in the walls of the stomach are organs for the excretion of lime, and that the gastroliths represent the lime removed from the absorption areas previous to the molt. Upon this theory their retention and absorption is an incident of no special importance (see *149*, p. 93).

The gastrolith of one of the common crayfishes (*Cambarus robustus*) when 4 inches long is about the size of a split pea, 7 millimeters in diameter by 5 millimeters thick. It shows no divisions into ossicles, but is a hard mass. The convex face is dull white and nearly smooth, while the flattened side presents a brown circular scar with a white center. In form and appearance it suggests a small mushroom with the stem cut off close to the cap. In sectional view it shows concentric striations.

Chemical analysis [a] has proved that lime salts as carbonates and phosphates form about half the constituents of the hard shell, there being from three to five times as much carbonate as phosphate. We also find that in the cast shell of the lobster the proportion of organic matter present is considerably less than under other conditions. An absorption of organic matter thus takes place during the period in which the new shell is formed, and this fact explains the fragility of the cast-off shell. Small quantities of alumina and silica are normally present in both the shell and gastroliths.

[a] See article by Prof. A. W. Smith, *252* of bibliography.

The composition of the gastroliths is similar to that of the shell, a conclusion which we should be led to draw from the fact that these bodies are specialized parts of the dead chitinous integument. The same substances are found in both, but in different proportions. The gastroliths are far richer in lime, chiefly in the form of carbonate ($CaCO_3$), than is the shell, and the amounts of magnesium carbonate ($MgCO_3$), alumina (Al_2O_3), ferric oxide (Fe_2O_3), and silica (SiO_2) are more or less reduced.

Lime estimated as carbonate ($CaCO_3$) constitutes about three-fourths of the gastrolith, but less than two-fifths of the carapace. Lime reckoned as phosphate ($Ca_3(PO_4)_2$) forms about 10 per cent of the gastrolith and but little less in the case of the shell; about 10 per cent of the gastrolith is water and organic matter, probably mainly chitin, and the rest is made up of various salts and oxides. In the only molted shell analyzed about 38 per cent was water and organic matter, while in two hard-shell lobsters this percentage was considerably greater, 42.21 in one case and 51.80 in the other.

Since the total quantity of lime contained in the gastroliths is but a small fraction of the amount necessary for building up the hard crust, the rapidity with which the new shell hardens depends in some measure upon the individual, and particularly upon the quality of its food. Lobsters when young and sometimes when adult not only eat their own cast after molting, but swallow fragments of shells and other calcareous materials, which are dissolved in the stomach and help to strengthen the new shell.

Williams (*279*), who has recently studied this subject, has added some important facts to our knowledge of the gastroliths. He found that while absent in the larvæ they made their appearance at the fourth stage, when the shell begins to receive deposits of lime, and at about the middle of this period. After the next molt the gastroliths were dissolved in the course of a few hours, either remaining in place or falling to the bottom of the stomach sac, to be later broken up. With their dissolution there was observed a gradual hardening of the gastric teeth, mandibles, and later of the chelipeds and other parts.

> As soon as the gastroliths are dissolved [says Williams], the lobster attacks his cast, beginning to eat the bristles and small parts and proceeding to devour more or less of the harder parts. The newly molted lobsters seldom seriously attack their sloughs within three or four hours, and generally eat the greater part of the cast within twelve or eighteen hours.

He therefore supports the older view that the gastroliths represent a store of lime and other minerals reserved from the old shell for the immediate hardening of the new, with the additional statement that this reserve is destined for particular parts—gastric teeth, mandibles, and chelipeds—so that the cast and other calcareous matter within easy reach may be quickly available.

Stebbing (260), who also has criticised the view that the gastroliths are primarily excreted products, does not believe that such nicely adjusted structures can serve as "mere off scourings of the body."

The difficulties in the way of supposing that these interesting bodies are necessary rather than incidental sources of lime to the newly molted lobster are by no means removed by the observations quoted above. To be of service at all the carbonates of

the gastroliths must be dissolved, absorbed into the general circulation, and converted into phosphates. There is no reason to suppose that the gastric teeth or any other part can make exclusive use of this lime, or use it at all except through the roundabout course open to all lime-absorbing cells. Moreover, the total amount of mineral matter in the gastroliths is so small that when equally disseminated it is difficult to understand how it could be of vital importance.

It seems altogether more probable that the parts mentioned by Williams are hardest in the end because they have the hardest chitinous base in the beginning, and that all parts receive only their due proportion of lime.

Assuming the problem of the gastrolith to be similar in both lobster and crayfish, the spicular character of the former may have no special significance. In the crayfish these bodies, as we have already seen, are solid stones, which, according to Chantran,[a] are slowly ground down rather than dissolved, their complete dissolution taking upward of three days in an adult animal.

Turning to the other side of the question, the absorption of lime from definite areas of the shell is of the utmost importance. Deformity or death awaits every animal in which the absorption areas are not duly formed. The production of such areas involves the excretion of lime through the medium of the blood. Their actual development proceeds, in some measure at least, with the growth of the gastroliths.

Accordingly, while the question may still be regarded as somewhat involved, we still believe that the theory earlier given, that the gastroliths are primarily excreted products and represent mineral matter removed from the shell in preparation for molting, and that their use for hardening the new shell is purely incidental, is the only one which meets all the facts in the case with any degree of success.

If it could be experimentally shown that the gastrolith is essential to life after the molt, as we now know it to be for the safe passage of the molt itself, a theory early maintained but not satisfactorily proved, the present status of the question would be changed.

HARDENING OF THE NEW SHELL.

A lobster which molted while under observation was watched particularly with reference to the hardening of the shell. One hour after the molt the cuticle seemed to the touch of the finger to be perceptibly hardened, but this may have been due to the turgescence of the tissues. Eighteen hours after shedding the cuticle had a leathery consistency, and the tubercles and spines had hardened slightly. The shape of all the parts was perfectly normal. Four days after the molt, when the animal died, the cuticle was still coriaceous, and but slight increase in the stiffness of any parts had occurred.

Another animal which also molted in confinement was kept for a period of 25 days. The carapace at the end of this time was easily compressible between the thumb and finger. The large claws could be made to yield in the same way, but not without

[a] Comptes rendus de l'Académie des sciences, t. LXXVIII. Paris, 1874.

using considerable force. It was in the state which the fishermen designate as a "paper-shell" or "rubber-shell" lobster. If sent to market it would have been classed as a soft-shell lobster. It is possible, of course, that in this space of time an animal under natural conditions would have become harder. It is safe to conclude, however, that from 6 to 8 weeks are necessary, under ordinary conditions, to produce a shell which is as hard as that cast off, and if the lobsters were destined for the market they would probably be in a still better condition in 10 weeks or 3 months. Many lobsters with soft shells are caught and sent to market, but their flesh is then watery and of inferior quality. When cooked, the fine meat of the claws, which will serve as a good index of their condition, shrinks to an almost unrecognizable remnant. According to the opinion of a canner of lobsters in Maine, 7 pounds of soft-shelled lobsters in summer or fall will yield no more than 4 pounds in spring, when the flesh is more solid.

RELATION OF WEIGHT TO LENGTH IN THE ADULT.

The lobster's weight does not bear a constant ratio to its length, but is very variable owing chiefly to the loss of limbs, and particularly of the great claw-bearing legs. These alone represent from one-fourth to one-half of the weight of the animal, and probably in all giants of the 20 to 30 pound class, which are invariably males, the weight of the great chelipeds is fully two-thirds that of the entire body. The lost limbs are promptly regenerated, as we have seen, but never completely without the intervention of one or more molts, so that a lobster with an undersized claw is a common occurrence.

The length of lobsters is commonly measured from apex of rostral spine to the end of the telson, not including its terminal fringe of hairs. More exact comparisons can be made from measurements of the nondistensible carapace or back shell alone. This method of measuring the lobster was adopted by the legislature of Maine in 1907, and should be generally followed. The Maine laws require the marketable lobster to measure 4.75 inches from the beak to hinder margin of the carapace, which is equivalent to a 10½-inch animal under the old standard, the ratio of carapace length to full body length being approximately 45 per cent for animals of average size. When the rostrum is defective the total body length can be taken. Under such a relatively inflexible standard the fisherman is not tempted to stretch his lobsters in order to put them into the "counter" class, and to sell animals which are likely to die from injuries thus received.

The weight is subject to considerable variation in consequence of molting, when a dense armor is exchanged for a much lighter though larger one. In the soft lobster the specific gravity of the solids and fluids of the body is considerably reduced, but on the whole the weight is chiefly affected by disparity in the size of the big claws.

The male is heavier than a female of the same length, at least after passing the 8-inch mark. The 10-inch males are about an ounce heavier than females of corresponding length. From this stage onward the balance in favor of the male becomes most pronounced. Thus the 11-inch male exceeds the female of this length by a full

quarter of a pound. In a lobster 12.5 inches long there is a difference in favor of the male of 7.5 ounces.

It is evident from the data earlier presented (see *149*, table 31) that the greater size of the male, which is a sexual characteristic, does not appear until the animal has passed the 8-inch limit. At this period the sexes are of about equal weight, but from this point the male surpasses the female in weight, owing chiefly to the greater development of the large claws.

The average weight of females without and with eggs proves that females with spawn are in a poorer condition or weigh relatively less than females without eggs attached to the body. In one-third of the cases recorded the weight of females with eggs was actually less than that of females of the same length without eggs. In the 10-inch series 184 females were examined; 36 of them had eggs and weighed on the average but one-tenth ounce more than those without eggs. The average quantity of eggs borne by a 10-inch lobster is 1.73 fluid ounces, and since a fluid ounce of lobster eggs weighs very nearly an ounce avoirdupois, the average weight of the 10-inch female deprived of her eggs is 22.13 ounces, as compared with 23.76 ounces, the average weight of nonegg-bearing females of this size. There is thus a difference of 1.63 ounces in favor of the female without eggs. In the case of the 9.5-inch female lobsters, where 169 in all and 24 bearing eggs were examined, the average weight of the spawners was less by 0.09 ounce than that of the corresponding females without eggs.

The facts which have just been stated do not support the conclusion of Buckland and his associates on the fisheries work in Great Britain that "the lobster, when berried, is in the very best possible condition for food."

The average weight of the 10.5-inch male lobster (the present legalized length limit in Maine, New Hampshire, and certain districts of Canada) is about 1.75 pounds, a corresponding female without eggs weighing about an ounce less. At 9 inches (legalized in New York, Rhode Island, Connecticut, in Massachusetts since 1907, and in certain parts of Canada) the average for both sexes is nearly 1.25 pounds. The lobster 8 inches long (the present legal gauge for England, Norway, and parts of Canada) of either sex, has an average weight a little short of a pound, or 15.16 ounces. At the 12-inch length the male weighs approximately 2 pounds 12 ounces, the females being about 2 ounces lighter, while lobsters 15 inches long will weigh on the average 4.25 to possibly 4.5 pounds.

A lobster 17.75 inches long weighed nearly 10 pounds (though in this case the cutting claw was undersized), and the mammoth specimens recorded in table 1, weighing from 19 to 34 pounds, varied only from 19.5 to 23.75 inches in length. Indeed between the 18-inch and 20-inch length, as well as beyond this limit, great variation is seen in the weight of normal individuals of either sex of the same length as in the case of smaller lobsters, and due to the same causes, namely, variations in the size and the corresponding weight of the large claws or to the condition of the shell with respect to molting. Beyond the 20-inch size a slight increase in length may imply a great addition to the weight.

PROPORTION OF WASTE TO EDIBLE PARTS IN THE LOBSTER.

Atwater (*11*), in his chemical analysis of the flesh of the lobster, gives the proportion of the edible parts and shell as follows:

	Per cent.
Total edible portion	39.77
Shell	57.47
Loss in cleaning	2.76
	100.00

The proportions of water and dry substance in the edible portion are estimated as follows:

Water	82.73
Dry substance	17.27
	100.00

In this relation the analysis given in table 3 will be of interest. These data were obtained from a 13-inch (boiled) female lobster, with shell of medium hardness. Literally all of the soft and edible parts were carefully removed from the skeleton and weighed. This, without doubt, accounts for the higher percentage of "edible" parts obtained when compared with the result quoted above, it being assumed that all of the soft tissues of this animal are edible and wholesome excepting the stomach and intestine.

The flesh of the lobster is rich in nitrogenous or proteid substances and contains a considerable amount of phosphorus and sulphur. Its nutritive value as compared with beef taken as a standard is 61.97 per cent (*11*).

TABLE 3.—SHOWING RELATION OF EDIBLE TO WASTE PARTS IN THE LOBSTER.

Edible parts.	Pounds.	Ounces.	Waste.	Pounds.	Ounces.
(1) Tail muscles	0	8¾	(8) Shell and "lady" or stomach sac	1	3¼
(2) Meat of great claws, including joints of great chelipeds	0	7¼	(9) Liquids	0	6
(3) "Cream," or clotted blood from great chelipeds	0	1¼			
(4) Fine picked-out meat from linkwork of body and smaller appendages, including gastric, mandibular muscles, and green glands	0	7¾			
(5) "Cream," or clotted blood from body under shell	0	2⅞			
(6) "Coral," or ovaries	0	2			
(7) "Tomally," or liver	0	2⅛			
Total weight of claw and tail meat, 1 pound.					
Total weight of edible parts	2	.....	Total waste	1	9¼

Total weight of items 1 to 9, 3 pounds 9¼ ounces.
Estimated living weight, 4 pounds 4½ ounces.
Dead weight, 3 pounds 9¼ ounces.
Percentage of clear meat in claws and tail, 27.
Percentage of all clear meat and edible parts, 55.
Total cost at current retail-market price, at 25 cents per pound, at Tilton, N. H., June 27, 1903, 90 cents.
Cost per pound of clear meat of big claws and tail (items 1 and 2), 90 cents.
Cost per pound of clear meat and other edible parts not usually saved (items 4–7), 45 cents.

Chapter V.—ENEMIES OF THE LOBSTER.

PREDACEOUS ENEMIES.

The adult lobster, whether with eggs attached to its body or not, is the prey of numerous fish which feed upon the sea bottom, like the sharks, skates, and rays. When of considerable size or in soft condition it is also devoured by the cod, pollock, striped bass, sea bass, tautog, and probably by many other species. In fact every predaceous fish which feeds upon the bottom may be looked upon in general as an enemy of the lobster.

Next to man with his traps, the codfish is probably the most destructive enemy of the lobster, for it not only takes in the soft and hard shell animals alike up to 8 inches or more in length, but is very partial to the young from 2 to 4 inches long.

If the lobster is thus attacked and destroyed in large numbers by fish after it has acquired the habits of the adult and has many devices to avoid its enemies, what shall we say of the destruction which is wrought on the young during the first three or four weeks of their life? From the time of hatching up to from the fourth or fifth stage the young lobster swims at the surface and becomes an easy prey to all surface-feeding fish, some of which, like the menhaden, roam about in vast schools, straining the water as effectively as the towing net. When lobsters settle in relatively shallow water the greedy cunners or even fish of smaller size would doubtless prove vastly more destructive. During this period the lobster measures from one-third to three-fifths of an inch in length, and is not only helpless in the hands of its animate enemies, but is subject to a vast amount of indiscriminate destruction from the forces of inanimate nature.

PARASITES AND MESSMATES.

But two parasites in the strict sense have thus far been known to infest the lobster, although it is probable that others will he discovered. One of these, a trematode worm (*Stichocotyle nephropis*) first noticed in the intestine of the Norwegian lobster, was later detected in the American form, about 2 per cent of these animals being infested by it. Its final host is probably some species of fish which preys upon the lobster, but the adult trematode is unknown.

The only other strict parasite which has been found to trouble the adult lobster is the large gregarine (*Gregarina gigantea*), discovered in the intestine of the European lobster by Van Beneden (*269*).

The European lobster is commonly infested with a small colorless worm, *Histriobdella homari*, of remarkable habits and doubtful relationship. Discovered in 1853 by Van Beneden on this lobster's eggs at Ostend, it was regarded as a larval serpulid, but later (*108*) shown by him to be an adult and placed among the leeches. An account of its anatomy was given by Foettinger (*108*) in 1884, but for the most exact anatomical analysis of this curious semiparasite or commensal we are indebted to Shearer (*324*), whose work has but recently appeared. He found that it not only lived among the eggs of the berried lobster, but took up its abode in the branchial chamber and on the gills of both sexes also, passing readily back and forth when its host was a female in berry. It crawls slowly, but is more active among the lobster's eggs, to which it attaches its own ova freely, as well as to the carapace side of the branchial chamber. It is very sensitive to changes in the sea water, and its selection of such lodgings seems to indicate clearly the need of an abundant supply of oxygen. Development is direct, there being no larval stage, and little is known of its distribution or the means by which this is effected. Though possessing toothed jaws, and though seen to bite one another, these parasites are not known to molest either the gills or eggs of their host, and since they often devour diatoms in quantity they may be the lobster's bosom friend rather than its enemy. So far as known at present, *Histriobdella* is not attached to the American lobster.

But although parasites are rare, the lobster is encumbered with a great variety of messmates, which attach themselves to the external shell. Whenever the lobster is confined in inclosures, or compelled for any reason to lead a sluggish life, the common barnacle fixes itself to the arched carapace and begins to secrete its tent-like covering as securely as it might upon a stone; mussels of various kinds insinuate themselves in convenient angles of the shell and joints, and small tunicates sometimes become attached firmly to the underside of the shell between the legs. Tube-forming annelids, lace-like bryozoa, form incrustations in various parts, and red, brown, and green algæ often decorate the antennæ and carapace with long streamers which are waved with every movement of the animal. At each molt the lobster of course frees itself completely from these troublesome companions. (For fuller account of parasites and messmates see *149*, p. 122–124.)

When young lobsters are hatched and reared in confinement they are apt to be troubled with a variety of parasitic fungi and algæ, including many species of diatoms, as well as stalked protozoans. Young lobsters captured at sea seem to be peculiarly free from foreign matters of every kind, but when the young of almost any crustacean are confined they are liable to become clogged with solid organic and inorganic particles of many kinds, including living bacteria, spores of fungi, and diatoms. The hairs which garnish the body and appendages of crustacean larvæ serve to gather up and hold particles from the water, so that one of the first considerations in the artificial rearing of these animals is to give them as clean a water supply as possible. Old lobsters, in which the molting periods have become very infrequent, are the worst sufferers from enemies of this kind, but the physiological condition of the animal is a most important consideration.

DISEASES AND FATALITIES OF THE LOBSTER.

There are few specific diseases to which adult lobsters are subject so far as known, yet they sometimes die off so rapidly as to lead one to suspect that they have fallen a prey to infectious disease.

Mr. N. F. Trefethen, of Portland, Me., relates the following experience: In May, 1893, he placed 100,000 lobsters in a pound at South Bristol, the area of which is about 3 acres. Very soon they began to die, and in a few days all of them were dead. There was from 12 to 13 feet of water in this pound at flood tide and not less than 9 feet at low tide. The pound was probably very much overstocked, but it is difficult to understand why these lobsters should have all died so suddenly, unless they were either poisoned or attacked by disease.

In the summer of 1889 a lobster with a large bunch on the side of the carapace was captured in Vineyard Sound. On the top of this tumoid growth was a crater-like depression covered with a membrane. This was probably a sore resulting from a wound which the animal had received in the back, and which failed to heal. A similar case is mentioned by Rathbun. Further, according to Prince (*218*), Professor M'Intosh has described a tumor-like growth in a large lobster which originated in the wall of the stomach sac, finally perforated the carapace and caused its death.

In another place I have alluded to the experience of the U. S. Bureau of Fisheries at Woods Hole in feeding the young lobsters with shredded menhaden. The larvæ became infected with a fungus, which spread to all parts of their tissues and was soon fatal.

To paraphrase the words of Hardy,[a] the lobster, like many other aquatic animals, is confronted by the same problem that has so long puzzled the shipbuilding world. Larvæ and spores are constantly settling upon the exposed surfaces of its body, where they tend to develop growths which would interfere with their movements unless some method of destroying or removing them were adopted. Hardy believes that "the presence of a film of soluble slime on the surface of an animal immersed in water would, like the copper sheathing of ships, mechanically prevent the occurrence of parasitic growths by continually forming a fresh surface," and further that this slime may in some cases have a specific poisonous power, directed chiefly against vegetable parasites.

The lobster apparently secretes no slime, but its shell is studded with the openings of the tegumental glands, the exact function and rôle of which is still in doubt. At all events it will do no harm to raise the question whether these bodies may not help to free the animal from such pests. That molting alone is not able to do this and that some additional aid is often needed is amply proved by the great variety of messmates or semiparasites which we have described.

Lobsters from a few inches in length up to the greatest size are sometimes driven ashore and stranded on the beach, where, stunned or crushed by the force of the waves,

[a] Hardy, W. B. The protective functions of the skin of certain animals. Journal of Physiology, vol. XIII, no. 3 and 4. London, 1894.

they are often left to perish. Well-nigh incredible accounts of the "windrows" of dead lobsters left by fierce storms on the shores of New Brunswick and of other maritime provinces were current in the earlier days of the fishery. Thus Prince (*218*) speaks of a memorable storm along the Shippegan shore, Gloucester County, New Brunswick, in 1873, and states that as many as 2,000 dead lobsters were counted in the distance of 2 rods.

The writer quoted above also speaks of the fish crow (*Corvus frugilevus*) as very destructive to lobsters on parts of the coast of Nova Scotia, where he says "when the tide goes down these birds destroy the lobsters left amongst the seaweed. They pierce the shield of the lobster where the heart and main blood vessels are situated, and the crustacean is at once rendered helpless and is devoured by its assailant." I have seldom known the lobster to be stranded in this way in calm weather. The adolescent lobsters, which alone remain in near the shores, ordinarily go deep down among the loose stones, where neither crow nor any other bird could possibly dislodge them.

Chapter VI.—ANATOMY OF THE LOBSTER, WITH EMBRYOLOGICAL AND PHYSIOLOGICAL NOTES.

Both the lobster and the crayfish have long been regarded as classical exponents of a zoological type and have figured so prominently in text-books that the elementary facts of the anatomy of few invertebrates are better known; yet there is still a wide field for more exact research in nearly every direction, as we have found whenever it was possible to dip below the surface. In the present chapter it will be necessary to restate certain elementary facts, but my embarrassment would be greater were this work intended solely for professional zoologists, who will probably find more that is new in the chapter which follows.

In attempting to give a fairly consistent account of the lobster's anatomy I shall not hesitate to enter into details, but shall endeavor to emphasize those parts of most zoological interest from the standpoint of morphology, physiology, and development. Numerous anatomical drawings are given, including the entire series of adult appendages, which may serve for more exact comparisons with the larval stages than have been possible hitherto.

THE BODY.

The lobster's body (pl. XXXIII and table 4), which the fisherman compares to a pistol in shape, but holds by the "barrel," is made up of a series of 21 somites or body segments (or of 18, omitting 3 of doubtful value), all but the last of which bear paired and jointed appendages. The first 14 are united into one piece called the cephalo-thorax or "barrel," while the last 7 form the flexible abdomen or tail. This primitive segmentation which is expressed chiefly in the exoskeleton or the hard and soft skin extends also to the nervous system, as well as to certain muscles and blood vessels, but does not involve the soft parts of the body as a whole. A cuticle, which is strengthened with lime and other minerals to form a hard crust wherever greater protection or rigidity is needed, follows every inward fold of the skin and covers every part of the body down to a microscopical hair.

The skeletal parts of head and thorax are fused on the upper and lateral surfaces to form a large cephalo-thoracic shield or carapace, often called simply the "shell," which is "buttoned" on to the tail by small overlapping pleura of the first small somite of this part. The carapace is marked and sculptured in a very definite manner by symmetrical folds or grooves, tendon marks, and absorption areas, not to speak of protective spines, and smaller tubercles, fringing sensory hairs, and the very minute depressions with which it is stippled all over, the hair pores to be later described. The light median stripe which runs, as if drawn with pen and rule, from the rostrum to the hinder border of the carapace represents an absorption area of the greatest importance to the molting lobster. A prominent fold known as the cervical groove crosses the carapace

at a point about midway on the back to a triangular depression, representing a tendon mark, and is thence continued forward on either side as a groove, which ends between the antennæ and the mandibles. In a soft lobster a penknife can be readily inserted into this fold on the midline. Inwardly the pocket is continued into three divergent endotergites, which give attachment to parts of the posterior gastric muscles, but are absorbed previous to molting. Immediately below the forward end of the groove is seen the "grater," a peculiar roughened area of the shell at the outlet of the branchial cavity; just before reaching this place the groove rises slightly, as if to avoid a prominent swelling, which marks the position of the ball of the outer hinge of the mandible, to be seen upon opening the branchial cavity. A branchio-cardiac line passes backward from each tendon mark toward the hinder border of the carapace, and with the cervical groove divides it into cardiac, gastric, and branchial regions. These lines are obscure in young animals, but become prominent grooves later, and deep furrows in lobsters of mammoth size. The gastric mill underlies the shell immediately in front of the cervical groove; a puncture behind this fold draws blood from the pericardium or the heart, while one below the branchio-cardiac line pierces the gill cover to the branchial chamber. The meaning of other tendon marks and muscle impressions on the carapace is given in a later section. Of the last 10 thoracic legs in the decapod, the first pair bear the big claws in the lobster and are its largest and most characteristic appendages. Its smaller and slenderer legs are chiefly ambulatory and sensory. The tail carries at either side on its under surface a bank of elastic oar-like feet of simple type, the swimmerets or pleopods for forward swimming, while the greatly enlarged and displaced sixth pair, or uropods, make with the telson the tail-fan already referred to.

INTERNAL SKELETON AND HEAD.

If we examine a well-prepared skeleton of a lobster we see that besides the outer hard crust there is a delicate internal skeleton, consisting not only of hard strap-shaped tendons at the joints of the limbs, but of a complicated linkwork of very thin plates or apodemes (pl. XXXIII and XLI). These unite to form partitions between successive sterna and their appendages in the cephalo-thorax, and form an internal or endophragmal skeleton. This intricate structure is produced by infoldings of the epidermal layer of the skin in the sternal and epimeral parts of the cephalo-thorax. The apodemes of which it is composed, are formed like the rest of the exoskeleton from matter secreted by the epidermis. Each plate or rod is thus double in origin, being formed in a flattened pocket like the tendons of the legs (*tp*, fig. 1, pl. XLIII).

According to Huxley[a] four apodemes are originally developed as ventral folds of the skin between any two successive somites of the body, the anterior wall of each pertaining to the somite in front, and the posterior wall to the somite behind. These four apodemes thus form a single transverse series, the two nearer the middle line being called the endosternites, and the two farther removed the endopleurites. The linkwork

[a] Huxley, T. H. The Crayfish, p. 158. New York, 1880.

which thus arises by the repetition of simple units on the ventral side of the thorax becomes more complex through the divergence and coalescence of both endosternites and endopleurites at a higher level to form an archway for the sternal sinus. The roof of this passage is discontinuous, being formed by the fusion on the midline of the inner processes or mesophragms of the endosternites of each side, while their outer processes or paraphragms unite with corresponding horizontal plates of the endopleurites.

The endophragmal skeleton greatly increases the area for the attachment of muscles, and serves to bind the somites of the cephalo-thorax together with greater rigidity, as well as to protect important organs, for not only does the archway securely lodge the large blood sinus, but it also gives passage to the nerve-cord, access to which from above can not be had without cutting through its roof (pl. XXXIII and XXXIV). Since, as is well known, this linkwork is shed in one piece, how do the central nervous system and the parts adjacent to it escape unharmed? I have never heard this simple question raised, but the answer is given by the molted shell, in which it will be seen that the roof of the archway is completely absorbed as well as a large part of the intersegmental and dividing partitions of the bulkheads referred to above, so that the whole under surface of this part of the body with the delicate gills can be withdrawn with impunity.

The endophragmal skeleton bears the hinges for the articulation of the limbs, the arrangement of which is peculiar (pl. XXXVII and XXXVIII). The central hinges which lie close to the mid-line are all cups and are borne on the sterna and close to the endosternites, while the outer or peripheral hinges are all balls and are borne on the epimeral surface of the branchial cavity, close to the endopleurites. The transverse partitions are parallel with the axes of articulation of the appendages in successive somites.

The hard skeleton of the lobster's head immediately in front of the mouth, representing apparently the sterna of somites ii to iv, consists of a conspicuous plate shaped like an Indian arrowhead or spear, with the point drawn out into a sharp spine lying between the first segments of the lesser antennæ, while its broad base, raised into a ridge, bears the soft upper lip or labrum; immediately in front of the ridge this triangular plate is traversed by a deep furrow, in the midst of which lies a small closed pit, most obvious in a soft-shelled animal. This marks the position of a median endosternite to which are attached certain small muscles leading ventrally to the esophagus and dorsally to the membranous covering of the brain.

Upon examining the skeleton of the head from the inside, it is seen that the epimeral and tergal parts are fused to form a ring into which the eye stalks open, close to the brain. On the upper side at the base of the rostrum the ring forms a solid bar, which Professor Huxley thought might represent the tergum of the antennulary somite in the crayfish, and from either side of this bar spring two large leaf-like divergent plates, the procephalic processes, to which the anterior gastric muscles are attached. Below the ring the calcified epimeral surface surrounds the large paired openings for the antennules and antennæ, and is continued to form the wall of the branchial chamber on either hand.

APPENDAGES.

The 20 pairs of appendages of the lobster are developed as tubular folds or outgrowths of the body wall, and consist of ectoderm with mesodermic cores, a rule which seems to be broken only in the case of regenerating limbs, where ectoderm appears to contribute to the renewal of both muscles and nerves. The order of embryonic development is: (1) Antennules, (2) mandibles, (3) antennæ, (4) maxillæ and the thoracic limbs in regular succession. Four pairs of swimmerets (somites XVI–XIX) are released together in the second larval stage (fig. 41); the uropods in the third stage (fig. 42) and the first pair of pleopods, which are the last to appear, are not usually recognizable until the sixth molt or later.

The eyestalks, which are omitted from the enumeration given above, and the antennules are prostomial in origin, while the originally postoral antennæ reach a position in front of the mouth by the twentieth day, when the compound eyes are distinctly lobate. Segmentation in the limbs is a gradual process, constrictions early marking future joints, while the division into outer and inner branches begins at the apex of the appendage except in the antennules, as noted below. Most parts of the adult appendages are recognizable in the first larva, and all, excepting those of the XV somite, in the lobsterling. From the fourth stage on through the adolescent period the changes are gradual and relatively slight, excepting only those which involve the

TABLE 4.—THE BODY SEGMENTS AND APPENDAGES OF THE LOBSTER

Divisions of body.	No. of somite.	Name of somite.	Name of appendage.	Functions of appendage.
Head (6)	I	Opthalmic	Eyestalk	Visual
	II	First antennal	Antennule	Olfactory or chemical, chiefly through outer branch, and static.
	III	Second antennal	Antenna	Tactile chiefly, and probably chemical
	IV	Mandibular	Mandible	Crushing and triturating small, hard parts of food.
	V	First maxillary	First maxilla	Masticatory and chemical, but chiefly for passing the food.
	VI	Second maxillary	Second maxilla	Respiratory chiefly; also chemical, masticatory, and for passing on the food.
	VII	First thoracic	First maxilliped	For passing, and like the maxillæ possibly subserving the chemical sense.
	VIII	Second thoracic	Second maxilliped	For transference of food, the chemical sense, and respiration.
	IX	Third thoracic	Third maxilliped	Chiefly masticatory, with brushes for cleaning.
Thorax (8)	X	Fourth thoracic	Great cheliped, or first pereiopod.	Chelate; big claws adapted on one side for crushing and on other for seizing and rending prey; respiratory, tactile, and possibly olfactory.
	XI	Fifth thoracic	Second pereiopod	Chelate; ambulatory, tactile, and possibly with chemical sense, for seizing, testing, and transference of food; respiratory.
	XII	Sixth thoracic	Third pereiopod	The same
	XIII	Seventh thoracic	Fourth pereiopod	Nonchelate; the same
	XIV	Eighth thoracic	Fifth pereiopod	Nonchelate; the same, and for cleaning swimmerets.

great chelipeds and the first pair of swimmerets. The complex and varied relations of the successive somites and appendages of the lobster in the larval and adult state are outlined in table 4.

In their type form (fig. 2 and pl. XXXVI, fig. 5) the appendages consist of an inner and outer branch borne on a basal stem, known respectively as endopodite, exopodite, and protopodite. The protopodite is composed of two segments, a proximal coxa, or coxopodite, and distal basis or basipodite. The coxa of each limb from the maxillæ to the fourth pair of pereiopods (somites V–XIII) bears a hairy respiratory plate or epipodite, from which rises a gill or podobranchia on all but the first two of these somites. The primitive type of crustacean limb was probably biramous, since in the course of development we frequently find the uniramous condition produced by loss of the more transitory exopodite, and further, since the foliaceous form of appendage of the lower branchiopod crustacea is secondarily assumed by certain of the mouth parts of the lobster and other decapods. The undivided form of limb is permanently preserved in metameres I and X–XV, in the last of which the appendage is modified in the two sexes to perform distinct functions. The origin of the two-branched antennules will be considered presently. The exopodite is frequently abortive, or multiarticulate and elastic, as in the swimmeret, a condition which the endopodite has also preeminently assumed in the long whips of the antennæ.

WITH THEIR CHIEF FUNCTIONS AND MODIFICATIONS IN LARVA AND ADULT.

Relation of appendage to type form.	Relation of adult to embryonic and larval appendage.	Apertures of body.
Doubtful; stalk in two segments	Transitory ocellus in first larva; compound eye relatively large, and stalks short.	
Doubtful. Basal segment lodges statocyst sac	Bifid, and later uniramous in embryo; finally biramous in first larva; inner flagellum a secondary outgrowth from primary stalk. Prostomial.	Pore of statocyst on upper surface of basal segment.
Exopodite wanting; exopodite reduced to scale, and endopodite irregularly segmented.	Bifid, and later completely biramous in embryo; poststomial in origin, but later advance in front of mouth.	Papilla for opening of renal organ on coxa.
Biramous; two distal segments of palp supposed to represent the endopodite.	Body and palp at comparatively late embryonic stage.	Mouth, screened by labrum, between mandibles.
Foliaceous; exopodite wanting; endopodite of two modified segments.	Early larval condition similar to adult, but endopodite unsegmented.	
Biramous and foliaceous; respiratory fan formed by fusion of exopodite and epipodite.	First larval condition similar to adult	
Biramous and foliaceous, and like maxillæ, with protopodite modified for testing and passing the food. Endopodite 2-jointed.	The same, but epipodite without fold for "bailer"	
In type form; endopodite 5-jointed, and epipodite with rudimentary gill.	First larval state similar to adult	
In type form, modified for mastication, and cleaning; second and third podomeres fused, and exopodite reduced. Epipodite with functional podobranchia in IX–XIII.	In first larva with long swimming exopodite, lost at fourth stage, and third joint free; no cleaning brushes, and no teeth on ischium.	
Uniramous through loss of exopodite in fourth stage. Second and third podomeres modified for autotomy, and fused "breaking joint" between them.	Biramous to fourth stage. Big claws nonprehensile in first larva; of toothed type in fourth, and symmetrical up to sixth or seventh stage. Torsion of limb completed at fourth stage, after which big claws are horizontal, and dactyls face, opening toward mid-line of body.	
Uniramous through loss of exopodite in fourth stage.	Swimming exopodite shed at fourth stage	
The same	The same	Oviduct opens on coxa.
The same	The same	Seminal receptacle.
The same, without epipodite and podobranchia	The same; torsion of terminal segments away from mid-line of body completed at fourth stage, when limb is directed backward.	Vas deferens opens on coxa.

TABLE 4.—THE BODY SEGMENTS AND APPENDAGES OF THE LOBSTER WITH

Divisions of body.	No. of somite.	Name of somite.	Name of appendage.	Functions of appendage.
Abdomen (7)	XV	First abdominal	First pleopod	Modified in male for copulation, and reduced in female to prevent attachment of eggs. Uniramous.
	XVI	Second abdominal	Second pleopod	Biramous; for forward swimming; in female for holding and aerating the eggs, and possibly for secreting the glue by which they are fastened to certain of the setæ; tactile, with chemical sense in doubt.
	XVII	Third abdominal	Third pleopod	The same.
	XVIII	Fourth abdominal	Fourth pleopod	The same.
	XIX	Fifth abdominal	Fifth pleopod	The same.
	XX	Sixth abdominal	Sixth pleopod, or uropod.	Enlarged and modified for forming with telson, the tail-fan, for backward swimming; tactile.
	XXI	Telson	Wanting	

In the typical thoracic leg (pl. XXXVIII) the endopodite is divided into 5 segments, which, with the two divisions of the protopodite, give the limb 7 podomeres, numbered[a] and named from base to apex as follows: (1) Coxa or coxopodite, (2) basis or basipodite, (3) ischium or ischiopodite, (4) meros or meropodite, (5) carpus or carpodite, (6) propodus or propodite, and (7) dactyl or dactylopodite. These successive segments are articulated to the body and to one another by soft membrane and usually by hinge joints which limit the movements of each to a single plane at right angles to the articular axis, or to the line joining the two hinges; each segment, with the exceptions to be noted later, is actuated by opposing muscles, a larger flexor and a smaller extensor, the fibers of which are implanted over the hard shell of their respective segments and are inserted on strap-shaped tendons which react on the distal podomere (fig. 1, pl. XLI). The tendon is derived from an ingrowth or flattened pocket of interarticular membrane (fig. 2, *mb.*, pl. XLI, and fig. 1, *tp.*, pl. XLIII), and is sometimes closely united to the shell of the distal segment. Each joint or articulation is therefore crossed by tendons which belong to the proximal podomere and pull on the distal one.

In the successive somites of the tail the axes of articulation are all parallel, and at right angles to the longitudinal axis of the body so that movement is limited to the vertical plane. In the appendage, on the other hand, the direction of the axis of articulation varies in successive podomeres (see figs. 6 and 7); moreover the initial direction of movement of the base of each limb, which depends upon the angle which its articular axis makes with the long axis of the body, varies greatly from head to tail (135° in the mandibles, about 55° in the great chelipeds, and 90° in the swimmerets). Accordingly each segment acts as a lever of the third order, and the successive thoracic limbs are capable of universal movement, and in a variable field. By reference to figures

[a] This order seems preferable to the reverse, which is sometimes adopted, since the protopodite has been less modified than either of its branches, and we thus avoid the ambiguity of speaking of the seventh segment of a pleopod or of an antenna

THEIR CHIEF FUNCTIONS AND MODIFICATIONS IN LARVA AND ADULT—Continued.

Relation of appendage to type form.	Relation of adult to embryonic and larval appendage.	Apertures of body.
Uniramous, presumably through loss of exopodite.	Appear as buds in fifth to eighth stage; and sexually differentiated in eighth to tenth stage.	
In type form, with endopodital spur in male.....	Appear as bifid buds beneath cuticle of first larva; released as rudimentary limbs in second larva; fully functional at fourth stage.	
In type form.....	The same.....	
The same.....	The same.....	
The same.....	The same.....	
The same, with protopodite undivided, and 2-jointed endopodite underlying exopodite.	Appear as buds at base of telson in second stage; released in third and completely functional in fourth.	
.....	Bifid in an embryo of two weeks; later elongated and forked; released in larva as a triangular swimming plate, with terminal fringe of large spines and small setæ, which are more distinctly plumose and greatly elongated at the fourth and later stages.	Anus on lower side at base.

1 and 2, plate XLI, the working of this effective mechanism is readily understood. In the sectional view of the big claw and walking leg the tendons of the terminal joint lie in the plane of the paper, and the axis of articulation is at right angles to it; a contraction of the large flexor muscle (*fl.* 6) pulls on the large inner tendon and thus closes the claw, while an impulse sent into the extensor (*ex.* 6) draws on the opposite tendon (*t.* 6), which springs from the opposite side of the dactyl, and thus opens the claw. Contraction of the flexor of the next segment (*fl.* 5) would raise the whole claw toward the eye, and so on. In this case, where considerable power is required, there is a double or divided tendon for this muscle. Owing largely to the variation in the field of movement of the successive pereiopods, referred to above, the lobster is able to cover a wide front in defense, move forward, sideways, or backward, reach every part about the mouth, and scratch the underside of its tail.

Whether the stalked eyes of decapods are metameric appendages or not is a question upon which zoologists are not agreed. In the lobster the eye-stalk (fig. 1, pl. XXXV) is composed of two segments, the basal of which is minute, and imperfectly calcified, as in the protopodite of the swimmeret, and that flagella-like outgrowths occasionally follow partial excision or injury of the eye is well known. "I think," says Professor Brooks in his monograph on Lucifer, "that the presence of a distinct ocular segment in *Squilla* compels us to recognize an homology between the stalked eyes and an ordinary appendage, although it is no doubt true that all the groups in which stalked eyes occur can not be traced back to a common ancestor, and also true that the stalked eyes themselves can not be traced back to ordinary appendages."

The first antenna (fig. 4, pl. XXXV), as we have seen, is first in the order of embryonic development, arising on about the ninth day, just behind the thickenings which form the optic diks, and before the mouth invagination is formed. The latter appears a few hours later than the antennules, and on a line drawn through their posterior margins, so that these appendages are essentially prostomial. The mandibles come next in order, followed

in a few hours by the second antennæ, both arising as simple buds, and all three pairs become concentrated about the mouth in the early egg nauplius stage, which is thus reached at the tenth or eleventh day. Both pairs of antennæ are then distinctly divided at the tips, as if about to branch, but the second pair only becomes biramous, the first remaining as single constricted stalks up to near the end of embryonic life. When the larva emerges, what is to be the inner and slenderer branch of this appendage is seen arising as a small bud from the base of what becomes the outer and thicker flagellum (fig. 34). The inner branch of the antennule is therefore probably not homologous with an endopodite. The outer branch develops its club-shaped "olfactory" setæ in the second larval stage, and remains very short and stout up to the fourth or fifth stages, when it rapidly lengthens.

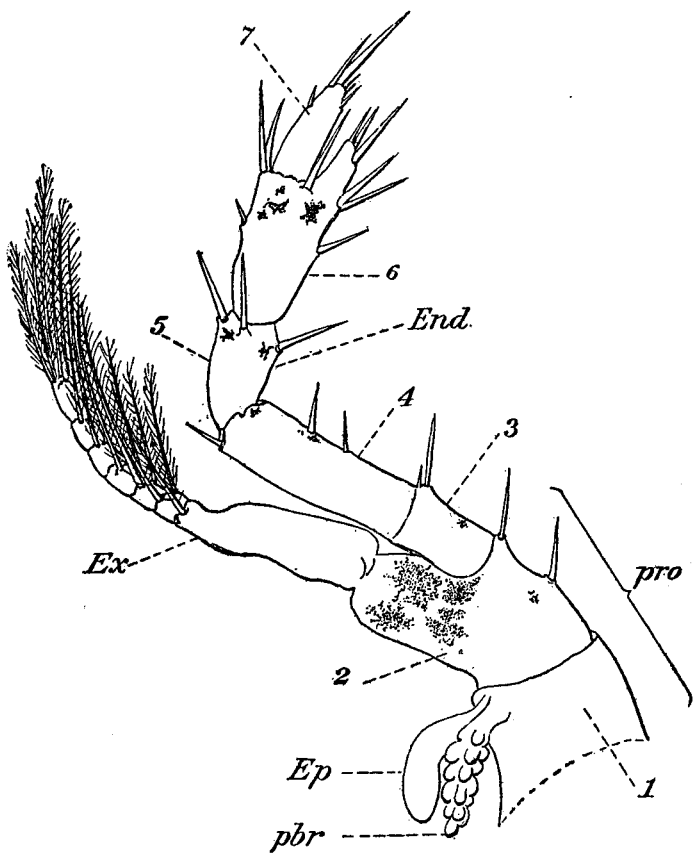

FIG. 2.—Left second pereiopod of first larva of lobster, showing the primitive divided form of the limb, with successive segments or podomeres of protopodite (*pro*, segments 1–2), and permanent inner branch or endopodite (*End*, 3–7). *Ex*, deciduous swimming branch or exopodite; *Ep*, epipodite or gill separator, with its gill or podobranch (*pbr*).

It should be noticed that the lower or sternal part of the head faces forward instead of downward, as a result of cephalic flexure which arises in the course of embryonic development; in consequence of this the anterior sterna are bent upward through nearly a right angle, so that the eyestalks and both pairs of antennæ are directed forward, and their originally anterior faces have become their upper sides. (Pl. XXXIII.)

Assuming that neither the eyes nor antennules are metameric appendages, and that the telson is not a true somite, the body would consist of a prostomium bearing the two pairs of articulated processes named, eighteen metameres, and a terminal telson, the first four somites being fused with the prostomium to form the head, with appendicular antennæ, mandibles, and maxillæ.

Since it will be necessary to examine the swimmerets, the compound eyes, and statocysts in relation to other organs, the account which immediately follows will be

limited to the mouth parts and certain adaptations found in the walking legs, further details being given in table 4. The history of the big claws is reserved for the following chapter.

MOUTH PARTS.

In addition to labrum and metastoma, we designate as mouth parts the six pairs of limbs which are concentrated about the mouth opening, and which are modified in some degree for dealing with the food.

When the mandibles open, a conspicuous pink fold of fleshy tissue is revealed overhanging the median V-shaped fissure which is the lobster's mouth (pl. XXXIII). The labrum is shield-shaped and compressed in a peculiar manner, being keeled above and below on the middle line, with a thin free edge or border, so that it presents two upper and two lower concave surfaces. The lower keel by fitting into the slit of the mouth forms the upper bound of this opening as it passes into the dorsal wall of the esophagus; the fissure is limited below by a soft, round papilla, from the sides of which spring a bifurcated "lower lip," or metastoma. The metastoma on either side consists of a short strap-shaped blade fitting closely over the convex body of the mandible; it is slightly ridged on the outer side and sparingly sprinkled with setæ. Both labrum and metastoma are richly supplied with organs which there is reason for regarding as sensory buds. The sides of the mouth are formed by rounded swellings of the esophageal wall, and are directly continuous with the metastoma below. When the jaws are closed and their outer masticatory ridges meet on midline just over the mouth fissure, the concave sides of the labrum fit into deep grooves which traverse the opposing mandibular surfaces, and since the groove of each mandible lies below the level of its cutting ridge, it is impossible for the lobster to "bite its lip." The V-shaped mouth described leads through a very short esophagus directly to the large stomach sac. All of the mouth parts which succeed the mandibles are thin and leaf-like up to the somite VII; and all conform to their outer convex surfaces.

The six pairs of appendages which are concentrated about the mouth are abundantly supplied with sense organs, and are charged with a variety of functions, the most obvious of which are handing the food along to the mouth and mincing it in the course of passage; that they further serve as organs of the chemical sense and of touch more or less completely is not to be doubted.

The mandibles of the adult lobster (fig. 7, pl. XXXV) are in form like hinged double doors set in front of the mouth, and so hung to the cephalothorax of the animal that they are capable of swinging only a little way in or out, or toward and away from the middle line. The body of the mandible, which probably represents the coxa of a typical limb, is a triangular convex bar, with a very oblique axis of articulation corresponding to its long anterior side; the opening tendon of the abductor mandibuli muscle is inserted on the anterior border, near the outer socket and exerts a pull sufficient to open the "door." The posterior border bears at a more favorable point near its middle, a long tendon, from which fan out the fibers of the powerful adductor mandibuli muscle (see p. 242). These muscles arise from the inner surface of the carapace on either side in front of the

cervical groove, and between two white tendon marks; when they work the "doors" are swung to with force.

The masticatory surface of each jaw is represented by the short side of the triangle which meets its fellow on the midline in front of the labrum. It is divided by a deep groove into an outer cutting ridge, capped with a dense mass of yellow chitin, and a lower and flatter surface, which appears to be available for mastication in but a slight degree, if at all. The groove (*g*, fig. 7, pl. XXXV) not only protects the fleshy upper lip, but gives play to a 3-jointed hairy palp, the two distal segments of which are supposed to represent the endopodite. The palp is actuated by muscles lodged in the body of the mandible itself, and possibly serves to direct food particles to the mouth, below the level of the groove, and just beneath the tip of the labrum.

The lobster's mandibles work essentially on the principle of the modern stone-crushing machine; little or no lateral motion being possible in an animal with a hard shell, they can serve only by repeated closing movements to divide and triturate the larger particles of food, which, having resisted the preceding mouth parts, get pinched between the meeting edges of the swinging "doors."

The leaf-like first pair of maxillæ, the smallest of the mouth parts (fig. 1, pl. XXXVI), bear on their first segment a fringe of stiff hairs and on their second a comb of bristles, which help to pass up the food or mince it when soft. The second maxilla serves chiefly as a "bailer," or rather as a fan for driving water out of the respiratory cavity in front. (Fig. 2, pl. XXXVI.) This thin elastic plate lies nearly horizontal, the divided protopodite and rudimentary endopodite closely fitting over the mandible and the conforming first maxilla, and is formed by the fusion of an anterior exopodite and posterior epipodite, the upper side of the former and lower side of the latter, when not in rythmic movement, resting against the sides of the respiratory cavity. (For action of fan see p. 247.) The "masticatory ridges," or setigerous coxa, and basis of the second maxilla are partially cleft and distinctly separated by a superficial fold.

The first pair of maxillipeds (fig. 3, pl. XXXVI), except for one or two particulars, are modified only in minor details from the condition seen in the first larva. The parts are all rather soft, flattened, and curved to fit over the swelling mandibles and one another; the setæ of the meeting borders of the bases and coxæ are soft and useless for mastication; the exopodite lies against a shallow groove on the outer side of the two-jointed endopodite, the groove being marked by independent rows of setæ and the branch presenting a modified four-sided appearance. There is a long respiratory epipodite which carries no gill, but a part of its outer border is folded or turned under so as to form a trough, *fd* in which plays the posterior blade of the "bailer," or scaphognathite.

In the slender, outwardly swelling second maxilliped (fig. 4, pl. XXXVI) there is a fused joint (*x*) between the ischium and reduced basis. The brushes of setæ which fringe the inner border of this compound segment and the long curved meros are all soft, and on the small knob of the dactyl only do we find short stiff spines which can in any way effectively react on the food in mastication. Both epipodite and podobranchia are rudimentary.

The third and last pair of maxillipeds are similarly curved and conform perfectly to the typical limb, with the exception of a fused third joint between ischium and basis. (Fig. 5, pl. XXXVI, *x*.) The three terminal segments of this appendage are flattened and, as commonly carried, crooked downward upon the longer and more modified meros and ischium. The latter podomeres are curved upward and outward, are three-sided, and, like the former, bear double fringes of dense setæ which are used, among other purposes, as cleaning brushes (see p. 179). In place of the upper or inner fringe, however, the trihedral ischium is provided with a serrate crest, or row of about twenty closely set "incisor" teeth. These tooth-like spines increase in size distally and end over the joint in a strong curved fang. They work on the principle of an old-fashioned nutcracker, but in this case with toothed jaws which are very effective in cutting the coarser pieces of food delivered by the slender claw feet before they are passed on to the smaller mouth parts. The first three segments of this limb are closely appressed and quite flat where they meet on the midline, the coxa bearing two flat and hairy spurs.

The third pair of maxillipeds are the only really effective "jaw feet," and with the mandibles the only appendages which play an important part in reducing the food. Of the other mouth parts, the maxillæ, especially the smaller first pair, and the second maxillipeds without doubt help in the mincing process to which the food is subjected, but their chief function, as in the first maxillipeds, is without doubt sensory and for passing the food up to the mandibles. When the latter have finished their work the "grist" is ready for the gastric mill.

THE SLENDER LEGS.

The ten thoracic legs, which are designated as the pereiopods in the higher Crustacea, consist of the great chelipeds and four pairs of slender walking legs (pl. XXXVIII), the first two of which bear weak compound or double claws and the last two end in simple dactyls.

The successive segments of these limbs move on hinges, a description of which is given in chapter VII, and are actuated by opposing muscles in the typical way with the exception of basis and ischium, in each of which a flexor is absent. (Fig. 1, pl. XLI.) The basis has but one ventral or posterior extensor, with movement limited to a few degrees of arc, and the ischium two posterior extensors inserted upon two tendons, which are set close together on the margin of the shell at the opening of the meros. Accordingly these limbs can not be flexed at the fourth joint. There are no fused joints in the slender legs, which commonly break between basis and ischium, and are regenerated from this plane.

Aside from their direct use in locomotion, the smaller pereiopods present a variety of functions, the last pair possessing brushes for cleaning the abdomen (see p. 303), and incidentally serve as picks to steady the animal as it crawls over the bottom. Far more significant, however, are the clusters of sensory setæ (*s. s.*, pl. XXXVIII) arranged in symmetrical rows on the last two segments of the slender legs. One can count a

hundred brushes upon a single leg, and each brush contains from 50 to 100 setæ, the bundles themselves being gradually concentrated toward the tip. In other words, each limb is furnished about its apex with from 5,000 to 10,000 sensory hairs, each of which is supplied with at least one nerve element. With such sensitive feet the lobster can feel its way securely at every step, whether by night or by day, as well as test every object before handing it up to the mouth.

THE CENTRAL NERVOUS SYSTEM.

The nervous system, the coordinating and regulating mechanism of the body, is composed of a complex series of distinct but closely related nerve elements, and each element consists of a ganglion cell and one or more outgrowing processes, the principal of which in certain cases is termed the nerve fiber. Three kinds of nerve elements or neurons have been described, as follows: (1) Coordinating elements, which lie wholly within the central system, the probable function of which is to coordinate the action of its parts; (2) motor nerve elements, which consist of a ganglion cell in the central mass and of a fiber process which passes out to a muscle or gland; and (3) sensory elements, composed of specially modified cells of the outer layer of the skin and of sensory fibers which enter the ganglia of the nervous system proper. Certain nerve fibers which pass out to the skin or its immediate neighborhood end in close relation with sensory cells and serve to convey impulses from them to the centers, while others conduct motor impulses from the centers to the muscles or glands. The epidermic cells of the skin may be regarded as the simplest sensory cells, or as the direct ancestors of such, and all the specialized sense organs, such as the eye or statocyst, are essentially modified patches or pockets of the outer skin layer.

The most primitive sense being that of touch, it is not surprising to find in an animal like the lobster that virtually every part of the skin is capable of receiving and distributing either tactile or chemical sense impressions. The proper sense organs, however deep their final position in the skin or tissues, come into close relation with the nerve fibers with which each is abundantly supplied. The sense organs are thus a primary means by which any form of energy to which they are able to respond starts a series of changes which are finally translated into what are known to us as sensations, feelings, and other mental states.

The lobster has a nervous system of the relatively simple "ladder" or "chain" type characteristic of the higher invertebrates (pl. XXXIII), in which segmentation, begun at a lower level in the animal scale, is the dominant character of its structure and instinct the ruling method of its response. Its reflexes and instincts are very precise and very stable, but not necessarily invariable, and, as we shall see at a later page, the lobster even at the fourth stage is able to modify its actions in relation to experience and to form habits, and thus is gifted with a certain degree of what is usually defined as intelligence in vertebrates. The uprights of the ladder are the long commissures of the chain, the rungs the transverse commissures, while the paired ganglia for each somite lie at the junctions of these parts. In addition to this cord with the

appendicular and other nerves which spring from it, the lobster has certain stomato-gastric nerves and ganglia which have been described as a rudimentary sympathetic nervous system.

The brain or compound supra-esophageal ganglion (pl. XXXIII) is united, by means of a ring-commissure which embraces the esophagus, to the chain of paired ganglia; this traverses the mid-ventral portion of the body and is protected by an archway of the internal skeleton in the thorax. The brain, which is thus the only ganglionic part of the central nervous system dorsal to the alimentary tract, appears as a small whitish mass at the base of the rostrum and between the stalks of the compound eyes. It gives origin to the following paired nerves: (*a*) The large optic nerves, which terminate in the optic ganglia and the compound eyes of the eyestalks; (*b*) the antennular nerves supplying the first pair of antennæ; and (*c*) antennal nerves which innervate chiefly the second pair of antennæ. The brain thus represents the fused ganglia of the first three somites and is connected by esophageal commissures with the central cord.

The subesophageal ganglion, or first ventral link of the chain, lies below the mouth and is composed of the ganglia of the mandibles, the maxillæ, and the maxillipeds (segments IV–IX), more or less intimately fused together, the ganglia of the large maxillipeds being nearly or quite independent.

Then follow five pairs of thoracic ganglia, which supply the legs and body wall, and six abdominal ganglia, the last of which sends nerves into the terminal telson. The longitudinal commissures between the twelfth and thirteenth somites diverge to admit the sternal artery, which thereupon divides, one of its branches passing forward and the other backward immediately under the nerve cord. (For nerves of cheliped, see ch. VII, p. 265).

In the embryo and larva the nervous system is much more concentrated than in the adult, and according to Allen (2) the thoracic ganglia are fused into one mass, which is united by short commissures to the brain. The hinder part of the embryonic brain is connected by a bridge commissure, which in the adult lies immediately behind the esophagus.

The nervous system is composed of a central "Punkt-Substanz" or neuropile, which, though granular in appearance, is in reality a felt work of fibers running in all directions, and an outer covering of ganglion cells. According to Allen the posterior ganglia of the chain give off two pairs of nerves, an anterior and posterior division; the anterior nerve becomes a double branch in the adult lobster and supplies the limbs, while the posterior division innervates the body wall.

THE PERIPHERAL STOMATO-GASTRIC SYSTEM.

In passing down the esophageal commissures, at a distance of about two-thirds of their course from the brain, a small commissural ganglion is seen upon either side lying against the wall of the esophagus. The delicate bridge commissure, which indirectly unites both sides of the brain, lies immediately behind these small ganglia and toward the lower side of the gullet, as already seen. Each commissural ganglion gives off two

nerves, a dorsal medio-lateral and a ventral or antero-lateral nerve of Huxley, which send branches to a diffuse esophageal ganglion to be seen resting against the upper anterior wall of the esophagus (pl. XXXIII); from this ganglion, moreover, a median bundle, the anterior visceral or azygos nerve, runs up the wall of the stomach sac, to end in a minute gastric ganglion lying between the origins of the anterior gastric muscles. A smaller anterior median nerve also joins the esophageal ganglion to the brain.

The stomato-gastric system thus consists of four peripheral ganglia, two of which form a pair, and of peripheral nerves, which spring from them, in addition to a smaller ganglion belonging to the labrum, to be mentioned presently. The dorsal or medio-lateral nerve gives off two branches to the wall of the esophagus and bifurcates, a dorsal division going to the esophageal ganglion and a ventral forming the labral nerve, which has hitherto escaped notice. I have found that the two labral nerves end in a small labral ganglion embedded in the fleshy mass of this organ; from it issue fibers which presumably supply the sense organs of this part (see p. 237). The ventral nerve gives off a small branch to the esophagus and divides, one section going to the esophageal ganglion and the other passing to a plexus of fibers on the lower border of the mouth; from this plexus a very diminutive median nerve is sent to the esophageal ganglion.

Allen has traced with great skill the origin and course of the fibers in various nerves. Many of these fibers, which have bipolar cells in their course and which terminate on the walls of the esophagus, are possibly concerned with sensory cells.

SENSE ORGANS.

Special-sense organs, in so far as they are definitely known to exist in the lobster, are (1) the eyes, and (2) the sensory hairs or setæ, distributed over the body and appendages, if we omit from this category those organs of equally wide distribution which have the appearance of sensory buds and have received the general designation of tegumental glands. The hairs embrace (a) tactile setæ, which, though apparently aimlessly scattered over the appendages, are really distributed in a definite manner, including the setæ of the statocysts, and (b) chemical setæ, which abound on the antennules and where for a long time they have been supposed to possess an olfactory function, as well as on the mouth parts, to which a gustatory sense has been ascribed, and indeed upon the surface of virtually the whole body, where experiment seems to prove that chemical sense organs of some sort exist.

EYES.

At the time of hatching, the lobster possesses three visual organs, a median cyclopean ocellus, a mere rudiment of the simple type of eye which proved useful to its ancestors and is still retained in the lower orders of Crustacea, and the paired lateral or compound eyes. The latter, so conspicuous at all later stages of life, appear very early, and at the close of the fourth week their black pigment can be detected as a dark crescent-shaped line on either side of the head of the embryo. The eye is first disk shaped, then

lobate, and finally stalked. In the first larva the stalks are immobile but very large, being relatively four times longer than in the adult. From the fourth stage the faceted eye is typically borne at the apex of a cylindrical movable stalk, which projects from either side of the base of the rostrum. Each stalk (fig. 1, pl. XXXV) is capped with a hemispherical surface, over which the cuticle has become modified into a thin flexible membrane as transparent as glass. Through it is seen the black pigment which defines the retinal area. This window-like cornea is interrupted by a process which juts in like a peninsula from the opaque shell at a point where the field of vision seems to be interrupted by the rostrum.

After the first larval stage the eyestalks recede somewhat until the lobster attains a length of from 1½ to 3½ inches, when their prominence is again very marked. In short, they now assume the form and relative size of certain fossil Crustacea from which the modern lobsters have probably descended.

The structure of the compound eye of the crustacean appears to be extremely complicated, because it is composed of units repeated many thousands of times. As was shown in 1889,[a] it is wholly derived by differential growth from a single plate of columnar ectodermic cells, the optic disk, which arises very early in development on either side in front of the future mouth and before the buds of the antennules are formed.

When the lobster's eye is examined with a hand lens, its clear corneal membrane has the appearance of a glass mosaic, composed of minute square disks of great uniformity both in size and arrangement, especially in its central parts (fig. 2 and 3, pl. XXXV). Each disk is the facet of an eyelet or ommatidium of the compound eye, and each supplies a part of the mosaic image produced in vision when the light is sufficiently strong. Each eyelet is developed from a cell cluster of the optic disk and this in turn from a single columnar cell of the primary optic plate.

The axial part of the ommatidium consists of (1) the corneal lens secreted by 2 underlying cells, (2) the refractive cone derived from 4 cone cells, and (3) a long striated and sensitive rod, the rhabdom, secreted and sheathed by 7 retinular cells, in addition to 2 peripheral pigment cells which surround the crystalline cone; in this rod also a nerve fiber terminates at the level of a basement membrane which divides the proper eye from the complex optic ganglia, muscles, and other tissues contained in the rest of the stalk. In ordinary daylight each eyelet is completely isolated by its sheath of black pigment cells, all of which display ameboid movement, but which respond differently to the intensity of the light stimulus.

In 1890, while working at the laboratory of the U. S. Fish Commission at Woods Hole, Mass., I showed by experiments upon the prawn *Palæmonetes vulgaris* that when this animal was placed in total darkness there was an immediate adjustment of the pigment cells of the ommatidium, in consequence of which the whole eye became intensely black and prominent, and that when returned to the light the eye began to lighten in a few minutes and in a relatively short time assumed its normal daylight appearance. It was shown that the blackening was due to a forward movement of processes of the

[a] The development of the compound eye of Alpheus. Zoologischer Anzeiger, bd. XII, p. 164–169, fig. 1–5. Leipzig, 1889.

distal pigment cells. One shrimp was kept in darkness 38 days, but the change was the same whether the interval was one of a few hours or weeks.[a] The true significance of this response was clearly established by Exner in his remarkable work on the physiology of faceted eyes in insects and crabs, published in 1891.[b] It was shown that the distal and proximal pigment cells or the "iris" and "retina" pigment moved in opposite directions in response to waning light, the former in its "night position" moving up to the cornea and leaving the refractive cone exposed and the latter crowding down upon the basement membrane, thus exposing the sensitive tip of the rhabdom. In the "day position" the converse movement takes place when the eyelet is completely isolated, and only those rays which are parallel to its long axis can enter and reach the rhabdom.[c] When the pigment screens are separated and drawn wide apart at night, on the other hand, light rays of any angle can pass freely from one ommatidium to another to be refracted by the exposed cones upon the upper ends of the exposed sensitive rods. The response is thus an adjustment to economize light, though at the expense of clearness of image. At dusk the lobster can presumably distinguish moving objects, but only dimly, since the eye at this time can produce no clear mosaic images.

The compound eye of the house fly is said to have about 4,000 facets, that of a dragon fly 20,000, while in a 12-inch lobster I estimated the number to be 14,000. Assuming that the ommatidia are equally well isolated and equally sensitive in each case, the relative efficiency of mosaic vision in insect and crustacean would be proportional to the number of facets. Upon this showing the lobster has a rather poor eye when we consider the unfavorable medium in which its visual powers must be exercised. The image produced by this organ, as Exner showed by a photograph made through the medium of the faceted insect eye itself, is single and upright; sight is attended by great loss of light, and must be very imperfect except for short distances and when the animal is moving in shallow water strongly lighted. The fact that the lobster is most active at night, that it is abundantly supplied with tactile organs for feeling its way about, and that the greater part of its life is spent at depths where clear vision is impossible for lack of light, show us further that its visual organs can play but a subordinate part in the activities of its daily life.

SENSORY HAIRS.

Certainly the most numerous and probably the most important sense organs of crustaceans generally are the sensory hairs or setæ, which are all of epidermic origin. Each hair consists of a hollow, conical, or nearly cylindrical shaft of chitin, continuous with the general cuticular basis of the shell, and is associated with one or more sensory nerve elements connected with the central nervous system.

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[a] Memoirs of the National Academy of Sciences, vol. v, 4th mem., p. 454. Washington, 1893.

[b] Exner, Sigm. Die Physiologie der facettierten Augen von Krebsen und Insecten. Leipzig, Wien, 1891.

[c] It has been found by Congdon that increased temperatures cause movements in the pigment cells, which are probably of a non-adaptive character and are reverse in direction to those caused by light. See Congdon, E. D: The effect of temperature on the migration of the retinal pigment in decapod crustaceans. Journal of Experimental Zoology, vol. IV, p. 539–548. 1897.

The exact analysis of the sense organs of the higher Crustacea is still a vexed problem, and the literature of the subject far from satisfactory.[a] In the description to be given I shall follow in the main the account of Prentiss (*217*), who worked upon the common prawns, *Palæmonetes* and *Crangon vulgaris*, with which the lobster undoubtedly agrees in these particulars. The sensory bristles of decapods have been found to conform to two types: (1) The tactile, and (2) the olfactory, or better, the chemical setæ which are sensitive to chemical stimuli. The former have straight, long, and often plume-like shafts, and at the base of each a spherical enlargement is formed, which, owing to its thin wall, permits the hair to swing freely as upon a joint. Bristles of this type occur all over the body and appendages, and the "auditory hairs" of what has been called the "ear-sac" or otocyst (fig. 2 and 4, pl. XXXV) are of this form. According to Prentiss, each is supplied with a single nerve element. The "olfactory" or "chemical" bristles are shorter, more cylindrical, or less tapering chitinous tubes, with no marked basal swelling. Their tips are either perforated or possess so thin a wall as to permit the ready diffusion of chemical substances from the water to the inside of the shaft. Each bristle is supplied with a cluster of nerve elements, which may be very numerous, their fibers ending free in the shaft, but not penetrating to its apex. Such setæ are apparently more highly specialized and are restricted to the small antennæ, where they are called olfactory hairs, or to the mouth parts, where they are often spoken of as gustatory bristles, though it is probable that their functions are the same wherever found.

RELATION OF THE SETÆ TO HATCHING AND TO MOLTING.

The way in which these sensory hairs are formed and renewed at each molt is very interesting. The subject has been investigated by a number of naturalists, but in the brief account which follows we shall depend mainly upon the observations of Prentiss. Each hair is secreted by a number of matrix cells which send their processes up into its shaft. In preparation for the molt the protoplasm recedes from the shaft of the hair and its matrix cells sink into the tissues and with other cells form a "papilla" around the nerve fiber and begin to secrete a new hair. This condition lasts for a long time in an adult animal, but for a few days only in the larva, which often passes several molts in the course of a week. The cuticle which is to form the new shell and hair is secreted under the old which is soon to be cast off, but the new hair is invaginated, so that below the level of the skin its wall is double, while its tip only projects into the hollow shaft of the old hair above it. The walls of the double hair tube are thus continuous with each other and with the general cuticle which is to form the new shell.

In this condition the hairs may be compared to the fingers of a glove which have been pushed in or telescoped, so that their tips only project from the surface. When the lobster is ready to molt every new hair on its body is in this condition. Now at each molt we always find between the old and new cuticle a sticky, homogeneous substance which adheres both to the old shell and to the tips of the new hairs. Molting

[a] For a review of this subject, see Bell: The reactions of crayfish to chemical stimuli. Journal Comparative Neurology and Psychology, vol. XVI, p. 299–326. 1906.

thus becomes a means of drawing out or evaginating every microscopical hair of the newly-formed armor.

This adjustment is even more complicated in the young lobster about to hatch. Its "swaddling clothes" are so pinned together that all come off as one piece; the animal hatches and molts at the same time. The outer egg membrane splits lengthwise like the skin of a pea; it is glued in certain places to the inner membrane or true egg shell; this adheres to the outer deciduous cuticle, which in turn sticks at innumerable points to the hairs; by the time the animal has kicked off its covers it is thus ready to swim, for every hair is drawn out to its full length.

In hatching the eggs of lobsters by artificial means in jars or boxes, this delicate adjustment often fails at one point, and the little animal is doomed. The egg membranes fail to stick, and thus to pull out the swimming hairs, so that the young lobster is hatched in a helpless condition. It struggles in vain, a prisoner inside of its own skin, which it is unable to shed.

Blood pressure is another factor which enters into this important process of evaginating the setæ, and in all adult lobsters withdrawal of the blood from the great claws is an essential condition of the molt. As a consequence, when the animal escapes from the old shell, the hair clusters on the deformed plastic flesh of the great claws are scarcely visible, while they are prominent in other parts. With returning blood pressure the hairs of the toothed claw are fully evaginated. It seems evident that when once the shell has become hard no further evagination of the hairs is possible.

From the method of formation of new hairs it follows that at each molt, as Prentiss has shown, the nerve fibers lose their connection with the old hairs and enter into relations with the new ones.

TOUCH, TASTE, AND SMELL.

As long ago as 1868 Lemoine (*179*) suggested that the senses of taste and smell in higher Crustacea might be blended with that of touch, and while many able workers have since attacked this problem and produced far better results, we are still unable to speak with much exactness upon the subject. As I have shown by earlier experiments, nearly every part of the lobster's body is subject to tactile or chemical stimulation, and must therefore be supplied with sense organs of some sort. (See *149*, p. 129.) We found that the parts most richly supplied with setæ, with the exception to be noted below, were most sensitive, and it seemed evident that all the soft setæ, whether fringing and protective or not, were sensory. It was further observed that the greater sensitiveness was lodged in the antennules, and especially in their outer whips, which bear the peculiar club-shaped setæ, the antennæ, the tips of the slender legs, and in younger animals, at least, in the fingers of the big claws. Stimulation with various gases and liquids, injected with a pipette upon a given part, gave more or less prompt reflexes either in the limb itself or in the appendages nearest the part affected. If any stimulus, whether electrical, tactile, or chemical, be applied to the right second maxilla or right first maxilliped, vigorous chewing movements are immediately started in the affected appendage of that side, and may spread to the side opposite.

The swimmerets of the lobster were also proved to be quite sensitive under most conditions, as well as the thoracic sterna, the wings of the seminal receptacle of the female, and even the hard carapace, which was nearly as responsive to weak acids as is the soft skin of the frog, and the scratching movements made by the legs in the direction of the stimulated part are essentially the same in each case. We concluded that the sense organs were the setæ, reenforced by sensory buds, which lie in the tissues beneath the hard shell, but open upon it by capillary ducts. For other reasons these perplexing structures were given the name of tegumental glands. We have found no reason to alter this conclusion, and can still point to the upper lip as a supporting case. The labrum while possessing no true setæ is highly responsive to chemical stimuli, and is full of the organs in question, which open by ducts all over it in the lobster, but are most abundant on the under concave surfaces, to which a greater sensitiveness was attributed in the crayfish by Lemoine; here the ducts are clustered in large sieve-like plates bearing 60 to 70 holes each. We have further shown (see p. 232) that the labrum is not only well supplied with nerves, but possesses an independent ganglion of its own. That these labral organs are not glandular in function might be also indicated by the fact that the upper lip is always clean in the lobster, and free from anything suggesting a glandular secretion.

Experiments on the crayfish by Bell and others have shown conditions essentially similar in most respects. In getting food, sight plays little part, the blinded crab or crayfish going unerringly to the bait. This is certainly true of the lobster, as the experience of fishermen amply proves. Apparently through their chemical sense organs, for we do not seem warranted in using either the word "smell" or "taste," they become aware of the presence of food, and are attracted to it, while in the crayfish accuracy in the localization and in the seizure of the food seems to be secured through the medium of touch.

Bethe, who performed some strking experiments with the common green crab, *Carcinus mœnas*, found that the chemical reaction was the most important in its search for food.

> The mouth parts, says Bell, in summarizing Bethe's results, seem to be more sensitive to chemical stimulation than the antennæ or the antennules, since the animals react when the latter are removed. The threshold of chemical stimulation is extremely low, for the animals react most vigorously to the trail left in the water by a finger that has been in contact with meat, and greedily devour filter paper which has barely touched meat, but to really clean filter paper they pay no attention.

Holmes and Homuth [a] have repeated Bell's experiments on the crayfish and tested its reactions to chemical stimuli after removal of the antennules and antennæ, and after destruction of the brain and a section of the ventral nerve-chain. They confirmed the old opinion that the olfactory sense was lodged chiefly in the outer branches of the antennules, but found it exercised in a lesser degree by the antennæ, the mouth parts, great chelipeds, and the slender legs. Destruction of the brain or nerve cord tended if anything to slow down the reactions, but did not put an end to response.

[a] Holmes, S. J., and Homuth, E. S.: The seat of smell in the crayfish. Biological Bulletin, vol. XVIII, p. 155-160. Boston, 1910.

The lobster feels its way in the dark or gropes about in twilight by the aid of the sensory hairs with which it is abundantly supplied. From 50,000 to 100,000 of these organs are present on the big claws and slender legs alone. In most cases we do not find it possible to discriminate between hairs which are solely tactile or for the chemical sense alone. The lobster finds its way, however, to the fisherman's baited trap after dark or in dim light by the aid of all those setæ which respond to the chemical stimulus, and chiefly no doubt by those on the anterior appendages, the hairs which project from the lower sides of the outer whips of the antennules being probably the most sensitive. Fine particles of the bait which diffuse through the water from all sides of the trap, or are carried by currents, furnish the stimulus which draws this animal to their source.

BALANCING ORGANS OR STATOCYSTS.

It is commonly observed that while a living fish swims with its body erect and poised, a dead one floats on its side, and that the former position is one of unstable, and the latter one of relatively stable equilibrium. The upright unstable position is maintained in life by compensating movements which are automatically called into play by aid of special sensory bodies called static organs. This is true of the lobster, and of all animals which carry themselves upright, in opposition to the force of gravity.

There is now considerable evidence to show that what were formerly regarded as true "otocysts," or ear sacs, in the basal segments of the first pair of antennæ, are static rather than auditory in function, and accordingly they have been more appropriately called statocysts or organs of equilibration. The sac of either side (fig. 2) fills nearly the entire segment, and is open to the outside by a fine pore barely large enough to allow a minute grain of sand to pass, or to admit the point of a pin. The membrane overlying this sac is thin and taut (fig. 4, pl. XXXV, *mm.*); long setæ encircle it, and also surround the mouth of the sac.

The sac originates as a shallow pit of the skin, sinks into the tissues, becomes horizontally flattened, and remains attached to the cuticle along its transverse front, the opening being gradually constricted to a minute pore on the inner side of the thin membrane. Upon dissection and examination of the sac from within, we see on its floor a semicircular or horseshoe-shaped sensory ridge (*s. r.*, fig. 3), studded with a median row of about 75 plume-like hairs and four times as many shorter setæ arranged on either side or crowded about its mouth. Three hundred and seventy-five hairs were present in a single case examined, but the number may be considerably greater. Some of the hairs have bent shafts; some are thread-like, and scattered among them and often glued to their tips are numerous fine sand grains, the "ear-stones" or otoliths, as they have been called. In one of the sacs examined there were several hundred grains, ranging from one-fortieth to one-six-hundredth inch in diameter, the smaller being far too minute to be picked up with the points of the finest forceps. Each hair of the sac is supplied with a nerve-element, and as Prentiss has shown, with but a single one, as is the case with all tactile setæ.

From the foregoing account it will be seen that in the water-filled sacs just described, with their rich supply of sensory hairs, many of which, having little weights in the form of sand grains glued to their tips, and all being subject to the impact of free particles with the least displacement of the body, we have what would seem to be an admirable apparatus for enabling the animal to carry itself erect in walking or swimming. Any swaying of the whole body would sway the little hairs, or rattle the sand over them, and the stimulus thus given, would act as a sign to which the nervous system of the animal could respond in an adaptive and useful manner.

The study of development throws some light on the probable use of these peculiar sense organs. As shown by my earlier studies but first carefully worked out with histological definiteness by Prentiss, the sacs are developed in the free-swimming stages. They are barely visible as shallow depressions in the second and third larvæ, but in the fourth stage sensory hairs and sand grains are present, and closure of the sacs, which has now begun, is gradually effected with each successive molt. As Prentiss has shown, this "sudden leap" in the appearance of the sacs at the fourth stage is probably related to the abrupt change in form and method of swimming exhibited at the fourth molt.

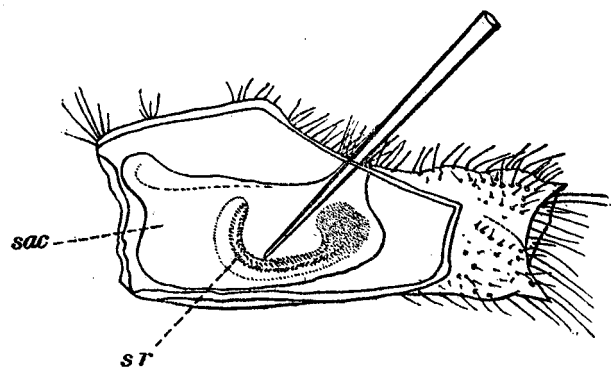

FIG. 3.—Sectional view of antennal segment to show statocyst, with needle inserted in pore at surface and pointed to sensory ridge, *s r*.

Every one who has watched the swimming movements of the young lobsters up to the fourth stage (fig. 34 and 42) has noticed how unsteady they become whenever the water is in the least degree disturbed. In ordinary swimming, when their equilibrium is not upset, the thorax is horizontal and the abdomen bent; in rising the head is inclined downward, but at best they are very unstable, and frequently pitch and reel to and fro, swimming now on their backs, now with their heads directed up or down. (See fig. 40.) It should be added, however, that under certain conditions, as in dull light, the young larva, as Hadley observes (*131*), swims with grace and precision, and there is no doubt that the eyes act before the statocysts as organs of orientation.

At the fourth stage (pl. xxxi) the little animals uniformly bear themselves erect like an adult and move about with great speed and definiteness. Prentiss has pointed out that when the young at this stage are unable to get sand for the statocysts, their movements again become uncertain, like those of an adult animal from which the sac has been removed. It is thus evident that while other organs, such as the eyes and antennæ, may help a crustacean to maintain its erect attitude, the sacs are indispensable for this purpose, at least after the larval stages.

It seems to be established that the supposed response of aquatic animals to atmospheric sounds of ordinary intensity is a myth, for sound waves propagated in air are almost totally reflected from the surface of water, but since sound vibrations are transmitted by water it does not follow that aquatic animals are necessarily deaf. An animal so abundantly supplied with tactile organs as a lobster has little need of ears, since sounds transmitted through the water would be perceived or felt by means of the sensory hairs. "The range of the average auditory organ in mammals," to quote from the work of Prentiss, referred to above, "is from 30 to 16,000 vibrations per second; waves of less than thirty vibrations per second do not usually produce auditory sensations, but are appreciable to the tactile sense. It is important to note that decapods respond most vigorously to low notes, and not at all to high notes or sounds produced by very rapid vibrations. This fact would seem to be good evidence that the vibrations imparted to the water and perceived by decapods correspond to those which produce tactile rather than auditory sensations in vertebrates." It has been noticed that the so-called "auditory" hairs of certain crustaceans will vibrate to different musical notes, as will the hairs on the back of one's hand or the strings of a violin, but they are not auditory, as Prentiss remarks.

It is only natural to find that the senses of touch and hearing grade into each other, and in either case it is the effect of a vibration which is perceived. While it is a matter of convention how these sensations are described, it is evident that an aquatic animal like the lobster has no organ strictly comparable to a vertebrate ear or even to the auditory or chordotonal organ of insects, and that if possessed of such an instrument it would have little occasion to use it. The basal segments of the large antennæ of *Palinurus* possess a peculiar structure often called a "stridulating organ," but nothing seems to be known of the real uses which it serves. (See p. 160.)

To return for a moment to the sacs, which have the form of a narrow-necked bottle, and are carried in the antennulæ, how do the sand grains find their way through their minute openings, guarded with hairs? Professor Brooks has seen the megalops larva of the crab, *Callinectes*, pick up the grains and place them in the sac with its claws. As an illustration of animal instinct, this is truly remarkable, for it is peculiar to the larvæ alone, the adult crab having no sand grains or otoliths of any kind in its sacs. The lobster at the fourth stage nearly corresponds to the crab megalops, but it has never been seen to behave in this manner. Whatever method the young may adopt to replenish their stock of sand after each molt, it is evident from the microscopical proportions of the grains that adults behave in a different manner. The animal in all probability thrusts its head in the sand, while the smaller grains, selected by the one opening of the "strainer," gradually sift into the sac by the force of gravity. The spiny lobster (*Palinurus*), which also keeps its antennal sacs well supplied with sand, has no claws with which to pick up anything, and must have recourse to a similar method. In reference to this peculiar need of the animal, it is interesting to notice that molting lobsters often burrow in the sand, where they remain for some time after casting the shell.

THE MUSCLES.

The muscles of the lobster's body are of two kinds, the striped or striated and the non-striated, distinguished in higher animals as the voluntary and involuntary muscles. The involuntary muscular tissue is inconsiderable in quantity, excepting the "fine meat" at the tips of the claws, being mainly confined to the walls of the alimentary canal, the blood vessels, and sexual organs. The heart and powerful skeletal muscles are composed of distinctly striated fibers.

The skeletal muscles, of which the large adductor of the mandibles is a good example, are attached to the hard shell on the one hand, and to tendinous ingrowths of the softer cuticle on the other. Just how the union with the shell is effected is a somewhat vexed question. In the first larval stage of the lobster the prominent muscle just referred to is distinctly striated up to the basement membrane. (Fig. 2, pl. XLVI, *bm.*) At this level its fibrillæ are directly continuous with attaching fibers within the cells of the epidermis; the basement membrane is accordingly penetrated at this point. Examination of earlier embryonic stages shows essentially the same conditions. The epidermis of the shell in the area of attachment (*fb. ep.*) is modified in a characteristic manner; its cells are columnar and elongated, and their cytoplasm develops fibers which appear to fuse with those of the muscle-fibrillæ; moreover, their nuclei are eventually reduced and spindle-shaped, though this was not the case in the specimen figured. The basement membrane in this region is a distinct cuticular sheet, to which blood cells and other elements (*ms.*) presumably of mesoblastic origin also attach themselves, with long axes parallel with the surface, thus making a distinct lamella. The horizontally placed lamellar cells can be detected beneath the modified epiblast, where the cuticular portion of the membrane appears to be reduced or absent. In some cases the epiblastic fibrils brush out perceptibly at their periphery against a concavo-convex layer of chitin, upon which the outermost stratum of the shell is molded. Since the clearer inner chitinous layer frequently peels off in preparations, it may represent a renewal of the shell at this point previous to molting.

In his study of regenerating limbs in the lobster, Emmel (*97*) has found that the striated muscles are regenerated from ectoderm, and that the outer ends of the myofibrillæ are differentiated as tensile elements, which pass between the proper epidermic cells, are frequently spread out in branches, and are fused directly to the chitin of the shell.

The muscles of the tail, which form a great part of the edible flesh of the lobster (pl. XXXIII) consist of two paired masses, the dorsal extensors, by the contraction of which the abdomen is straightened, and a much larger pair of ventral muscles, mainly flexor in function, which form the principal source of power for locomotion. As we have seen, the segments of the shell in this region are united by flexible membrane, and move over articular surfaces as well as upon double hinges of the typical ball-and-socket form, and that the parallel and horizontal arrangement of their articular axes limits the flexion of the tail to the vertical plane. The ventral muscles are very complex, being composed of external bundles attached to the side walls of successive segments, and of interlooping or enveloping strands, which are fixed to the lower or sternal parts of the skeleton. A

twisted rope-like mass is thus formed, the forward strands of which are attached to the linkwork of hard tendons in the thorax. There are also in the thorax, rotator abdominis, ventral thoracico-abdominis and tergo-epimeral muscles, as well as flexors of the telson and tail fan in the abdomen.

The weaker dorsal muscles (pl. XXXIII) form a pair of segmented strands overlying the alimentary canal and dorsal blood vessel. They are inserted into the anterior border of each abdominal somite and diverge as extensor abdominis muscles in front, where they are attached to the walls of the thorax below the cervical groove. When the ventral muscles suddenly contract at the command of the nervous system, the combined pulls on successive joints bring the tail with expanded tail fan quickly and violently down upon the thorax, and the animal shoots backward through the water. By the contraction of the weaker extensor muscles the body is again brought into a horizontal position, and ready for another downward stroke. Raising the abdomen tends to send the animal forward, but owing to the obliquity and slowness of the stroke after closure of the tail fan the speed is but little checked. The muscular equipment of the great claws and legs are described in chapter VII.

Two prominent light spots are conspicuous on either side of the carapace of an adult lobster, one at a point about an inch behind the base of the large "feelers," and the other about as far behind the first, close to the irregular depression known as the cervical groove. (See p. 220.) The first, which is large and very conspicuous at the sixth stage, when the animal is barely five-eighths inch long, is the mark of a straight rod-like tendon which binds the carapace firmly to the internal skeleton below. The latter was without doubt originally a tendon-mark also, but in place of a distinct tendon, short muscle fibers issue from its margin, and from the groove in front, to be attached to the wall of the gill chamber. The scar-like impression conforming to the groove and immediately in front of it marks the attachment to the shell of the posterior suspensory muscles of the stomach sac. The powerful adductor of the jaws, by the contraction of which their cutting surfaces are brought to bear on the food, divides to give passage to this gastric muscle, one section of which is attached to the carapace in front of the groove, and the other just behind it on the endotergites, which as stated above are tendinous ingrowths from the fold itself. The anterior gastric muscles are inserted on the procephalic plates.

Some fourteen pairs of extrinsic and intrinsic gastric muscles have been described by Williams (*279*). These serve either to suspend the stomach sac to the inner wall of the carapace (anterior gastric, anterior dilators, and posterior and lateral gastrics) or to move its nicely articulated framework, bring the food to mill, work the grinding teeth, and to effect in some measure the sorting and straining of the comminuted food particles.

THE BLOOD AND ORGANS OF CIRCULATION.

The blood of the lobster when freshly drawn is quite colorless, leucocytes or white blood cells being the only corpuscles present, but after exposure to the air for a few minutes it becomes tinged with blue, and thickens or coagulates. The bluish color is imparted by a respiratory pigment called hæmocyanin, which like the haemoglobin of

red blood becomes deeper in color as it takes up oxygen. The bluish tint of the larval lobster is probably due in part to the hæmocyanin of its blood. The blood is also regarded as the bearer of other pigments, the lipochromogens, which are probably elaborated in the digestive gland, transmitted by the blood, and laid down in the pigment cells and the shell.

The heart begins to pulsate rythmically when the lobster is an embryo, between 4 and 5 weeks old,[a] at a time when the black pigment spots of the compound eyes have begun to show, but when the nervous system has been only roughly blocked out and long before any nerves are developed. The heart, although later brought under nervous subjection and control, is at first quite automatic and independent in its movements.

The circulatory system of the lobster (see pl. XXXIII) consists (1) of a muscular heart for driving the blood, (2) of arteries or definite channels for conveying it to the tissues, and (3) a system of irregular channels called sinuses or lacunæ, besides certain well defined vessels, the veins for leading it back to the pericardial chamber and heart. The arteries end in microscopic capillaries which open directly into the lacunar system.

The freshly aerated blood of the lobster is driven from the gills to the pericardial sinus, enters the heart through the ostia, is pumped thence by the rhythmical contractions of its walls into the arteries, and by their subdivisions is distributed over the entire body. Having performed its physiological work of giving up to the tissue cells dissolved oxygen and food materials, and having received from them carbon dioxide and other waste products, it returns by the lacunar system to the large ventral sinus, which surrounds the ventral nerve-chain; thence the venous blood is driven to the gills, where aeration is effected by the absorption of oxygen from the fresh streams of sea water in which they are constantly bathed. More simply expressed, the path traversed is heart, body, gills, heart. The gills are placed in the returning blood stream, so that the vessels which both supply the gills with venous blood (afferent branchial vessels) and which conduct arterial blood from the gills to the heart (efferent branchial and branchio-cardiac vessels) may be described as veins.

THE HEART.

Examining the heart more closely, it appears as a boat-shaped or somewhat hexagonal body, rounded below, flattened above, and broader in front. It is pierced by three pairs of openings, the dorsal, ventral, and lateral ostia, which admit blood from the pericardial sinus. Each ostium is provided with valves which open inward, so that the blood once admitted to the heart can not be regurgitated to the sinus.

The heart gives off a series of arteries, five in front and two behind; these are also supplied with valves (or at least in the largest of them, the sternal), so that the heart can empty only into the arteries, while it can fill only from the sinus.

THE PERICARDIAL SINUS.

The chamber in which the heart is suspended, called the pericardial sinus, lies at the extreme upper and hinder part of the carapace; it is lined with connective tissue

[a] The beating of the embryo lobster's heart has been noted in winter (December 14) at 100 times per minute.

and muscle fibers,[a] and has an arched roof and floor, with sloping sides. This chamber lies close to the back, so that if the shell is perforated anywhere in the cardiac area the animal will quickly bleed to death. The convex floor of the sinus covers the sexual organs and the digestive gland, while at the sides only the thin shell of the body wall (inner epimeral surface) separates the sinus from the upper part of the branchial cavity. Moreover, the extensor muscles of the tail virtually pass through the sinus and are inclosed between its sides and floor.

The heart beats rythmically and heat accelerates its action. Plateau (*214*) found that the isolated lobster's heart, when placed in a moist chamber, would beat for nearly an hour; according to this investigator the movements of the decapod heart are governed as follows: (1) By a cardiac nerve which arises in the stomato-gastric ganglion and ends in the heart muscle; (2) by ganglion cells within the tissue of the heart itself, by means of which its automatic movements are maintained, and (3) by depressor nerve fibers which moderate the heart's action, but the real courses of which are not known. The brain is found to have no direct influence upon the action of the heart.

THE ARTERIES.

Of the five anterior arteries the ophthalmic or cephalic runs along the middle line just beneath the shell, and makes straight for the brain, which it supplies, together with the eye stalks (upper side), giving off a few twigs to the stomach sac in its course. The paired antennal arteries issue from the side of the ophthalmic, and in passing forward along the surface of the gastric glands they give off numerous small branches to the following organs: The glands themselves, the gastric muscles and walls of the stomach, the sexual organs, the thoracic muscles, and the body wall, or the integument of the carapace and the inner epimeral wall of the branchial cavity; finally the same vessel sends twigs into the eyestalk, the antennule, the adductor mandibuli muscles, the antenna, and the green gland which lies at its base. The paired hepatic arteries supply the gastric glands. Both ophthalmic and antennary arteries are subject to considerable variation in both the lobster and crayfish. (See fig. 1, pl. XLIV.)

Two arteries issue from the hinder end of the heart, where it swells into a bulb, namely the sternal artery, which passes straight down and penetrates the nerve cord, and the superior abdominal artery, which supplies the greater part of the tail. The sternal gives off twigs to the sexual ducts before it swerves to pass the intestine, and entering the ring formed by the long commissures between the fourth and fifth ganglia of the ventral chain (somites XII and XIII), gains the ventral side, where it divides or gives off a posterior branch, the inferior abdominal artery, which supplies a small part of the ventral surface of the abdomen, but none of the appendages. The main branch of the sternal, the inferior thoracic artery, runs forward under the nervous system, and supplies the slender legs, the great forceps, and the mouth parts.

[a] According to Dogiel (*72*), the pericardium also contains blood vessels, which can be injected from the superior abdominal artery, as well as nerves supplied by a trunk (nerve of Dogiel) which is given off from the ganglion of somite XII. The valves of the heart are further regarded as properly sphincters, rather than of the bilabial or semilunar form. On the other hand the sternal artery, of which the superior abdominal may be considered a branch, is provided with true valves of the bilabial type.

ARTERIAL SUPPLY OF THE SWIMMERETS.

The dorsal or superior abdominal artery passes backward just above the intestine and gives off six pairs of segmental lateral vessels, which, besides supplying the intestine itself, send arterial blood into the great muscles of the tail, the posterior lobes of the gastric glands, and the sexual organs. To complete the statement, however, it must be added that the main branches of the lateral segmental vessels are curiously continued around the sides of the body to the swimmerets or pleopods, which they feed with arterial blood.[a]

The swimmerets have been invariably described as receiving their blood from the inferior abdominal artery, both in the lobster and crayfish, an error which may have arisen in the first instance from failure to inject the vessels or from inference, probability favoring the inferior vessel, on the principle that organs as a rule draw their blood supply from the nearest source. The error, started in some such way, has escaped the scrutiny of such keen observers as Professors Huxley, T. J. Parker, and Howes, and is to be found in all the text-books and literature dealing with these forms. It can be seen, however, without recourse to much dissection, that the inferior abdominal artery is too diminutive and passes altogether too small a quantity of blood to supply the swimmerets, which are the most active of all the appendages, excepting only the respiratory plate or "bailer" of the second maxilla.

The superior abdominal artery divides at the hinder border of the fifth somite into two branches, which embrace the intestine where it gives off a short cæcum on its upper side, and which run backward and diverge to supply the sixth somite and tail fan.

The principal artery of the big claw (pl. XL) traverses the lower side of the limb and gives off numerous branches to the muscles of the segments. In the fifth podomere it sends off a shoot which enters the big claw, passes to the abductor muscle along the inner border of the big tendon, and ends in the fine meat of the dactyl. The main artery, upon entering the claw, again divides, giving rise to four branches, three of which supply the big adductor muscle and the fine meat of the propodus, while the other passes to the adductor muscle and divides, sending a branch to both dactyl and propodus. The division to the dactyl is united by a cross branch to the vessel which supplies the abductor and enters the propodus from the fifth joint. In the index and dactyl the arteries ramify in tree fashion, and apparently break up into a lacunar system of irregular spaces in the fine meat. From this situation the blood returns by a large irregular channel and enters the sternal sinus, whence it reaches the gills.

It has been shown by Emmel (97) that as the returning sinus of the great cheliped passes the ischium or third podomere it is divided into two channels by a septum of connective tissue. These dorsal and ventral sinuses, moreover, possess valves which originate as folds from the septum and become operative to staunch the flow of blood from the breaking joint the moment a claw is shot off (see p. 282).

[a] I am indebted to Prof. Carl B. James for first directing my attention to this fact, which must have been noticed by other teachers in the laboratory.

THE GILLS.

The adult lobster is provided with 20 pairs of gills, 1 of which, belonging to the second pair of maxillipeds, is rudimentary. Of these, 6 are podobranchiæ, 10 arthrobranchiæ, and 4 pleurobranchiæ, distributed according to the following table:

TABLE 5.—BRANCHIAL FORMULA OF THE LOBSTER.

Thoracic segments and appendages.	Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.	Totals.
		Anterior.	Posterior.		
VII, first maxilliped	0 (ep.).	0	0	0	0 (ep.).
VIII, second maxilliped	1 rud. (ep.).	0	0	0	1 rud. (ep.).
IX, third maxilliped	1 (ep.).	1	1	0	3 (ep.).
X, first pereiopod	1 (ep.).	1	1	0	3 (ep.).
XI, second pereiopod	1 (ep.).	1	1	1	4 (ep.).
XII, third pereiopod	1 (ep.).	1	1	1	4 (ep.).
XIII, fourth pereiopod	1 (ep.).	1	1	1	4 (ep.).
XIV, fifth pereiopod	0	0	0	1	1
Total	6 (ep.).	5	5	4	20 (1 rud.).

ep.= epipodite. rud=rudimentary.

The first larva has no rudiment of a podobranchia in the eighth somite, but all the other branchiæ are represented. The podobranchiæ of the following segments are very small and are partially exposed, together with their reniform epipodites (fig. 34). In the second larva the podobranchiæ are covered by the carapace (fig. 41) and the branchial formula is complete.

The gills are developed in the embryo as simple folds or pouches in the body wall. (fig. 8, *g. fil.*) They belong to the trichobranchiate type, the respiratory surface being gradually increased by growth of multiserial branchial filaments.

In the fourth larva the podobranchia carries four rows of filaments, and the mastigobranchia, or epipodite proper, is a long, tapering, hairy plate.

The adult gill (pl. XXXVIII), suggesting by its form a bottle brush, is a pyramidal tuft, consisting of a central stem and numerous longitudinal rows of branchial filaments, which enormously increase the area of the surface exposed to the water. The number of rows of gill filaments gradually increases with the size of the animal and with its need of a greater respiratory surface, until it reaches between 30 and 40 in an adult 10½ inches long, while the total number of filaments in such a gill is between 3,000 and 4,000. The filaments are "parted" into two groups by a median longitudinal furrow and in the larger posterior section tend by transverse partings to separate into quadrangular masses. The filaments gradually lengthen in passing forward or backward on either side of the "part" and terminate in several rows of short filaments next the efferent division of the stem, opposite the body wall. Further, the filaments are so regularly spaced that they come to assume an arrangement in circular rows from base to apex of the branchia, corresponding to the circular efferent vessels (fig. 2, pl. XLVII *c v*) with which they communicate.

THE BRANCHIAL CAVITY AND RESPIRATION.

The branchiæ are lodged in a cavity of peculiar form upon either side of the body, where they are securely protected by the broad sides of the curving carapace. The gills (pl. XXXIV) arch upward in pyramidal form from the bases of the limbs and the sides of the body to which they conform, those of successive somites being divided by the gill separators or epipodites, which are hairy respiratory plates, springing from the basal segments of the limbs. Currents of water set upward and forward from under the free edges of the carapace, pass over the myriads of fine filamentous processes of branchiæ, and are led into a trough or groove at the forward end of this curved narrow passageway on either side of the body. From this trough the water is fanned out by the rythmic beating movements of the "bailer" or respiratory plate of the modified second maxilla (see p. 228). The fan or respiratory paddle thus works with up-and-down strokes in a narrow passageway,[a] which is horizontal in front, and behind curves upward abruptly to the pyramidal apices of the gills. The lower bound of this passage is formed mainly by the epipodite of the first pair of maxillipeds, which is folded over so as to form a sort of trough in the part where the free inner division or epipodite of the bailer plays (pl. XXXVI, fig. 3 *fd.*). This fold presses against the side of the carapace and keeps water from entering the trough until it has passed over the lower half of the gills. The outgoing stream is thus essentially limited to the forward upper part of the gill cavity.

By the alternate beating of the hinder (epipodite) and anterior (exopodite) divisions of the bailer the water is driven forward and out of the cavity.

At the extreme hinder end of this chamber the carapace overlaps a small hairy leaf-like plate belonging to the fourteenth somite and bearing a small oval lacuna in its chitinous cuticle, just behind the pleurobranchia of this segment and above the hinge joint of the limb. This corresponds to similar lacunæ for the four pleurobranchiæ in front and without doubt represents the position of a former gill, every other vestige of which has now disappeared.

As blood slowly passes through the 20 pairs of gills and their protective plates the act of respiration is accomplished. Carbon dioxide diffuses from the blood through the thin walls of the filament, and from the air dissolved in the sea water the oxygen supply of the blood is renewed. The water in the respiratory chamber is kept stirred up by the legs, to the bases of which 10 of the gills are attached, while the incessant beating of the fan at the front end of the cavity (marked by the frothing which commonly occurs when the animals are taken from the water) causes an active forward flow through the chamber and over the gills as described above. If the motion of the fan is stopped the animal soon becomes asphyxiated. The lobster will live for a long time out of water, in some cases for upward of two weeks, provided the branchiæ are kept moist, and even in hot weather when the air is cooled by ice.

From the filaments the aerated blood is conducted down one of the efferent branchial veins on the inner side of the stem in each gill, and thence through a distinct channel, one of the branchio-cardiac veins, to the heart.

[a] The "fan" has been noticed to beat at the rate of 95 to 178 strokes per minute in summer, in lobsters which had been out of the water long enough to become quiet.

COURSE OF THE BLOOD IN THE GILL.

The description of the course of blood through the gill given above usually suffices for the text-books of zoology, but the physiologist wishes to know how the blood circulates in the gill filaments, for if these were simple capillary tubes it would tend to flow past rather than through them. The gill in reality is a complicated structure, and the actual course of the blood is not easy to follow.[a]

Each filament, like the stem of the branchia, is a double tube or vascular loop, consisting of outer afferent and inner efferent divisions (fig. 2, pl. XLVII.) All the blood must pass from the afferent branchial vein (*af. v.*) to the afferent divisions of the loops, thence to the efferent divisions, and then to the main efferent of the stem (*ef. v.*). The wall of the branchial afferent vein which carries unaerated blood to the filament suggests a cylindrical sieve or grater, with fine holes arranged in regular transverse rows. As the blood enters one of these holes it is conducted by a short passage to the afferent division of the loop or filament, but, as Dahlgren and Kepner have shown, the course by which the efferent half of the filament is reached is indirect. The venous blood in the afferent section enters a plexus of fine channels or capillaries, by which it is conducted around the filament and into the efferent loop. In the course of this passage the venous blood is brought close to the cuticular surface, but never quite touches it, there being always a cytoplasmic layer of the true epidermis of the filament, from which the cuticular covering is supplied at each successive molt. Thus, in passing through the filament the blood is kept in close relation to its surface, a condition which tends to promote the most active exchange of gases essential to respiration. These capillaries do not, apparently, have definite walls, but worm their way between or through the cells. The connective-tissue cells of the central core of the filament are described by Dahlgren and Kepner as being essentially peculiar and characteristic in possessing loosely branched protoplasmic processes. The efferent channel of each filament empties into a circular vessel (fig. 1, pl. XLVII, *c. v.*) which runs around the main afferent of the stem, and thus conveys the arterialized blood to the efferent vein (*ef. v.*).

The course of the blood through the gill is thus, in brief, as follows: Stem afferent to filament afferent, through filament capillaries to filament efferent, to circular vessel in wall of stem afferent, to stem efferent, to branchio-cardiac vein, to pericardium and heart.

This system of vessels is filled with blood, which, owing to the rhythmic contractions of the heart and the dispositions of its valves, is kept moving in the same direction, from heart to tissues, from tissues to gills, and from gills to heart again. The heart is "arterial," and the breathing organs of the crustacean are thus introduced into the returning stream of venous blood, the converse of the conditions found in fishes, where the heart is "venous" and the gills participate in the arterial system which leaves it.

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[a] The account of the circulation of blood in the gill given in this section was written six years ago, when the drawings illustrating it were made. Certain details concerning the capillary plexus have been added since reading the work of Dahlgren and Kepner, who, so far as we are aware, were the first to describe the histology of the filament and the course of the blood through it.

THE ALIMENTARY TRACT.

The alimentary tract (pl. XXXIII), extending from mouth to anus, consists of three parts, which are quite distinct in origin, namely: (1) The foregut (stomodæum of the embryo), formed by a tubular invagination of ectodermic epithelium; this remains distinct until late in embryonic life, and gives rise to the epithelial lining of the esophagus and grinding stomach; (2) the midgut (mesenteron of the embryo), lined with endodermic epithelium, and formed by the walling in of the great mass of the yolk by endodermic cells; paired outgrowths or folds of the endodermic sac arise early in embryonic life and eventually form the liver of the adult; aside from the liver or gastric glands, the mesenteron appears to take no part in the formation of the alimentary tract; (3) the hindgut (proctodæum of the embryo), formed by a solid ingrowth of ectodermic epithelium which subsequently becomes hollowed out, its walls merging with those of the mesenteron; it gives rise to the lining of the intestine and cæcum.

The foregut and hindgut, being infolded parts of the outer surface of the body, are covered with a cuticle which is continuous with the chitinous exoskeleton, and is cast off in the molt.

THE GRINDING STOMACH.

The higher Crustacea are the only animals which grind the food after it reaches the stomach as well as before it enters the mouth. Granivorous birds swallow their food whole, and with the aid of gravel stones or other hard bodies pulverize it in a muscular gizzard; in a number of gasteropod mollusks analogous organs occur, but the stomach mill of a decapod crustacean is a much more complicated machine.

When a bit of fish or clam is offered to a hungry lobster, it seizes the food with the claws of the slender forward legs and passes it up to the mouth, where it is held by the large maxillipeds. The cutting teeth and spines of the mouth parts, especially the maxillæ and mandibles, are successively brought to bear upon it, and chop it into mince-meat, while it slowly enters the mouth in a stream of fine particles.

The stomach of the lobster is truly a complicated mechanism, and could not be fully described without entering into great detail. In the brief account which follows I shall rely mainly upon a study of this subject by Williams (*279*), which is by far the best that has appeared.

The stomach sac (pl. XXXIII and XXXIV) serves for storing, grinding, sorting, and straining the food, as well as for delivering the finest particles in liquid streams along definite channels to the intestine and to ducts of the liver; for, as Jordan has shown, the huge gastric glands serve also for the direct digestion and absorption of food. Further, the coarser particles of the food may be sent to mill time and again to be reground, while the indigestible parts are regurgitated. Again, it should be added that newly molted lobsters instinctively devour their own cast, and I have found soft lobsters with their stomachs stuffed full of the shells of mollusks and other calcareous fragments (see *149*, p. 89), actions which point clearly to the need of the animals at such times to obtain a supply of lime as quickly as possible.

The stomach is divided into a larger forward, or cardiac division, for storage chiefly, and a smaller hinder, or pyloric section (pl. XXXIII and XXXIV), mainly for sorting and straining the food. Between the two lies the gastric mill, the grinding "stones" of which consist of a single dorsal median tooth and of two large lateral grinders. The wall of the stomach is composed of two layers of connective tissue, in the inner and looser of which are lodged the blood vessels and muscles, a gastric epithelium, and a chitinous lining. The lining of the stomach is thickened in certain areas and hardened by deposits of lime, to form the calcareous plates or ossicles which make up the framework of the gastric mill; the largest and strongest ossicles culminate in the "millstones," or teeth, just mentioned. The lining of this organ is further thrown into various permanent folds, pads, ridges, or bands, between which lie definite canals for the circulation of liquids containing the comminuted food. Most of these parts are thickly studded with short setæ, which in general point toward the gastric mill, and serve to direct the food mechanically into its proper channels, whether to or from the mill, whether into the pyloric strainer or from this to the intestine and liver.

Aside from the grinding mechanism, the most essential parts of the stomach, according to Williams, are the distributing and circulating canals (the upper and lower cardiac and the lower pyloric canals) and the five food gates or valves, namely, the cardio-pyloric valve between the two main divisions of the stomach and the four pyloric valves which guard the passage of food to the intestine and the liver. There is a small intestinal cæcum, which extends forward over the dorsal wall of the stomach, and the short duct of the liver or gastric gland opens into the intestine between the ventral and lateral pyloric valves on either side. The conspicuous horn-shaped processes at the base of the pyloric sac and in front of the intestinal cæcum are the lateral pyloric pouches, where the finer particles of food are sifted out for delivery to the liver. In addition to the canals mentioned there are also a pair which traverse the median section of the pyloric sac. A small rudimentary tooth (infero-lateral tooth) is seen projecting from between folds of the stomach wall immediately below the anterior end of the lateral tooth, on either side (pl. XXXIII).

Upon each side of the stomach sac, at its forward end, a large ovate plate (pl. XXXIII) is to be seen, called the gastrolithic plate (lying immediately above a small gastrolithic bar). This plate is composed of a modified epithelium, which between the molts secretes the rounded mass of snow-white prisms known as the stomach stones or gastroliths. Williams has found that the gastroliths make their first appearance in the fourth stage, when for the first time the skeleton abounds in lime.

Over thirty distinct plates, ossicles, and bars enter into the complex framework of this organ, governed by some fourteen pairs of intrinsic and extrinsic muscles, some of these serving to suspend the sac to the dorsal wall of the carapace (such as the anterior, posterior, and lateral gastric muscles), for "turning the wheels" of the gastric mill and feeding the "hopper," as well as for dilating or constricting the cardiac and pyloric chambers.

From the mouth the food passes into the short esophagus, through an esophageal valve, and into the cardiac chamber of the stomach sac. Thence it is delivered through

the cardio-pyloric valve to the mill to be ground. The contraction of the anterior and posterior gastric muscles reacts upon the articulated plates of the elastic frame in such a way as to bring the lateral grinders together and to draw the median tooth forward with great force. This upper middle tooth, or prepyloric ossicle, is shaped like a bird's beak and has brown indurated surfaces, while the lateral teeth, or surfaces of the zygocardiac ossicles, the principal grinders, are divided by parallel transverse furrows into a series of yellowish-brown hardened tubercles. According to Williams the forward and downward movements of the median tooth tend to drive much of the food back into the cardiac sac, so that it is reground again and again. Some of it, however, enters the pyloric division of the stomach, and filters back and forth in its chambers and canals. Here it is sorted and strained; the finer parts, suspended in fluids, are delivered by the canals to the intestine in four streams, while the coarser elements are swept up by bristles of the cardio-pyloric valve and sent to mill again. Two streams from the dorsal pyloric canal pass into the intestinal cæcum; a stream from the middle pyloric canal also delivers food to the intestine, while finally a current from the lower pyloric canal conducts food particles to the lateral pouch, where a final sifting occurs, the finest parts, suspended in fluids, entering the liver by the "bile ducts," and the coarser by way of the middle pyloric canal reaching the intestine.

When the muscles of the gastric mill relax, the elasticity of the framework is sufficient to separate the parts. While it is not possible to see these movements in the living animal, they can be roughly imitated by concerted pulls upon the anterior and posterior gastric muscles. Undoubtedly the clashing movements of the teeth go on for hours after a full meal until all of the food has been thoroughly stirred up, brought to mill, ground, and reground. After the soft and semiliquid parts have been filtered and delivered to the intestine and gastric glands, the indigestible residue is regurgitated through the mouth, as is the habit with many birds.

The intestine is a delicate tube of small caliber, and since there are no coils it is quite short. This suggests the need of a gastric mill, and the absorptive function of the glands, for the area of the intestinal surface being limited, the digestive process must be conducted as rapidly and efficiently as possible. As already seen, there is a cæcal enlargement on the dorsal side of the pyloric sac of the stomach. The intestine suddenly enlarges at the beginning of the sixth segment of the tail, where it gives off from its dorsal side another slender blind pouch or cæcum, which is apparently a rudimentary structure. (Pl. XXXIII.) From this point to the vent, which is closed by a sphincter muscle, and from the mouth to the beginning of the intestine, the canal is lined with cuticle which is continuous with that over the body and is accordingly renewed at each molt. The embryology of the animal shows that the inner wall of the intestine is primarily due to an ingrowth from the outside skin and in the early larvæ an intestinal cuticle can be detected, but if the latter is present in the adult it is reduced to a layer of extreme thinness.

THE LIVER.

The "liver" (pl. XXXIII and XXXIV), called also the gastric glands, hepatopancreas, and by the chefs "tomally," is the largest single organ in the body. It is paired of a green, bright yellow or yellowish green or yellowish brown color, and lies along the sides and partly below the alimentary tract of which it is a part.

The liver is a soft, lobulated mass, divisible on either side into three parts—a thick anterior lobe, a long posterior lobe, and a less clearly marked dorsal or lateral lobe. Each lobe is composed of many lobules, and each lobule of a multitude of short aggregated tubes called the cæca. The lobules are covered by a delicate transparent membrane, and when this is broken can be shaken out in water like tassels.

A part of the secretions of the cæca is gathered by a system of converging tubes and is finally admitted to the pyloric division of the grinding stomach, near the junction of the latter with the intestine. These ducts also serve to admit streams of food particles (see p. 249) to the glands themselves, where they are acted on by ferments and are directly absorbed.

THE KIDNEYS OR GREEN GLANDS.

The direct excretion of nitrogenous waste products is effected by a pair of glands which open at either side by a prominent papilla on the lower side of the basal segment of the first pair of antennæ. (Pl. XXXIII and fig. 6, pl. XXXV, *g. gl.*) In their fundamental relations these organs agree with the segmental nephridia of worms and vertebrates.

When unraveled, the entire organ has been found to consist of the following parts: A large, thin-walled peripheral vesicle or bladder, and closely applied to this, in front or below, the proper excretory organ or gland. Together these parts form a rounded or flattened body of a light green color, closely fitting in the convex depression over the articulation of the antenna on either hand and just in front of the stomach sac.

The bladder empties to the outside by a short duct, the opening of which on the papilla is guarded by a valve. The kidney proper is composed of a central saccule or end sac, and of a convoluted tubule, both of which are glandular. According to Dahlgren and Kepner (*67*) the tubule is lined throughout with nonciliated epithelial cells, and is covered by a tunic of connective tissue, it being in this section only that a cuticle is secreted. Upon taking a lobster in hand a fine jet of liquid is sometimes thrown from the papilla to a height of an inch or more. Inasmuch as water does not apparently have access to the bladder, the walls of which are contractile, the liquid is probably a true secretion. This fountain display of the green glands has been noticed but two or three times.

Chapter VII.—THE GREAT FORCEPS OR BIG CLAWS.

THE CRUSTACEAN CLAW.

The last ten thoracic legs of higher Crustacea all end in hard-pointed segments technically known as dactyls. In the account which follows, when not thus designated, they will be called "single claws," "nails," or "digits," the original meaning of the word. In *Palinurus*, the spiny lobster, all of the thoracic legs end in talon-like claws of this simple type; but in the true lobsters, crayfishes, crabs, and many other decapods a unique organ is developed in certain of the forward legs by the extension of an opposable finger-like process of the subterminal segment, the propodus, which is often large and powerful. In the great cheliped of the lobster (pl. XXXIII and XXXVII) this division is also called "the hand" and the terminal part of it the "index," as distinguished from the opposed "thumb" or dactyl. Thus is formed the admirable forceps, commonly known as the "claw" or chela.[a]

Those legs ending in forceps are described as chelate and the others as nonchelate, and the technical use of these terms is unobjectional. This, however, need not lead to the ambiguity of saying that the last two pairs of legs in a lobster or crayfish have no "claws." To avoid this absurdity, we may adopt Huxley's terms, "double claws" and "single claws" for the forceps of the first three and the nails of the last two pairs of legs, respectively, since they describe the conditions met with in both lobsters and crayfish exactly. The chelate legs all pass through the simple claw stage in either the egg or early larval state.

The big claws of the lobster are remarkable organs whether considered in the light of their structure, their development, or the process of their renewal, and the more we study them the more remarkable they appear.

In most of the higher Crustacea the great claws are the chief weapons for both attack and defense and very efficient means for seizing and rending the prey, as well as for grasping and holding the female in the act of pairing, when the spermatophores are transferred to her seminal receptacle or to some other part of her body.

While three pairs of pereiopods in this animal bear double claws or forceps, in the first pair alone are they entitled to be called "great." In many crabs, as well as in the lobsters and crayfish, the great claws are weapons whose grip is not to be despised.

In some of the crayfishes the great chelipeds are equal to about one-quarter of the weight of the entire animal, while in lobsters above medium size their proportionate weight sometimes reaches one-half, and tends to increase with age. Moreover, the disproportion between the big claws of either side, which are normally asymmetrical,

[a] Latinized from the Greek word for any armed appendage; in plural form chelæ, corrupted from chele.

tends also to increase with age and in favor of the "crusher," which in old males reaches an extraordinary size (fig. 1). Many crayfish when incautiously handled readily draw blood, and there can be little doubt that a lobster weighing upward of 30 pounds could easily crush a man's arm at the wrist.

The differentiation of the large claws is often very marked in crabs, and all degrees are represented. The character of the adaptation is equally varied, as may be seen in the common green crab (*Carcinus mænas*), the fiddler (*Gelasimus pugilator*), and in the "king crab" of the West Indies (*Caleppa marmorata*). In *Carcinus* the slightly larger claw is of the "knobbed" or crushing type. A singular differentiation has apparently been started in the same direction in the more remarkable *Caleppa*, where the great chelipeds have been modified in a different manner for the protection of the animal. The great trihedral claws of this singular species swing in and out in front of the head like double doors, and when these are closed or folded in, the crab is as secure as the tortoise in its shell.

In many of the small shrimps belonging to the *Alpheus* family, the huge "hammer" claw, which is usually largest in the males, is most interesting, whether considered as a "snapper" or popgun, as a saber for delivering a slashing blow, or as a means of controlling the development of its fellow in regeneration (see p. 277).

But of all the crustaceans known to me the shrimp-like *Jousseaumea* which I found at Nassau, Bahama Islands, in 1887, but did not describe, presents the most singular differentiation of the claws. When viewed from above this animal presents a very deceitful appearance, no formidable weapons of any kind being visible. In reality, it possesses a huge and ugly looking claw, which in rest is completely concealed, being nicely folded like a pocket rule and tucked under the grooved cephalothorax, ready at any moment to be shot out and to strike an unsuspecting victim. The fellow to this "pocket" weapon is very diminutive. Were this little shrimp as large as the common lobster it would be justly regarded as one of the most remarkable animals in the sea.

While in *Cambarus* and in crayfishes generally right and left claws may be more or less unequal in size, they are often very similar in structure and function, suggesting the primitive toothed type seen in the lobster, but not approaching it with any degree of detail. There is no lock spine in *Cambarus*, but the hooked tips cross, the dactyl underlapping the propodus. The armature consists of small rounded tubercules, set like a row of corn on a cob. When this claw is closed a large gap is left at the proximal end where the teeth are most numerous, and the fingers touch only at their tips.

THE GREAT CHELIPEDS.

The legs which carry the big claws consist of the 7 typical segments already enumerated (pl. XXXVII), united to the body and to each other by articular membranes, and moving in the way described on double hinges of variable form, excepting only the basis and ischium, or second and third segments, which after the fourth or fifth stage fuse into a single piece. This limb in the adult state therefore possesses 6 free podomeres and 6 free joints. The suture of the stiff joint (x in all figures) marks the "breaking plane," since whenever the lobster "shoots a claw," the limb always breaks at the suture of this joint.

The musculature of the great chelipeds is essentially normal and like that of the slender legs, with the exception of the basis or second segment, which has no muscles in the adult state, a condition to be considered in relation to autotomy and the breaking joint; as in the smaller pereiopods the ischium carries two posterior extensors only.

The hinges of this limb are quite peculiar, and suggest possible adaptations to the "breaking joint," and "interlock," considered in a later section. In place of anterior balls working in posterior sockets, as in the tail, we have proximal balls moving in distal cups,[a] with the exception of the first, fifth, and sixth podomeres, for the hinges between the carpus and big claw are so peculiar that they merit special attention. As we have seen, the order in the hinges of the basal joints of all the thoracic appendages is socket and ball of limb, united to ball and socket of the body.

LOCK HINGES OF BIG CLAWS.

By far the most peculiar joint and one of the most unique mechanical devices in the lobster's skeleton are the concealed, sliding hinges, by means of which the great forceps are securely locked and articulated to the rest of the limb. By referring to plate (XXXVII and text fig. 4) it will be seen that the great claw swings between flattened processes of the carpus, which embrace the upper and lower sides of its proximal end near the joint. These two processes (*u* and *l h p*) conceal the joint in question, and lock the claw firmly to the carpus, upon which it is free to move in the horizontal plane through an arc of about 135°, but from which it can not be removed without breaking either segment.

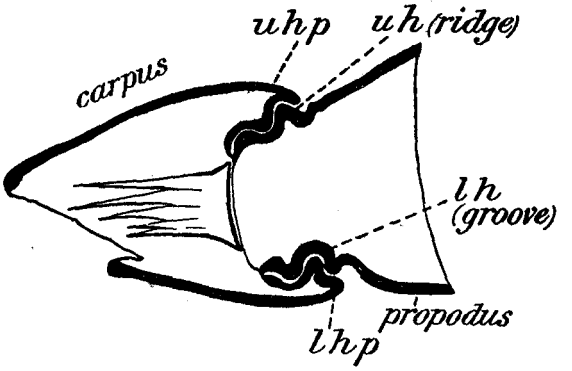


FIG. 4.—Locked sliding joint of big claw of lobster. Sectional view of left chela seen from side towards median plane of body, showing reversed grooves and ridges of upper and lower hinges. This locked joint is strengthened by the overgrowth of upper and lower hinge processes (*u h p* and *l h p*), which arise from the carpus.

When the hard shell is broken at this joint the upper hinge on the claw side is seen to consist of a prominent semicircular ridge, which fits into a corresponding carpal groove, but of greater length. Further, on the inner or proximal side of this groove rises a ridge of lesser arc, which runs in a corresponding groove under the curved ridge of the claw; in brief, circular ridge and groove of claw work on corresponding groove and ridge of fifth segment. To complete this adjustment there is an outgrowth from the hinge process of the carpus, which is outwardly curved, and runs in a corresponding groove distal to the articular ridge on the claw; this serves as an additional lock to the joint, but the proper articular surfaces are those described above. Turning now to the lower or originally anterior side of the claw, we find the conditions completely reversed, and instead of ridge groove we have groove ridge, with corresponding ridge groove on

[a] These terms are used for the successive segments of the limbs in reference to the median plane of the body. The dacty possesses proximal balls only.

the lower hinge process of the carpus. It follows from these relations that the articular surfaces of the carpus face, while those of the claw look in opposite directions.

This remarkable joint suggests the hinge of an ordinary folding pocket rule, but with a different locking device. It is neither a true pivot, tenon-and-groove, or ball-and-socket joint, and so far as I am aware its principle is not found embodied in any of the common mechanical devices. We find it well developed at the fourth stage, with little later change except in the further overgrowth of the hinge processes. (Fig. 9.) Such a joint works with great precision in its prescribed plane, with little or no appreciable lost motion, and would seem to be an adjustment by means of which the big claw is firmly secured to the supporting carpus, and the voluminous flexors of this segment can react upon the great weight of the claw to the best advantage.

In the crayfish (*Cambarus*) the big claw is not locked to the carpus, but moves loosely on double hinges of the typical ball-and-socket order, each hinge consisting of carpal ball, and propodal socket mounted on a round tubercle. In *Callinectes* and certain other Brachyura examined (text fig. 5) the great cheliped has suffered little or no torsion, and the dactyls open upward as in the larval lobster. The claws move on modified ball-and-socket hinges, which are firmly locked to the claw but in quite a different manner from that of the lobster. The propodus in this case bears cups (*l h* (socket) fig. 5) on both upper and lower sides, which are locked over the balls by processes (*u* and *l h p*) growing out from this segment and not from the carpus. The crab's claw thus swings vertically in and out through an angle of upwards of 90°.

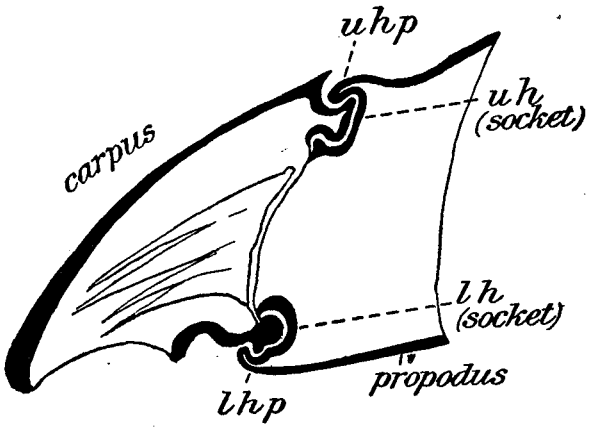


FIG. 5.—Locked sliding joint of big claw of crab (*Callinectes hastatus*); in same plane as represented in figure 3, showing modified balls and sockets, but with no reversal on upper and lower sides; hinge processes (*u* and *l h p*) here arise from the propodus of claw.

While the locked, sliding joint of the lobster, particularly in the reversal of its hinges, suggests the ordinary ball-and-socket device of the other limb segments, and even more that of the crab's chela, it would be difficult to decide whether one was better from a mechanical standpoint than the other, or to imagine how either could have arisen from the simpler type upon any principle of selection.

ASYMMETRY IN THE BIG CLAWS OF THE LOBSTER.

The marked dissimilarity of the big claws (pl. XXXVII) in regard to both their structure and chief functions in all lobsters above an inch or an inch and one-half long, has led to various distinctive names on both sides of the Atlantic. Fishermen often speak of the "knobbed" and "quick" claws. The larger is adapted for crushing the

food, and to emphasize the function, we shall call it the cracker, crusher, or crushing claw; the smaller and slenderer, which suggests a patent lock forceps with serrated jaws, is used for seizing, holding, piercing, tearing, and slashing the prey. We shall call it the lock forceps or toothed claw, in preference to the phrase "cutting claw" formerly used. In young animals from 2 to 5 inches long the teeth of this weapon are completely concealed by dense clusters of sensory hairs, which though seldom absent become less conspicuous with advancing age. It is therefore evident that the toothed claw is highly sensitive and "feels" the blows it gives as well as those it takes.

Przibram (*223*), who classifies the higher Crustacea according to the similarity or differentiation of the big claws into the "Homoiochelie," and the "Heterochelie," calls the larger claw the "Knoten" or "Knackschere," and the smaller the "Zähnchen" or "Zwickschere," in view of their form and function respectively. Stahr (*257*), who uses the terms "Zahnchenschere" (toothed claw), and "Knotenschere" (knobbed claw), as descriptive of their structure, after a discussion of their probable functions, says that he is justified in designating the claws of *Homarus gammarus* as follows, "the beautiful, regular, elegantly formed, thin-walled forceps, provided with periodic teeth and sensory hairs as the ornamental ("Schmuck-") and sensory claw ("Spürschere"), and the other, plump, oval, thick-walled form, provided with tubercles, as the crushing ("Knack-") and grasping claw ("Greifschere"). As will later appear, the development of these organs affords no warrant for regarding the toothed claw as an ornament, not to speak of the psychological difficulties involved.

TORSION OF THE LIMB.

Of greater interest than the difference in size and structure of the big claws is the complete change in their position on either side which takes place after birth, due to a twisting of the limb and mainly of the fifth joint or carpus or the third podomere reckoned from the distal end.

This curious torsion of the crustacean leg is of very ancient origin, dating from as early as the Cretaceous period, and is shared by many of the higher crustacea decapods (for first account of torsion and fuller discussion see *153*). It further affords a good illustration of how a very obvious fact may long escape the notice of naturalists, my own attention not having called to it until 1905, although drawings of the larval and adult stages had been repeatedly made.

In the adult lobster or crayfish the free dactyls of the smaller chelate legs all open upward and outward in a plane which is nearly vertical, while in the big claws the dactyls of opposite sides face and open inward or in a nearly horizontal plane. In the lobster at birth, on the other hand, and up to the fourth stage, all the chelæ have the same relative positions; all open vertically upward with an outward inclination. (Compare fig. 1, 6, and 7 with pl. XXVIII.)

It is thus evident that the position of the great forceps in an adult animal has been reversed through a rotation of either claw through an angle of 90°, toward the median plane of the body, in consequence of which their inner or anterior faces have become

their under sides. This rotation is completely effected at the fourth stage (pl. XXXI) and with the molt which registers so many other marked changes in the structure and habits of this animal. It is responsible for the torsion or twist to be clearly seen in the carpus of the limb. In conformity with this change in position, the claw has undergone a change in coloring, for the deep green chromogen pigments which cover the present upper surfaces are completely lacking from their pale red under sides.

It would appear in the highest degree improbable that this condition in the big claws could have been produced through the inheritance of slight variations leading to a greater and greater degree of torsion, and finally extending through so great an arc, although it is conceivable that such a variation may have been correlated with others which were of so favorable a character as to be of selective value and to have been "dragged" along with them.

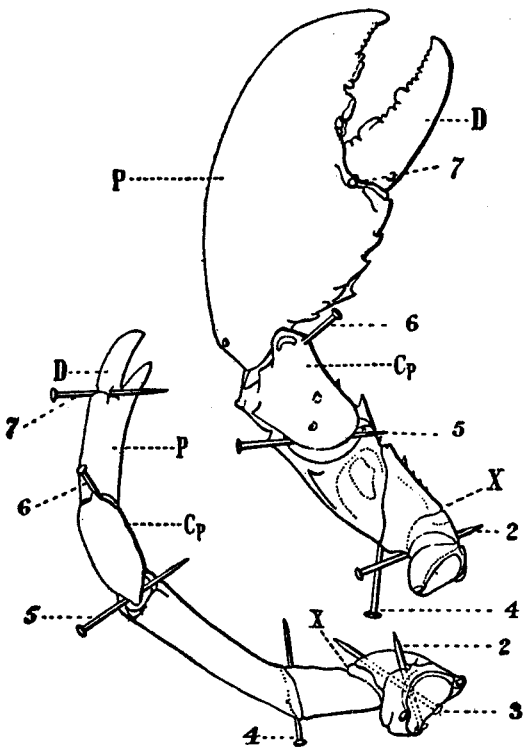


FIG. 6 and 7.—Great first and small left third claw feet of adult lobster with pins (no. 2–7) inserted in the axes of articulation of successive podomeres, to indicate normal torsion in the great cheliped. Position of the big claw up to the fourth stage is identical with that of the little claw of the slender leg. Compare plates XXVIII and XXXI, with figure 14 of text. Cp carpus; D, dactyl, and X, breaking joint. Podomeres or segments of permanent limb numbered, as in all succeeding figures, in Arabic numerals, from base to apex.

Again, it is even more difficult to regard this torsion of the crustacean limb as the resultant effect of use through inheritance. The carpal podomere has but one flexor and one extensor muscle, both of which react on the claw at points outside of the joint itself; at the same time the muscles, of course, pull on the shell of this part at their points of origin, but no conceivable position or strain of these fibers can convert the pull into a twist. If the increasing weight of the claws in the growing animal had any effect upon their ultimate position it should tend to turn them outward. In other words, their modification is just the reverse of what we should expect were the effects of strain or use inherited.

If we examine other crustaceans we find that the big claws open inward, upward, or outward, irrespective of their relative size or weight. In the Alphei, which usually have one claw of enormous size and of peculiar structure, the dactyls open outward, while in the fiddler crabs (*Gelasimus pugnax*) they incline inward, as in the lobster. This is true not only of the single huge claw of the male fiddler but of its diminutive fellow and of the small, almost rudimentary chela of the female. In the common crabs (*Carcinus*, *Callinectes*) the claws open obliquely outward. It therefore appears that in the rotation of the crustacean

limb we have an illustration of an adaptive variation, which in origin and the extent to which the process may be carried is independent of use and the mechanical strains to which the organ may be subjected.

Apart from their crushing or piercing teeth and sharp indurated tips, the large claws are armed along their facing edges by stout tooth-like spines, while the exposed surfaces and angles of the lower segments of the limb are similarly protected. These spines are generally directed forward and mostly upward and tend to guard the space about the head which the outstretched claws inclose (see, p. 273).

The terminal segments of the last pair of slender legs have undergone torsion but of a different character, as described in chapter IX, page 304.

BREAKING PLANE AND INTERLOCK.

We have seen that both of the large chelipeds have a stiff or breaking joint in the compound segment at their base, as well as peculiar hinges, which are not only adapted to the ordinary uses of such limbs, but possibly to the resources of the animal in sacrificing them for its own preservation. There has also been developed in relation to the breaking plane an interesting interlocking mechanism, which seems to have escaped notice up to the present, although its importance in the life of this animal would appear to be great.

This interlock (fig. 1, 3, and 4, pl. XXXVII) is a simple but effective adjustment by means of which it is impossible for an enemy to pull out or twist off one of the chelipeds, as may be done in a cooked lobster, without bringing autotomy into play, to which process it seems to form a sort of emergency "brake."

Turning the body of the lobster over and working the chelipeds by hand, we perceive that they move freely forward and backward, the striking or thrust movement, at the junction of coxa with basis. In such movements the lobster's most powerful blows are dealt, whether in attack or defense. We observe further that any lateral movement of this joint would be serious, and that is guarded against by huge interlocking spurs (s^1, s^3) on the first and third podomeres respectively. This condition seems to be related to the fact that the breaking joint (x) lies between these points, or peripheral to a free joint, so that when the strain upon this articulation and the interlocking spurs is too great or, in other words, sufficient, the limb is reflexly cast off in the breaking plane.

This mechanism, moreover, together with the complete fusion of the joint, is not developed until after the fourth stage, when there is probably less need of strengthening the hinges between these particular segments. Yet autotomy occurs at this stage, and we find the hinges strengthened in a degree by the interlock of distinct but different spines (fig. 8–10, s^4, and s^2), although this early adjustment is not quite so marked as in the adult animal. At all events in the lobsterling there is an interlock between the second and third podomeres, which evidently increases the resistance of the limb at its base during this period. These spurs of the fourth stage lobster become later reduced to rudiments, and new interlocking processes are developed in the adult animal

between the first and third segments. The principal spur at the fourth stage (fig. 8, s^2) is still to be seen in its rudimentary state in the adult lobster immediately in front of the large functional spurs already described. (Pl. XXXVII, fig. 1, s^2 *rud.*)

THE TOOTHED CLAW OR LOCK FORCEPS AND ITS PERIODIC TEETH.

If the armature of the smaller claw is closely examined, the teeth or spines are seen to be arranged in periodic sequence, a fact first noticed by the German naturalist, Stahr (*257*). Stahr's description is correct, so far as it goes, but we can not adopt his remarkable conclusions that this should be called the "ornamental" or "beauty claw," and that the æsthetic sense of this self-admiring crustacean is aroused as its eye wanders over the dentate margin of its "hand." We should fail, however, to do justice to the imagination of this writer without quoting directly from his work, in which he concludes "That it is not a far-fetched idea to recognize in the periodic teeth or rows of points of the ornamental and sensory forceps an embellishment—an architectural and artistic ornament. We may mention their close relation to music, poetry, and dancing, where we have to do with rhythm, time, measure, composition, everywhere with periodic sequences. * * * Thus it is only natural to suppose that the beauty sense of a crustacean would receive an agreeable impression as its eye wanders over the periodic points of its claw." [a]

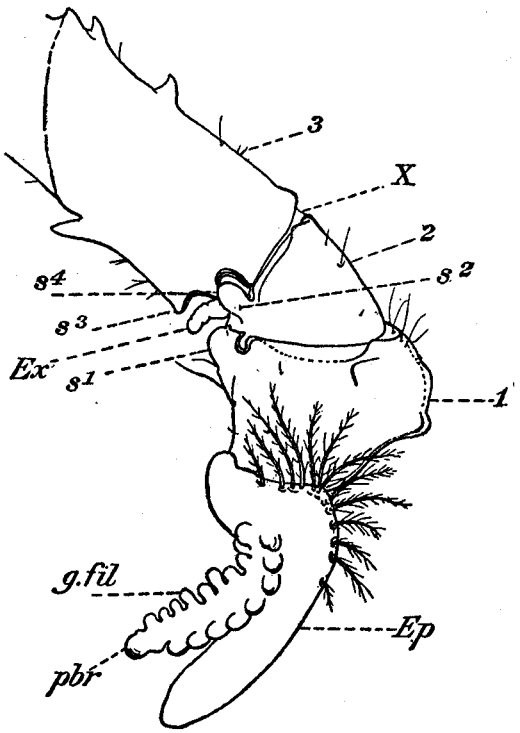


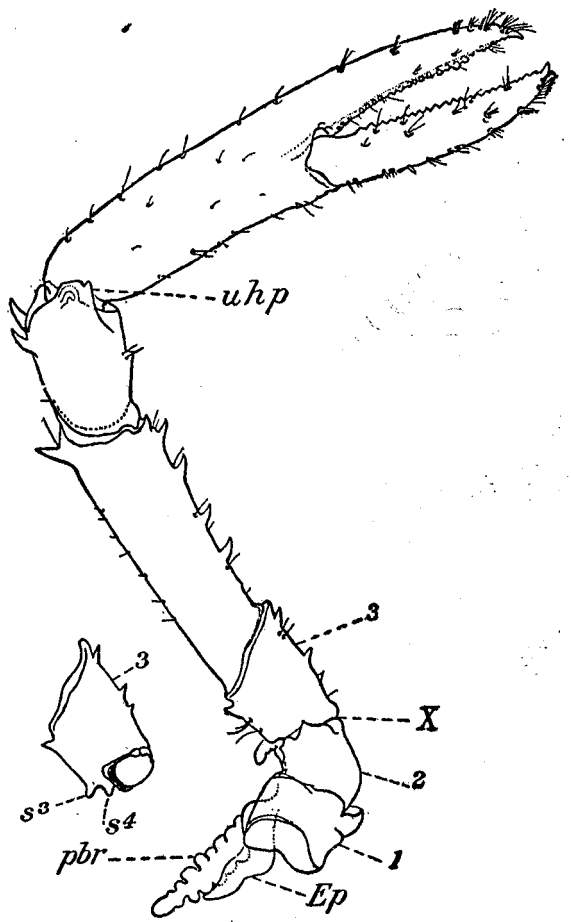
FIG. 8.—Base of right great cheliped of fourth stage lobster from below, showing future breaking joint free at surface, before complete fusion has occurred, a temporary interlock at this stage by spurs (s^2 and s^4) of the second and third podomeres, as well as rudiments of the spurs (s^3 and s^1) of the first and third segments, which form the permanent interlock of the adult limb. Compare with figure 13. Swimming branch or exopodite (*Ex*) functional up to this stage is reduced to a rudiment. Gill filaments (*g. fil*) are developed as secondary outgrowths of the primary filament, which is a fold of the body wall.

We have worked out the history of development of both types of claw, in the light of which their peculiar structure becomes more intelligible. The arrangement of the teeth or spines on the smaller claw may be expressed by a diagram (fig. 11), in which they appear as a linear series, made up typically of periods of eight. In respect to size and age, or order of development, the eight teeth of each period are symmetrically distributed and fall into four orders or series, of which the first and second contain one each, the third two, and the fourth four. On this basis the formula for each perfect period or sequence would

[a] All quotations from foreign languages in this work are freely rendered into English.

be: $1+1+2+4=8$, or, designating each spine by its serial number as in table 6, $1:4:3:4:2:4:3:4=8$.

About midway on the dentate margin of the "hand" (fig. 12 and 13) or propodus one finds a stout spur which I shall call the "lock spine" (*L* in all the figures). As we shall see, it is really a displaced spine of the first order. It fits into a shallow groove of the dactyl, which is often slight or wanting, and forms the lock of the claw. Upon closing, the dactyl falls on this spur, and, its teeth sliding under those of the opposed jaw, it is firmly locked in this position, so that no lateral motion is possible. (Fig. 1, pl. XXXVI.) To complete this adjustment, the tips of the forceps are bent like the mandibles of a crossbill, the dactyl underlapping. The spines of the propodus are bent upward, those of the dactyl downward so that in the claws of some individuals they make an angle of 45° with the lock spine, which is nearly vertical. Moreover, the spines are aligned very accurately, and in a peculiar manner. The spines of the "upper jaw" or propodus are all tangent to a line traversing its lower border, while those of the dactyl or underlapping jaw meet a line drawn along its upper margin. This reversal of the alignment it will be observed makes it possible completely to close and at the same time to lock fast the jaws of an instrument having this structure. It follows that the teeth do not interlock but overlap (fig. 12 and 29).



FIGS. 9 and 10.—Right great cheliped of fourth stage lobster, from above, showing upper hinge process (*u h p*) of carpus, and disarticulated ischium with interlocking process (s^4), and future interlocking spur (s^3), which is rudimentary. Compare text figure 8, and plate XXXIV, figures 1, 3, and 4.

The tendency of the spines to increase in geometrical ratio is often present and if effective would in the next progression give a period of 16 spines. Under these conditions the periods are generally incomplete, seldom yielding over 13 spines.

The formula given above seldom holds good for more than two or three periods, and in many claws no period is quite perfect. At both proximal and distal ends of the series the periods become irregular and the identity of the spines is lost. Some means

of identifying the principal periods, however, is necessary, if we are to follow the course of development and the changes which attend the molt. Fortunately two guideposts are always present at either end of the series, the lock spine (fig. 12 *L*) and a distal spur or tubercle on the lower side of the propodus near its tip (*Sp.*) For convenience of description we assume, then, that the first period lies proximal to the spur, and that the "lock" spine is the primary member of a hypothetical fifth period. Between these boundaries lie three, four, or exceptionally five, periods, of which the fourth is rarely perfect. This leaves three or at most four periods (numbered in all the figures I–IV) for special consideration.

Counting the tip of the claw as a primary spine (though it really is not, since it develops as a seta), we should have from five to seven periods between it and the lock

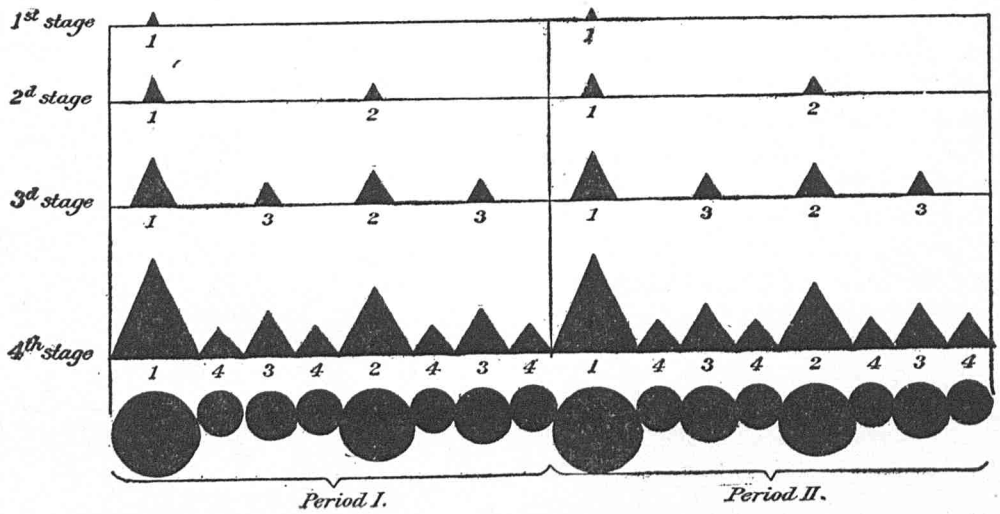


FIG. 11.—Diagram to show the serial arrangement of the spines in the toothed forceps of the lobster in periods of 8, and the development of these spines by interpolation from the first to the fourth stages. Arabic numerals indicate orders of teeth (here reading from left to right).

spine. Proximal to the lock spine, the linear series is completed by from three to five primary teeth, with small secondary spines among them, which like similar spines elsewhere are a fluctuating quantity. Consequently in the propodus there are from 8 to 12 primary spines which represent periods, of which never more than 3 or 4 are complete, or in eights. (Compare fig. 29.)

In order to set these relations in clearer light as well as to illustrate individual variation I append a table of formulæ for the teeth in the large segment of the toothed claw of 10 lobsters taken at random (table 6), and of the teeth before and after the molt in the claw of an adolescent (no. 11*a*, 11*b*, stages VII and VIII) and an adult animal (no. 12*a* and 12*b*).

TABLE 6.—SEQUENCE OF SPINES IN PERIODS I–IV OF TOOTHED CLAWS OF ADULT, AND IN PERIODS I–III OF MOLTING ADULT AND ADOLESCENT LOBSTERS.

No.	Period I.	Period II.	Period III.	Period IV.	Summation of periods.
1a	1 5 4 5 3 5 4 5 2 5 4 5 3 5 4 5	1 5 4 5 3 5 4 5 2 5 4 5 3 5 4 5	1 5 4 5 3 5 4 5 2 5 4 5 3 5 4 5	1 5 4 5 3 5 4 5 2 5 4 5 3 5 4 5	16+16+16+16=64
2a	1 4 3 4 2 4 3 4	1 4 3 4 2 4 3 4	1 4 3 4 2 4 3 4	1 4 3 4 2 4 3 4	8+8+8+8=32
1	1 4 3 4 5 2 4 3 4 5	1 5 4 3 4 2 4 5	1 4 3 4 3 4	1 4 3	10+10+8+3=31
2	1 4 3 4 2 4 3 4 5	1 4 3 4 5 2 5 4 5	1 5 4 3 4 2 4	1 4 3 4 3 4	9+11+9+8=37
3	1 4 3 4 5 2 4 3 4 5	1 5 4 5 3 4 5 2 5 4	1 5 4 3 4 3 4	1 4	10+12+10+2=34
4	1 4 3 4 2 5 4 3 4	1 4 3 5 4 2 4 3 4	1 5 4 3 4 2 4	1 4 3 4 2 4 3 4	9+9+9+8=35
5	1 4 3 4 2 5 4 3 4	1 5 4 3 4 2 4	1 5 4 3 4 2 4	1 5 4 3 4 2 4 3 5 4	9+9+10+10=38
6	1 4 3 4 2 4 3 4	1 5 4 3 4 5 2 5 4 5	1 4 3 4 2 4	1 4 3 4 2 3 4	8+11+8+7=34
7	1 4 3 4 2 4 3 4	1 4 3 4 2 4 3 4	1 5 4 3 4 2 4 3	1 5 4 3 4 2 4 3	6+7+7+8=28
8	1 4 3 4 2 4 3 4 5	1 4 3 4 2 4 3 4	1 6 5 4 3 4 2 4 3 4	1 5 4 3 4 5 2 4 3 4	7+8+10+10=35
9	1 4 3 4 2 4 3 4	1 4 3 4 2 4 3 4 5	1 4 3 4 2 4 3	1 5 4	5+9+7+2=23
10	1 4 3 4 2 5 4 3 4	1 4 3 4 2 4 3 4	1 4 3 4 2 3	1 3 4	9+6+6+3=24
11a (VII)	1 4 3 4 2 4 3 4 5	1 5 4 3 4 2 4 3 4	1 5 4 3 4 2 4 3		8+11+8
11b (VIII)	1 4 3 4 2 4 3 4	1 4 3 4 5 2 4 3 4 5	1 6 5 4 5 3 4 2 4 3 4		8+10+11
12a	1 4 3 4 2 4 3 4 5	1 5 4 3 4 5 2 5 4 5	1 4 3 2 4 3		8+10+6
12b	1 4 3 4 2 4 3 4 5	1 5 4 3 4 2 5 4 5 3 4 5	1 4 3 4 5 2 4 3		9+12+8

It will be observed that four periods usually occur between the spur and lock spines; that in ten individuals only seven regular 8-tooth sequences occur; in one there are two, and in four cases none. The disturbances arise from the interpolation of exceedingly small spines, or the tendency to advance to the next progression, which if complete would give 16 spines to the period. The largest number of spines to the single period given in the table is 12, but I have seen a case in which the third period contained 15 spines.

A fairly regular claw of large size is represented in profile and horizontal projection in figures 12 and 13, the formula of which for the four principal periods is 31 (table 6, no. 1), only one of the sequences being in eights, and the spines of the entire armature totaling 48.

The serration of the dactyl of the toothed claw is more regular than that of the propodus and similar except for the disturbance introduced by the "lock spine" of the latter. Three or four 8-tooth periods usually occur and the sequences are often perfect.

The toothed claw, as already remarked, is richly supplied with tufts of sensory hairs above and below the line of teeth and also along the margin of the claw near its tip. These are specially abundant on the underside, and with them the animal is constantly feeling the bottom when it assumes the common alert attitude with the tips of the claws bent down. These tactile setæ are arranged in bundles of 200 to 300 or more short, stiff bristles which, like little scrubbing brushes, project from depressions in the shell. The floor of each depression is a sieve plate, the perforations of which correspond to the number of setæ as well as to the number of nerve fibers supplying the bundle. In the adolescent stage, when the lobster has attained a length of 3 or 4 inches, the setæ of the lock forceps become large matted tufts which sometimes completely conceal the teeth. (Compare fig. 15 and 16).

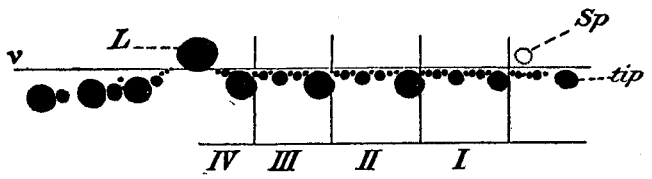


FIG. 12.—Projection of serial teeth in segment of big claw of large adult lobster represented in figure 13, showing alignment to lower or ventral (*v*), originally the anterior, side, the position of the *tip*, spur (*Sp*), and the large displaced lock spine (*L*), the two last serving as guide posts for identification of the periods i-iv. In this and following figures the periods are enumerated from the distal to the proximal end of the claw.

THE CRACKER OR CRUSHING CLAW.

In place of tooth-like spines the great crushing claw presents a number of rounded tubercles, both large and small, single or double, and arranged in a characteristic manner (fig. 2 and 3, pl. XLIII). These crushing tubercles are very dense, and in old hard-shell

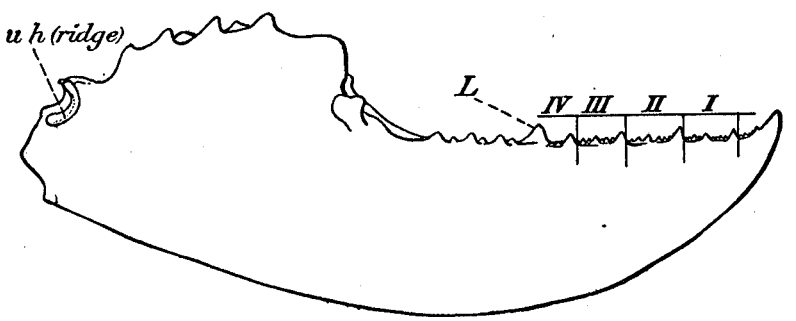


FIG. 13.—Large segment of right toothed claw from above, to show the periodic teeth; compare projection in figure 12; *u h* (*ridge*), upper ridge of sliding lock joint.

lobsters the pigment and enamel is completely worn away from long and rough usage. The tips overlap slightly, but the dactyl is curved, and not straight as in the toothed claw, consequently when closed there is often a wide gap between the jaws, the tubercles touching at but one or two points only. (Fig. 2, pl. XXXVII.)

The crushing claw, as shown in the drawing (pl. XL), has a far more powerful musculature than its fellow, and is accordingly richer in its supply of blood vessels and nerves. Two tendons (fig. 2, pl. XLI) spring from opposite sides of the proximal end of the free

dactyl and afford a surface for the attachment of the huge flexor and smaller extensor muscles. Each tendon is a keeled plate which is developed in a flattened pocket of the skin, but the closing muscle of the great claw being the largest and the strongest in the body requires the largest tendons. The tendon of the flexor (*t. fl.*[6]) is a broad leaf-shaped plate, keeled above and below, while that of the weaker opening muscle is narrow and strap-shaped.

At the time of molt these huge tendons, like all others in the body, are drawn out, attached to the cast-off shell, and leave deep open pockets into which in a large animal the little finger can be easily inserted. As soon, however, as the soft claw becomes tense with blood, the water is driven out and, the opposed surfaces of the pocket uniting, a new tendon is gradually formed. (Compare fig. 1, *t p*, pl. XLIII.)

The coarser flesh of the claws represents, as we have indicated, the characteristic flexor and extensor muscles, while the "fine meat" of the dactyl (fig. 3, pl. XLVI) and distal half of the propodus is composed of a sponge work of involuntary muscle fibers in addition to fine-blood vessels of the arterial system, nerves, glands, and connective tissue, the whole being enveloped by the soft pigmented skin (pl. XL). No special sense organs, aside from the setæ, have been detected in it. The meshes of the sponge work form a system of communicating sinuses into which the arteries appear to open through very small branches or capillaries.

During the molting process, when the fleshy mass of the claw is drawn through a series of narrow rings as if it were a piece of candy, the blood is of necessity withdrawn from these parts. The sponge work is an adjustment which meets this prime need of the molting period. At the time of molt the muscles are extremely tense and the flesh hard, and the contraction of the fibrous sponge work apparently keeps back the flow of blood until the animal escapes from its old shell, when it again becomes completely relaxed (see p. 206).

The abundant blood always found in the large claws, except when molting, is supplied by a large artery, which at the point of entry from the fifth segment divides into an inner and a smaller outer branch. The inner division passes between the two muscles, and gives off small twigs in its course; then as it curves outward over the distal end of the flexor muscle, it sends off somewhat irregularly a branch to the upper and lower division of each muscle, and to upper and lower parts of dactyl and propodus.

The nerves of the great cheliped (pl. XL) consist of two main bundles (n^1 and n^2), made up of a number of closely related strands. In the basal segments of the limb the larger and more complex bundle (n^2) is anterior while the smaller bundle (n^1), which is double, follows it closely on its posterior or outer side.

The nerves usually enter the claw in three closely related strands, one of which supplies chiefly the extensor, one the dactyl and flexor, while the outermost branch is distributed to the flexor and large "finger" of the claw. Both arteries and nerves regularly divide and subdivide in the terminal parts of the claw to form a very complicated system.

DEVELOPMENT OF THE GREAT FORCEPS.

How has the differentiation of the great claws been brought about? It is easy to follow the history of their development molt by molt from the first larval stage onward. This history clearly shows that the toothed claw represents an original or an older type, and that the crusher claw was later developed by a modification of this primitive pattern.

In the first larval stage of the lobster the future big claw (fig. 14) is distinctly of the embryonic type, relatively short and thick, and armed with few tactile bristles, its tips being drawn out, as it were, into long sharp-pointed spines. The dactyl, which bears the longer and straighter spine, is larger than the undeveloped index. This inequality is much more marked in the smaller chelipeds, where the index appears as a bud-like outgrowth, setate and bearing one or more stiff, barbed, or serrated bristles (fig. 2).

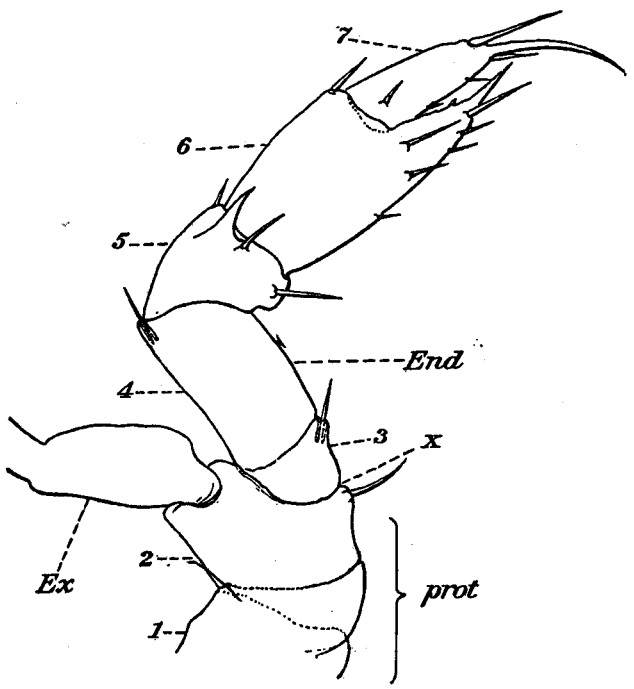


FIG. 14.—Left great claw-foot of first larva of the lobster, from above, showing outwardly opening dactyl, before any torsion of the limb has occurred, the short ischium (3), with free joint at future breaking plane (x), and base of swimming branch (*Ex*). Compare with text figures 6 and 9.

In the second and third larvæ (fig. 41 and 42) the claws become broader and more voluminous, while their spinous tips are reduced and both index and dactyl are curved.

In the fourth stage (fig. 9 and pl. XXXI) the great chelipeds suddenly become very conspicuous, bearing long slender forceps which now for the first time serve as organs of prehension with marked success. The jaws of the forceps are slender, dentate, and tufted with tactile hairs. The condition of symmetry, with this general structure, on right and left sides, continues through the fifth and in some cases up to the seventh or eighth stage, when the first traces of asymmetry begin to appear, though not necessarily apparent to the naked eye. (Fig. 15 and 16.) By the ninth stage, when a total length of about one and one-quarter inches has been reached, the differentiation of the crusher claw is easily recognizable, but the changes registered at each molt are slight. In the account which follows we shall consider in more detail the beginnings of asymmetry and the development of the teeth and tubercles which characterize the two types of big claw in the adult animal.

In the fourth stage the great claws are not only symmetrical, but of the toothed type. According to Emmel (*96*) the transition to the asymmetrical condition begins in the sixth stage, but in the material studied as a basis for this account it was impossible to detect any morphological differences until the seventh or succeeding stage. There is doubtless some variation in this respect. It is true that at preceding periods the big claws may differ in size or slightly in form as a consequence of molting or regeneration, but without implying the differentiation in question. Again at the seventh stage these

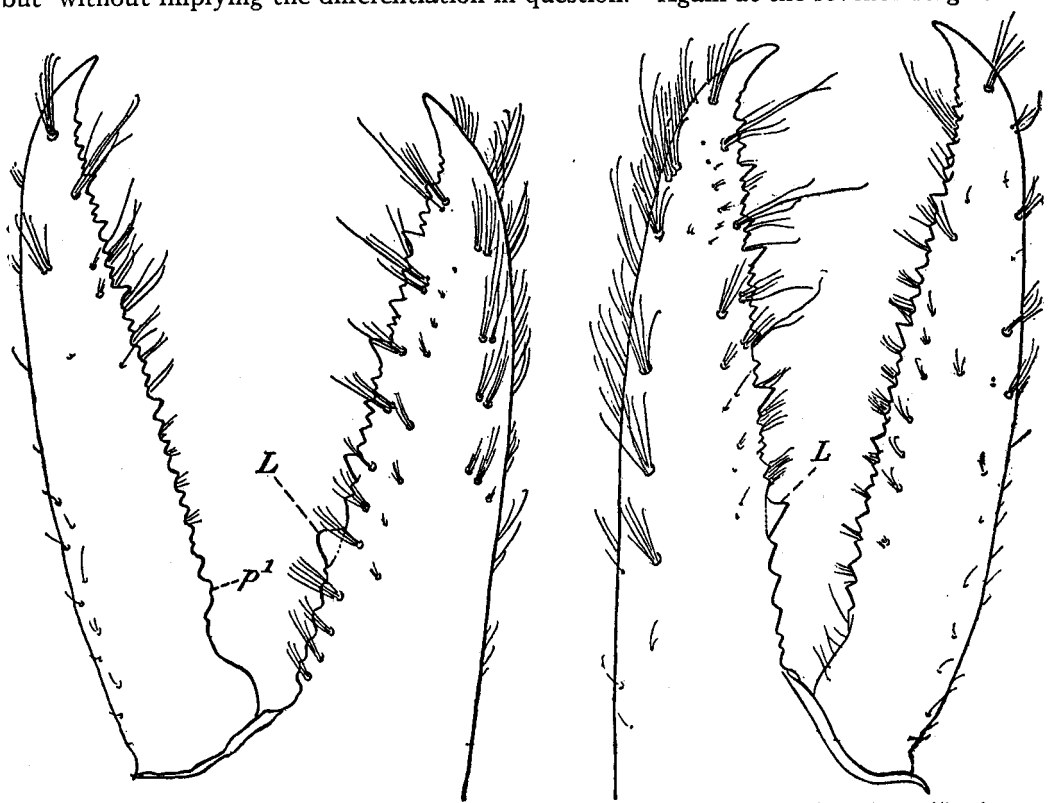


FIG. 15 and 16.—Left and right future toothed and crusher claws of lobster in eighth stage, seen from above. The claws are of equal length, and the differentiation of the crusher is not apparent to the naked eye. Compare with figures 21 and 22. *L*, lock spine; *p*, compound proximal tubercle of crusher claw. Enlarged about 34 times.

claws may appear to the naked eye essentially alike in form and size. Thus, to give a concrete example, a lobster in the eighth stage, measuring 19.75 milimeters, September 22, showed a rather striking similarity in the forceps, the dimensions of which were as follows:

	Millimeters.
Right claw (future crusher):	
Length	7
Breadth	1.7
Left claw (future toothed forceps):	
Length	7
Breadth	1.4

When these claws are magnified thirty or forty times (fig. 15 and 16) the first steps in the differentiation of the crushing from the primitive toothed type of claw become evident. They are expressed by a blunting or rounding off of the sharp points of the teeth, and a tendency to fusion among those situated at the proximal extremity of both divisions of the claw. (Compare fig. 21–24.)

We therefore conclude that during the fourth, fifth, and in some cases at least in the sixth or even seventh stages of the lobster, both of the big claws represent the older or phylogenetic type which is retained as the toothed or lock forceps of the adult. The chela destined to become the crusher is a little broader though not necessarily longer than its fellow, and its teeth which still show the periodic sequence are more rounded, as we have just seen, at the proximal end of the series. The tufts of sensory hairs are, moreover, less prominent on the future crushing claw, as apparent in all the later stages.

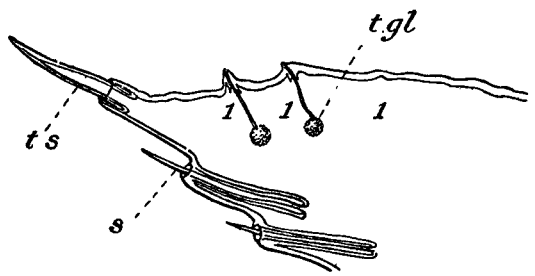


FIG. 17.—Outline of great claw tip, showing serrate margin of propodus, in first larval stage of the lobster, represented as a transparent object, from glycerine preparation. Note the invaginated sensory hairs or setæ (*s*), and claw-tip (*t s*), and three teeth of the first order (1, 1, 1) developing from apex to base, and representing the three primary periods (I, II, III), indicated in figures 11 and 18; also a tegumental gland opening at the tip of each of the two oldest spines.

The development of the toothed type of claw is represented by a series of drawings (fig. 17–25, and pl. XLII) from the first to the ninth or tenth stages, in which the orderly appearance of the spines can be followed with approximate accuracy up to stage 3, and with certainty beyond it. The large propodus only is represented in most of the figures.

The spines of the toothed claws are developed in a linear series, and the order in respect to size corresponds to that of age, or time of appearance. The larger teeth of the first order are the first to emerge. They are set at wide intervals and evenly spaced. From 2 to 3 are recognized in the chelæ of the first larva (fig. 17) and from 3 to 5 in the claw of the second stage (fig. 18). In the third stage the normal number of primary teeth are present (fig. 19), although some of them are very small, and in the intervals between them are interpolated rudiments of the teeth of the second order. In a single series the first trace of the third series of teeth may be detected also. At the fourth molt (fig. 20) a single period of eight may be completed by the intercalation of the four small teeth of the fourth order; but the process does not always stop here, and an attempt, so to speak, is often made at the seventh, eighth, or at some subsequent molt to introduce a fifth series of 8 teeth, which if completely

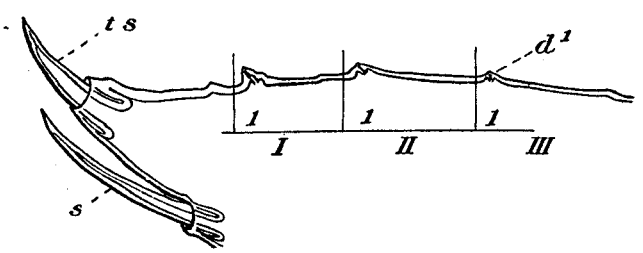


FIG. 18.—Outline of corresponding part of big claw shown in figure 17, but in second larval stage, showing the separated primary teeth, invaginated claw-tip, and setæ, as well as a new spine arising at either end of the series. Spine 1 of period III now bears the duct of a gland. See figure 11.

successful would increase the serial number to 16. A few cases are noted of the introduction of a tooth of the sixth series (table 6, no. 8, 11*b*). The process of interpolation is illustrated in the diagram (fig. 11) up to the usual 8-period stage, which is commonly attained at the fourth or fifth molt.

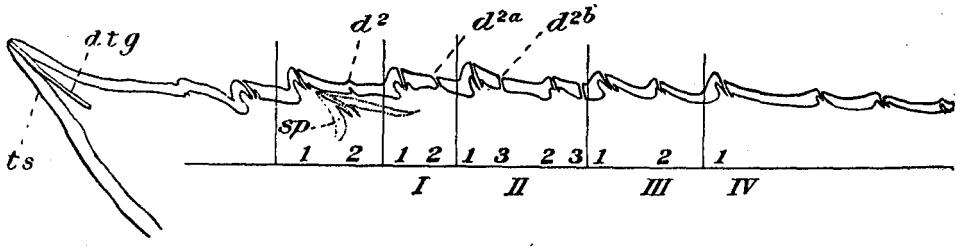


FIG. 19.—Outline of corresponding part of great claw shown in figures 17 and 18, but at third larval stage, showing spines of the second order, sometimes preceded by ducts of glands (*d 2a*, and *d 2b*), interpolated between those of the first, also spur (*sp*) and tip of claw (*t s*), both of which arise like the setæ, and like the teeth are provided with glands, the ducts (*d t g*) of which open at their summits. Compare figure 11.

The first teeth to appear apparently occupy the same plane, but at the seventh stage, or even before this, the alignment is similar to that of the adult claw, and the future "lock spine" or tooth (*L* in all the figures) is readily distinguished by its form and position.

It is interesting to notice that in all the early larval stages and up to at least the fifth or sixth molt, each serial tooth is regularly pierced by the canal of a single tegu-

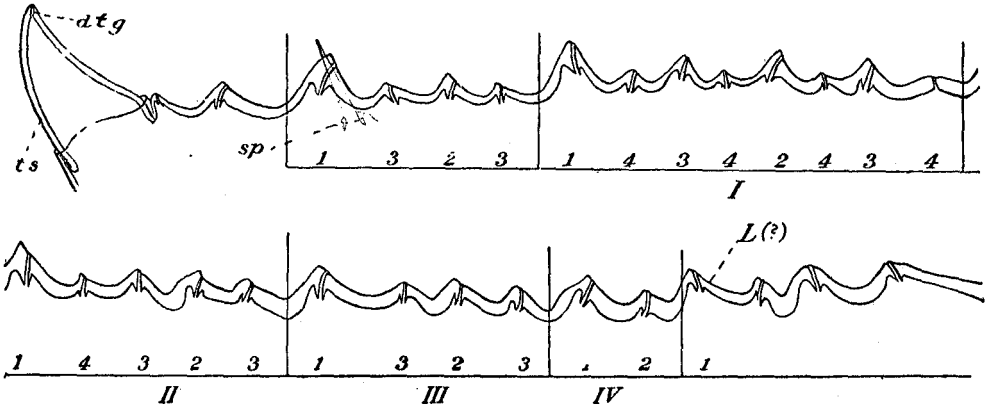


FIG. 20.—Outline of corresponding part of big claw represented in figures 17 to 19, but at fourth stage, showing spines of the third and fourth orders, and the establishment of a single period of 8, though the identity of the periods in this case can not be exactly defined. Invaginated claw tip still bears duct of gland (*d t g*), and the spur (*sp*) is still invaginated like a hair.

mental gland (fig. 17–20), which opens on its proximal side and just below the summit. In some cases the opening of the duct precedes the spine and marks its future position exactly (fig. 19 d^2 *b*). While the serial spines are always developed as outgrowths of the skin, the tips of the claw (fig. 17–20, *t. s.*) and peculiar tubercle or spur (*sp.* in all figures) originate like ordinary hairs, and like them are always invaginated previous to

molting.[a] It is to be further noted that as early as the third larval stage and for some time thereafter the claw-tip, like the tooth, gives passage to the duct of a gland (*d. t. g.*, fig. 19–20). I have not found glands of this type in the spines of the adult claw, and if present in older adolescent lobsters they are successfully concealed by the opacity of the shell. The adult spines were sectioned, but in all the young stages glycerine preparations were relied upon. A single tooth sometimes bears the ducts of three independent glands, in which case it is probably compound, resulting from the fusion of a corresponding number of teeth. Rarely a bifurcated duct is seen (fig. 2 pl. XLII), each

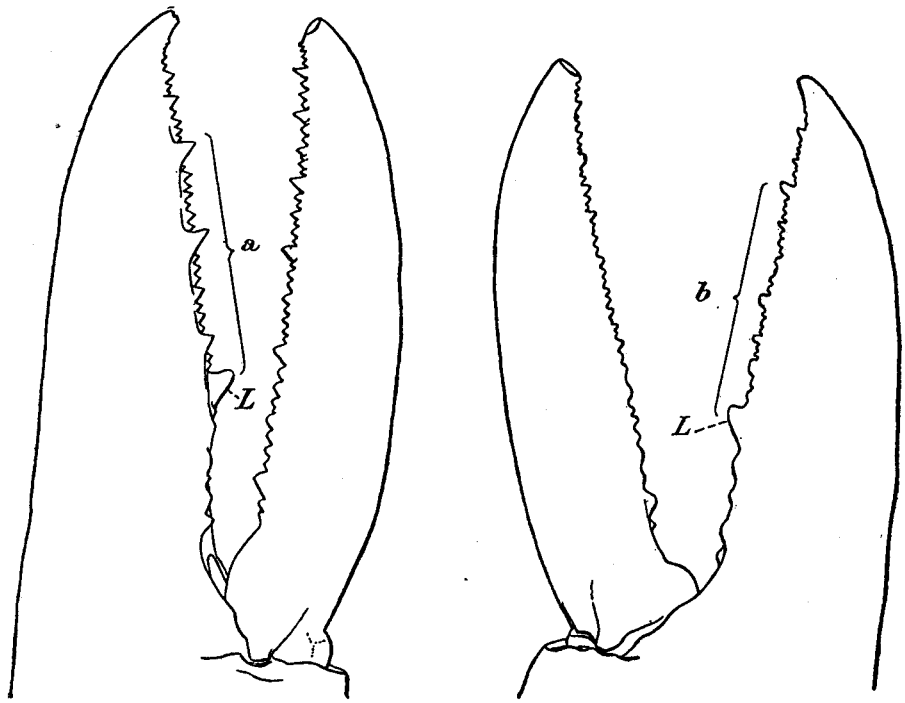


FIG. 21 and 22.—Right and left forceps of lobster 24 mm. long, reared in captivity, and 11 months old, in eighth or ninth stage; seen from above, showing early state in the differentiation of cracker (right) and toothed claws. Enlarged about 40 times. *L*, lock spine, as in all figures.

tube issuing from a separate gland, but with common opening at the summit of tooth. Whether these organs possess any special significance in these parts or not I am unable to say.

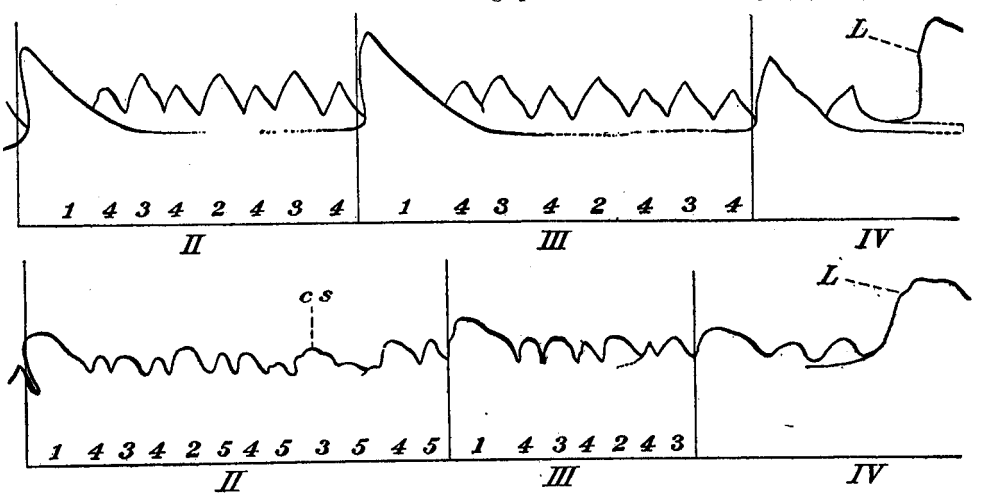
The first step in the differentiation of the cracker claw, as already remarked, is seen in the rounding or blunting of the teeth, particularly at the proximal end of the series (see fig. 22 and 24, and especially fig. 25). The teeth appear to be retarded in growth, and while these remain blunt and irregular, those of the toothed claw become

[a] The sensory hairs, as already stated, are derived solely from the epidermis, no mesoblast ever entering them, and they are invaginated with every molt. The claw teeth are tubular outgrowths of the wall of the appendage, and are never invaginated. The rostrum, as well as at least the tips and terminal spur or tubercle of the propodus, are seen to arise like the setæ, and like them are invaginated during the early molting periods, but they are eventually entered by mesoblast.

even sharper than before and retain their periodic character. The spines of the lock forceps are also noticeably larger for a time at least. Then follows a characteristic process of concentration and fusion in the spines of the future crusher claw (fig. 24, *c. s.*, and fig. 25, *d.*), which eventually leads to the reduction of their number. The crushing tubercle is thus formed by the fusion of a greater or lesser number of spines, like those of the toothed claw in the fourth to sixth stages.

In the light of this process are to be explained the "transition forms" which Przibram found to arise in the course of regeneration of the crusher claw, showing the knobs as fusing masses of teeth. The occurrence of such transitional stages has also been mentioned by Stahr and Emmel.

In the adult cracker claw (pl. XLIII, fig. 2 and 3) the propodus bears two large and six or more smaller tubercles. The big proximal tubercle (*p* (*L*), fig. 25) repre-



FIGS. 23 and 24.—Serrate margins of claws shown in figures 21 and 22, in regions marked a and b, and corresponding to periods ii-iv. Two perfect periods of eight sharp spines appear in the future lock forceps, and interpolations with fusions of teeth (*c s*) in the future crusher.

sents mainly the lock spine of the toothed claw, with the addition of lesser elements, while the great distal tubercle (*d.*) is composed of a fused mass of upward of thirteen spines, embracing the whole of the third and a part of the second periods. The dactyl of the crusher also possesses two tubercles of greater size, which close over the intervals between the "molars" of the propodus, besides a dozen or more small ones, resulting in each case from the fusion of several spines. There is also a small rounded tubercle on this segment at its proximal end and below the serial line.

The final differentiations established between the great crusher and lock forceps are illustrated by a perfect set of typical claws from a hard-shelled lobster which must have weighed approximately 12 pounds. In all measurements excepting length this crusher greatly exceeds its fellow, being one-third broader, weighing twice as much (in the dry shell), and having more than double the cubic capacity. In animals of adult size the slenderer claw has often a slight advantage in length over the more powerful

cracker, as in this case, and in giants the difference is sometimes striking. The dry shell of this crusher is so dense and strong that it will bear the weight of a man of average size without giving way. The measurements of these claws are as follows:

Crushing claw:		
Length propodus	inches..	8½
Greatest breadth	do....	4 9/16
Greatest girth	do....	11⅛
Contents	cubic centimeters..	680
Weight of shell (8¼ oz.)	grams..	235
Toothed forceps:		
Length propodus	inches..	8⅝
Greatest breadth	do....	3½
Greatest girth	do....	8 1/16
Contents	cubic centimeters..	320
Weight of shell (4⅛ oz.)	grams..	116

The armature of this cracker claw (fig. 2 and 3, pl. XLIII) is typical and does not essentially differ from that found in giant lobsters weighing upward of 25 pounds.

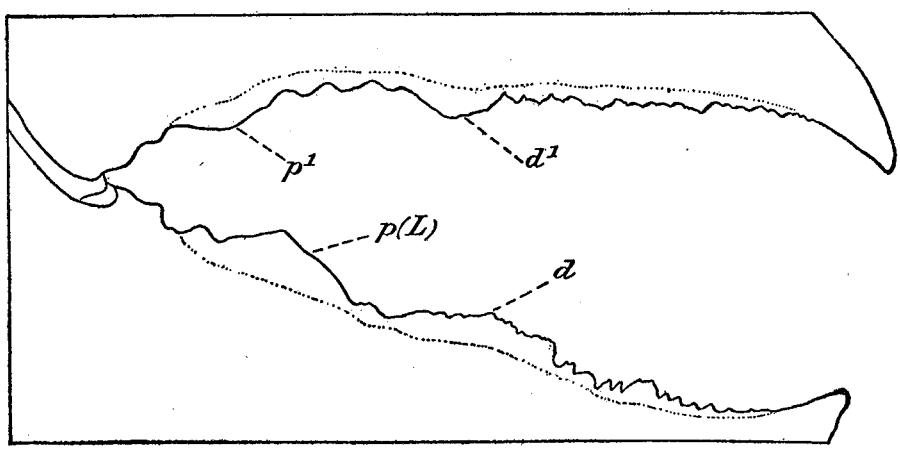


FIG. 25.—Armature of right crusher of female lobster 35 mm. long, and at approximately the tenth stage, showing origin of "molars" by fusion of spines. The proximal tubercle of the propodus (p (L)) is derived from the lock spine, while the distal (d) is composed of a fused mass of over a dozen teeth, embracing the whole of period II, and part of III. Length of claw 14.5 mm.

As in their case also the blunted end of the dactyl meets the big distal "molar" of the propodus, which, in the Belfast lobster, is worn flat and is 1¾ inches long by 1¼ inches broad. The dactyl in the slenderer claw is considerably longer, and as noticed above in mammoth lobsters the toothed forceps tends to surpass the crusher in length.

Since writing the preceding paragraph I have had the opportunity of reexamining the New Jersey lobster, which holds the record for size and weight (see no. 9, table 1), and find that the great claws which here reach the extreme known development of such organs, conform to the types already described and to conditions met with in mam-

moth lobsters generally. The cracker claw of this giant is remarkable for its swollen ovoidal form, its girth being 20½ inches, and for its worn and blunted tips; the blunt end of the "hand" is even recessive, the tubercular margin being convex as is frequently noticed in very large animals, and this in spite of the fact that the big molars are worn nearly flat. The worn-off end of the dactyl strikes about midway on the big distal tubercle, while the arrangement of the tubercles themselves is typical and essentially that given above; the propodus showing only two big "crushers," with one small intermediate and two paired or double proximal tubercles.

In the lock forceps of this specimen the hooked points are broken, rasped, and worn down, while its serrated margins are slightly convex, as is often the case in the fourth or fifth stage. The dactyl of this claw presents 7 to 8 primary spines. The huge, pyramidal lock spine of the propodus is much worn, and the first period distal to this bears 10 spines, having the formula: $1+1+2+4+2=10$. Then follows a long and probably compound period of 17 spines; then a primary spine and several smaller ones opposite the "spur." Thus, in this huge claw from lock to spur there are only three or at most four periods represented, as in all the younger stages hitherto discussed. This again illustrates the fact that while the procession of spines is constantly "on the move," the "dental formulæ" for the toothed claw never being identical for any two successive molts, the losses are so well balanced by the gains that the toothed claw, which attains its characteristic form from the fourth to the seventh molt, remains essentially unchanged throughout life.

We have seen how the toothed type of claw, which Stahr considers an ornament fitted to please the "æsthetic sense" of these animals, has arisen, but the wonder is not that the teeth are arranged in periods of eight, but that they are developed in order at all. The problem is similar to that of the orderly arrangement and appearance of the paired mesentaries of certain coral polyps, and fundamentally the same as that of the orderly development of the parts of all organic bodies, concerning the mechanics or the regulative control of which nothing is definitely known.

When we consider the known structure and development of the great claws in relation of the known habits of their possessor, we find no warrant in considering them as an "ornament" or in any other light than that of most efficient tools and weapons, chiefly for defense, for the capture of prey, for rending it in pieces, and afterwards for handing over the edible parts to the grinding mechanism which begins with the mouth parts and ends in the stomach. The developmental history of the lock forceps and its periodic teeth, as narrated above, renders any criticism of Stahr's fantastic theory, on the ground of comparative psychology, superfluous.

On the inner margins of the great claws appear certain prominent spines (fig. 2, pl. XXXVII *up. ser.*, and *l. ser.*), which are very regular in form and position, but vary somewhat in number. They consist of an upper series of 4 to 6 stout spurs curved upward and forward, and a lower of 1 to 3 teeth of lesser size, alternating with the first, and bent downward and forward. They probably originate from a single series, by displacement. They are eminently protective, while the proximal and often double spur on the upper side may act as a buffer when the claw is folded inward. Greater

attention, however, is called to the serrated jaws of the forceps themselves, owing to the origin of their teeth by interpolation in the way described, and to the periodicity thus established, but the biological significance of one set of spines may be as great as that of the other.

VARIATION IN THE POSITION OF THE GREATER FORCEPS.

As was long ago remarked by Aristotle,[a] it seemed a matter of chance whether the crushing claw were on the right or left side of the body, but this is not altogether the case. The large claw occurs about as frequently upon the right side as upon the left, without distinction of sex, as shown by the following table, in which 2,433 individuals are recorded:

TABLE 7.—SHOWING VARIATION IN POSITION OF BIG CLAWS.

Sex.	Crushing claw on right side.	Crushing claw on left side.	Claws similar and of toothed type.
Males.....	562	628	1
Females.....	602	638	2
Total.....	1,164	1,266	3

I have shown that in *Synalpheus brevicarpus*,[b] of the Bahama Islands, where the large hammer claw can be recognized even before the animal is hatched, the members of a brood are either right-handed or left-handed, that is, have the hammer on the same side of the body. This seems to be a case of direct inheritance from the parents, though not enough data were collected to settle this point.

Since the issue of that work my early observations have been extended by Coutière and our combined results are tabulated below.[c]

TABLE 8.—SHOWING POSITION OF BIG CLAWS IN BROODS OF SYNALPHEUS.

No.	Great claws of mother.	Number in brood.	Right-handed larvæ.	Left-handed larvæ.
1	.....	40	.....	40
2	.....	[d] 30	.....	30
3	Left.....	16	.....	16
4	.....	3	2	1
5	Right...	6	4	2
6	Left.....	4	1	3
7	...do.....	44	.....	44
8	...do.....	22	1	21
		165	8	157

[a] "In the Carabi and in the Carcini the right claw is invariably the larger and stronger. For it is natural to every animal to use its right side in preference to its left. In the Astaci alone it is a matter of chance which claw is the larger, and this in either sex." Aristotle: The parts of animals; translated by W. Ogle, London, 1882.

[b] Herrick, F. H.: Alpheus: A study in the development of Crustacea. Memoirs of National Academy of Sciences, vol. v. ch. v, 4th mem., p. 370–463+, pl 1–38). Washington, 1892.

[c] Coutière, H.: Les "Alpheidae", Morphologie externe et interne; Formes larvaires; Bionomie. Annales des Sciences naturelles, 8e sér., Zoologie, t. LX, p. i–iv, 1–560, pl. 1–6, text fig. Paris, 1899.

[d] The exact number in this brood was uncertain, but all that were preserved were left-handed. No. 1–4 were observed by the writer, no. 5–8 by Coutière. No. 1–3 refer to *Synalpheus brevicarpus*, no. 4–8 to the small *Synalpheus longicarpus* which abounds in the big black *Hircinia* sponges along shore.

Out of a total of 165 larvæ all but 8 were left-handed and 4 of these last are known to have had a left-handed mother. Four "families" in which every one of the 130 members were left-handed are known in two cases at least to have had left-handed mothers, the position of the crushing claw not having been observed in the others. Where the children of the same family vary in this character, it is probable that the parents or grandparents varied also. However, as I pointed out in 1892, the position of the toothed or crushing claw is not haphazard in its primary condition, but is predetermined in the egg.

In the next section, however, we shall see that in *Alpheus* as well as in other genera a remarkable reversal of the position of the big claw may take place, as a result of loss, so that in the course of life the crusher may shift back and forth, being now on the right and now on the left side of the body. The question therefore arises whether the left-handed female (no. 7 of the table), whose 44 children were all left-handed, was herself left-handed at birth, and secondly, whether, as in the right-handed *Alpheus* (no. 5), two-thirds of whose young were right-handed and the other third left-handed, the shifting of the big hammer claw would influence the inheritance of the children. These questions can not be answered, but it is suggested that in *Homarus* as in *Alpheus*, where no loss of limbs or other serious disturbance to the processes of growth have occurred, the right or left handed condition is due to inheritance.

Emmel has recently shown that up to the fourth molt the large crusher claw may be made to develop upon either side of the body at the will of the experimenter by the amputation of one claw, thereby, as it were, throwing the greater quantity of energy into the other for the purposes of growth. This power of control, however, ceases during the fifth stage, as at all later periods when asymmetry has become established and when the amputation of either chela does not normally reverse the conditions present. Emmel concludes that the factors which control asymmetry are correlated with the conditions of growth from the time of hatching up to the fifth stage. His experiments show that the asymmetry of the big claws of any given animal is not necessarily due to inheritance, but it would appear that in the normal course of development heredity played a part, although its initial course may be subsequently changed.

SYMMETRY IN THE BIG CLAWS.

In 1895 (*149*, p. 143 and pl. 14) I described and figured a variation in the adult American lobster in which both big claws were similar and of the toothed type. This variation was exceedingly rare, as shown by table 7. Only three cases of this abnormal symmetry were found in this collection of 2,433 lobsters made in the Woods Hole region by Mr. Vinal L. Edwards, the veteran naturalist and collector of the United States Fisheries Laboratory.

Since that time several papers have appeared upon this subject by Stahr (*258*), Przibram (*220*), Calman (*45*), Emmel (*91*, *92*, and *93–96*), and myself.[a] The first of

[a] The account which follows is partly taken from an article on 'Symmetry in big claws of the lobster" (no. *155* of bibliography).

these writers seems to have found this variation of similar toothed claws much more common in the European lobster.[a] The history of development proves, as Stahr maintained upon theoretical grounds, that the toothed claw represents the more primitive and the crushing claw the more modified type. Therefore it seemed natural to infer, as he did, that the anomalous symmetry in these weapons had been brought about by loss of a crushing claw and a subsequent reversion to the primitive toothed condition in the regenerated member which took its place. This would give us a lobster with symmetrical toothed claws like the variation described.

The converse of this, or the production of a new crushing claw in place of a toothed "forceps," could not occur upon Stahr's theory of regeneration, and hence he inferred that my report of a case of similar crushing claws in a lobster was an error. It was later at first rejected on similar grounds also by Przibram, who regarded the report as incredible and "worthy of being consigned to the realm of fishermen's myths." It should be added, however, that this objection was withdrawn in a later contribution (*223*), and neither Stahr nor Przibram are to be blamed, for my report was based upon the statement of a fisherman. Still, however great the inaccuracy of fishermen in biological matters, I have yet to find a lobsterman who could not tell a "club" from a "quick" claw. It now seems that the maligned fisherman, for once at least, was right, and he should get his dues even if earlier theories have to be revised, for Dr. W. T. Calman, of the British Museum, has described a case of symmetrical crushing claws in the European lobster (*45*), and his account is accompanied by an excellent photograph, which he has kindly permitted me to use (pl. XXIX). In all other respects this animal was a perfectly normal male. It was caught near Stromness, Orkney, and its living weight was 4 pounds 10 ounces.

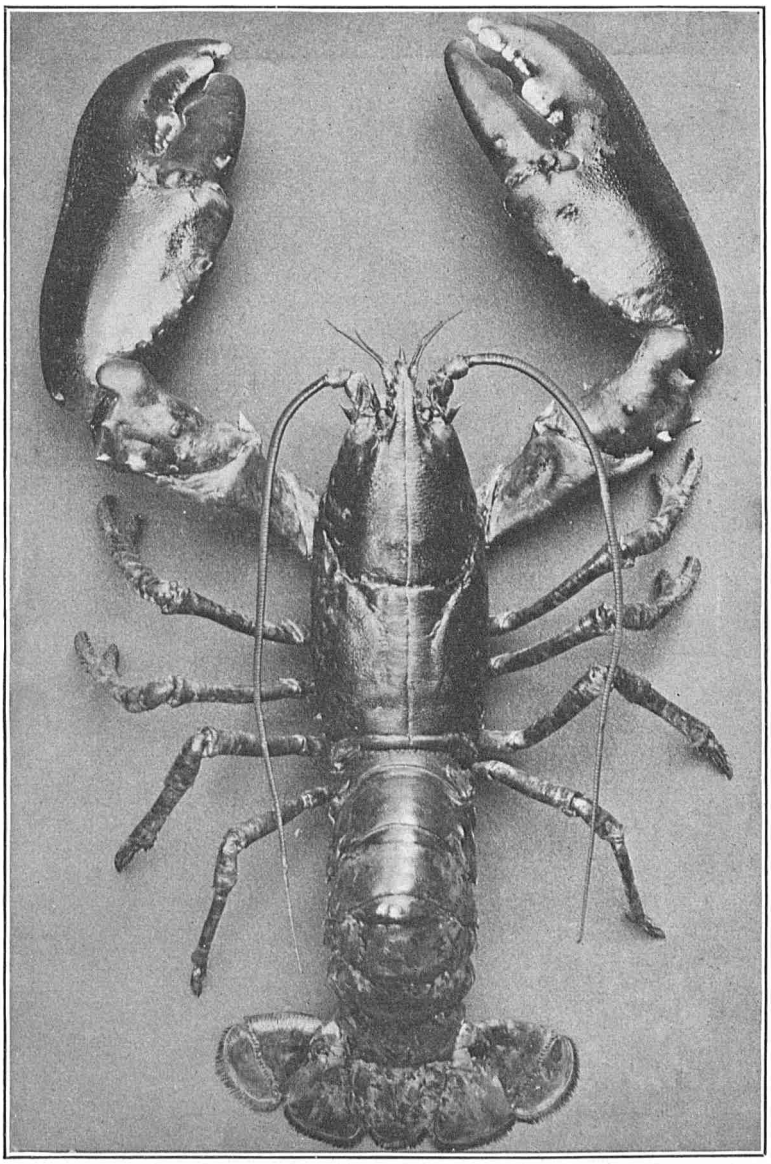
In a letter, under date of December 3, 1906, regarding this unique specimen, Doctor Calman says:

> The correspondence between the two chelæ as regards arrangement and size of the crushing tubercles is even closer than appears on the photograph, where slight differences of color have a little obscured the shape in one or two points. The differences are no greater than one would expect to find between the two sides of a normally symmetrical animal. In other respects the chelipeds are practically alike in size and shape, except that, as seen on the figure, the dactylus of the left is shorter than that of the right. The basal segments of the limbs show no trace of asymmetry, which is often associated with regeneration.

To return to Emmel's paper (*93*), we find that in two recorded cases, an $8\frac{3}{16}$-inch female and an 8-inch male, "crusher claws" were regenerated after amputation by autotomy of normal asymmetrical chelæ. Emmel further records the capture at the Rhode Island experiment station in 1895 of a single adult lobster with similar "nipping" claws. When these were removed by autotomy two similar claws were also reproduced, but in this instance of the "nipping" type, like those cast off.

While in the usual course of events regeneration of a large cheliped restores the normal asymmetry of an adult lobster, Emmel has clearly established the fact that it

[a] Przibram (*223*) has reported a case of similar toothed claws in a specimen of the Norwegian lobster (*Nephrops norvegicus*) preserved in the Hofmuseum of Vienna.



Male lobster (*Homarus gammarus*) with symmetrical claws, and both of crusher type. The first specimen of the kind, living under natural conditions, to be definitely recorded. For figure of lobster with both claws of toothed type see no. *149* of bibliography, pl. 14. Stromness, Orkney Islands; weight, 4 pounds 10 ounces. Reproduced from photograph by Dr. W. T. Calman.

can both produce and restore a condition of symmetry. Both Przibram (*221*) and Morgan (*203*), as well as Emmel, have called attention to the fact that when the crushing claw is thrown off the regenerated member at first suggests a transitional stage between the more primitive toothed and the more modern crushing type, but this is not always the case, for two of Emmel's lobsters developed similar crushing claws at a single molt. Emmel's experiments show that a change in the type of big claw may occur in the adult lobster, but whether this is to be regarded as a step in the process of complete reversal of asymmetry met with in the younger stages of *Alpheus* and other forms described by Przibram remains to be seen. As Wilson has already remarked, the removal of both forceps from the prawn, unlike the case of the lobsters referred to, led to no disturbance in the normal asymmetry of those appendages. In 1901–2 Przibram (*221*) showed that in the crabs similar claws could be experimentally produced through regeneration.

To follow the reversal phenomena of *Alpheus* more closely for comparisons: We have seen that this shrimp carries a huge "hammer" or snapping claw, which in some species is as large as the entire body of the animal, and a diminutive claw of more primitive form on the opposite side. Moreover, in the common *Alpheus heterochelis* of the southern coast the small chela presents an interesting sexual variation, and resembles the "hammer" more closely than does the corresponding simpler and more primitive claw of the female.

A striking example of heteromorphic regeneration or reversal of asymmetry is seen when the *Alpheus* "shoots" its "hammer," or for any cause loses its big claw, as was discovered by Przibram in 1891. The big claw seems to hold the little one in check, for no sooner is it lost than the smaller one grows apace and becomes differentiated into a "hammer" or "snapper," while, as if in compensation for this change, a diminutive chela of the primitive type replaces the great claw lost from the opposite side. Wilson (*284*) found that in both sexes the small claw, which was regenerated from the stump of the large one, was always of the simpler female type, and, moreover, that the small chela of the male was more rapidly changed into the big "pistol" or hammer claw because it was already further advanced on this line of development than that of the female. When the smaller claw is amputated, or when the "forceps" are removed from both sides of the body at once, there is no reversal, a new slender chela or hammer claw taking the place of the corresponding member lost. Many additional facts have been brought to light through the experimental studies of Wilson, Brues, and Zeleny.

Przibram (*223*) has also found by experiment that reversal of the claws takes place not only in *Alpheus*, but also in *Athanas*, *Carcinus*, *Callianassa*, *Portunus*, and *Trypton;* that the tendency is most marked in the younger stages, and that it decreases with age. His results are therefore similar to those obtained by Emmel (*92*) in the lobster, where the experimental control of asymmetry ceases, as we have seen, at the fourth stage.

In the lobster no reversal or compensatory regulation normally or usually attends the regeneration of any of its appendages. The crushing or the toothed forceps, when severed at the "breaking plane," are as a rule replaced by their like in due time after one or more molts. How, then, are we to explain the anomaly of similar claws? It

seems highly probable that the reversal, which regularly takes place in *Alpheus* when its great "hammer" claw is cut off, does actually occur, though but rarely, in the lobster, or, rather, that a step in the process takes place, there being no immediate compensatory change to restore equilibrium of the system of which the great claws form a part. Thus, when a "club" claw is "shot" or amputated by the experimenter, a chela of similar crushing type is usually regenerated in its stead, but rarely a toothed claw may appear. There is a change in the appendage, bringing about an abnormal condition of symmetry, but the process stops here, and we have as the result lobsters with similar toothed claws, like the specimen illustrated in an earlier work (*149*).

In like fashion the toothed claw of the lobster is usually replaced in regeneration by a limb of similar type, as is the rule with *Alpheus*, but in rare cases a "club" claw is substituted, and we get a lobster with symmetrical crushing chelæ, like the specimen described by Doctor Calman. This case is certainly much rarer than reversal from crushing to toothed claws. There is the possibility that these abnormal conditions of symmetry may be upset by a compensatory change in the appendage of the opposite side, but there is no evidence at present that this ever takes place.

When most of the preceding paragraphs on this subject were written I had not seen Emmel's valuable paper on the regeneration of crusher claws following the amputation of the normal asymmetrical chelæ in the lobster. Accordingly, the statement that the case reported by Doctor Calman was "for the present essentially unique in the literature of the subject" applied only to the fact of its occurrence in a state of nature or freedom, the two other lobsters reported by Emmel and referred to above being regeneration products resulting from amputations.

In discussing the significance of the substitution of the "crusher" for the primitive "toothed" type of claw, Emmel does not consider that any explanation is at present possible, either on the basis of "reversal" phenomena or of "compensatory regulation," and he thinks that we must be content at present with a record of the fact that substitution by regeneration takes place. I have endeavored merely to point out the probability that in such forms as *Alpheus* and *Homarus* we are dealing with processes which are essentially similar.

CHANGES IN THE TOOTHED CLAW AT MOLTING.

The adjustment of the blood supply in the big claws and the adaptation of their tissues to the process of molting, in the course of which their great bulk of muscles is pulled through the narrow ring at the base of the cheliped, are described in chapter IV. We shall now consider the interesting changes in the armature of the toothed claw or lock forceps, which are expressed at a given molt.

The behavior of the spines of this weapon suggests the movements of a company of soldiers at drill, and offers a striking illustration of that power of regulative control which distinguishes living things. The peculiar alignment of the spines of the forceps, by means of which its serrated jaws overlap, apparently effected by concerted but reversed movements of the teeth, and the behavior of the large "lock" spine, which gradually shifts to a position far out of line with its fellows, have already been described.

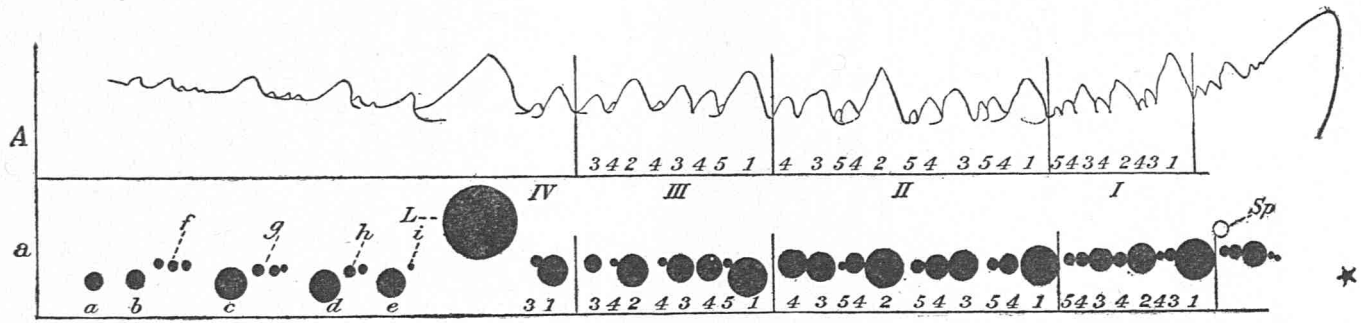


FIG. 26 and 27.—Profile and horizontal projection of larger division of right toothed forceps of male lobster immediately before the molt. Length of lobster before molting, 11¼ inches; length after, 12½ inches. Three periods and part of a fourth are present between spur (*Sp*) and lock spine (*L*). Enlarged nearly three times.

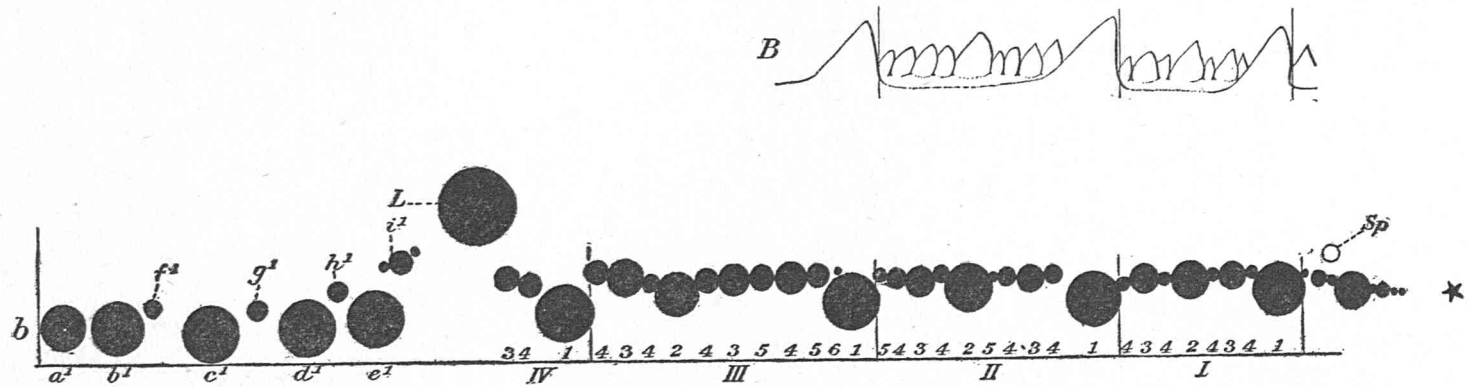


FIG. 28 and 29.—Partial profile, and projection of armature of same claw shown in figures 26 and 27, but immediately after molting; drawn to the same scale, and showing additions and losses in the periods, period 1 having acquired the typical formula in 8. Projections after camera drawings from clay impressions; periods in Roman, and orders in Arabi numerals, as in all figures, and reading from right to left. Claw-tip indicated by star.

The armature of the toothed claw of a seventh-stage lobster and that of the eighth stage from the same individual are given in figures 4 and 5, plate XLII. The formulæ for three typical periods in similar stages of another individual are also tabulated (table 5, no. 11*a* and 11*b*). It will be seen that five new spines have been gained in the course of this molt, and that one of them (the second in series III) belongs to the sixth order, while three have dropped out.

Similar changes were effected in the course of the molt of an adult lobster (lengths before and after molting, 11¼ and 12½ inches, respectively), and are illustrated in figures 26–29, where the spines are represented in profile and in horizontal projection. The "dental formulæ" are also given (table 6, no. 12*a* and 12*b*), from which it appears that five spines have been gained without corresponding loss in the three periods considered. More interesting changes have occurred at the proximal end of the jaw, where five characteristic large spines (*a–e*, fig. 27 and 29) have been retained, but the intermediate smaller groups (*f–i*) have lost from one to two members in three instances and in one case have gained two. Spine *i* has moved toward the lock spine, and bears two satellites, which seem to be thrown off as buds. The large tooth of the first order in the proximal period (IV, 1) has also received new recruits upon either hand (III, 4, and IV, 4).

Looking at the jaw as a whole, it has lost 6 teeth and gained 9, the first period alone having suffered no change in numbers. At the beginning of the molt the jaw was provided with 49 teeth, while at its close it possessed 52.

This suppression of old and emergence of new teeth probably goes on all the time in the life of this crustacean, but the changes must be compensatory, for no substantial losses or gains in the complete armature are finally registered in animals of great age. It will be observed that new spines often occur in the most crowded places, and it seems probable that such intercalated members arise as buds from their larger neighbor, as suggested above. In the earlier stages, however, there is no evidence of budding growth or division at the surface. As to why in certain parts (groups *f–h*, fig. 27 and 29) teeth are summarily suppressed, we can only hope that at some future time light may be thrown on such obscure questions.

Chapter VIII.—DEFENSIVE MUTILATION AND REGENERATION.

AUTOTOMY OR REFLEX AMPUTATION.

The casting of the big claws and of some of the smaller legs described as defensive mutilation, autotomy, or "self-amputation," is highly characteristic of the lobster. It is closely associated with the remarkable power of regeneration or replacement of lost parts, and less directly with the periodical renewal of the shell. These subjects have opened up wide fields for research, the borders of which we can only touch at a few points.

The power of reflex amputation is most perfectly developed in the large chelipeds of the lobster. When this animal is seized by the claws, and struggles to escape, amputation is likely to occur in both limbs. The animal surrenders its principal weapons, but may escape with its life. The powers of regeneration are at once enlisted in the complete renewal of the lost members. Every stage in the process can be found in animals kept alive in floating cars or in those sent to the markets. Out of 725 lobsters caught at Woods Hole, Mass., in December and January, 1893–94, 54, or 7 per cent, had thrown off one or both claws. The leg is broken off, as we have already seen, at a definite place, called the "breaking plane" or joint near its base, through reflex muscular contraction; there is but little bleeding from the old stump, and a new limb soon sprouts and is regenerated. The slender walking legs are sometimes lost and replaced in a similar way. Many, if not all, of the appendages, when mutilated or removed, are capable of regeneration, the time required for the process depending upon the proximity of the succeeding molt, the vigor of the animal, and the temperature of the water.

In autotomy the five distal segments of the limb are cast off, fracture taking place in the walking legs at the free third joint, between second and third podomeres, and in the great chelipeds at the corresponding breaking plane. On the second compound podomere of the first pereiopod of the adult the suture of basis and ischium is marked by a fine hairline or encircling groove, free from setæ, and it is always in this plane that disjunction occurs. If the terminal parts of the limb are amputated autotomy of the remaining stump usually occurs before the work of regeneration is begun. Mutilation of the claw alone, however, is not necessarily followed by the casting and renewal of the limb. Parts regenerated in any of the appendages are as a rule similar to those thrown off, except in the case of the eyes and big claws under certain conditions. The stalked eye can sometimes be made to produce an antenna-like structure, and while big crusher claw usually reproduces crusher, and lock forceps lock forceps, this is not invariably the case, and we occasionally find lobsters with both claws similar, and of either toothed or crushing type, as described in chapter VII.

Autotomy can be experimentally produced by seizing the animal by its claw or slender legs, or by stimulating the nerve of the limb directly, the reflex nerve center

having been found to lie in the corresponding ganglion of the cord, but if the animal is anæsthetized it will "forget" to shoot its claw. We have seen that the basis has lost its muscles, and that the ischium possesses two extensors only; in order that autotomy should normally occur it would seem to be necessary that the part of the limb distal to the breaking plane should offer a greater resistance than the traction of the small extensors of the ischium is able to overcome; ordinarily the clutch of an enemy furnishes the opposing force required, but since the action is purely reflex, "accidental" disjunction of a limb which happens to be suddenly opposed in its movements may occasionally happen. The probable relations of autotomy to the interlocking mechanism of the coxa and ischium are described in chapter VII.

While no tendons cross the breaking joint in the adult lobster, Emmel (*97*) has shown that this is not the case in the larvæ, in which he has discovered a transitory muscle of considerable interest; this muscle originates on the inner wall of the basis, crosses what is then a free joint, and is inserted upon the inner side of the ischium. It acts as a flexor during the first four stages of life, begins to dwindle in the fifth stage, and is reduced to a mass of degenerate tissue in the sixth. It has been maintained that in the lobster the breaking plane does not represent a lost joint (see no. *235*), but that a fusion has taken place between the third and fourth segments, a statement which is not easily understood. Thanks to the peculiar interlock of spurs on the first three podomeres, it is easy to follow the changes which these segments undergo from the fourth stage onward without difficulty (see ch. VII, p. 259), and if any further evidence were needed to show that the breaking joint, which is functional up to the fourth stage, corresponds to the articulation of the second and third segments, it would seem to be furnished by Emmel's discovery of a missing flexor muscle at this point.

While autotomy does not normally occur before the fourth stage, the limbs are often snapped off at the joint destined to become the breaking plane. Lobsterlings occasionally cast a claw at the articulation between the second and third segments which has the appearance of a free joint; fusion is not completed until the fifth stage, from which time onward autotomy in its typical form becomes a common occurrence.

An interesting adjustment to prevent excessive loss of blood in the stump of the reflexly amputated limb has been described by Emmel (*97*). We have seen, in referring to his account in another place (ch. VI, p 245), that as the venous sinus crosses the breaking plane it is divided into two channels by a septum in which are lodged the two arteries and two nerves of the limb; on the proximal side of the joint the septum gives off two folds, which are swung out by blood pressure after the break occurs and acting as valves to the small openings exposed, check the bleeding at once. It would appear from Emmel's work that the severed arteries must immediately contract so that their blood is discharged proximally to the folds or valves which he describes. Whether a similar adjustment to prevent excessive loss of blood is found in the other appendages, so far as I am aware, has not been determined. To continue this account further, when a claw is shot, a short jet of blood is thrown from the stump, but the bleeding soon ceases, followed by a slight swelling of the tissues over the fresh surface; if the valves are pressed open the bleeding is resumed.

Reflex amputation in crustaceans, whether considered in relation to shock or to fear, or as an independent mechanism, must be regarded as one of the most remarkable phenomena of invertebrate life. The loss of a considerable amount of tissue is always a shock to a higher vertebrate, while a lobster in autotomy of both its chelipeds may give up with impunity one-half the weight, or even more, of its entire body. In the higher animals fear may be due to inheritance or it may directly arise through association, by experience. The lobster, indeed, shows fear by hiding or by its hasty retreat from an enemy, but reflex amputation does not appear to have any necessary relation to fear. The reflex center of the cord is aroused to activity by a stimulus coming direct through the nerves of the limb, and not from the brain. We may be sure that the same center does not at one moment give the order to flee, and at the very next compel the animal to drop any of its legs. The lobster or crab does itself a grievous injury automatically in order to escape a worse fate. This kind of reflex surgery thus seems to be an afterthought of nature, as if an attempt had been made to repair an earlier mistake, or a compensation, as it were, for having originally endowed the crustacean with a frame too vulnerable to attack, or with a mind too feeble to successfully cope with its environment.

RESTORATION OF LOST PARTS.

The power of restoring lost or injured parts through the process of regeneration is very general throughout the body and appendages of the lobster. It is exercised very perfectly and promptly in the big chelipeds when thrown off by autotomy at the breaking plane, where the process has evidently been favored by natural selection or some other factor of evolution. Regeneration is also very active in the fragile antennæ and the walking legs. All of these organs are, at the same time, very liable to injury, and are essential to the maintenance of life by directing the animal to its food and enabling it to secure it. In conveying this food to the mouth and preparing it for the stomach the mandibles and other mouth parts are quite as important; the swimmerets also serve a variety of necessary functions, but all of these structures are far less liable to injury. Whether there is a causal relation between liability to injury and facility to restore the injured parts is another question. Morgan has reached a negative conclusion in his experimental studies on the hermit crab, and concludes that "regeneration is a fundamental attribute of living beings." The question, however, does not depend upon a single relation; the relations are undoubtedly very complex, and it can not be denied that in such animals as the lobster the external organs which are most exposed to injuries of every kind and which are of immediate necessity for the maintenance of life possess the most active power of regeneration.

Emmel has shown (*89*) that the power of regeneration varies at different levels in the limbs and that even the swimmerets may regenerate more rapidly than the legs if the latter are cut off but a short distance below the breaking plane. Therefore the rate of regeneration depends upon the place of injury as well as upon the amount of surplus energy available at that point.

The regeneration of a large cheliped in the fourth and fifth stages is essentially the same as in the adult. At the moment the limb is broken off there is but little loss of

blood, which coagulates and forms a protective crust over the stump. In a short time a small white papilla, which represents the rudiment of the new limb, appears in the midst of the brown, hardened clot. This papilla continues to grow independently of the molting process, though covered with a cuticular membrane, until a miniature appendage is formed. The papilla lengthens, and gradually the constrictions which mark the future joints of the new limb make their appearance. At first colorless, the new appendage becomes bright, transparent red, with bluish pigment at the constrictions of the joints. In this stage the limb is surrounded by a thickening cuticle and soon ceases to increase in size until after the next molt. If autotomy occurs just after a molt, the appendage will reach a much greater size than if it happens a short time before, but within the limiting period referred to below. When the molt finally takes place the new stump becomes very much larger, and now resembles the normal appendage in all respects except size. With each succeeding molt the normal size is gradually attained.

The large cheliped of the young lobster in the fifth stage may be regenerated in from 15 to 18 days after a single ecdysis, or it may require a month's time, during which the animal may pass two molts. The normal size, however, according to Emmel, is not attained until after the third molt. He also found that by the repeated removal of the same appendage in sixth to eighth stage lobsters the rate of growth in the mutilated limb was repeatedly reduced, but the experiment was not carried very far. This observer has also found that the thoracic legs will not begin to regenerate if removed immediately before a molt. The limit varies from 2 to 4 days in sixth to seventh stage lobsters. In more mature animals the limiting period is 16 days at its shortest duration. Accordingly, if accidents happen shortly before the molt, the animal must wait until this crisis is over before nature can give any attention to the restoration of the parts lost. Apparently in this case the energy required to renew the entire cuticular covering does not leave any surplus immediately available for the growth of new limbs and tissues. If the tips of the large chelipeds are clipped off, autotomy does not always or usually occur, and the limb is completely repaired after one molt. If the limb is injured below the propodus, it is usually cast off at the plane of fracture.

The antennæ are very liable to injury, particularly the delicate, sensitive flagella. Autotomy does not occur in these appendages, but regeneration may take place at any articulation in the flagellum or stalk.

In the young the whip of the second antenna may be completely restored without a molt taking place, while in the adult one molt at least appears to be necessary for complete restoration. In the fifth stage lobster, already mentioned, the antennary flagellum was restored in about 15 days. This appears first as a papilla or bud, which becomes sickle-shaped and finally coiled so as to resemble a small spirally twisted red wax taper.

The cuticle of the limbs in process of restoration must be elastic and capable of considerable distension, although the limit of this distensibility is, in most cases, soon reached.

According to the studies of Miss Reed upon the process of regeneration in the crayfish (*235*), the membrane or the inner half of the double fold which remains after autotomy, and the blood cells beneath it serve to protect the end of the stump, but take no part in

the regeneration of the new limb. To summarize briefly her account, the process of actual regeneration begins in about 5 days after the loss of the original member by an extension of ectoderm over the opening, which thus replaces the blood plug formed at the time of injury. Later these same cells secrete chitin and form a thickened disk over the broken end of the nerve. The ectoderm pushes out into a growing, expanding tip; its cells become elongated, join the cells of the old nerve, and reconstruct those of the new one. As the bud grows out, muscles and nerve are regenerated from ectoderm cells and folds in this layer appear, thus marking out the future podomeres of the new limb. The folds, which arise as ingrowths of ectoderm, also secrete chitin; they split to form the folds of the joints and, finally, at their ingrowing ends give rise to the tendons of the muscles and to the muscle fibers which are attached to them.

Emmel (*97*) has obtained similar results in working upon the lobster, wherein the wound caused by autotomy is soon covered by a plate of migrating epidermic cells. The wall of the limb and possibly its core were found to be epidermic, the old muscle and connective tissue cells of the stump appearing to contribute little to the new appendage. Both new nerve and new connective tissue elements seemed to owe their origin to the epiblast of the regenerative bud.

MONSTROSITIES.

The curious monstrosities that occur in the appendages, particularly in the large claws of the lobster, have attracted the attention of naturalists from early times. They were noticed by Von Berniz over 200 years ago, and some good figures of the deformed claws of the crayfish were published by Rösel in 1755.[a] Among the later students of variation Bateson (*19*) has shown that in most of the cases of supposed duplication of limbs in both insects and crustaceans the extra parts are double instead of single, as where two dactyls are formed at the extremity of the claw instead of a complete claw consisting of dactyl and propodus. He has also formulated certain principles according to which supernumerary appendages make their appearance in secondary symmetry. If the normal appendage which bears the extra ones is a right leg, "the nearer of the extra legs is a left and the remoter a right."

The monstrosities noticed in the chelipeds of the lobster are mainly the result of a secondary outgrowth from one of the two terminal segments. Rarely the appendage is duplicated or triplicated. In some cases the extra appendages are perfectly formed, while in others deformation has been carried to excess, resulting in irregular branching processes or grotesque contortions. Injuries to the claws are excessively common, while duplication of the parts is rare. Defective or deformed claws, the result of injuries in different stages of repair, are met with every day by dealers, while thousands of lobsters may be examined without meeting a single case of repetition or duplication of parts.

If the tips of the claws are snipped off near the articulation of the dactyl, the lost parts are restored at the next molt without autotomy taking place. This is called simple regeneration by Przibram (*221*). This restoration is often perfect, but not

[a] Insecten-Belustigung, dritter Theil. Nuernberg, 1755.

always so. Distortions arise which may have been caused by a pinch and arrest of growth while the claw was soft or by injury to the stump. In the latter case the member might be only partially restored, and unequal growth would account for the defect.

A small budlike swelling is sometimes seen near the apex of either division of the claw, and it formerly seemed to me improbable that this could be due to a simple injury since such appearances are rare, while injuries to the big claws must be excessively common. I further assumed that, given such an outgrowth, a progressive series of changes might take place with successive molts, the swollen part becoming bifid and eventually completely divided. To continue the account upon this basis: With the growth of the animal, the superadded part, whether it be upon dactyl or propodus, seems to be shifted at each molt farther and farther back upon the claw, and meantime, in most cases, to undergo fission in a vertical or somewhat oblique plane. This fission apparently proceeds until one or both of the supernumerary dactyls are entirely separated. The opposing edges of these become gradually toothed, so that each is almost an exact copy of the original. According to the principles laid down by Bateson, the part which is nearer the original joint corresponds with the appendages on the opposite side, that which is farthest away with those on the same side of the body. Many cases occur, however, which do not conform to this and apparently to no other rule (see *149*, p. 144–148).

Since the appearance of my earlier work referred to above, the excellent researches of Przibram (*220–223*) and Emmel have added greatly to our knowledge of this subject. The former has shown that in all probability monstrous growths of every kind result from a regenerative process following upon injury. However, such growths are comparatively rare and follow only upon injury of a certain kind, or upon an injury inflicted at a certain time with respect to the molting period, or under certain conditions of the animal which are not fully understood.

Przibram found that when an injured leg was retained duplication of the part might arise through a division of the regeneration rudiment, as in vertebrates, and it was further shown by Miss Reed that when a leg of the hermit crab is thrown off, if the base is split lengthwise so as to divide the nerve, there often appear two new legs, each connected with one end of the nerve. It would thus appear that duplication of a limb is subject to the will of the experimenter, and that duplicated parts may often arise in nature through an accidental injury to the nerve rudiment. Further, in 1905 Zeleny (*290*) obtained by experimental means the regeneration of a double chela in the fiddler crab. Two cases where duplication of parts of the big claw followed directly upon injury to the claw itself or to a regeneration bud have been recorded by Przibram (*223*); the first concerned a specimen of *Portunus hastatus*, which suffered in an aquarium the loss of both points of its big right claw in an irregular manner, and regenerated within three months; after molting, the dactyl became doubled, while the propodus was unchanged. The second case arose through an artificial division of a normal regeneration bud of the last walking leg of a *Carcinus mœnas*. The operation was performed with fine scissors on May 14, 1901, and after the molt, which occurred on June 2, the protopodite showed two separated dactylopodite buds. Since this animal died on

the day after the molt, it was not possible to test the hypothesis outlined above, of progressive changes following each molt. Przibram further expressed the belief that similar claws in the lobster were due to regeneration, since in crabs individuals with similar claws could be experimentally produced, a view confirmed later by the experiments of Emmel, already referred to.

Emmel (*92*) has described three additional cases in which abnormalities have been artificially produced through the process of regeneration. In two instances similar crushing claws resulted, and in a third case a triplication of the claw occurred in one of the walking legs. This adds greater weight to the conclusion that all deformities in the limbs of these crustaceans, as well as the condition of abnormal symmetry rarely met with, may arise in nature through the process of regeneration, directed by some injury or abnormal condition in the nerve end, the regeneration bud, or the growing or developing limb.

Monstrosities occur in the early and late embryos, and are therefore regarded as congenital in their origin (see *149*, p. 216). It is well known that embryonic or larval monstrosities can be produced by subjecting the eggs of many animals to unnatural and unfavorable conditions, and it is possible that the causes which produce a double-headed larval lobster are similar to those which bring about the duplication of a big claw in the adult. Perfect twins are occasionally produced from the same egg (see p. 321).

Emmel has also recorded a striking case of the triplication of a big (right) crushing claw in a 10-inch male lobster taken alive on the coast of Maine. The normal claw was the smaller and transitional in type, while the two supernumerary claws were considerably larger and typical crushers. Of these the outermost was an inverted right, with lighter colored surface uppermost, and the other a normally disposed left. The abnormal chela was removed by autotomy, in anticipation by the experimenter of some interesting results at the next regeneration, but to the regret of all students interested in the problems of regeneration this animal died in September, 1906.

Emmel remarks that if the duplication of the big claws and other similar deformities which appear in the lobster were congenital in origin, we should expect to meet with cases in the larvæ and the later stages of growth, but after an examination of over two thousand fourth and fifth stage lobsters not a single abnormal case was observed. Examination of thousands of larvæ have everywhere given the same result.

What was described in the newspaper press as a "lobster pearl" was taken from a claw of a cooked lobster by Mr. F. W. Denton, of Hollis, Long Island. Through the courtesy of Mr. Alfred Eno, of Jamaica, N. Y., the writer was able to examine this interesting specimen, an account of which, with illustrations, has been published (see *157*). The "pearl" is a globular body 11 millimeters in diameter and of the same creamy tint as the inside of a lobster's shell, with which it agrees in every physical and biological character.[a] It probably represents a freak of the regeneration process following injury to the claw, and a more or less permanent invagination of the skin at a certain point. It is safe to say that no true pearl can be formed in any arthropod.

[a] Dr. W. T. Calman, of the British Museum, writes under date of January 14, 1911, that a similar specimen was received from a fishmonger in London several years ago, but in this case the body was "embedded in the abdominal muscles of *Palinurus valgaris*," and is now preserved in the Museum of the College of Surgeons.

Chapter IX.—REPRODUCTION.

Since every attempt at the artificial propagation or rearing of animals must be made in imitation of nature, the more exact our knowledge of the reproductive life and habits of old and young the more likely are we to succeed. Apart from their economic bearings, however, the problems suggested are the most interesting with which the zoologist has to deal. In the case of many animals the facts which lie at the surface can be gathered and utilized with comparative ease, while in others, as with the common eel, whose breeding habits baffled naturalists for centuries, opportunities for making the essential observations are seldom, if ever, presented. In some respects the lobster belongs in the latter class; its life is spent at the bottom of the sea, and when confined in aquaria, where alone continuous observation is possible, the normal play of its reproductive functions is apt to be disturbed. While much attention has been given to the subject, and many important facts have been learned, there are certain questions to which a confession of ignorance is the best answer that can be given. In reviewing the matter in hand we shall endeavor to make it clear whenever a plausible conjecture is offered in place of well-attested facts.

SEXUAL DISTINCTIONS.

In general form and color the sexes agree so perfectly as to be indistinguishable to an inexperienced eye when examined from above. The female abdomen is relatively broader than that of the male in adaptation to the protection and safe carriage of the eggs, while length for length the male is heavier, this advantage in weight being seen in his slightly larger claws. Above the 8-inch size, as we have already observed, males are usually heavier than females of the same length, even when the latter carry eggs.

Upon turning the animal over, the sex is readily determined by a glance at the swimmerets, the first pair of which is rudimentary in the female, and bears but a single hairy blade, the endopodite (fig. 1, pl. XXXIX). This may be considered as an adaptation for the benefit of the eggs, for were these appendages of normal size they would catch so many ova at the time of spawning as to make it impossible for a large animal comfortably to fold her tail, a difficulty actually experienced by egg-bearing lobsters over 16 inches long. The seminal receptacle appears as a bright blue shield wedged between the bases of the last two pairs of thoracic legs on the underside of the body. (Pl. XXXIII, and fig. 4 and 6, pl. XLIII.) Its function is to receive and hold the sperm until the eggs leave the body and are ready for fertilization. Just in front of this organ the oviducts open close together on the basal segments of the second pair of small claw feet. Each duct is closed by a valve and faces its fellow with an inclination backward. When the eggs are emitted from the mouths of the ducts their natural course in the case of an animal lying on its back would be downward and backward over the seminal receptacle.

Turning to the male and confining our attention for the moment to external anatomy, we find correlative structures of great interest. The seminal ducts open to the outside much as do the oviducts, but on the basal segments of the last pair of walking legs. The openings face the middle line obliquely and are directed backward and downward. The underside of the tail is armed with a median row of four sharp spurs, which project downward and backward from the sternal bars of the second to fifth abdominal somites; in the mature female these protective spines are rudimentary, a condition which certainly favors the safe storage and carriage of eggs.

In place of the seminal receptacle we find in the male small corresponding wing-like processes diverging to form a deep V-shaped groove in which rest the tips of the stylets or modified first pair of swimmerets (fig. 5, pl. XLIII and fig. 1, *a*, pl. XXXIX). The inner branch of the second pair of pleopods bears a peculiar short spur, and it is to be noticed that when the swimmerets of the male are directed forward the stylets meet on midline between the wings of the sterna just mentioned to form an imperfect archway or covered passage, while in the divergent angle behind rest the short hairy spurs. That these parts are concerned in the passage of the spermatophores to the seminal receptacle of the female can hardly be doubted. Their structure and function will be more fully considered after the several organs themselves have been examined.

THE RIPE OVARY.

The ovaries, or "coral" as they are sometimes called, are immediately exposed upon opening the dorsal body wall. They consist of two cylindrical rods of tissue united by a transverse bridge, behind which each lobe gives off a short, straight duct (fig. 1, pl. XLIV). The ovarian lobes traverse about two-thirds the length of the body, extending from the forward end of the stomach to the third, fourth, or fifth segments of the tail, and when approaching maturity are of a rich dark-green color. The ripe ovaries are so much swollen that they fill all the available space in the upper parts of the body. The bead-like eggs are clearly seen through the thin ovarian wall, and when this is cut they flow out, if perfectly ripe, in an uninterrupted stream. When the congested ovary is not mature the loosened eggs stick together and can not be easily disengaged without injury. A female with eggs approaching maturity can be readily distinguished by extending the translucent membrane between the tail and carapace, through which the color of the ovary is at once apparent, but since the eggs can not be pressed from the unyielding body of the animal, there is no way of telling when these are ripe short of actual dissection.

During the long period of growth, which leads up to the production of the first generation of eggs, various changes ensue, which are essentially uniform except for variations in color imparted by the yolk to the immature ova. After the first generation of eggs is expelled a normal reproductive rhythm is established, and during each cycle which follows, from egg laying to egg laying, the ovary undergoes a definite series of changes, unless the normal rhythms are disturbed by unusual and unfavorable conditions. A complete change in environment may necessitate a change in repro-

ductive habits, and it is remarkable how quickly this crustacean can on occasion adapt itself to new conditions, as seen in the successful transportation of the lobster 12,000 miles through the Tropics to New Zealand in 1906–8 (see p. 176).

The history of the ovary will now be considered on the basis of the periodic events noticed above and as they have been found to occur on the coast of Massachusetts.

DEVELOPMENT OF THE OVARY TO THE FIRST SEXUAL PERIOD.

The ovaries (pl. XLV) are first recognized in well-advanced embryos as minute paired ovoidal masses of mesoblastic cells below the forward end of the heart and close to the pericardial wall. Later they appear as solid rods composed of a wall or capsule and a lining epithelium. The ovaries do not originate as hollow tubes, but virtually possess a tubular structure at the time the ripe eggs are expelled by contractions of their muscular walls. Egg laying is followed by a collapse of these walls and the immediate return of the ovary to a solid condition. It will, however, be easier to understand the structure eventually attained by conceiving the organ as possessed of a tubular form, the entire wall of which is composed of two parts, namely, (*a*) a capsular layer consisting of involuntary muscle, connective tissue, blood vessels and sinuses, and (*b*) a lining epithelium. Between these parts the blood finds ready access in irregular channels after leaving its definitive vessels. The ovarian epithelium consists of a basement membrane and epithelial cells from which the eggs and egg follicles are differentiated (fig. 1, pl. XLVI). The superficial area of this epithelium becomes greatly increased by irregular inwardly directed folds or invaginations. Through the reentrant sinuses thus formed blood penetrates to every part of the organ. The egg follicles are eventually composed of a thin sheet of tissue, the cells of which, as we have seen, are homologous with the ova. These follicles separate each egg from its fellows, form a medium for the transfer of nourishment to it from the blood, and soon begin to secrete about it the transparent egg shell or chorion. Owing to the manner in which the invaginations of the ovarian epithelium arise, the ova at a certain stage are arranged in irregular, radial and longitudinally directed tiers; each tier is embedded in opposing sheets of follicular tissue, while each ovum is completely inclosed, and the largest and oldest eggs are peripheral.

Along the central ridges of the epithelial folds the primitive ovarian cells mulitply and become differentiated into the future ova and follicular elements which are crowded or discharged into what corresponds to the lumen of the ovary, or into its central parts. (Fig. 5, pl. XLV.)

The process of early differentiation and growth of the eggs seems to proceed in the following manner (fig. 1, pl. XLVI): Along the crests of the central folds referred to above, the ovarian cells become columnar and often greatly elongated; each narrow cell appears to be attached to a corresponding thickening of the basement membrane, which forms the lining of a blood sinus. To this is due the "pitted appearance" mentioned by Bumpus (*41*). The nucleus of a cell destined to become an egg, which lies close to the basement membrane, swells into a large spherical vesicle, about which a thin layer of cytoplasm, without boundary wall, may be discerned. Granules of yolk appear almost

immediately in the cytoplasm, and henceforth the growth of the egg is determined by additions to the store of yolk, the materials for the manufacture of which are supplied by the blood. At an early stage the eggs probably multiply by division, and where they do not immediately break away from the parent epithelium they become elongated by mutual pressure, so that their long axes are parallel to each other and perpendicular to the basement membrane. Irruptions of ova, however, always occur at certain points, so that the young eggs appear in bunches along the crests of the original folds.

The nuclei of those cells destined to form a part of the follicle are easily distinguished by their smaller size, rod-like form, and by the relation to the young eggs which they promptly assume. The nucleus or germinal vesicle grows apace and continues to expand until, at the close of the first year after a given ovulation, it attains a diameter of one-eleventh millimeter. Rarely two or more nucleoli are developed in the young eggs; there is usually but one nucleolus and this of large size.

When sections of the ovary are examined, after treatment with the usual killing, fixing, and staining fluids, we find the nucleoli of all the eggs lying against the nuclear wall in the same relative positions; that is, at the "bottom" of the nuclei or on the side which was lowest at the time of fixation. The nucleolus is apparently released from its suspension in the nuclear reticulum by the action of the fixative employed, and responding promptly to the influence of gravity, drops like a shot in a bag. The ultimate position of the nucleolus is thus solely determined by the direction of gravity, and in reference to the egg itself by the position of the tissue at the time of fixation.

The growth of the first generation of eggs is exceedingly slow, occupying from four to five or more years, during which the ova must derive their nourishment indirectly from the blood. Swarms of new cells which continue to arise along the axial folds tend to drive the largest and oldest eggs toward the outer walls, a condition which is maintained until these ova approach maturity. When the limit of growth is reached the eggs are dehisced from their capsules, fill the lumen of the ovarian tube, and crowd the germinal folds and younger eggs of the next generation farther and farther toward the periphery.

We have already referred to the variable color of the organs during this period of their growth. Bright yellow, flesh and salmon color, light olive green, with many intermediate tints, are commonly noticed, while after the first eggs are produced, uniformity in the color of the organs prevails. With rare exceptions, after the first egg laying the ovary in due time assumes a characteristic light pea-green color and becomes progressively darker with age until maturity is reached.

CYCLICAL CHANGES IN OVARY AFTER THE FIRST SEXUAL PERIOD.

We have finally to consider the changes which the ovary normally undergoes during each successive reproductive period. After the eggs are laid the collapsed organs assume a grayish-white tint and appear flecked with green spots—the residual ova which fail of emission and stick fast in the lobes and ducts. In the course of 36 hours or less the ovaries are again solid masses with central germogenal folds, the larger eggs lying nearer

the periphery, where the epithelium has become decidedly glandular in appearance. (Fig. 4, pl. XLV.) These gland-like organs apparently contribute to the growth of peripheral eggs for a short period and subsequently disappear. Amœboid cells pass from them into the eggs, where their nuclei degenerate, giving rise to swarms of fine chromatin-like granules, which persist for a considerable time. In 5 weeks from the date of oviposition the gland-like bodies are reduced to shrivelled remnants, of which later no vestige can be recognized.

While the massive yolk of the eggs is mainly derived from materials drawn from the blood and laid down at first in the cytoplasmic reticulum, the migratory cells just described contribute in a minor degree toward the supply, and the glandular follicles possibly manufacture yolk directly, although the evidence which seems to support this idea may be wholly deceptive, owing to the presence of degenerative elements.

In the course of 5 or 6 weeks the ovary, flecked with degenerating eggs which failed of passage and now of a bright orange color, begins to assume a light-green tint. Examination of the larger ova shows that the pigment, a green lipochromogen, is first formed in the yolk spheres immediately around the nucleus and thence spreads centrifugally until it involves the entire yolk mass. In a year's time, or at the beginning of the summer following ovulation, the peripheral eggs, while but little larger, are more uniform in size and color, and the whole organ presents a characteristic pea-green tint. A second period of active growth ensues, followed by a second interval of quiescence during the winter. At the beginning of the third summer after the last ovulation these eggs enter upon their third and last period of active growth and are soon ready for extrusion. (Fig. 5, pl. XLV.)

Owing partly to the presence of the egg membrane or chorion, absorption of the residual eggs at each period of laying is exceedingly slow. After the lapse of 2 years traces of them can be detected, and the presence of these orange flecks in the ovary of any lobster tells us conclusively and at a glance that it has already spawned once at least.

The ripe eggs, as spawning time approaches, lie free in the lumen of the ovary, which they distend to an unusual size, its elastic walls becoming very thin in consequence. Maturation may be completed in the ovary itself, but fertilization is possible only after the eggs have been expelled from the body. The massive yolk is inclosed in a flexible and transparent shell or chorion, secreted, as we have seen, by the egg follicle or sac, and by the time the ovum has reached the ducts its nucleus (female pronucleus) has migrated to the surface. The ripe egg possesses a single membrane only.

DISTURBANCES IN CYCLICAL CHANGES OF THE OVARY.

It is convenient to notice here what the fishmonger in England sometimes calls "black lobsters." During the summer months the English lobster dealer is said to examine his stock daily and to cull for immediate sale such animals as show a tendency to blacken. It seems that whenever females with ripe ovaries happen to be caught and are either sent to market or kept in floating cars, the normal reflexes which attend

the reproductive functions are apt to be disturbed. The eggs, instead of being expelled in the natural way, perish in the ovary, possibly by having their requisite supply of oxygen from the blood curtailed, and absorption of this inert mass begins, in part at least, through the agency of the blood. By taking up the green pigment from the eggs the blood becomes very dark in color, thus giving all the tissues an unpalatable greenish-black appearance, very noticeable at the articular membranes.

The green color of the eggs, like that of all parts of the integument of this animal, is due, as we have seen, to the presence of dissolved pigments of a very unstable character. In consequence of partial absorption and coincident changes in the pigment which remains, the degenerating eggs gradually assume a yellowish-orange color. Whether the animal survives these conditions and succeeds in producing another batch of fertile eggs in due course has not been determined, but the chances would seem to be wholly in its favor.

While physiological disturbances of this kind are commonly induced by unnatural conditions, a single case has been observed in which the eggs of an animal recently taken from the sea were partially absorbed. Degeneration had spread irregularly throughout the entire organ, which at this stage of the process presented a remarkable appearance, being dark green, marbled with light lemon yellow. All the tissues pervaded by the blood seemed to be steeped in a green dye, which the organism was trying to throw off.

The structure of the ovaries, as outlined, suggest certain questions of considerable economic interest, such as the age at which sexual maturity is reached, the limits of the breeding season, and the length of the reproductive cycle or the frequency of spawning. We shall endeavor to show what light direct observation and anatomy have shed upon these matters.

PERIOD OF ADULT LIFE OR SEXUAL MATURITY.

The age of sexual maturity varies greatly in individuals, extending over an interval in which lobsters vary in length from 7 to 11½ or 12 inches. Out of thousands we should expect to find here and there one of possibly less than 7 and more than 12 inches in length coming to maturity for the first time. We may safely conclude that the majority of these animals are mature when 10½ inches long. Very few are with spawn before attaining a length of 8½ or 9 inches. In order to test this question traps must be put down at a certain point, kept there for a long period, and the catch noted day by day and month after month. This was done in the harbor at Woods Hole, Mass., where traps were laid by Mr. Vinal Edwards December 1, 1893, and the daily catches recorded until July 1, 1894, the conditions as to molting and the presence of eggs being noted in each individual. A summary of the catch showing the proportion of each sex and the presence of external eggs is recorded in table 9. During a period of 6 months 1,344 female lobsters were captured, and of these 168 carried eggs; of 249 females measuring from 6 to 8 inches but 3 bore eggs, while of those under the 9-inch length but 11 were berried.

TABLE 9.—RECORD OF THE TOTAL CATCH OF LOBSTERS IN THE HARBOR OF WOODS HOLE, MASS., FROM DECEMBER 1, 1893, TO JUNE 30, 1894, SHOWING THE NUMBER AND SIZE OF EGG-BEARING FEMALES.

Length in inches.	Number of males.	Number of females.	Females with eggs.	Total.	Length in inches.	Number of males.	Number of females.	Females with eggs.	Total.
6	3	4	.....	7	10⅛	.....	1	1	1
6¼	1	.....	.....	1	10¼	62	71	17	133
6½	3	4	.....	7	10½	79	103	28	182
6¾	5	.....	.....	5	10⅝	1	.....	.....	1
7	45	47	1	93	10¾	18	18	2	36
7⅛	.....	1	.....	1	11	31	62	20	93
7¼	10	4	.....	14	11¼	10	11	.....	21
7½	66	47	.....	113	11½	11	30	4	41
7¾	20	9	.....	29	11¾	2	2	.....	4
8	168	140	2	308	12	9	14	3	23
8⅛	.....	1	.....	1	12¼	1	.....	.....	1
8¼	44	29	.....	73	12½	4	7	.....	11
8½	143	115	7	258	12¾	.....	1	1	1
8¾	26	27	1	53	13	4	4	.....	8
9	170	166	13	336	13½	1	.....	.....	1
9⅛	.....	1	1	1	14	1	.....	.....	1
9¼	32	38	4	70	14½	1	2	.....	3
9½	148	169	24	317	15	.....	3	.....	3
9¾	27	29	3	56					
10	167	184	36	351		1,313	1,344	168	2,657

The reproductive curve, based upon body length, is seen to begin with the 7-inch lobster and to rise very slowly between this and the 9-inch size.

We do not assume that lobsters are always uniformly distributed, or that had the experiment been conducted elsewhere the results would not have been somewhat different. Where thousands of lobsters are captured at any point a considerable number measuring 8 inches or less may be found to have eggs outside of the body, but the proportion of this number to the total number of animals of the same length captured in the same place for the entire period will undoubtedly be very small.

LIMITS OF THE BREEDING SEASON.

Much confusion formerly existed concerning the time when the lobsters laid their eggs. This arose mainly from the fact that the eggs are carried by the females for a period of 10 months before they are hatched, and because of occasional departures from the common rule to which the majority conform. The following conclusion was reached in 1895: "About 80 per cent of spawning females lay their eggs at a definite season in the summer months, chiefly in July and August. The remainder, about 20 per cent of the whole number, extrude eggs at other seasons, in the fall and winter certainly, and possibly also in the spring." While this statement seems to me now to be in the main correct, I consider it very probable that considerably less than 20 per cent of the whole number of spawners lay eggs out of season, as was then suggested. It is not necessary to review the data by which it was definitely proved that eggs are at least occasionally deposited in winter and fall. The only way to check these results is to determine the retarding influence of a temperature varying from 67.1° to 32.1° F. (September to February, Woods Hole, Mass.) upon different batches of eggs laid out of the usual season. When normal eggs in the egg-nauplius stage, which in summer

is outlined on the tenth day and well formed on the fourteenth, are found in winter; when segmented eggs are taken in November, and unsegmented eggs in February, it is evident that the production of fall and winter eggs is not a unique occurrence in this animal.

At the western end of Vineyard Sound and in the region about Woods Hole the greater number of spawners lay eggs during the latter part of July and the first half of August. The summer spawning for each year lasts about 6 weeks, and fluctuates from year to year backward and forward through an interval of about a fortnight. This variation in the time of egg laying is not remarkable, since the period of growth of the ovarian ova extends over 2 years. Any disturbance of the vital conditions of an adult female during this period would be likely to affect the time of spawning. The spawning season in the middle and eastern districts of Maine is about 2 weeks later than in Vineyard Sound. In 1893, 71 per cent of eggs examined from the coast of Maine were extruded during the first half of August.

According to the testimony of various observers, the eggs of the European lobster are generally laid and hatched from July 15 to August 31, in the northerly parts of its range, including Scotland, the west coast of Norway, and Helgoland. Larvæ may exceptionally appear, however, at the end of June, or even as late as the first part of October. In the Skager Rack and Cattegat, at the straits of the Baltic, the hatching period, at least, is about two weeks earlier (see no. *305*), while in the English Channel, at Plymouth, Allen found that the old eggs were hatched chiefly in May and June, and the new ones laid chiefly in August.

FREQUENCY OF SPAWNING.

The conclusion reached in 1895 that the American lobster as a rule lays her eggs but once in 2 years having been questioned, the subject was again taken up in 1902, and more conclusive evidence of the truth of this general statement was given.

It was suggested that "the best way to test the question by experiment would be to take a female which had recently hatched a brood and keep her alive until the following summer, when the next batch of eggs would be due, in case the spawning period is a biennial one." I attempted to try this experiment when, on June 19, 1900, Mr. Vinal Edwards, acting under my direction, through the U. S. Fish Commission, placed in a floating car at Woods Hole 36 lobsters from which the old light eggs, when close to the hatching point, were removed to the propagating boxes. I wished to ascertain three things: (1) Whether any eggs were extruded in the fall, which, according to the idea of an annual breeding season, ought to occur; (2) what changes took place in the ovary during the entire period from summer to summer; and (3) how many lobsters among those which might survive would lay eggs in the following season, one year from date.

In order to follow the behavior of the ovary I directed that at the beginning of each month one of the lobsters should be killed and its ovaries preserved, a proceeding which Scott (*248*), in a paper on the spawning of the European lobster, quoted in another

place, criticises as follows: "There is nothing to show that the eggs carried by the lobsters at the beginning of the experiment hatched out naturally and were therefore extruded during the previous year." On the contrary, all were of the class which we call "old egg" or "light egg" lobsters, which taken in June means that these eggs were laid the previous summer, and can mean nothing else, unless the rarely occurring "fall" and "winter" eggs which I have described can reach the hatching point in June, a supposition still awaiting proof. There is, further, no evidence that the removal of the mechanically attached eggs from a lobster in June alters its physiological condition. Mr. Scott says further: "There was no obvious need to kill one lobster each month to discover whether it was going to extrude eggs or not." This would seem to be an obvious conclusion, but it should have been equally clear that this step was taken for another purpose, namely, to follow the changes which were taking place in the ovary itself. The condition of the ovary tells us at once whether growth of the ova is active or slow, or whether an absorption of the eggs already formed is going on. The step was far from needless, for after July it proved that there was no preparation for the production of fall or winter eggs. In other words, it showed that in these animals there was no tendency to produce eggs in each of two consecutive years, the chief point in the experiment. It was impossible to foresee how many of these animals would die in the course of their confinement or because of it, but had all of them lived two-thirds of the total number at the start, or 24, would have had a chance to spawn in 13 months from the time the experiment began.[a]

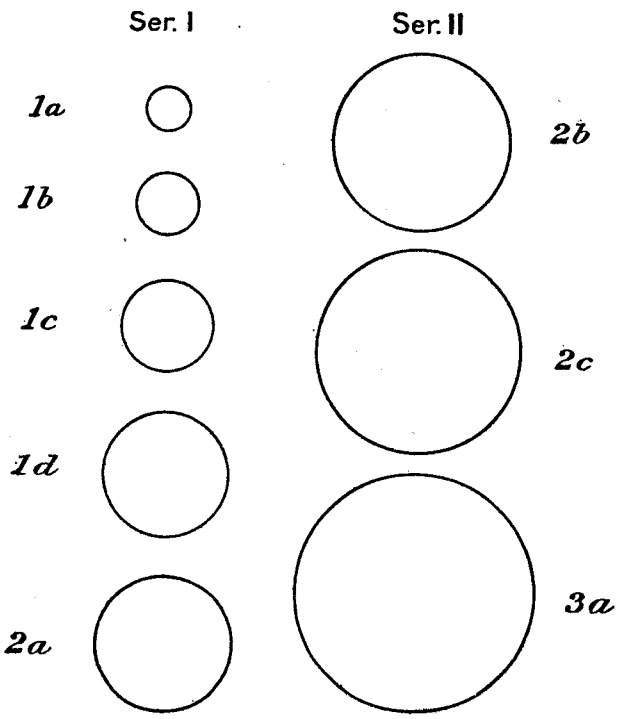


FIG. 30.—Diagram to illustrate growth in a single generation of lobster's eggs during a period of nearly 3 years, from an initial stage in ovary to time of hatching. Ser. I, internal or ovarian eggs; Ser. II, external or attached eggs. *1 a*, ovarian egg immediately after egg-laying; *1 b*, the same, 15 days after; *1 c*, the same 42 days after; *1 d*, the same 1 year after; *2 a*, the same in second growth period, 1 year and 10 months after egg-laying; *2 b*, fresh laid egg; *2 c*, "strictly" fresh, but removed from ovary or duct; *3 a*, last period of growth in shell, or egg-embryo about to hatch. Sizes deduced from averages of 10 eggs in nearly every case. Enlarged about 20 diameters.

[a] The experiment would have been more satisfactory if the directions, which were as follows, had been carried out: "Preserve the ovary of one lobster the first day of each month from July to December. If the number of lobsters should warrant it, continue to preserve the ovaries of one animal from January 1 until July. If, however, the remaining lobsters are few in number, and do not stand the confinement well, keep all as long as possible, preserving the ovary of each one that dies. * * * In case the lobsters die rapidly in late summer or early autumn, preserve ovaries of those only which die, giving the date."

By means of the animals killed it was shown that from June 19, 1900, to May 1, 1901, during a period of 10 months and 12 days, the ovaries had undergone a slow and gradual growth, a very important fact, which, if the conditions of growth were normal, is strong evidence that in the American lobster annual spawning is not a usual occurrence.

It was further demonstrated that the ratio of growth of the ovarian eggs for stated periods implied a reproductive cycle of 2 years. (Compare fig. 30.)

In conclusion we found that the theory of biennial spawning is supported: (1) By the statistics of the fishery; (2) by the anatomy of the ovary of the adult female taken at different seasons; (3) by the ratio of growth of a given generation of ovarian ova for stated periods; (4) by observation on animals kept alive for long periods; and (5) by the evidence of the rapid growth of ovarian eggs of spawners for any given year during the height of the breeding season.

Any rule to which the majority conforms may be expected to have exceptions. A lobster may exceptionally lay eggs in two consecutive seasons, and it is possible that in some cases the normal biennial period may be even prolonged.

When the preceding paragraphs were written I had not seen a paper of Appelöf (*6*) in which he confirms the theory of biennial spawning in the European lobster by an experiment conducted on a larger scale at the fisheries station at Stavangar, Norway. His statement is as follows:

> Since the matter (the question of spawning) had not been decided by experiment, I selected 100 lobsters, which were kept in a natural basin in the neighborhood for this purpose. It can now be maintained with complete assurance that in fact 2 years elapse between each egg laying.[a]

As already seen, a number of spawners, probably a very small proportion, lay out of season, in fall and winter. How can we account for these exceptional cases? An experiment tried by Mr. Cunningham (*63*) in the summer of 1897, on the European lobster, suggests an answer to the question. At Falmouth, England, five female lobsters, bearing external eggs which were nearly ripe, were placed in a floating box during the summer. After their ova were hatched these females were kept confined with two males until after October 14, when one was found to have newly spawned. This proves that it is possible for the European lobster to produce eggs in two successive years, but it does not prove that this is the common habit of the species in European waters. It also strongly suggests that these October eggs may correspond to the fall and winter eggs occasionally produced in the American form. By accelerated growth of the ovary the ova might be laid in fall or winter when not normally due until the summer following. Under such circumstances the ovarian eggs would come to maturity in 15 instead of 23 months. It would be interesting to know when these autumnal eggs hatch. The suggestion which we formerly made that they do not give rise to regular summer broods should be withdrawn, for it seems to us now that more confirmatory evidence is required before we can accept the statement that the young of the American lobster are ever hatched in the sea outside the period embracing the months of May, June, and July.

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[a] In referring to later experiments conducted at the lobster park, at Kvitingsö, Appellöf remarks: "The conclusion that the female lobster on the west coast of Norway normally lays its eggs only once in two years, I later found year after year to be completely confirmed." (See *305*, p. 23).

A later notice of the annual spawning of the European lobster after transplantation to artificial ponds in New Zealand has been given by Anderton (5), whose observations on the molting and breeding habits of this animal under a complete change of environment are most interesting and are referred to in various parts of this work (see p. 302). At the time of writing, when his observations had extended over 3 years, several of the lobsters had laid two batches of eggs, and one, which bore attached eggs at the time of shipment, was known to have spawned three times in 3 years and 7 months. The record for the latter lobster is as follows:

Arrived with a few eggs still attached, January, 1906.
First molt, in absence of male, January, 1907.
Second molt, followed by copulation, November 21, 1907.
First spawning under new conditions, January 24, 1908.
Hatching of first batch of eggs, November 23 to December 28, 1908.
Second spawning; date not determined, but before March 12, 1909.

These animals were confined in small ponds with concreted bottom, and regulated tidal flow, and were regularly fed and skillfully cared for. It is interesting to notice that while the seasons are reversed in the southern hemisphere, the local range of temperature in New Zealand is similar to that at bottom of Vineyard Sound, Massachusetts, the lowest average temperature of 3° C. (37⅖° F.) being recorded for July (compare p. 182), and the highest average of 13° C. (55⅖° F.) from December to February.

An interval of 65 days ensued between copulation and spawning, and the fosterage period from egg laying to the hatching of the first young was 10 months to within a day. While it can not be maintained that these novel conditions give the usual spawning habits for *Homarus gammarus* until similar results are obtained within its natural range (compare Appellöf's experiments, given above), they show that the lobster is remarkably plastic and able to withstand considerable change when directed by skillful hands.

NUMBER OF EGGS PRODUCED.

The freshly laid eggs are of a dark green, almost black hue, when seen in mass, and somewhat irregular in shape, but they soon plump out and become nearly spherical or ovoidal in form. As the eggs develop they increase in size, become elongated, and, owing to the gradual assimilation of the dark yolk, lighter in color. (Compare fig. 33, *a b*.) This is most noticeable toward the close of the period of development, when the phrase "old" or "light" egg lobster is commonly used by fishermen to distinguish them from the "black" egg lobsters, which have more recently spawned.

The fresh egg measures approximately $\frac{1}{16}$ inch in diameter (1.5 to 1.7 mm.) and weighs $\frac{1}{6000}$ ounce or $\frac{1}{821}$ gram. A fluid ounce of eggs weighs about 1 ounce avoirdupois. The number of eggs laid is proportionate to the volume of the ovary and of the body, and varies from about 3,000 to nearly 100,000 in animals from 8 to 19 inches long.

TABLE 10.—PRODUCTION OF EGGS.

Length of lobster.	Smallest number of eggs.	Largest number of eggs.	Average number of eggs.	Number of lobsters examined.	Length of lobster.	Smallest number of eggs.	Largest number of eggs.	Average number of eggs.	Number of lobsters examined.
8 inches	3,045	9,135	4,822	6	13 inches	6,090	48,720	28,610	321
8¼ inches	6,090	7,612	6,851	2	13¼ inches	24,360	48,720	33,495	5
8½ inches	3,045	12,180	6,935	9	13½ inches	6,090	54,810	32,858	146
8¾ inches	6,090	9,135	7,105	3	13¾ inches	42,630	42,630	42,630	2
9 inches	3,045	18,270	7,902	143	14 inches	6,090	85,260	36,960	426
9¼ inches	6,090	12,180	9,083	35	14¼ inches	21,315	60,900	42,968	90
9½ inches	3,045	20,792	9,297	241	15 inches	12,180	97,440	46,524	280
9¾ inches	3,045	15,225	9,947	55	15¼ inches			54,810	1
10 inches	3,045	24,360	10,555	514	15½ inches	24,360	97,440	53,795	45
10¼ inches	6,090	22,838	11,622	61	15¾ inches	48,720	54,810	50,750	3
10½ inches	3,045	36,540	12,905	532	16 inches	24,360	97,440	57,146	103
10¾ inches	6,090	24,360	14,067	45	16¼ inches			66,990	1
11 inches	3,045	48,720	15,410	568	16½ inches	36,540	85,260	66,053	13
11¼ inches	6,090	25,882	17,102	43	17 inches	12,180	85,260	63,336	30
11½ inches	3,045	42,630	18,668	307	17½ inches	60,900	73,080	64,960	3
11¾ inches	12,180	24,360	17,993	11	18 inches	60,900	91,350	77,430	7
12 inches	3,045	54,810	21,351	414	19 inches	54,810	91,350	77,647	4
12¼ inches	18,270	27,405	23,396	8					
12½ inches	9,135	42,630	24,812	156	Total number examined				4,645
12¾ inches	18,270	42,630	26,390	12					

In table 10 (reproduced from *149*) we have given the smallest, largest, and average number of eggs removed from the bodies of 4,645 individuals. These animals were "old" egg lobsters and were caught in Vineyard Sound and vicinity from April to June. The numbers were determined as a basis of 6,440 eggs to the fluid ounce. These tabulated results show great variability in the number of eggs borne by individuals of the same length, which may be attributed in part to loss of ova, but more to variation in the period of sexual maturity. Thus in 514 lobsters of the 10-inch length the number of external eggs varied from 3,045 to 24,360, with an average of 10,555. For the 12-inch size the corresponding numbers were 3,045, 54,810, and 21,351. We have seen that the period of sexual maturity is exceedingly variable in different individuals and that one animal may lay its first batch of eggs when 7 inches long, while another may not rear a brood until its body is 5 inches longer and has increased greatly in volume. The phenomenon is not remarkable in view of the slow growth of the ova, but it is important to recognize the fact.

Consideration of the average number of eggs produced suggested a general tendency which was expressed as follows: The number of eggs produced at each reproductive period tends to vary in a geometrical ratio, while the lengths of the animals producing these eggs vary in an arithmetical ratio. The average production in lobsters 8 inches long being 5,000 eggs, the average product for lobsters 10 inches long would be 10,000; for the 12-inch length, 20,000. This high rate of production is not maintained beyond the length of 14–16 inches. The lobsters with the largest number of eggs measured from 15 to 16 inches in length and carried upward of 97,000 eggs, which measured 16 fluid ounces and weighed nearly a pound.

Lataste (*177*) in a critical paper on that section of my earlier work dealing with the fecundity of this animal observes that the number of eggs carried by the lobster at any given time should be proportional to the volume of the body or to the cube of its length. If N represents the number of eggs carried, l the length of the animal,

and k denotes a constant, according to Lataste, the relation of these quantities would be expressed by the following equation:

$$N = kl^3;$$

$$\text{Whence } k = \frac{N}{l^3}.$$

He has drawn up a table (based on table 15 of *149*), from the data of which he deduces the cubes of lengths, the ratios of the average number of eggs to cubes of length (k), and the means of these ratios.

In the lobster the reproductive powers are manifested suddenly at a certain age, after which they increase steadily, reach a maximum, and then presumably slowly decline. Accordingly during the first period only does the fertility increase proportionately to the increasing volume of the body, as expressed in the equation given above.

We have no definite information upon the duration of life, or decline of rate of growth in these animals. It is certain, however, that the renewal of the shell is quite as necessary for the continuance of life as of growth, since in the course of time death would result were not the injured and abraded shell restored. In higher animals the skin and at least some of the tissue cells are being continually renewed throughout life, while size limit of the body is early attained, and it is not likely that a dense and heavy shell like that of the lobster could be sloughed without increase in the size or volume of the body. The decline in sexual vigor may therefore result from the tax which molting continues to levy upon the capital stock of energy at every period of life. According to Lataste: $k = f(t)$, k being a function of age which has no real value, except as it is confined within certain limits.

In conclusion, we wish to observe that upon the principle of correlation of parts the ratio of the number of eggs to body length should correspond in a general way to the ratio of the volume of eggs to the total volume of the body were the latter a constant quantity, but owing to the frequent loss of the great claws this is not accurately represented by the cube of the length. All that we can say is that in the long run there is a tendency to produce in such a ratio, but the physiological condition of the animal is an inconstant and indeterminable factor. The high birth rate of the lobster teaches us to expect a correspondingly high death rate, a subject which will be later considered.

BREEDING HABITS AND BEHAVIOR IN CRAYFISH.

The breeding habits of lobsters, so far as they were then known, were described in 1895. Since that time a number of important facts have been ascertained, but our knowledge of the subject is still defective at many points. The behavior of the American lobster at the time of pairing and extrusion of the eggs has probably never been witnessed in a state of nature, and certainly but seldom in any of the higher Crustacea. We have had more or less circumstantial accounts from Chantran, Ishikawa, and Cano, regarding the time and process of egg laying in the crayfish, shrimp, and crab. The pairing habits and process of laying the eggs in the European lobster have been described by Anderton and Scott, as will be noticed later, while a remarkably

full and accurate account of the habits of the American crayfish during the breeding period has been given by Andrews.[a]

Since the activities of the breeding crayfish are without doubt similar in some degree to those of the lobsters, and since they are at present far better known, I shall now give a summary of the instinctive acts and events in *Cambarus* for the period in question, drawn entirely from the work of Andrews referred to above.

Pairing in *Cambarus affinis* takes place in spring (February–April) and fall (October–November). The male catches the female by the antennæ or about the head, rolls her on her back, seizes her by the claws, stands over her body, and holds her in this position from 1 to 10 hours, during which time the sperm is transferred to the annulus or sperm receptacle on the ventral side of her thorax. This process may be repeated by "either male or female," both of which are in hard shell.

The male holds with his big forceps all the claw feet of the female in a bunch on either side, her abdomen being coiled under his, which closely presses it, he meantime supporting with his left or right fifth leg the abdominal appendages which are to transfer the sperm to the annulus. The first two pairs of abdominal legs or modified pleopods of the male are directed downward and forward against the ventral surface of the thorax of the female. Since the pleopods tend to lie flat against the body, they thus fold or close upon the the fifth leg, which stops them, forming a rigid support, and at the same time giving them the necessary elevation. The male then presses close upon the female so that his pleopods are directed toward the annulus and are forced into it, where the sperm is deposited. Spines on the legs of the male further tend to hold the pair firmly interlocked. *Cambarus affinis* has a prominent spine on the third joint (ischium) of the third pair of chelipeds, which fits into the base of the fourth pair of legs of the female. Spines or hooks of this character are wanting in the lobster. Thus rigidly interlocked, the transfer of sperm goes on slowly and may last for hours.

The vas deferens of the male is protruded or evaginated, as may be readily observed in all copulating males, forming a soft translucent double-walled tube, the lips of the opening being tightly closed. This evaginated duct fits in the groove which passes down the outer side of the first pleopod, and serves to conduct the sperm towards its tips. The appendages are rigid, sharp-pointed tools which are inserted into the annulus, and against which the modified second pair of pleopods are closely pressed. Sperm issues from the ducts as in the lobsters (compare fig. 2, pl. XLIV) in long vermicelli-like packets, or gelatinous capsules known as spermatophores, and guided possibly by the second pair of pleopods, passes slowly down the groove of the first pair to the receptacle or chamber of the annulus. The female is remarkably passive and appears as if dead, while the excitement of the male is marked.

While the spermatic receptacle of the lobster (pl. XXXIII and fig. 4 and 6, pl. XLIII) corresponds in function to the annulus of *Cambarus*, the latter appears to represent only the unpaired wedge-like middle piece of the former. The development of the seminal receptacle in the lobster proves that the middle piece in this animal is the anterior

[a] Andrews, E. A. Breeding habits of the crayfish. American Naturalist, vol. XXXVIII, p. 165–206, fig. 1–10. Boston, 1904.

section of the sternum of the eighth thoracic segment. The divergent wing-like processes in front of the annulus in the crayfish evidently correspond to the convergent wings, which are the modified sternum of the seventh thoracic somite, and which, united with the middle piece, form the elastic lips of the shield-shaped receptacle in *Homarus* (*st.* XIII, fig. 4).

The laying of eggs in the crayfish may not occur for some weeks after sexual union, and as Andrews remarks, some protection such as the annulus affords is necessary, since sperm can not long survive exposure to water.

PAIRING HABITS IN THE LOBSTER.

Both Boeck (*24*) and Fraiche (*109*) have referred to the union of the sexes in the European lobsters as if they had witnessed the act, but the errors which they exhibit tend to discredit their statements, however brief. Fraiche remarked that copulation in both the common and Norwegian lobsters took place in fall (October and November), and in the case of the former that it was extended into winter. "As with the crayfish, the sexual act is accomplished belly to belly, and so closely and firmly do they clasp each other, that, if taken from the water at this period, it is with difficulty that they can be separated."

But the only reliable observations under this head have been made by Anderton (*5*), of the Marine Department of New Zealand. The sexual act was noticed on a number of occasions among the European lobsters kept under observation in small artificial ponds. The general succession of events was as follows: Molting in early summer (November and December), followed in the course of a few hours by coition between a soft female and a hard male, and by the laying of eggs about two months after this event.

One of the female lobsters kept under observation by Anderton molted on November 21, at 3 p. m., and lay for some time beside her cast shell. "Two hours afterwards," to continue his account, "it was seen roaming round the pond and frequently approaching the various shelters, returning regularly and fearlessly to a shelter containing a large male. On approaching the entrance to this shelter the large claws were extended in a direct line with the body and the antennæ were thrust within the shelter. After a few moments the rostrum of the male appeared, the female meanwhile rapidly whipping her antennæ across the now projecting rostrum of the male, which in turn showed increasing signs of excitement, the antennæ being whipped very rapidly over the female in the same manner. After an interval of perhaps a minute the male gradually withdrew from his shelter, the female at the same time turning over on its back. Coition took place at once, the act occupying only a few seconds, the male retiring at once to its own shelter and the female into another. The following day both were observed to be living in one shelter, and they continued to do so, on and off, for several weeks."[a]

[a] In reply to certain specific questions regarding the pairing of lobsters, Mr. Anderton has kindly written under date of August 21, 1910, as follows: "The female lobster after casting does appear to seek out a male as soon as the distressing effects of molting have somewhat worn off. Male and female have frequently been observed living in one shelter for some days and even weeks after coition. The act of coition is very brief, and will not occupy more than half to a whole minute. They copulate, as you express it, "belly to belly," and head to head. The large chelæ do not come into use during the act so far as I have observed. The female voluntarily turns over almost completely onto her back, the excited male completing the process for her."

Three other cases of copulation were witnessed, and in every instance between a soft-shelled female and a hard male and always within a few hours after the female had cast. In one instance when the water in the pond was run off the body of the male was left partly exposed. I have already noticed two cases in which the American female lobster was impregnated when in the soft condition and when she also bore eggs; but there are other facts which show that molting is not necessary for the impregnation of the female. In the case of the American species we have found females of all sizes from 8 inches and upward in length impregnated at all times of the year, and the adult female lobster when taken from the sea, in whatever condition of shell, is likely to have her receptacle well supplied with sperm, even when preparing to molt. On the coast of Massachusetts in June and July I have found lobsters with newly laid eggs and a lobster with brood just hatched and about to shed, with receptacles full of sperm, which was in the first instance certainly, and in the last probably, newly acquired, and when the shell was hard. We know that the sperm is endowed with great vitality; that it can endure for months, and possibly for years. It is further probable that copulation is more or less indiscriminate, and more than one union is sometimes necessary to secure the fertilization of a given hatch of eggs.

Pearce [a] has presented strong evidence to show that crayfishes have no power of discriminating sex, his conclusions being based upon *Cambarus blandingi acutus* Girard, *C. diogenes* Girard, and *C. virilis*, observed in confinement. "The male," says Pearce, "tries" every crayfish which it meets, whatever the sex, a female instinctively remaining passive, while a male attempts to escape. The sexes meet by accident in the course of their random movements in the search for food. Males were found to even copulate with dead females, and in one instance with a female of another species, when the male stylets were inserted in the usual way in the copulatory pouch or annulus.

After taking into account all the facts at present known it seems highly probable that the lobsters are actuated by similar instincts when breeding and that they possess no greater powers of discrimination.

The probable method of transfer of the spermatophores is considered in a later section.

PREPARATION FOR EGG LAYING—CLEANING BRUSHES IN THE LOBSTER.

Preparatory to laying, the female *Cambarus*, as Andrews points out, retires for a number of days to the dark corners of her abode and is busily engaged in cleaning the under side of her abdomen for the reception of the fresh cargo of eggs. Her attitude and behavior in this instinctive act are peculiar. Standing as upon a tripod on the tail fan and the tips of the great claws, with her body raised high above the ground, she picks, brushes and scrapes every particle of dirt from the swimmerets and under surface of the tail, using chiefly the last pair of walking legs, the modifications of which, especially in the last two joints, render them very effective, combining as they do in one instrument the advantages of pick, comb, and brush.

[a] Pearce, A. S. Observations on copulation among crayfishes, with special reference to sex recognition. The American Naturalist, vol. XLIII, p. 746–753. New York, 1909.

The brush-picks of the lobster, especially those on the last two pairs of ambulatory legs, resemble similar instruments in the crayfish, as described by Andrews, and there can be no doubt that they serve a like purpose. That they are used as cleaning brushes has been often observed, but no one has yet studied the behavior of the lobster in the critical period before egg laying is accomplished.

Nevertheless I have recorded an observation (*149*, p. 47) which, read in the light of the foregoing account, suggests that the lobster has the cleaning instinct also and carefully prepares her abdomen for the reception of the ova. In two cases which I had been watching the lobsters laid their eggs in aquaria, and then industriously picked and scratched off nearly every one of them in the course of a few days. Now, these eggs were all of small size and the ovaries did not give up more than a third or a half of their contents. Under these conditions it would not be surprising to find the attunement of the instincts at fault. Interpreted in this way, the lobster by cleaning off her eggs was only preparing herself for the reception of the ova which still clogged the ovary.

In the lobster the terminal joint or dactyl of the last pair of legs (*cl. br.*, fig. 4, pl. XXXVIII) is developed as brush and pick, there being no comb on the under side. It is cone-shaped and traversed from apex to base by three nearly equidistant rows of hairs or setæ, those of the upper row being long, dense, and serrated. The subterminal joint bears three conspicuous tufts of saw-tooth hairs, quite similar to the "scouring brushes" described for the crayfish. In place of the strong spines or picks on this segment of the *Cambarus* is a single blunt spur almost concealed by the brush of hairs in the lobster. Just above it, near the base of the line of long dense setæ is a rudimentary comb or short linear series of spines.

If the short process which bears two spurs or picks in *Cambarus* were extended, it would form, as Andrews suggests, a double claw or forceps similar to those of the smaller chelate legs. In this case, however, the chelæ would all have the same relative positions or work in parallel planes. In the second and third chelipeds the claws work up and down, or in a nearly vertical plane, on the hinge joints. The great claws, however, have undergone a twist or torsion, in consequence of which their inner or anterior surfaces have become their lower sides. (See p. 257.) The dactyls consequently face and open inward, working in a horizontal plane. Now, the terminal segments of the last pair of legs have suffered a backward rotation or twist, in consequence of which their anterior surfaces are directed obliquely outward. If this limb were chelate, the dactyl would move obliquely outward and backward instead of upward, as in the smaller chelipeds, or inward, as in the great forceps.

In the lobster the torsion of the two terminal segments of the fifth pair of walking legs has gone a step further, so that the comb and spur of the dactyl, instead of being on the lower and anterior side of the limb, as in *Cambarus*, are upper and hindermost in *Homarus*, and, further, they no longer lie midway between the hinges of the joint, as in the crayfish. The torsion and other adjustments in the fifth pair of legs in the lobster evidently fit them for reaching and brushing the swimmerets and under side of the tail.

EGG LAYING.

On two different occasions, as already related, lobsters which I had under observation laid eggs in aquaria, in the night or early morning. These eggs were fertile and normally fixed in each case, but the extrusion was not complete, and the instincts of the female did not run their normal course. In the absence of any direct observations on the laying of eggs in the American species, the following account of the spawning of the European lobster, given by Scott (*248*), has a special interest:

> The lobster turns onto its back and by the aid of the two large claws and ridge of the abdomen makes a tripod of itself, the head being considerably higher than the posterior portion. The abdomen is then strongly flexed, forming a pocket, and the setæ on the edge of the abdominal segments make the space along the sides perfectly tight. A Λ-shaped opening into the pocket is formed by the telson and the sixth abdominal segment. This opening, when the abdomen is flexed, is slightly posterior to the first pair of swimmerets. The eggs then flow from the two genital openings in a continuous stream, one at a time, and pass along at the bases of the last walking legs and into the opening of the "pocket." The course of the eggs into the "pocket" is further assisted by a constant pulsation of the first pair of swimmerets, causing an indraft, which carries them rapidly inside. None of the eggs are lost on the passage from the genital openings to the "pocket" unless the lobster is disturbed. As the eggs leave the oviducts they become covered with an adhesive substance which causes them to stick together and to the swimmerets. The period of oviposition in the lobster under observation was just over four hours. Half an hour after the eggs had ceased to flow the lobster righted itself and walked into a corner of the tank, eventually getting into a nearly perpendicular position, with the head downward. It remained in this position for the rest of the day. Next day it was walking about the bottom of the tank in the usual way of a berried lobster. That the adhesive power of the eggs was imparted to them before leaving the oviducts was proved by collecting some just as they emerged from the genital openings. When these samples were placed in a glass of sea water and collected into a heap, they all became attached to one another and also to the glass. Moreover, the adhesive material only remains soft for a short time, as when the individual eggs were isolated and prevented from adhering upon the glass it was found that at the end of half an hour the adhesive property had entirely disappeared.

ARRANGEMENT AND DISTRIBUTION OF EGGS AND THEIR ATTACHMENT TO THE BODY.

Ishikawa, who watched the prawn *Atyephyra* lay her eggs in an aquarium, says that the act is performed in the early morning, and that it is preceded by a molt the night before, an order of events which has been often noticed in the higher Crustacea. The eggs were "almost rod-like" when they came from the ducts, and were laid down in an orderly manner, the anterior swimmerets receiving the first, while those deposited later were driven backward by the last pair of thoracic legs. The abdomen was incurved to form a pouch during the process, and the thoracic legs as well as the swimmerets and their corresponding segments were in constant movement.

In the lobster the ova adhere principally to certain setæ of the appendages of the five anterior segments of the abdomen (pl. XXXIX), and since hairs are absent only from the articular membranes of this region, they become bunched about the stalk of each appendage, and extend over the sternal bar and inner (epimeral) wall of the corresponding somites. In a full-berried female the swimmerets are embedded in a solid mass of eggs up to their branches, comparatively few being fixed to the free blades, and these

only to their inner or proximal ends. The eggs, however, are so completely adherent to one another that if every hair were severed the entire cargo would float off in a single mass. It should be noticed that the stalks of the swimmerets are inclined inward toward the median plane of the body, and not away from it as in the thoracic region, and also that three tufts of long setæ are borne on the inner margin of each, two on the lower part of the inner blade or endopodite, and one on the adjoining end of the stalk or protopodite (fig. 3 and 4, *a*, *c*, *d*); further, that upon these setæ a vast number of eggs find anchorage, and that glands are very abundant beneath the skin of these parts. Four smaller tufts (*e*, *f*, *b*, *g*, fig. 3) also carry eggs, and like the former are non-plumose. Assuming that the cement is derived in part at least from the tegumental glands, and that the eggs are engulfed in it when they reach the abdominal pouch, it is difficult to understand how in the lobster the true swimming hairs catch so few eggs and in the prawn *Alpheus* none at all, unless it be due to gravity or the ability of the animal to direct the course of the egg stream while lying on her back and gradually changing her position. The difficulty of explaining this simple fact is not lessened by assuming that the cement originates in the oviducts.

ORIGIN OF THE EGG GLUE AND FIXATION OF THE EGGS.

Upon reaching the sea water in the abdominal pouch the eggs are fertilized by the sperm with which the seminal receptacle is charged, and, as seems probable, all are mixed in a secretion coming from the tegumental glands as well as from the oviducts by the beating movements of the swimmerets; the cement gradually becomes viscous, hardens, and eventually incloses each egg in a thin capsule; the individual eggs of the entire mass are eventually fastened to one another and to certain hairs of the abdominal appendages by the spun sheets and threads of the glue. The latter is an ectodermic product and resembles chitin in its appearance and behavior. A knowledge of its chemical and physical properties when combined with sea water, at the time of its secretion, would probably include the answer to a number of puzzling questions.

There are three subjects, apart from the more special problems of cytology, concerning the pairing of the higher Crustacea about which exact knowledge is particularly needed. These are: (1) The exact rôle played by the cement-producing organ; (2) the kind of stimulus or stimuli needed to arouse the sleeping sperm in its receptacle, set it in motion, and direct its course to the eggs; and (3) more light on the action of the rays, and the "explosive capsule," by means of which recent students have endeavored to explain the forced entrance of the head of the sperm into the egg. Direct observations are too limited at present to afford a basis for the final settlement of any of these matters.

The origin of the cement has been attributed, on the one hand, to the sexual organs and especially to the epithelial lining of the oviducts, and on the other to the tegumental glands of the swimmerets and lower side of the abdomen and to the egg itself.

The older writers, among whom were Cavolini (1787), Rathke (1840), and Erdl (1843), generally favored the first hypothesis. Lereboullet (1860) was the first to attribute the cement to the abdomen, and Braun (1875) the first to describe "cement glands" in the crayfish. Tegumental glands are found in practically every part of the body covered by the skin or invested by its folds, occurring even in the alimentary tract, the gills, seminal receptacle, and the "ear sacs." Feeding experiments with carmine seem to have shown that they have an excretory function in some degree at least, but it is equally certain that in some parts of the body they give rise to definite secretions. At the time of oviposition the pleopods of the female are swollen with what appears as an opaque whitish substance, which is seen upon microscopic examination to be composed of thousands of these organs. Each gland is hardly an eighth of a millimeter in diameter, and each opens to the exterior by a capillary duct, the entire length of which, not including the part which traverses the cuticle, is scarcely more than $\frac{1}{10}$ millimeter and its diameter only $\frac{1}{125}$ millimeter. Such organs are absent or found but sparingly in the pleopods of the male. After ovulation these glands appear to be for the most part in an exhausted condition, zymogen-like granules filling the central ends of their clustered cells. In one case examined, in which the animal had recently hatched eggs and was about to molt, the glands were shrunken and transparent.

While these facts may be entirely misleading, an observation of Prentiss (*217*) seems to show that this is not the case, inasmuch as glands of this type occur in the sensory cushion of the otocyst of the crayfish and probably in that of all crustaceans in which sand particles are adherent to the sensory hairs. Until some more probable source of the secretion is discovered, it is reasonable to infer with Prentiss that these glands furnish the glue by which the otoliths are fastened to the pinnules of the sensory setæ.

THE OVIDUCT AND ITS PERIODIC CHANGES.

The evidence regarding the part played by the epithelium of the oviducts will not be perfectly satisfactory until much more is known concerning the nature of the secretions of these organs during the period of egg laying. Our studies of the histological changes which the oviduct undergoes are limited to two significant stages, one in which the ovary was nearly ripe and the other from a female with external attached eggs in yolk segmentation.

It is evident from a comparison of the critical stages that cyclical changes occur in the oviduct, no less marked in character than those which arise in the ovary itself, and to which they are evidently related.

By the time the eggs are ready to be laid the oviducal epithelium is distinctly glandular in type (fig. 3 and 4, pl. XLVII). Its cells become greatly elongated and distended, while after egg laying they are shrunken to less than one-fourth their former size. When treated with the common hardening and staining reagents before egg laying, the cytoplasm is clear; the nuclei are also clear, elongated by the pressure exerted in the direction of the short axes of the cells, and lie well down toward the basement membrane. After ovulation the cytoplasm of the shrunken cells is more vesiculated; the nuclei are more

granular, more deeply stained, oval in form, and are farther removed from the basement membrane. Furthermore, large vesicular cavities occur within or between the cells next the lumen of the glands, where products of nuclear degeneration are not wanting.

It thus seems evident that the glandular epithelium of the oviducts pour an abundant secretion over the eggs when these are delivered into the abdominal pouch. According to the account of Scott quoted above, the eggs are viscous when they leave the ducts, become adherent in sea water, but soon lose this property. So far as I have been able to ascertain, eggs to all appearance ripe, which were taken directly from the ducts shortly after egg laying, were nonadherent and showed no trace of cement or a secondary egg membrane, but at this time the action of the glands had ceased.

In the lobster with external eggs in segmentation, referred to above, the oviducts were beaded with ripe eggs, or as Duvernoy expressed it, stuffed like sausages, with eggs which failed of passage arranged in line, but they were not viscous at the time of examination, and were surrounded by the chorion only. Assuming that the oviduct contributes to the formation of the cement, some other chemical products would seem to be needed to render this effective. These are possibly supplied by the secretions of the tegumental or "cement" glands of the swimmerets in the presence of sea water. At all events it would seem that there is poured into the pouch at the time the eggs pass into it an abundant milky or turbid secretion from these glands, which under the microscope is seen to be swarming with minute floating particles or spherules. A similar secretion occurs in the crayfish, which after the setting of the cement is found to cover her eggs in a sort of protective "apron," as Andrews calls it, a sheet of grayish mucus or glair. When this is removed the eggs appear bright and fresh beneath it. This "apron" seems to be a residue of unused material, the presence of which may be needed not only to hold the eggs and sperm in the pouch but to take part in the production of the liquid hydraulic cement.

COMPARISONS WITH THE OTHER CRUSTACEA, AND THEORIES OF FIXATION.

In the lobster the glue forms a thin transparent sac about each egg (fig. 5, pl. XLIV *mb*^{2}), and the capsules of adjoining ova are united by short solid ribbons, or flattened strands of the same material. Similar bands adherent to the hairs and often coiled spirally about them hold the entire egg mass to the body. The cement is thus a continuous sponge work, which is imitated in the manufacture of certain kinds of nut candy, where the kernels are stirred in the thick sirup and held immersed when it hardens.

Coutière[a] describes a slightly different mode of fixation in the Alpheidæ (*Alpheus* and *Synalpheus*), where the eggs or egg-groups adhere only to the stalk of the pleopods, and never to the fifth pair of swimmerets, nor to the abdomen directly. The supporting hairs are bunched at the two extremities of the basal stalk and are nonplumose, as in the lobster.

Where the eggs are few in number, as in *Synalpheus longicarpus*, they are glued direct to the hairs, but where more numerous several hairs are cemented into a cable

[a] Coutière, H.: Les "Alpheidae," Morphologie externe et interne; Formes larvaires; Bionomie. Annales des Sciences naturelles, 8^e sér., Zoologie, t. LX, p. I—IV, p. 428.

by a flattened membrane with double walls, representing the expanded capsule which surrounds the egg. In most cases the hairs furnish support to but a small part of the egg mass, the individual eggs being freely united with their neighbors. Thus in the prawn *Eucyphotes*, according to Coutière, the capsular cement gives off three or four flattened bands, each of which is soldered at its apex to similar strands from other eggs. The point of union is marked in each band by a lozenge-shaped or circular thickening. This would indicate that the eggs are surrounded by a layer of the viscous cement, and separated by sea water until they come together. Each lozenge-shaped thickening would then represent the original points of contact of egg with egg, the strands being spun from the sheath by a mutual pulling strain, due to the weight of the moving eggs.

This condition is especially interesting since it seems to prove that such eggs must have received their coat of cement before leaving the body. Unless it should appear, however, that the marks of contact may be completely effaced by fusion of the united strands, it offers no basis for a general conclusion regarding the origin of the cement substance in other decapod crustacea, like the lobster and crayfish. It is probable that in this as in many other particulars there is no absolute uniformity.

A much more anomalous method of fixation of the egg to the swimmeret is described by Williamson (*281*) for the crab, *Cancer pagurus*, and in Brachyura generally. According to this observer, the eggs lie thick upon the hairs of the inner branches of the swimmerets, and are attached by independent and often intertwined stalks, but there is no union of egg to egg, as in *Synalpheus*, *Homarus*, and other Macrura. The eggs are attached to single hairs, which garnish the endopodites, and usually to hairs only. There are said to be two membranes in either ovarian or attached egg, namely, a delicate vitelline membrane and a chitinous chorion. Between these a slight perivitelline space is formed upon contact with sea water. How does it happen that the eggs escape the hairs of the exopodite, and how are they suspended to the silken hairs of the endopodite without a single case of adhesion of egg to egg, and with little sticking of hair to hair?

Williamson in brief offers this explanation: "The intimate relationship between the egg and the hair is due to the hair acting as a skewer, upon which the eggs are impaled and strung." Further, the hairs are supposed to penetrate the chorion and pass through a perivitelline space without injury to the vitelline membrane. The chorion thus pierced collapses, and a little albuminous perivitelline fluid is pressed out, which becomes adhesive in sea water and serves to glue the chorion to the vitelline membrane and the egg to the hair; later the glue and chorion is pulled out into the sheets or cords by which the egg is anchored to the hair.

The solution of the problem of fixation in the eggs of the blue crab appears to carry us into deeper water than before. In order to make comparisons I have examined the eggs and abdominal appendages of the blue crab, *Callinectes hastatus*. *Callinectes* lays upward of 4,500,000 eggs,[a] and the endopodites of the swimmerets are buried out of sight by the mass. As in *Carcinus* these myriads of

[a] Smith, S. I.: Report on the decapod Crustacea of the Albatross dredgings. Report of the Commissioner of Fish and Fisheries for 1885, p. 618–619. Washington, 1886.

eggs are attached exclusively to the long silken tufted hairs of the inner branches of the second, third, fourth, and fifth pleopods. They are distributed, therefore, in 8 bunches, with over half a million eggs to a bunch. The appendages are flattened, and excepting the anterior face near the tip and a portion of the posterior face near its base, the endopodite is studded with remarkably long silken setæ. Each hair carries from 150 to 200 eggs, and each egg is glued by an independent stalk to the hair. Each egg is, moreover, extremely minute, measuring about $\frac{1}{108}$ of an inch ($\frac{2}{10}\frac{3}{0}$ mm.) in diameter, or smaller than the dot of the letter *i* of this type. The hairs are extremely slender, varying in diameter from $\frac{1}{200}$ of an inch at base to $\frac{1}{700}$ of an inch at middle, beside which a human hair is very coarse and a silken thread a veritable cable. These attenuated hairs taper gradually to a sharp point.

The exopodite of the swimmeret is fringed with a dense row of plumose setæ, which are not more than one-fifth as long as the egg-bearing hairs of the inner branch and which, according to Williamson, serve in *Cancer* as a barrier to prevent the escape of the ova from the brood-chamber before they become attached. Strange to say, they do not catch a single egg.

Upon the theory of Williamson, and the assumption of an average cargo of 4,500,000 eggs, we can appreciate the nice work in fencing which would have to be performed by the silken hairs of *Callinectes* and indirectly by the appendages of the crab. Some 22,496 hairs would be required to spear and string 200 eggs each, and the feat would have to be done in the dark, as it were, and upon an egg so small as to be hardly visible upon the point of a fine cambric needle. But this is not all; the thrusts of the hairs must pierce a perivitelline space, that is, penetrate a tough chitinous membrane and be deflected from a semiliquid envelope. If this really happens, it is certainly a most wonderful performance.

Our objection to such a theory of attachment is based upon general principles, and before accepting it we should wish to have answers to the following questions. How is it possible for these delicate hairs to spear anything, and least of all solid spheres like an egg, suspended in water, and therefore in unstable equilibrium? The hairs have no more rigidity than a silken thread; they can hardly stand alone; and when loaded with eggs at their tips the spearing of additional eggs would seem to be impossible. (2) How is it possible for a spear or needle to penetrate the tough outer coat and avoid piercing the egg, for the suppositional inner membrane really does not exist at the time the egg is laid? (3) Are the almost microscopic eggs pushed along like beads on a string or birds on a spit, 200 or more crowded in line, and each leaving a viscous trail, without clogging the line, sticking together, or crowding one another off? (4) How is it possible for drops of an albuminous liquid to ooze from a hole in an egg without spreading over that egg, for a hair in contact with the egg would certainly not conduct this liquid against the force of gravity, and myriads of eggs must occupy every position with respect to the hair? Perhaps we can get a better idea of the physical difficulties involved by imagining a fly-fishing rod reduced to great tenuity and used as a spear for apples. How many apples of whatever size could its tip hold?

Before the question of egg attachment in the crab can be settled we must have very full and exact observations of the behavior of these animals during the period of egg laying. Now in *Callinectes* the endopodites are packed full of "cement" or tegumental glands; the exopodites contain fewer glands but an excess of cell disks or concretions (see *149*, p. 108). In fact, Braun called attention to the presence of glands in these Brachyura over thirty years ago.

If the secretion of the receptaculum seminis of the crabs is limited only to the uses of the sperm, as seems probable, we are inclined for the present to accept the older theory, namely, that eggs are glued to the hairs by a cement which is secreted by glands which lie at their base.

Why the eggs of the *Callinectes* are not stuck together or why neighboring hairs do not more frequently adhere is not apparent, and can not be explained until we know more about the physical properties of the glue itself. The hairs of *Callinectes* are covered with a continuous sheet of glue, but are not often adherent. Possibly the eggs stick to them before they have a chance to become entangled. Each egg is tethered by a thin spun sheet of glue, which is continuous with a narrow band or sheet, in which the entire hair is embraced up to the tip or very close to it.

As was pointed out by the writer in 1892 and as had already been demonstrated by Mayer in 1877, the crustacean egg does not possess a yolk-membrane. The ovarian ovum and the mature egg when it issues from the ovary, in crustaceans as well as in insects, is provided with a single membrane, the chorion, which is secreted by the "ovi-sac" or egg follicle. The great mass of the egg is made up of inert yolk; the protoplasm, which alone has formative power, is practically restricted to the center of the egg. When in the course of segmentation or later the protoplasm has reached the surface, a delicate membrane is secreted by the blastoderm. This often glues the egg fast to the chorion and gives much trouble to the embryologist. No doubt it was this membrane which gave rise to the mythical "Dotterhaut," or vitelline membrane of Erdl, Rathke, and the older school of embryologists.

A single membrane only, the chorion, is apparent in the eggs of *Callinectes*, but since the cord of attachment spreads out over its surface without any apparent break, the egg is probably covered with a thin layer of cement which has the same index of refraction as the chorion to which it is inseparably glued.

Williamson endeavors to extend his ingenious theory of fixation by "spearing" and the liberation of the cement from the egg itself to the lobster and other Macrura. Thus he says that the secretion "is not a true cement" capable of forming an outer envelope, but an albuminous substance, and that "the weight of the egg tends to stretch out the ductile chorion into long thin stalks." It is quite certain that the egg of the lobster, as in all the higher Crustacea, possesses a single membrane when it leaves the ovary, but the egg attached to the body has acquired a second and distinct membrane which is continuous with the stalk of attachment. The two are easily separable in picro-sulphuric acid; the second or outer layer is the "cement membrane" (fig. 5, pl. XLIV).

As we have already seen (p. 305) the eggs of the lobster are attached to the non-plumose hairs of the swimmerets as well as to the abdomen and to each other. Here at

least it is impossible to apply any theory of fixation which does not involve a fluid cement substance, engulfing both hairs and eggs, capable of setting under sea water and possibly in chemical relation to it into a firm "hydraulic" cement which is non-ductile under ordinary pressures when it is once set.

I have spoken of the chorion as a tough membrane. That this is true is proved by the vicissitudes through which it passes unharmed. In egg laying the egg is compressed, being rod shaped in some forms when it passes the duct; it is therefore elastic, but it is only slightly ductile and then only when under great pressure. The freshly laid lobster eggs are spherical and as we have seen measure $\frac{1}{16}$ inch (1.5–1.7 mm.) in diameter; the egg embryo when ready to hatch is oblong, and measures about $\frac{1}{12}$ inch (2.1 mm.) on the average of the short and long diameters (fig. 33). This swelling in size, due to embryonic growth, stretches the chorion to great tenuity, until the limit of elasticity and ductility is reached, and the membrane bursts under the pressure, aided to some extent by the exertions of the larva.

THE MALE SEXUAL ORGANS.

The paired testes of the male are either distinct or united by a transverse bridge, and each give off a coiled duct or vas deferens, which opens by a valvular orifice on the inner side of the first segment of the last thoracic leg (fig. 2, pl. XLIV). The duct consists of a proximal division which conducts the sperm from the testes, an enlarged glandular part, and a terminal muscular or ejaculatory segment. A linear milk-white mass marks the course of the sperm through the transparent tube. In the coiled glandular division it is embedded in gelatinous envelopes or spermatophore-sacs (*sph.*) secreted by the lining epithelium. A sphincter muscle (*sp. mu*) produces an abrupt swelling at the beginning of the ductus ejaculatorius, the function of which is to eject the spermatophores. The latter have the appearance of semitransparent rods of vermicelli about an inch long, and consist only of opaque masses of sperm and the gelatinous medium described. When pressed out artificially, they imbibe water and swell perceptibly.

SPERM CELLS, THEIR ORIGIN AND STRUCTURE.

The sperm cells of the lobster (fig. 31) were apparently seen for the first time by Valentin in September, 1837, and he gave a brief account of his discovery in the following year. A more accurate account by Kölliker, who also remarked on the apparent immobility of the "rayed cells," appeared in 1843, with figures, and notice of the "seminal sacs" or spermatophores.

The structure and genesis of the spermatozoa of the lobster have been studied with much detail by Grobben, Gilson, Hermann, Sabatier, and more recently by Brandes (*33*), Labbé (*175*) and Koltzoff (*172*). Probably few structures in the animal kingdom have been more puzzling than the rayed cells of the decapod Crustacea. The puzzle consisted in harmonizing the following conditions as generally found in these animals. The large eggs of crustaceaus are surrounded by a tough chitinous membrane in which neither pore nor micropyle has been discovered. The sperm cells may be rounded or columnar, but

whether devoid of processes of every kind, or provided only with three stiff rays as in the lobster, under ordinary conditions of observation these cells are absolutely immobile. Still every thoughtful observer who has pronounced the decapod sperm to be immovable must eventually recant, and like Galileo declare, "E pur si muove." How then could such sedentary bodies seek, find, bore through the tough shell and fertilize the egg? Brandes, Labbé, and Koltzoff have offered or worked out fertile suggestions, which afford a satisfactory solution to the general problem, subject to a course of verification and extension in different species of crustaceans.

That the "immobile" sperm cells really did move, has been maintained for thirty years or more by Owsjannikow, Hermann, and Cano. Thus apropos to this subject Grobben (*122*) remarks: "The stiffness of the rays does not prove that these cells are completely immobile. Moreover, the observation of Owsjannikow that the rays sometimes draw themselves in, and certain structures which I have examined, enables me to conclude definitely that these rays are living protoplasm and that they represent amœboid processes, remaining almost in a state of rest." (Compare the observation of Cano quoted below.)

In 1890 Hermann (*138*) had described movements of the processes of sperm cells, and in 1893 that excellent observer, Cano (*46*), spoke of seeing "certain of the sperm cells, especially the rayed ones, in amœboid movements in the sperm receptacle of the crab *Maia*."

In 1896 a remarkable statement regarding independent movement in the sperm cells of the lobster was made by Bumpus (*42*), to the effect that he had "seen the spermatozoa in active movement, swimming across the field of the microscope with the same nervous contractions that are characteristic of the Hydromedusæ."

In 1897 Brandes (*33*) asked how it was possible for the decapod sperm to enter an egg where no micropyle could be found, and especially in sperm cells like those of *Astacus*, which have no pointed head, but which are spherical and of considerable size. "I suppose that the sperms at the moment of contact with an unfertilized egg undergo a change, which consists in this, that a more or less pointed part of the anterior end of the sperm, the so-called clapper, the "tigelle" of French writers, is evaginated and so the membrane of the egg which at the moment of egg laying is perhaps somewhat yielding, is perforated." This ingenious suggestion, which was elaborated at greater length, has proved very fruitful, for it was confirmed by Labbé in 1903, and especially by Koltzoff (*172*) in 1906, who has worked out the development and structure of the sperm cell in a number of Brachyura, such as *Portunus*, *Maia*, *Pagurus*, and *Eupagurus*, and of Macrura in *Homarus*, *Galathea*, and *Scyllarus*.

According to these later observers, the sperm cell is a very complicated and delicate machine, beside which a clock or watch seems like a crude affair, especially when we consider the vast difference in size. This cell may be compared to a self-propelling torpedo, designed to move in a certain direction, and to explode the moment the cap or head strikes the hull of a vessel, or any opposing object.

In the following description of the genesis and structure of the sperm cell of the lobster, I shall follow in the main the account of Koltzoff (*172*), from which I have constructed a number of diagrams (fig. 31, *1–3*, and fig. 32). This account, whether correct in all particulars or not, is at least intelligible, and we are able to understand the remarkable evolution in form which these cells undergo in consequence of changes in osmotic pressure. It is very different from that of Sabatier, who devotes 37 pages to the sperm cells of the lobster, yet leaves it difficult to understand his descriptions and impossible to construct any consistent diagrams from his figures.

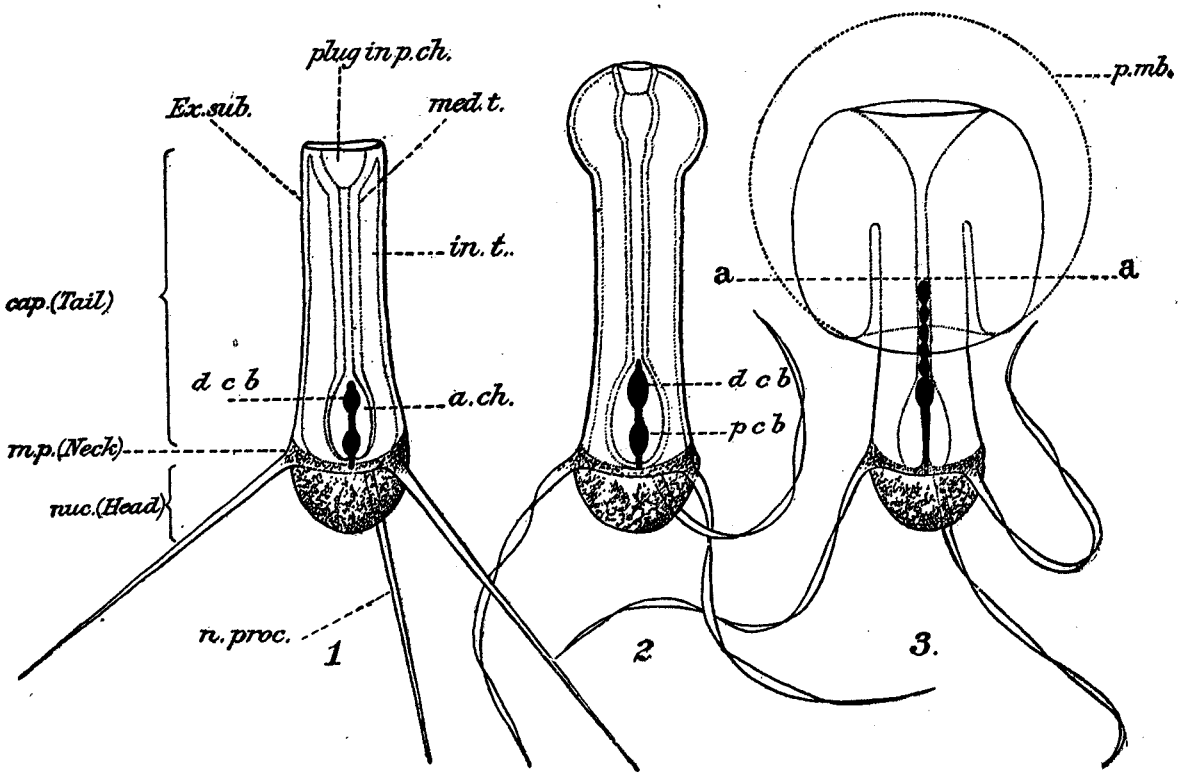


FIG. 31.—Diagrams of sperm cells of the lobster before (1), during (2), and after (3) capsular explosion, based upon Koltzoff (see *172*). *a a*, plane of section in figure 36; *a. ch.*, anterior chamber; *d c b*, distal central body; *Ex. sub.*, external layer; *in. t.*, inner tube; *med. t.*, medium tube; *n. proc*, neck process or ray; *p c b.*, proximal central body; *p. ch.*, posterior chamber; *p. mb.*, outer protoplasmic (?) membrane.

According to Koltzoff the sperm cell is derived by metamorphosis from a spermatid which in turn arises by division from a spermatocyte of the testis. The centrosome divides into two parts, and for some time remains united by fibers to the nucleus. The cell body is stuffed with granules which exhibit a difference in staining power, and in fact become differentiated into two important parts of the sperm, the mitochondral body and the capsule.

In the course of these changes the mitochondral becomes pressed against the nucleus, and molded upon it. A vesicular sperm cell is thus formed, peculiar to the

decapod crustacean but comparable to the flagellate spermatozoa of other animals. The crustacean sperm becomes differentiated in three parts, namely, (1) the nucleus or head, (2) mitochondral body (a partly fibrous and partly granular structure) representing the neck or middle piece, and (3) the explosive capsule or modified tail.

The sperm cell develops processes (fig. 31, 1) which in the lobster arise from the neck. They ordinarily appear to be immobile and are distinctive of the decapod sperm. The number of these processes varies from 1 to 10, but 3 is a common number, which is found in *Homarus*, *Palinurus*, and *Galathea*, as well as in some of the crabs. The number is of physiological importance, since they are used for orienting the sperm upon the egg in fertilization. In the true crabs the processes arise from the head and are therefore nuclear in origin. It may be added that in the prawns (*Caridida*) the usual processes are lacking, but the capsule ends in a sharp thread-like tail. In the crayfish (*Astacus*) and many crabs, as well as in *Gebia* and *Callianassa*, the neck and capsule are reduced in size and pressed against the head.

The processes are supported by a central mitochondral, skeletal fiber, or bundle of fibers. If in the course of development of the spermatid, these strong skeletal fibers project from the cell body with free ends, appearing to draw after them the more fluid constituents of the cell. The skeletal fibers can be demonstrated by plasmolyzing the cell or surrounding it with a solution of higher osmotic pressure. These skeletal fibers are really bundles of fibrils, which have a tendency to spiral winding.

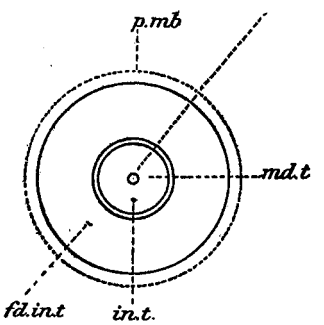


FIG. 32.—Diagrammatic section of sperm cell in capsular explosion, as seen in plane *a a*, figure 31 (3); *fd. in. t.*, folded inner tube.

The capsule (fig. 31, 1 and 2) is a double walled cylindrical body, a median tube running through it from end to end. This tube is formed by a median invagination extending from the hinder end forward to the neck, and is expanded at either extremity into a widechamber. The distal opening is closed by a plug of chitin. A peculiar rod or "Polster" of stainable substance is pressed from the central body into the anterior chamber. In the ripe sperm the outer capsular wall and the axial tube consist of chitin, and may be regarded as continuous, except at the point pierced by the "Polster." This stainable rod is often constricted into a proximal central body in the neck and a distal central body in the capsule (*p* and *d c b*).

FERTILIZATION.

In the lobster the sperm cells pass a long latent or resting period in the sperm receptacle, and may retain their vitality for from one to two years, and possibly longer. When the eggs are laid, the sperms leave their receptacle, find the eggs, and fertilize them. The spermatazoa are either pressed out by mechanical force, or else they must be aroused to activity by a definite stimulus, probably of a chemical nature.

By pressing the lips of the spermatic receptacle of a female with internal eggs nearly ripe, I have observed the sperm in a thick grayish mass which gave up its cells freely to sea water. This at all events suggests the possibility that the lobster herself is the direct agent in emptying her receptacle. In any case it is highly probable that the sperms are directed by chemotropism to the eggs after reaching the water. Nothing is known by direct observation of the phenomena of fertilization up to this point.

What are the locomotor organs by which the sperms leave the sperm receptacle or by which they seek and find the eggs in the brood chamber? In our search for an answer to this question we must remember that the lobster lies upon her back when the eggs are laid, so that the force of gravity is a bar rather than a help to the movements of the sperm at this critical period. We may assume first that in leaving the receptacle the locomotor organs of the sperm cells are the rays or processes, which I showed in 1895 to be rigid in the testes but limp in the receptaculum. This movement is probably amœboid in character, consisting in the lengthening and shortening of the protoplasmic element of the process which flows from the neck of the cell. As with the amœba a solid support is necessary for the process of locomotion to be effective, for according to a recent observer this animal probably draws itself along by the adhesion of its pseudopodia to the surface over which it creeps.

How does the cell make its way through the water to the egg? No satisfactory answer can now be given, but if Bumpus was not entirely mistaken in his report of movements of the lobster's sperm, as quoted above, we might plausibly suggest the following solution, which is of course purely hypothetical. Upon reaching the water the plug of the capsule is loosened and falls out. Water then enters and fills the inner tube. This water is subsequently ejected by contraction of the vesicle, and the cell is drawn forward by inertia. It should be added here that in some forms (*Eupagurus*) the capsule is covered by a thin protoplasmic layer, and that in this membrane contractile fibers are sometimes seen; transverse rings can be demonstrated in the lobster. The action is supposedly recurrent. The processes direct the cell, as do barbs the arrow. The eggs are big targets, and the moment one is struck orientation of the sperm upon its surface begins.

At this point speculation gives way in a measure to direct observation, and I return to the account of Koltzoff (*172*) who, like other observers, was unable to see the minute sperm enter the huge opaque egg. Disclaiming the ability to give a complete account of the movements of the sperm cells, he says: "My observations and experiments can naturally clear up only certain phases of these processes, and a whole string of hypothetical conclusions is needed to unite them into a harmonious whole."

Contact with a large and possibly moving body, or thigmotaxis, seemed to furnish the most powerful stimulus to the cell processes, which have been observed to shorten and lengthen, though not to the extent of more than one-tenth of their length. Once in touch with the egg the sperms begin to orient themselves in such a way that the cell comes to stand upon its thin elastic processes as upon a tripod, so that the head is placed in direct contact with the surface of the egg. The elastic process or processes in con-

tact with the egg possess an adhesive power; they seem to shorten, and thus to pull the sperm cell into position.[a]

In this critical situation when the conditions for fertilization are favorable something pulls the trigger and fires the gun. That is to say the capsule explodes and shoots backward, while the head in consequence of the rebound leaps forward and is driven through the chorion and into the egg.

The space between the inner and the outer capsule is filled with a peculiar explosive substance, which according to the ideas of Koltzoff possesses the property of swelling up when it meets with water. Water must either enter through pores of the inner tube or be absorbed through the outer wall of the capsule. The extension or swelling of the explosive material is rapid and is usually attended by an evagination of the inner tube and discharge of the central body.

The sperm cell is thus deformed by the action, and since the character and degree of the evagination varies with the physical and chemical conditions present the number of these apparent artifacts is very great.

In actual conditions or in 4.2 per cent isotonic solutions of calcium chloride in sea water, it is possible to follow every step of the discharge. Labbé in 1894 described the discharge of the capsule as the final developmental stage of the sperm. The explosion of the capsule seems to liberate the elastic energy of a coiled spring represented by the central body, which may show a spiral form in *Pagurus* or a series of beads, bands, or granules.

In abnormal capsular explosion, according to Koltzoff, there is a double spring of the sperm, first forward and then backward. If the suggestion of the free movements of sperm given above, and for which I am alone responsible, should prove to be an error, these abnormal explosive movements might account for the contractile pulsations described by Bumpus.

According to Koltzoff the energy of the explosion is contained in the explosive material. When the chitin plug of the inner tube is driven out, water enters and eventually penetrates to the inner capsule and brings on the explosion. My suggestion that water might enter the inner tube and be driven out by a contraction of the protoplasmic layer surrounding the capsule, thus causing the cell to move forward, presupposes that water does not at once penetrate the capsule and reach the explosive substance. If this really happens the suggestion regarding locomotion would be untenable.

No special stimulus was found which would effect a normal capsular explosion, and it is possible that the sperms respond to a coordinated series of stimuli. Nothing is yet definitely known upon this subject.

According to Koltzoff the head and neck containing the proximal central body are driven into the egg and take part in fertilization, while the capsule, with its processes, in whole or in part, and the distal central body, are left outside and disappear.

Notwithstanding the difficulties, owing to the great size and opacity of the egg and the small size of the spermatozoa, Koltzoff observed a single case where a normal sperm

[a] Koltzoff also offers a different and contradictory explanation of the adhesion of the sperm cell to the egg, namely, that the egg membrane appears in many cases under the microscope to be finely porous, and that the processes are driven like so many splinters into these pores.

having oriented itself on the surface of the egg exploded and penetrated the chorion; this happened in three different species of crabs. The capsule of the normally oriented sperm exploded while in view, and the nucleus was drawn into the egg, but it was impossible to distinguish anything whatever within the opaque ovum. He inferred, but did not prove, that this series of events represented a true fertilization process.

Several attempts were made at artificial fertilization of lobster eggs at Woods Hole in 1891, but like the experiences of Koltzoff in 1906 they were unsuccessful. There are the difficulties of first obtaining perfectly ripe eggs, and, secondly, of meeting the other conditions of fertilization in which the secretion of glands from the ovaries, oviducts, or integument of the swimmerets may play a part. I made glycerine extracts from the ovaries and oviducts in the hope of finding a chemical stimulus for the sperm, but did not succeed, the primary difficulty of getting the organs in the proper state of maturity being at that time insurmountable. It was impossible, also, to get any secretions from the swimmerets by applying electrical stimulation to the ventral nerve chain, from which they are innervated.

THE SEMINAL RECEPTACLE, COPULATION, AND IMPREGNATION.

The habits of the lobsters at the time of sexual union, so far as at present known, have been already described. (See p. 302). We have now to consider how the female is actually impregnated, that is, how the spermatophores are transferred by the male to her receptacle. According to the account quoted above the transfer is quickly made while the female lies on her back, and in the three or four cases observed when her shell is soft.

While no direct observations on the further course of events are as yet available, the structure of the spermatophore, the male stylets, and the female receptacle render plausible at least the following account, which is purely conjectural. Before proceeding with this, however, it will be necessary to examine the secondary sexual structures with greater care. The seminal receptacle (fig. 6, pl. XLIII) lies on the underside of the female immediately behind the opening of the oviducts and between the bases of the last two thoracic legs. (Compare p. 301.) It presents the appearance of a light blue shield with deep median groove. When examined closely it is found to consist of a pair of wing-like processes, the enlarged sterna of the seventh thoracic somite, with a middle piece belonging to the succeeding segment wedged between their posterior extremities. The lips of the median groove are elastic, and if forcibly depressed are seen to open into a membranous pouch, in which the spermatozoa are carried. The pouch is laterally compressed and extends directly upward at right angles to the long axis of the body and is supported on the link-work of the internal skeleton. (Fig. 4, pl. XLIII, *sac.*) We should notice that this sac, far from being a delicate structure, is well adapted to receive rough treatment with impunity. Within, the middle wedge-shaped piece is continuous with a pair of calcareous rods which form a solid frame for the posterior and upper part (or bottom) of the sac, where they are firmly sutured to the endophragmal skeleton. Within the pouch this sternal bar is prolonged into a stout keel, where it is

strengthened with yellowish deposits of chitin of a horny consistency. (Fig. 3, pl. XLIV, *bar.*)

The stylets or modified appendages of the first abdominal somite in the male (fig. 1, a, pl. XXXIX and fig. 5, pl. XLIII) have stout stalks and a single terminal blade. The latter is nibbled at the end, grooved along the median side, and bent in such a manner that when the stylets are opposed they form a covered way. At their hinder extremity they leave a wide open angle, but partially closed by the spurs of the second pair of swimmerets (fig. 2, a, pl. XXXIX, *sp.*) when these appendages are naturally extended forward On the anterior or upper side of the opposed stylets a deep groove on the stalk of each leads obliquely into the arched passageway. The tips of the stylets when held in this position diverge slightly, and when pressed into the seminal receptacle the elastic lips of the latter catch on the nibs and hold the appendages until they are forcibly withdrawn. The indurated tip of each stylet is interrupted by a minute oval area of soft membrane, but this does not appear to be the outlet of any peculiar organs. The tissues of the stylet itself, like those of the swimmerets, generally abound in tegumental glands and large glycogenic cells. In copulation the animals undoubtedly lie with ventral surfaces together, but apparently do not remain in this position long. After seizure of the female, the spermatophores are emitted and possibly with the aid of other appendages are conducted to the passage formed by the stylets, the tips of which are inserted nearly vertically into the spermatic receptacle and there held in the manner indicated. The spermatophores not only swell and soften in water, but possibly may be disorganized before the sperm are free to enter the receptacle, but this is not probable.

The crustacean sperm, as we have seen, is like a submarine torpedo, loaded and primed, capable of piercing the membrane and forcing a passage into the egg the moment its latent energy is set free.

While much of the preceding account is based solely upon inference derived from a study of the organs and of the changes which some of them are known to undergo, its presentation may be worth while, if only to call attention to the wide gaps still remaining in our knowledge of the whole process of fecundation in the higher Crustacea.

Chapter X.—DEVELOPMENT.

ANALYSIS OF THE COURSE OF DEVELOPMENT.

The entire course of development for each individual may be conveniently divided into embryonic, larval, and adolescent periods, which close, respectively, with hatching, the emergence into the fourth stage, and the acquisition of the secondary sexual characters and full adult power, reached in the female, according to Hadley, at the twenty-third molt. The age of sexual maturity or the entire period from larva to adult is subject to great fluctuation, owing to individual variations, changes in the environment, and to other causes. A 10-inch female lobster may be from 5 to 6 years old, or even older. There are really no sudden transitions, but only gradual progressive changes, the nature of which especially at the fourth stage is often disguised by the abrupt passage of the molt.

The embryonic life within the egg membranes is the most constant, occupying approximately ten and one half months on the coast of Massachusetts, during which the stored yolk supplies the materials and energy for growth. When this period is closed at hatching, the egg membranes burst, and together with a larval cuticle are cast off, thus leaving the animal free to enter upon an independent career. A remnant of unabsorbed yolk always remains, however, in the mid-gut region and serves to tide the little lobster over a critical interval before it is thrown entirely upon its own resources.

Pairing probably does not continue long after sexual union has been accomplished, yet when confined in ponds lobsters have been known to hold together for several weeks, and even to occupy the same shelter. (See p. 302.)

Parental instinct developed in the mother is mainly directed to the safe fosterage of her eggs. The young disperse as soon as hatched, rising to the surface, where they swim as free pelagic organisms until their larval life is over. Development proceeds through a series of metamorphoses or individual changes, externally marked by a corresponding series of molts, in the course of which the old cuticle is periodically shed in its entirety and as one piece to give place to the new covering already formed. The abrupt molts thus furnish a ready means of following the development and growth of the crustacean step by step from infancy to old age. The embryo virtually molts several times, though its cast cuticle seems to be mostly absorbed. The first of these membranes to be shed and absorbed in the egg is secreted by the blastoderm, and was mistaken for a true yolk or egg membrane by the older observers. As we have already noticed, the ripe crustacean egg possesses but a single protective envelope, the chorion or flexible shell, which at hatching time has been reduced to a layer of great tenuity.

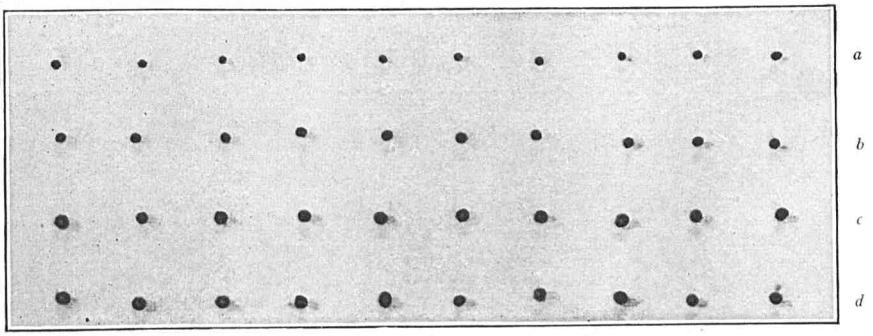


Fig. 1.

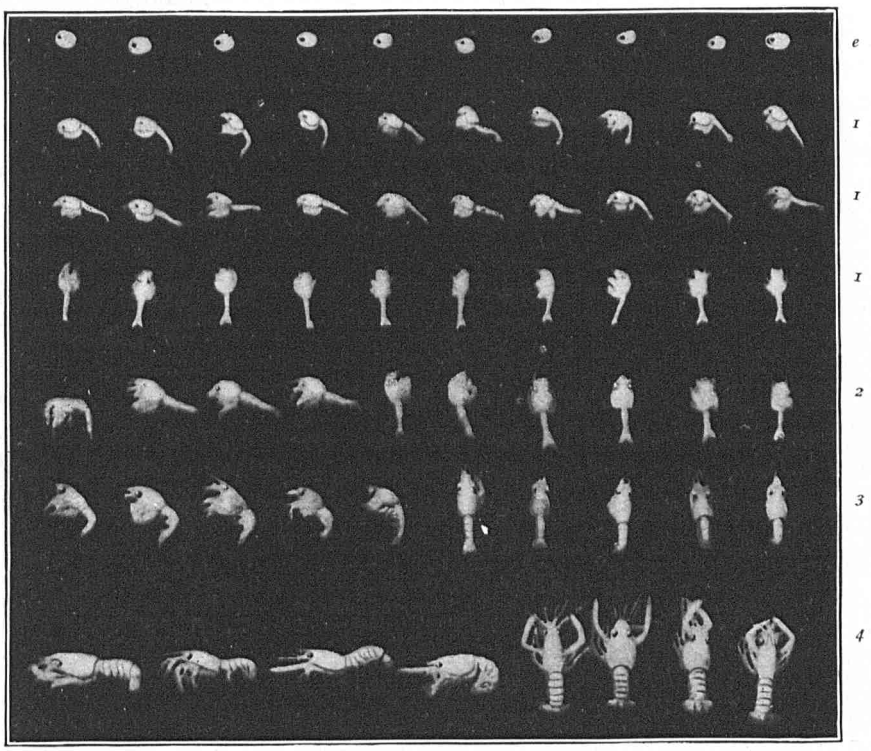


Fig. 2.

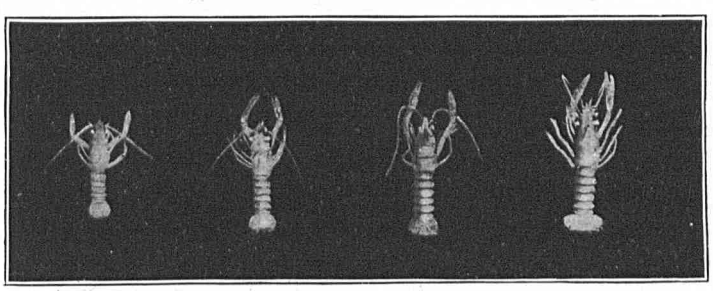


Fig. 3.

FIG. 1.—Growth stages of lobster eggs and young to illustrate relative sizes attained at Woods Hole, Massachusetts. *a*, ovarian ova in June; *b*, external egg in invagination stage, July; *c*, egg-embryo, September 1; *d*, embryo, March 1. In this and following figures, all represented in full size from alcoholic materials.

FIG. 2.—Growth stages of young lobsters continued. *e*, Embryo at hatching (July); *1* (first line), first larva, not free from first molt; *1* (second and third lines), first free larval stage; *2*, second larva; *3*, third larva; *4*, fourth stage.

FIG. 3.—Growth stages of the lobster continued. *4*, Fourth stage; *5* and *6*, fifth and sixth stages, respectively.

When the lobster is ready to hatch, it is therefore covered from head to foot with a close-fitting chitinous tunic which must be shed before active life is possible. As explained earlier, this outer garment sticks to the egg coverings and is kicked off when these are cast aside.

Before hatching and therefore before the molt which occurs at birth, the terminal telson is forked, and in this respect recalls the more primitive protozoëa larva, which has been attributed to the lobster without any further warrant than this fact; the first larva resembles an overgrown zoëa, and the fourth corresponds in some degree to the megalops state of the crab.

Since the first larval stage is preceded by a true molt, failure to pass which is often fatal in the operations of fish hatcheries, it has seemed best to recognize this fact. The molts and stages will therefore be named and numbered uniformly; molt 1 introduces stage no. 1, and not stage 2, according to most writers on these subjects; molt no. 4 precedes stage no. 4, and so on.

The first larva (fig. 34 and pl. XXVIII) is about one-third of an inch long, and continues to swim near the surface for from 3 to 5 weeks, or until the fourth (pl. XXXI) or fifth molt, when it sinks to the bottom and passes the remainder of its life essentially like an adult animal. The life of such a crustacean is thus made up of a series of stage periods, each of which represents the time passed between successive castings of the shell. The first four periods during which growth is most rapid and change most profound are passed rapidly. After this point, and particularly after the sixth or seventh stage, except for increase in size, there is comparatively little change from molt to molt.

During the three early stages the larvæ lack the power of very precise orientation. They will move steadily for a time with nicely coordinated movements, when their equilibrium is suddenly upset and they begin to reel or turn over completely. This seems to be due to the fact that their statocysts, which are the most important balancing organs, are not well developed until the fourth stage.

Twins and monsters are occasionally born, a fact noted by Brightwell in 1835, but this seldom if ever occurs under normal conditions. (See ch. VIII, p. 287.) In two cases of twins observed by Anderton in the European species one larva was released earlier than the other, which continued to rotate in the egg until set free.

The following changes in structure and instincts take place at the fourth molt or beginning of the fourth stage, which marks the most surprising leap in the whole history of development: Loss of the primitive swimming branches of the thoracic appendages; the cuticle becomes shell-like, containing more lime; the pigments are denser, the colors brilliant, and the color pattern variable; otocysts are present and orientation is perfect; rotation of great forceps is complete; the animal, during at least a part of this stage, moves toward the light and swims steadily at the surface with great claws directed forward and held close together; the preying instinct is more marked; the fighting instinct, the instincts of fear, "feigning," and hiding are all developed at the beginning or close of this stage or in the fifth, which follows, when the animal goes to the bottom to stay.

When a bottom life is finally adopted, the instincts of burrowing, hiding, wariness, pugnacity, and preying become strongly accentuated. The animal is negatively phototactic and tends, as in all later stages upon the whole, to avoid strong light.

In the larval lobsters the big claws are prehensile organs solely, by which the food is seized and transferred to the mouth parts. At the fourth stage the great double claws are perfectly developed, similar in structure, and of the primitive toothed type. The smaller chelæ and other appendages are in perfect symmetry. At about the sixth or seventh stage a difference in the big claws begins to appear, the claw on one side developing crushing tubules and becoming larger and heavier in accordance with the greater development of its muscles. The smaller forceps, the jaws of which have developed serially arranged teeth, retains its primitive form. Whether right or left claw shall be of the toothed or crushing type is predetermined in the egg, all members of the same brood in all likelihood being either right-handed or left-handed. (See p. 274.) Injury or mutilations, however, may determine the position and character of the claw in after life.

At the seventh molt the cast shell is blue with some green and brown pigments on the tergal surfaces. Pigment is thenceforth more and more deposited in the outer calcified layer of the shell, which becomes wholly responsible for the color of the animal. The dorsal median stripe of the carapace, which marks an absorption area of distinct service in molting, is much narrower than when first observed in the fourth stage. At the time of the fourth molt this linear area is one-eighteenth of the width of the carapace at its widest part. It gradually narrows until in the adult state it is in the proportion of one-sixtieth or less.

The sex can be determined as early as the eighth stage by the openings of the sexual ducts, which in the male arise in the coxa or basal segment of the last pair of thoracic legs and in the female on the coxæ of the third pairs of pereiopods. The sex can not be determined by the modified swimmerets of the first abdominal somite until some time between the eighth and the tenth molt. At about the eighth stage also the peculiar seminal receptacle of the female begins to undergo its characteristic differentiation.

During the adolescent stages, when the lobster of either sex measures from 1½ to 4 inches in length, there are certain marked characteristics—the relatively large size of the eyes, recalling those of the shrimp *Penæus setiferus* and probably a relic of an ancestral stage, the fringe of long setæ on the tail-fan, and the tufts of hairs about the ends and along the serrate jaws of the toothed claw.

With this introductory sketch, we will examine more closely the embryo and larva, although it is not our intention to enter minutely into all the details of their structure.

EMBRYO.

The freshly laid eggs are dark green, almost black in color owing to the presence of the soluble pigment, a lipochromogen, in the yolk, and the glass-like transparency of their membranes. (Compare p. 298.) The golden yellow variation, which is often associated with dark green, as in the eggs of certain shrimps, has not been observed in

the lobster, but its eggs are occasionally straw color, grayish-green, or yellow-green. When plunged in alcohol or hot water the ova respond like the shell of the animal and become light red, a more stable pigment, a lipochrome, soluble in alcohol, being formed. By adding alternately hot and cold water the eggs may be turned to red and green several times in succession.

The fresh-laid eggs, which are seldom seen, can be detected by examination with a hand lens. The transparent capsule closely invests the yolk, which presents a very fine-grained and uniform texture, quite different from that which the ova later possess. Maturation is without doubt completed by the formation of polar cells either in the ovary or during the passage of the eggs to the outside, although we have never been able to find these bodies in stained sections of the egg. External segmentation of the yolk follows in from 20 to 25 hours after oviposition, and the large yolk segments which are early formed can be detected by the naked eye. A clear perivitelline space, apparently filled in part with exudatian from the egg, soon appears between the shell and yolk. At the close of this process, or after invagination has begun, the living egg, when examined with a hand lens or low power of the microscope, is likely to be mistaken for one freshly laid. The ova, however, are not so closely adherent, are somewhat lighter in color, and the yolk has a coarser and more irregular texture. The first division of the protoplasm is central or subcentral. In the second and third segmentations, with four and eight cells, the products begin to separate and migrate outward. The greater number tend to move toward the side which marks the animal pole, where the yolk becomes distinctly flattened, and the shell correspondingly elevated. The cells which migrate toward the surface of the depressed area bring about the first segmentation of the yolk into hillocks. As they multiply by indirect division their products diffuse over the egg, and at the fifth segmentation, of 32 cells, the entire surface of the yolk is thrown into hillocks or inverted pyramids. The segmentation is rythmical, the early periods lasting about 4 hours, but the rythms of individual cells are not in harmony, and the segments are unequal. Later when about 110 cells are present the periodic divisions become more uniform over the entire egg. With each division the protoplasm approaches nearer the surface, and meantime a limited number of cells are formed by tangential divisions and migrate to the depths of the yolk. By a continuation of this process the yolk becomes surrounded by a thin mosiac of cells, or rather by a single tier of several thousand minute columnar cells or diminutive yolk pyramids of uniform size. Their "apices" blend into the central yolk mass, which harbors a few wandering and degenerating cells.

Cell division then becomes more rapid over a considerable area of the surface, which includes the animal pole, and at a certain point an invagination of superficial cells occurs. This begins by the in-wandering of a few cells, and is followed by the rapid multiplication of those thus immersed in the common food stock of the developing egg, and by the sinking of a small area of the blastoderm about this point, forming what is usually called the "egg gastrula" stage. The depression is at first shallow, and becomes a well-defined circular pit, but is never very deep. It is subject to marked

individual variation, but commonly elongates transversely to the long axis of the future embryo, endures 4 or 5 days, and then completely disappears. In front of the pit a wide embryonic area is defined by rapid divisions of the surface cells. The latter, which are the direct descendants of the enormous yolk pyramids or hillocks, become distinctly separated into a single stratum of yolk-laden and columnar cells. Below the point of invagination the ingrowing plug of cells expands by rapid divisions of its elements, and like columns of smoke from a steam engine a dense cloud-like mass is spread into the yolk. Many of the cells break loose from the syncytial mass and worm their way through the yolk like independently moving amœbæ. Many of them degenerate, while others creep forward and attach themselves to the embryonic area. The cells introduced by invagination give rise, in terms of the germ-layer theory, to the hypoblast or endoderm, and to at least a part of the mesoblast. It is almost certain that the yolk-wandering cells receive many recruits from the surface of the embryonic area; the yolk cells introduced earlier for the most part degenerate before the stage of invagination is reached. By multiple divisions cell nests are formed, particularly in the embryonic region at the surface, or more commonly just beneath it in the midst of spheroidal masses or balls of yolk.

Death waits close upon the birth of new cells, and from an early stage to the later egg-nauplius period degeneration is a marked characteristic of this and many other arthropod embryos. Nebulous clouds of chromatin strew the paths of cell migration, and are carried to every part of the egg, where they remain until absorbed. In the early stages at least embryonic layers do not exist, and attempts to reconstruct them out of a mass of rapidly multiplying, degenerating, and moving elements, by the aid of theory and the imagination, have thus far proved neither successful nor profitable.

The appendages are the first of the distinctly embryonic parts to make their appearance; they are formed by paired tubular folds of the body wall. They possess solid yolk cores which are gradually absorbed and replaced by mesoblastic cells which migrate from the embryonic region. The limbs arise in pairs in the following order: (1) First antennæ, (2) mandibles, (3) second antennæ, (4) first maxillæ, and the remaining thoracic appendages in regular succession. The second antenna soon becomes bilobed, the inner branch representing the future long "whip" or flagellum of this limb. The first antennæ remain single until shortly before hatching, when the inner flagellum buds out from the inner lower surface of the primary stalk (see p. 226). The optic disks, at first paired rounded areas of rapidly dividing cells, soon become elevated into lobes and form the rudiments of the large eyestalks. The mouth appears at about the ninth day as a median pit on a line drawn through the hinder margins of the buds of the first antennæ and before the second antennæ are formed. At the tenth day the three pairs of nauplius-appendages are present as buds; a day or two later the upper lip or labrum has grown down over the mouth and a larger fold representing the abdomen and a part of the thorax has grown forward from the region of the thoracic-abdominal plate, marked by the earlier point of invagination. At 14 days of age the latter fold is divided at its extremity, which represents

the forked telson-plate of the larva and touches or overlaps the lip. In 3 weeks the conical eyestalks are most prominent; 8 to 9 pairs of appendages are present, and the telson overlaps the brain. The brownish black eye pigment of the retinal cells begins to appear in the fourth week as a thin crescent at the base of each lobe, and gradually extends in area until in 3 or 4 months time it forms the large, rounded eye spots, so conspicuous a mark from this time onward. A cuticle to be later absorbed surrounds every part of the embryo, and rudimentary setæ are beginning to appear on the telson plate and antennæ.

Up to the fourth week internal changes, which we shall not attempt to describe, have led to the already complex foundations of the nervous and muscular systems, the heart, and alimentary tract. Of the latter the stomodæum or oral invagination gives rise to a distinct pouch from the epithelial lining of which the cuticular coat of the mouth opening, esophagus, and stomach sac are derived. The proctodæum, to which the anal opening and lining of most of the intestine is due, is similarly formed through a median ingrowth of ectoderm near the posterior end of what becomes the thoracic abdominal fold. The cuticular lining of the intestine when formed, like that of the stomodæum, is continuous with the outer skin and must be shed at every subsequent molt. The proctodæal invagination is at first solid or nearly so and is not sharply bounded from the yolk, which with its inclosed cells distinguished as hypoblast, represents the embryonic section of the digestive tract, called the mesenteron, and gives rise to the gastric glands and to the epithelial wall of a small section of the tract into which they open. The walls of the mesenteron become continuous with those of the proctodæum and are gradually extended forward on all sides until the entire yolk mass of the egg is inclosed within the folds of the paired gastric glands and forward division of the intestine. At a later period of embryonic life the screen which separates the stomodæum from the yolk is absorbed and its walls unite with those of the mesenteron. At the time of hatching the residue of the yolk lies in the folded walls of the lobulated gastric glands, from which it is finally absorbed. This residual yolk sometimes appears to pass to the masticatory stomach, but if this ever happens it must be due to secondary displacement, as will be readily understood from the relation of the yolk to the mesenteron just described. The functions of digestion and absorption, which the gastric glands or liver display on a large scale throughout the embryonic period, are retained in adult life as already noticed. (See p. 249.)

The intestine in the higher Crustacea, excepting only its terminal portion, is commonly described as arising from the endodermal or hypoblastic wall of the midgut, or mesenteron, but this is certainly not the case in the lobster, which sheds an intestinal cuticle during its pelagic stages. A median longitudinal section through the body of the larva at the time of hatching shows a distinct cuticle passing forward along nearly the entire length of the intestinal tube, and finally shading off and disappearing opposite the gastric glands. The epithelial lining of the intestine is therefore almost wholly of ectodermic origin and continuous with the epithelium of the skin, a conclusion which embryological study fully supports. Apparently in the adult animal the cuticular

lining terminates abruptly at the forward end of the rectum, but this is not the case in early life.

During the course of development the ova increase considerably in size, and, losing their original globular form, become distinctly oblong (fig. 33, *a* and *b*). The bright red pigment cells or chromatophores, which are distributed in a characteristic manner, particularly on their basal segments and on the sides of the carapace, are prominent for a long time before hatching. These, together with the interference colors of the huge eye-spots and the rich green of the unabsorbed yolk, give the eggs of the lobster exceptionally brilliant color patterns.

EXCLUSION AND DISPERSAL OF THE BROOD.

It was found that when the eggs at the point of hatching were removed from the mother lobster and placed in jars at Woods Hole a full week elapsed before the entire brood was set free. Possibly the period is shorter when the animal is undisturbed and left to her own devices in the sea. When other conditions are favorable, the warmer the water the more rapid will the emissions occur. The individual variation in the eggs entailed by the long period of fosterage render it certain that all can not hatch simultaneously. Fullarton (*113*) found that in the European lobster the time required for the hatching of a brood varied from one to three weeks or even longer, but it is not likely that this period is extended to very great lengths under natural conditions.

FIG. 33.—Outlines to show relative sizes of lobsters' eggs when laid (*a*), and when ready to hatch (*b*). Enlarged about 3½ diameters.

The egg-bearing lobster instinctively folds its tail, thus securely inclosing the eggs in the abdominal pocket when in danger of enemies, while at other times she is seen at intervals to extend her tail and, standing upon her legs and incurved tail fan, move her swimmerets back and forth. In this way the eggs are aerated and cleaned, and such actions proceed instinctively during the 10 months of parental care which they receive. The cargo of eggs shows the effects of the treatment, for they pass the storms and stress of winter with remarkably little loss, and come to point of hatching bright and clean. It is rare to detect a single barren egg or broken embryo among the thousands of perfectly formed young. Yet when the egg-bearing lobster or crayfish are too closely confined, or the normal conditions of their environment seriously disturbed, sediment soon clogs the eggs and parasitic protozoa and other organisms attack and destroy the egg glue to such an extent that the ova fall off of their own weight and soon perish.

It might prove to be a point of some interest to determine whether the rhythm of the swimmerets is fairly uniform or not from the beginning to the end of the period of fosterage, but nothing can be said on this subject at present.

The behavior of the American lobster at the time of the emission of the young has not been studied with sufficient care under natural conditions; accordingly, I transcribe the following observations made on the European species by MM. Fabre-Domergue and Biétrix (*101*).

In order to ascertain as exactly as possible the age of our young lobsters, we determined to collect them for the space of twelve hours, a circumstance which led us first to find that hatching never takes place by day. At from six to seven o'clock in the evening not a larva was visible in the water of the float. Two hours later we could see several hundred of them swimming about. If we removed all of the latter with care, no new arrivals appeared before the evening of the following day. To what was the rapid emission of larvæ in so short a time due? The continual observation of our float during the first hours of night soon showed us the key to the enigma.

Toward seven to eight o'clock in the evening the female commenced to stir herself in her prison by presenting an attitude altogether unusual and characteristic. Her feet are stretched out almost rigid, her tail extended to the full in a horizontal direction, forming, with the rest of her body, a nearly straight line. She walks, as we might say, upon her toes, so careful is she to hold her entire body as far away as possible from the bottom of the aquarium. This feat lasts for a certain time; then quickly lowering her head and the fore part of her body until she rests upon the ground between her outspread claws, with tail on the other hand raised at an angle of 45 degrees and kept stretched, we see her violently shake her swimmerets with such rapidity that the eye cannot follow the movement, and a veritable cloud of larvæ are sent far to the rear and dispersed in all directions.[a] This phenomenon lasts from 15 to 20 seconds, and the female thereafter returns to her habitual attitude, to depart therefrom no more until the following evening. We have repeatedly verified the fact by observing always that the larval emission is produced in certain cases by two series of distinct movements, lasting some minutes, the second producing much fewer larvæ than the first.

The hatching does not therefore proceed independently of the mother and does not take place at all times of the day and night, but is confined to the hours of eight to nine o'clock in the evening.

The first molt which follows hatching is effected in the hours which precede the emission, and it is without doubt the movement of the larvæ under the abdomen of their mother which causes in her these signs of agitation and unrest already described. If, in short, one tries to draw the female out of the water when in this condition, we can see in her movements of defense the downfall of a great number of larvæ previously hatched but doubtless united to their mother by the molted membrane which her violent movements sufficed to break or to detach. Unfortunately we have been unable to assure ourselves whether, as Laguesse has observed in the crayfish, the young are found attached by the telson to the debris of the shell or of the molt (compare p. 167).

It should be noted that on occasion larvæ appear to be normally hatched in the daytime, and that a few may even resist the movements of their mother to disperse them, and remain for some little time attached to her body, though capable of swimming. In regard to the hatching of the European lobster when confined in ponds at the marine fish hatchery and biological station at Portobello, New Zealand (see p. 298), Mr. Anderton has written to me as follows: The hatching "almost always takes place at night. I say *almost* advisedly, since this last season a batch has frequently been hatched during the afternoon by a violent aeration of the tank water. I think about 1,700 has been the largest number hatched from a single individual during one night."

THE HATCHING PROCESS.

As already observed, what we shall consider the first molt of the larva is passed at the time of hatching, and in this act the larval cuticle and shell membranes are shed together. The stalked secondary egg membrane, representing the glue or fixative by

[a] With this specific and graphic account compare the brief statement of Coste, made nearly a half century before, that "The brood females straighten their tails, which up to now have been carried bent against the plastron, gently oscillating those appendages to which the bunched embryos are attached, as if to scatter the larvæ, and to aid them in breaking the shell, and hus free themselves in the course of a few days of their entire cargo." (55, p. 205).

which the eggs are attached to each other and to the body of the mother, in consequence of internal pressure, splits lengthwise of the embryo and its two halves separate like the skin of a pea. The primary eggshell or transparent "chorion," reduced by distention to a sac of great tenuity, adheres to the outer capsule at a point usually beneath its stalk and is in turn apparently adherent in some degree to the embryonic cuticle. Further, the invaginated hairs or setæ of the larva about to issue stick by their tips to the cuticular sheaths of the corresponding setæ. Consequently, successful hatching in the lobster means shedding the egg membranes with the old cuticle and the pulling out of the invaginated hairs of the new chitinous covering at the same time. Hatching and molting thus go hand in hand, and the first larval stage, like every period which follows, is preceded by a molt. The fact that hundreds of the larvæ which are hatched by artificial means get clear of the eggshells, but die through inability to cast this embryonic cuticle, illustrates the importance of these nicely adjusted relations.

It is thus evident that we can not help the little lobster out of its shell, but must let it escape in its own way, and if healthy it will cast in a few minutes. Its old covering must be shed in one piece and with the loss of as little energy as possible. The infant lobster hatches, molts, and unsheaths its swimming hairs at the same time, as was explained more fully in an earlier chapter (see ch. VI, p. 236). The eggshell, as we have also seen, sticks both to mother and child, while the cuticle of the latter is in turn glued to the swimming hairs of the new skin, so that every tug at the shell helps to free the little lobster from its hampering cloak and at the same time to perfect its swimming apparatus.

The young lobster is very compactly folded in the egg, which becomes ovoidal in consequence of growth. At the time of hatching this marked ovoidal form of the embryo is largely determined by the form of the carapace, which is longer than broad. The body is bent, but not twisted, the tail, as in all crustaceans, being folded against the thorax and head, the tips of the telson plate even reaching beyond the compound eyes and to a point overlying the masticating stomach. The mouth is thus covered by the overlap of the hinder part of the fifth somite of the abdomen, which also presses against the downwardly bent rostrum and the mouth parts. The antennæ are directed backward along the free borders of the carapace, while the thoracic appendages with their outer branches, like a double bank of oars, are directed downward over the abdomen and forward toward the middle line. Hatching thus implies not only release from the egg membranes, but casting off a complete cuticular molt and at the same time the evaginating or drawing out of every telescoped hair and spine of the body, including the rostrum; further, in addition to this and aided by it, the unfolding of the abdomen and the straightening of the telson and the various appendages.

Little difference in the size of the eggs was noted by Anderton (5) in the European lobster until the last month of development, when they increased as much as 3 millimeters in length in conformity to the shape of the embryo, and when convulsive movements of the embryo itself were often violent enough to move the egg from under the object glass.

THE FIRST LARVA.

[Pl. XXVIII and text fig. 34.]

When the lobster has successfully escaped from the egg capsule and shaken itself free from its cuticle, it emerges as a free-swimming animal and eventually rises to the surface, where it remains rising and sinking, but probably never far removed from the actual surface until its pelagic life is over.

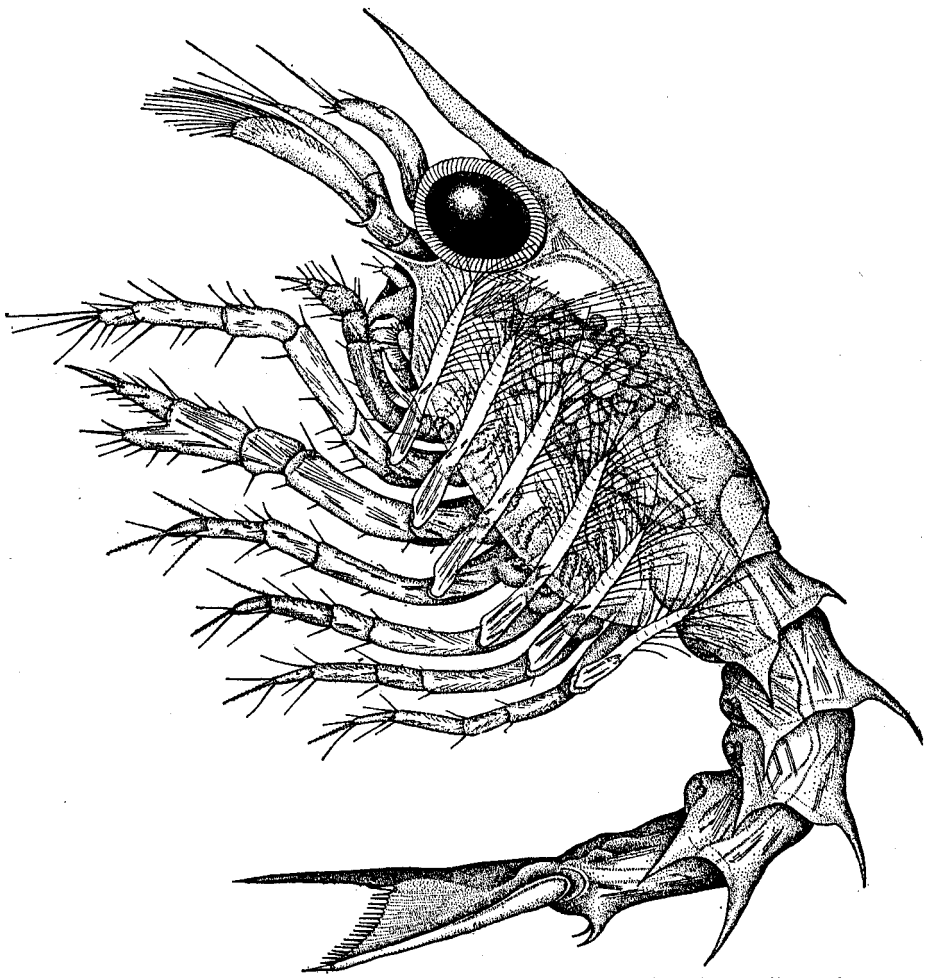


FIG. 34.—First larva, or first swimming stage of the lobster in profile. For drawing colored to life, see plate XXVIII; for natural swimming hold page sidewise with head of animal down, and compare figure 40 of text. Length about 8 mm., or a little less than ⅓ inch.

The animal is but little over a third of an inch long. The body is segmented as in the adult form, the most striking characteristics being the enormous eyes, the conspicuous rostral spine, which projects like a sharp spear in front, the triangular telson, and the biramous swimming legs, which, from their resemblance to the permanent swimming

organs of the schizopods, have given to this and the two succeeding larvæ the name of the "schizopod" or "mysis stage." Functional appendages are wanting only in the abdominal segments, where, however, very small buds of the adult swimmerets can be seen beneath the cuticle in the second, third, fourth, and fifth abdominal somites.

The cuticle of the larval lobster is now as translucent as glass, and such organs as the heart and blood vessels, the alimentary tract, and the rudimentary gills are seen with

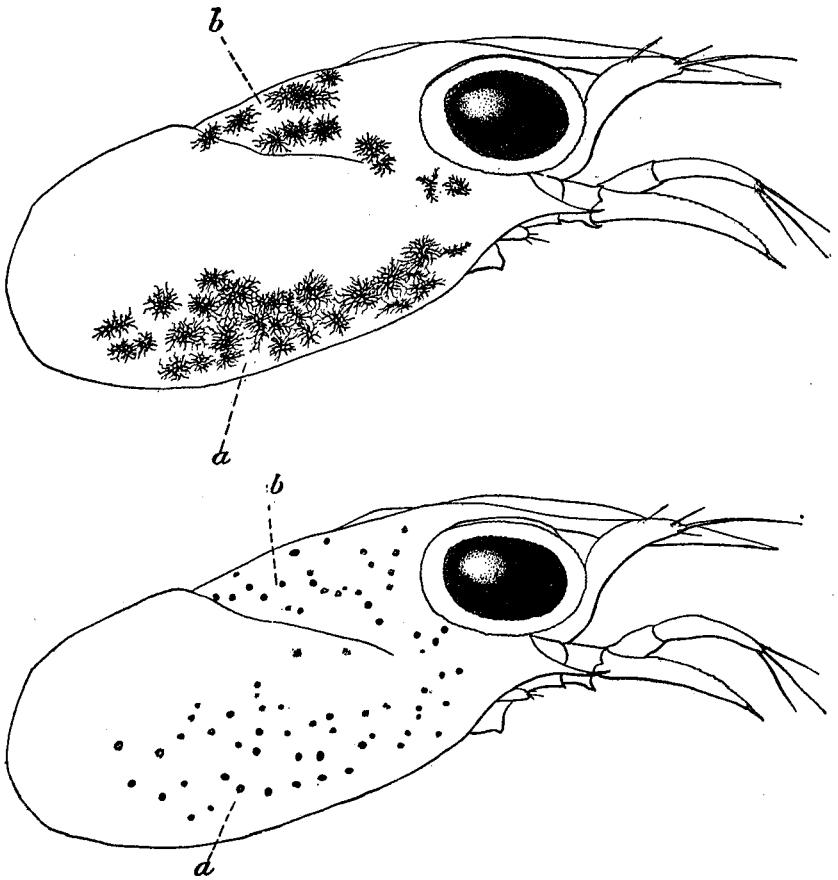


FIG. 35.—Cephalothorax of lobster in first stage when under stimulus of pressure, drawn immediately after reddening, through expansion of chromatophores. *a*, *b*, Lateral and dorsal red chromatophore groups; yellow pigment not here shown.

FIG. 36.—Cephalothorax of the same individual 10 minutes after release from pressure, and after paling from contraction of chromatophores. Both the red (solid) and yellow (dotted) pigment cells are indicated.

great clearness. The green food yolk has disappeared entirely or is reduced to a mere remnant now more yellow than green, in the masticatory stomach. Perhaps the most conspicuous internal organ is the yellowish-brown "liver," or gastric glands, the form of which on either side of the body resembles a cluster of grapes.

Color of the larva.—The gay coloring of the larval lobster, aside from that contributed by the internal organs and contents of the ailmentary tract, is produced by a blue pigment dissolved in the blood plasma and by red and yellow chromatophores which lie in the dermal layer of the skin, besides the pigment cells of the eyes. The distribution and grouping of the red chromatophores is very characteristic, and it is to these that the brilliant colors of the larvæ are largely due. The red cells are the larger and play the most prominent rôle. The expansion and contraction of the chromatophores, by which the animal becomes brightly colored or pale, ordinarily requires from 10 to 15 minutes when stimulated by pressure and released (fig. 35 and 36). The chromatophores are distributed in a number of well-defined regions, namely the carapace, in front of the cervical groove, the gill covers or sides of the carapace, the large claws and bases of the cephalo-thoracic appendages, and the dorsal surface of the abdominal segments, including the telson. These centers of color distribution are well marked from a late embryonic period to the lobsterling or fourth stage, when the change in the lobster's coloring is no less profound and abrupt than that of its structure and habits. When the chromatophores contract under the influence of a stimulus the animal becomes pale blue and very translucent; when they expand the vermilion cells give it a much more decided color. Pale blue at night, bright red by day is the rule, and among external agents sunlight seems to provide the main stimulus which causes the chromatophores to expand, but other changes, like raising the temperature or applying pressure to the body, will produce a like result. If the young lobsters are suddenly placed in darkness they tend to become paler and if returned to the light to redden more or less promptly. But the internal conditions or physiological states of the animal evidently present another and highly variable factor. All larvæ do not redden in the sun and all do not pale in darkness, while some respond more promptly to all such changes than others.

When the larvæ are seen struggling on the bottom of an aquarium, to get free from their old cuticle, when crippled in any way, or as Hadley remarks, when starved for some time, they so often turn red that this color has been regarded as a sign of weakness. On the other hand, if thousands of larvæ hatched and reared indoors are suddenly set free in more brilliantly illuminated water outside, a large proportion of them will redden, though not all. It has been asserted that the young and adult in all stages are upon the whole more active by night than by day, and that the young tend to move toward the source of light, or toward the surface where they find their suspended food. If the latter statement were true, we should expect to find the young larvæ at the surface of the ocean in the daytime and in active movement. Prof. S. I. Smith has taken the larvæ in all stages in the surface waters of Vineyard Sound in the daytime, and in several instances when using an electric light at night. These larvæ are often seen to pursue their prey by sight, and it has been shown that they can orient themselves through the medium of the eye. We thus seem to become entangled in a web of contradictory statements. The larvæ are more active in twilight or at night, but seek the light, and pursue their prey in the daytime, by the aid of sight. Red is a symptom of weakness, but they redden in the light.

The difficulty seems to lie in the fact that any given reaction is the resultant of complex conditions, which can be regularly repeated only when those conditions remain uniform. The life of the lobster during all of its free swimming life is apparently one of incessant activity, whether swimming at the surface or at whatever distance below it, and at all times of the day or night. In the account of their reactions to light, which later follows, it will be seen that their behavior is very complex and very variable. Certain responses may not only vary but even disappear altogether in consequence of changes in the organism or in the stimuli which affect it. Further, since the chromatophores as well as the muscles of locomotion are under reflex control of the nervous system, it is not more surprising to find variations in the responsive behavior of the pigment cells than in the activities of the body as a whole.

All that can be definitely said at present concerning the gay and plastic coloring of the larvæ is that it is an expression of chemical and physical changes in the body, due to stimuli, some of which are unfavorable, and that they have no protective significance. If every larva remained pale while swimming at the surface in the daytime, and took on color only at night, which is not the case, there would be no reason for supposing that there was a relation between the origin of the habit and the protection which it afforded because of the vast indiscriminate destruction which all such larvæ suffer at the hands of inanimate nature. That any such hypothetical protection would really count for nothing is further shown by the fact that the young lobster emerges at the fourth stage in a richly colored dress which renders it more conspicuous at the surface where it still swims than it would be if it remained colorless. For the continuance of the race a single lobster in the fourth stage is worth many hundreds in the first, and we should hardly expect to find nature at one moment using certain measures to protect life and at the next the same means for destroying it.

Both the blue pigment of the blood and the yellow and red pigment of the chromatophores, as already remarked, are lipochromogens, which are converted into lipochromes under a variety of conditions whether the animal is dead or alive. The stomach and liver are sometimes bright red, which recalls an observation by MacMunn, who concluded from spectroscopic evidence that in the lobster (*Homarus gammarus*) the enterochlorophyll of the liver might be carried to the hypodermis and converted into a lipochrome.

Structure and habits.—The most striking habits of the little lobsters immediately after birth are their incessant and apparently aimless activity, their preying and fighting instincts, and their voracity, which invariably results in cannibalism whenever the food supply is insufficient or unsuitable and where the young are too closely crowded in either vertical or horizontal limits; their seeking or avoidance of light under the variable sum of all the conditions which influence their behavior; their unstable, vacillating movements in the daytime or when stimulated by strong light; the total absence of the instincts of fear and concealment so clearly expressed at a later stage; their sharp vision for small floating particles at close range; their lack of precise discrimination, snapping up many inorganic particles or dead organic substances which are useless as food; their pursuit

and often successful capture of copepods and other members of the plankton or floating population, showing that they can direct their movements with a certain degree of precision when necessary or when the light and other conditions are favorable.

The body of the little lobster is armed at most vulnerable points with defensive spines, and its various appendages bristle with tactile hairs or setæ, as well as with more diminutive spines, which may afford some slight degree of protection against smaller enemies when they do not assist it in seizing and tearing its prey.

The free margin of the "paddle," or forked telson plate, as commonly seen in the larvæ of the higher Crustacea, is garnished with very uniform and symmetrical spines and plumose hairs.

It is interesting to observe that certain spines and the setæ whatever their size or function, from the rostrum or tips of the claws down to the smallest microscopic hair, agree in their essential structure, and are all developed as tubular folds or outgrowths of the integument. In the course of the prenatal molt all the spines as well as the hairs are telescoped or invaginated. (Compare p. 269–270.)

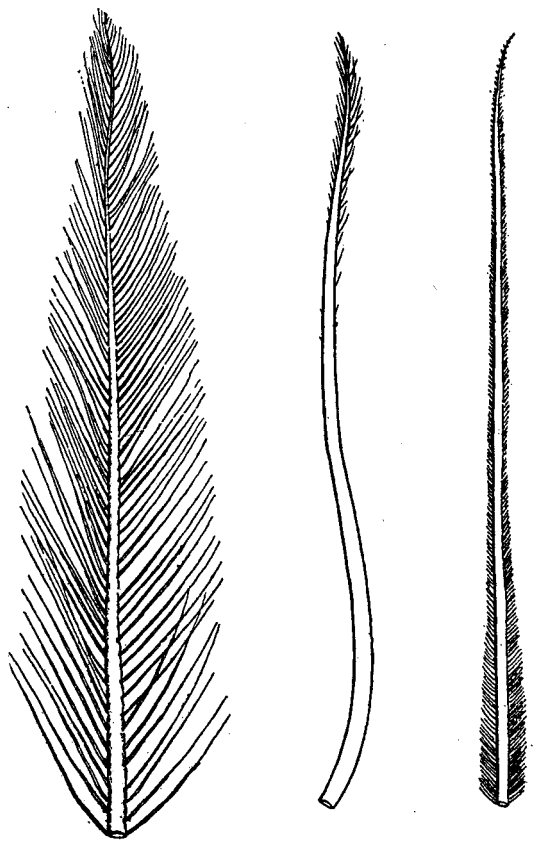


FIG. 37, 38, and 39.—Parts of setæ from cheliped of larval lobster, showing different degrees of reduction from typical plumose type. Enlarged 85 times.

In swimming the young lobsters use the outer branches or exopodites of the thoracic limbs (segments IX–XIV, table 4), by the beating movements of which they are slowly driven upward, downward, or forward (compare fig. 40), and the abdomen, by the sudden folding of which and by the aid of its broad telson plate, they dart rapidly backward. Each thoracic leg, in conformity to the type of decapod limbs, consists of a short stalk or protopodite and two diverging branches, the outer branch or exopodite which serves as a flexible "oar," being flattened and fringed with long feather-like hairs.

The "oars" work independently of the inner branches, which in the larva are mainly prehensile organs, and which with the stalk alone give rise to the adult limbs. The concerted vibratory strokes of these minute flexible oars is so rapid and so uniform in vigorous larvæ that at a short distance from the eye it is impossible to follow their movements.

The exopodites atrophy, and are reduced to microscopic rudiments in the fourth stage, and completely disappear in the fifth. No doubt in this respect there is variation, however, as Williamson (*282*) has found to be the case in the European lobster.

In rising with head inclined, the body is usually bent into a quadrant, and according to Hadley (*131*) when the appendages are extended forward the exopodites strike somewhat forward as well as downward and thus drive the lobster upward and backward (fig. 40, *c*); when on the contrary the thoracic legs are contracted or drawn backward the larva is driven forward and upward. Whatever the direction of movement, as this observer has also pointed out, the animal always heads away from the source of light. In swimming near the surface the thorax is sometimes held horizontal with tail bent at an angle of 45°, more or less (*a*); when riding down another larva, feeding upon its carcass, or grappling with a lobster's egg the body is straightened (*b*); in the ascending currents of a hatching jar the young frequently come to the surface tail uppermost, and body vertical (*d*). By bending the body the weight is concentrated, which is especially advantageous in swimming upward. As Williamson remarks, the position of the body is correlated with the beats and direction of motion of the exopodites.

In hovering over the bottom, "standing on their heads," and as it might appear, probing the sediment with the rostrum (fig. 40 *f*), they are not trying to escape the light, as one observer has suggested, but are oriented for rising, being too weak, however, for any sustained effort. In every hatching jar or container many weakened individuals gradually settle into the sediment, a veritable trap for them, at the bottom, at first kicking away with strokes of the tail or standing erect with every oar in motion, but finally keeling over on their backs and beginning the death struggle to which there is usually but one ending.

The mutual destructiveness of the young lobsters when too closely crowded in aquaria has already been mentioned. When one lobster attacks another under these conditions the pursuer usually endeavors to get astride of his victim and with its sharp-pointed prehensile legs nip into the abdomen at its junction with the carapace. When the prey is an object too heavy to float, the lobster is frequently carried to the bottom; but if the animal is healthy it will be usually seen swimming about the aquarium dragging its prey with it and feeding upon it as it goes (fig. 40 *b*).

The beating of the heart and circulation of the blood begins at about the fifth week of egg development, or even earlier, and in the larval stages the heart and blood vessels have acquired the same general relations that we find in the adult.

The lobster at first possesses 19 pairs of filamentous gills distributed as in adult lobsters. The podobranchs are rudimentary, as are also the gill separators or epipodites, which are minute reniform plates exposed below the free border of the carapace. In the second stage these plates are taken completely into the gill chamber and the rudimentary gill of the eighth somite appears, which completes the branchial formula (see p. 246).

The nervous system of the lobster is highly developed in the larva and indeed before hatching, as shown by the admirable researches of Allen, (*2*), and brain, nerve

cord, motor and sensory elements, as well as the complex stomato-gastric system, have essentially the same relations as are found in an adult animal.

Natural food of the larva.—It is not to be doubted that the incessant activity of this larva, which apparently knows no rest day or night, is needed, as Mead remarks to

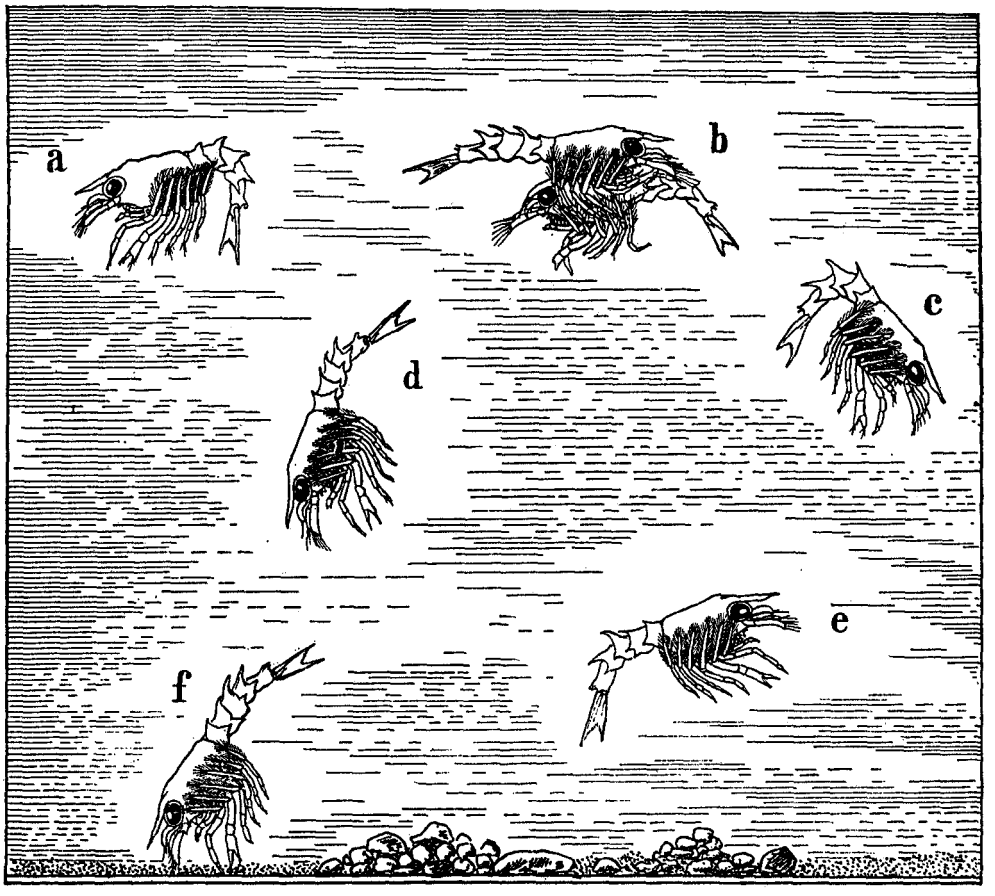


FIG. 40.—Swimming attitudes of young lobsters in the first free stages; *a*, lobster swimming with body bent in the usual quadrant form, the head directed downward and often at a greater angle; the swimming branches (and the permanent limbs rather more than here shown) directed backward, in "posterior" position of Hadley; resulting movement upward and backward; *b*, young lobster playing cannibal, swimming astride the carcass of another which it has nipped at the junction of the carapace and abdomen and holds with its prehensile legs; *c*, swimming with the thoracic legs directed forward; in "anterior" position of Hadley; resulting movement upward and forward; *d*, rising position occasionally assumed; *e*, slowly moving or "floating" position sometimes observed; *f*, lobster "standing on head," apparently probing the bottom with rostrum, but really too weak to rise.

bring them into contact with the minute suspended bodies upon which they feed. All the rearing experiments that have been conducted by Mead and others with any degree of success during the past 15 or 20 years, whether in Europe or the United States, have clearlv shown that the larvæ must have their food suspended and in fine particles; the

water must be gently agitated so that larvæ will not settle and become smothered in a mass of decomposing food and sediment at the bottom.

The natural food of the larval lobster consists of minute pelagic organisms, whether animals or plants, which through their own movements or their lightness remain suspended near the surface, such as diatoms and other protophytes, copepods, the larvæ of crustaceans, echinoderms, worms, and mollusks, the floating eggs of fishes, and, in fact, any member of the pelagic fauna which comes into their zone and is not too large for them to master.

The young lobster does not show, however, a very precise discrimination in its food. It will snap up almost any moving object, living or dead, which it is able to seize and swallow. Thus I have found in the stomachs of the older larvæ vegetable fibers, the scale of a moth or butterfly, and fine granules of sand.

An examination of the stomachs of a number of larvæ which were reared in aquaria to the fourth and fifth stages, when they measured 13 to 14 millimeters in length, revealed the following substances: (1) Diatoms in abundance, chiefly *Navicula* and the long tangled ribbons of *Tabellaria;* (2) remains of crustacea, probably parts of young lobsters; (3) bacteria in great numbers; (4) cotton and linen fibers and parts of algæ; (5) amorphous matter, with sand grains. The sediment of the jar contained the same species of diatoms in abundance, and amorphous débris similar to that found in the stomach and intestine.

Analysis of the stomach contents of a lobsterling captured in Vineyard Sound August 12 (length, 15 mm.) gave the following organisms: (1) Parts of crustaceans; (2) diatoms; (3) shreds of algæ. In another young lobster taken at the same time (length 17 mm.) there were (1) parts of crustaceans, (2) large numbers of diatoms, (3) filaments of green algæ and thin sheets or shreds of vegetable tissue, (4) the scale of a lepidopterous insect, (5) bacteria, and (6) amorphous matter in large masses. The diatoms and small amorphous particles of every kind may be regarded as partly or wholly incidental—that is, taken in with more important food material.

Williams (*279*) carefully examined the stomachs of one hundred larval and fourth-stage lobsters, which were being reared in the hatching bags at the Wickford (R. I.) station, and were fed with finely chopped clams. Thirty-seven contained copepods to the amount of 37 per cent of the total quantity of food present, and these favorite crustaceans were especially abundant in the stomachs of the second and third stage larvæ. Larval lobsters were almost invariably absent from their menu, from which he concludes "that a lobster in the presence of abundant food will not attack his kind."

A further discussion of food for artificially reared lobsters is given at the close of this chapter.

The length of the stage periods and the size attained by the lobster in each are subject to variations to be considered later: Length of first larva, 7.50 to 8.03 millimeters, average 7.84 millimeters (of 15 individuals); stage period, 1 to 5 days (Woods Hole, Mass.); length, 8.2 millimeters; period, 2 to 3 days, which may be extended to 25 days with the temperature at 60° F. (Mead and Hadley for Wickford, R. I.)

THE SECOND LARVA.

[Fig. 41.]

Under favorable conditions the first larval stage of the lobster lasts from 1 to 2 days. Upon molting for the first time after birth, the animal emerges into its second larval, free swimming stage.

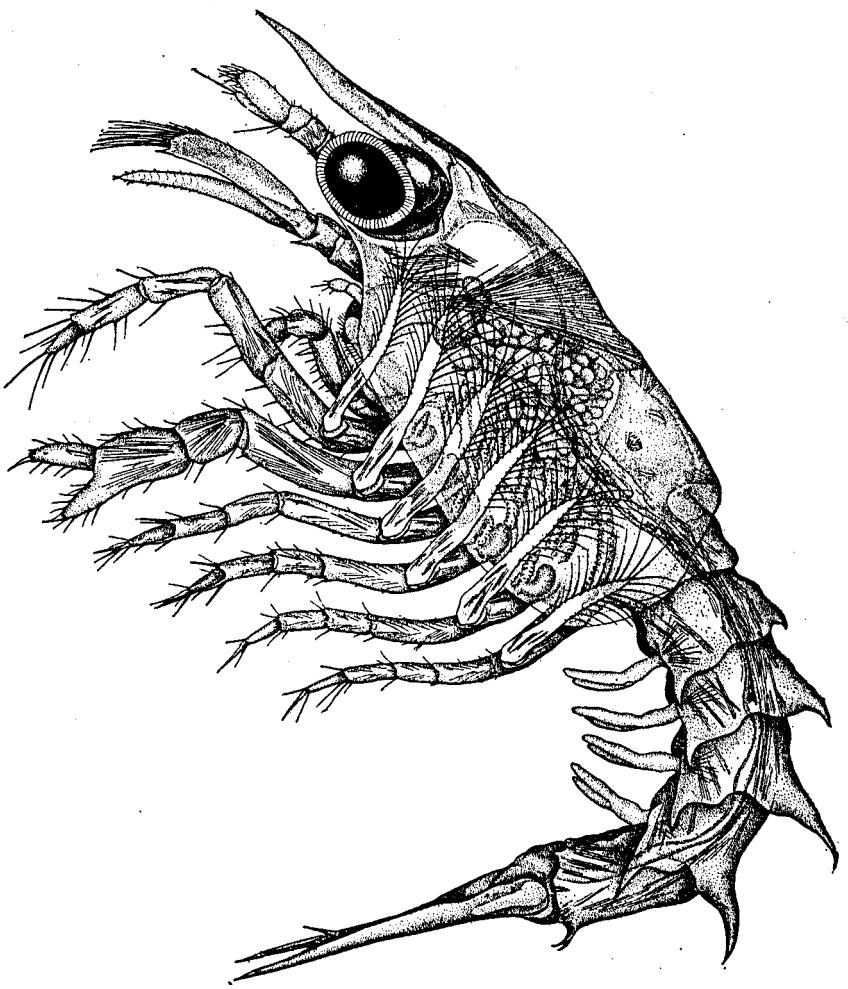


FIG. 41.—Second larva, or second swimming stage of lobster in profile. For natural swimming position hold page sidewise with head of animal down, and consult figure 40 of text. Length 9 mm., or 0.35 inch.

In habits and color the second larva resembles the first closely, but is distinguished by its slightly larger size and by the presence under the tail of four pairs of swimmerets on the second, third, fourth, and fifth abdominal segments, which appeared as minute buds beneath the cuticle of the first larva at birth. These appendages lack the swimming hairs, and do not become completely functional until the fourth stage.

Slighter structural changes which appear upon closer examination of the second larva are as follows: The rostrum is broader and its margins are serrated; the sides of the carapace completely cover the gills and separators; the sixth pair of abdominal appendages, the uropods of the tail fan, can be seen through the transparent cuticle as rudiments at the base of the telson; the stalk of the antennule is divided into three segments as in the adult, and its inner secondary flagellum, which is present in the first larva as a minute bud on the lower side of the primary flagellum, is much larger and shows traces of segmentation, while the stouter primary branch bears on its inner margin numerous clusters of sensory hairs. The long terminal spine of the outer flagellum has disappeared; the second antenna shows a reduction in its exopodite, the outer leaf-like scale with fringe of plumose hairs, which progresses with the following molts, and an extension of its segmented whip or endopodite; the chelæ or double claws borne on the first three pairs of walking legs are more perfect, and those of the first pair, which are destined to become the big claws of the adult, are perceptibly larger but otherwise similar. Both of the "great claws" gradually develop into the primitive toothed type, reached in the fourth stage, with teeth arranged in periods of eight; the primary and secondary spines only are present in the second larva. (See ch. VII.) Average length of second larva, Woods Hole, Mass., 9.3 millimeters; extremes, 8.3 to 10.2 millimeters (47 measurements); stage period, 2 to 5 days; Wickford, R. I. (Hadley), average length, 9.6 millimeters; average duration of stage period, 3 days; extremes, 2 to 7 days.

THE THIRD LARVAL STAGE.

[Fig. 42,]

Molting for the second time after hatching, the larva enters upon its third free swimming stage, in which the exopodites of the six pairs of thoracic legs (segments IX–XIV) are still functional. In habits, in color, and in general appearance the first three stages in the pelagic life of the lobster show no striking differences. The third larval stage, however, is readily distinguished from the second by the larger size of the animal, the presence of the completed tail fan, and the less rudimentary condition of the swimmerets upon the second to the fifth abdominal somites. The telson is reduced, though relatively much longer than the uropods; its terminal border is still incurved as in the first larva, but its lateral spines are longer. The inner whip in both antennæ is relatively larger and distinctly segmented, that of the second pair being considerably larger than the scale.

The "big" claws, though somewhat larger, still conform to the same type. They present a series of uniformly spaced spines, corresponding to the largest teeth of the lock-forceps or toothed claw of the adult, with rudimentary intermediate spines of the second order, or, if the latter are not present, the ducts of tegumental glands only, which mark their future position, may appear on the surface of the shell.

Like the earlier larvæ, they swim with head pointed downward, and with incurvated tail when rising, falling, or moving either forward or backward in the water, and they dart rapidly backward by sudden flexions of the tail. Yet Hadley observes that

toward the close of this period they become more sluggish, as if already affected by those profound changes which at the next molt deprive them of their rowing organs and start them upon a new career. Upon the bottom, however, the third-stage lobster is nearly as helpless as at an earlier period, and while it may make the attempt to steady itself upon its legs, it can not long maintain an upright position. Its future balancing organs

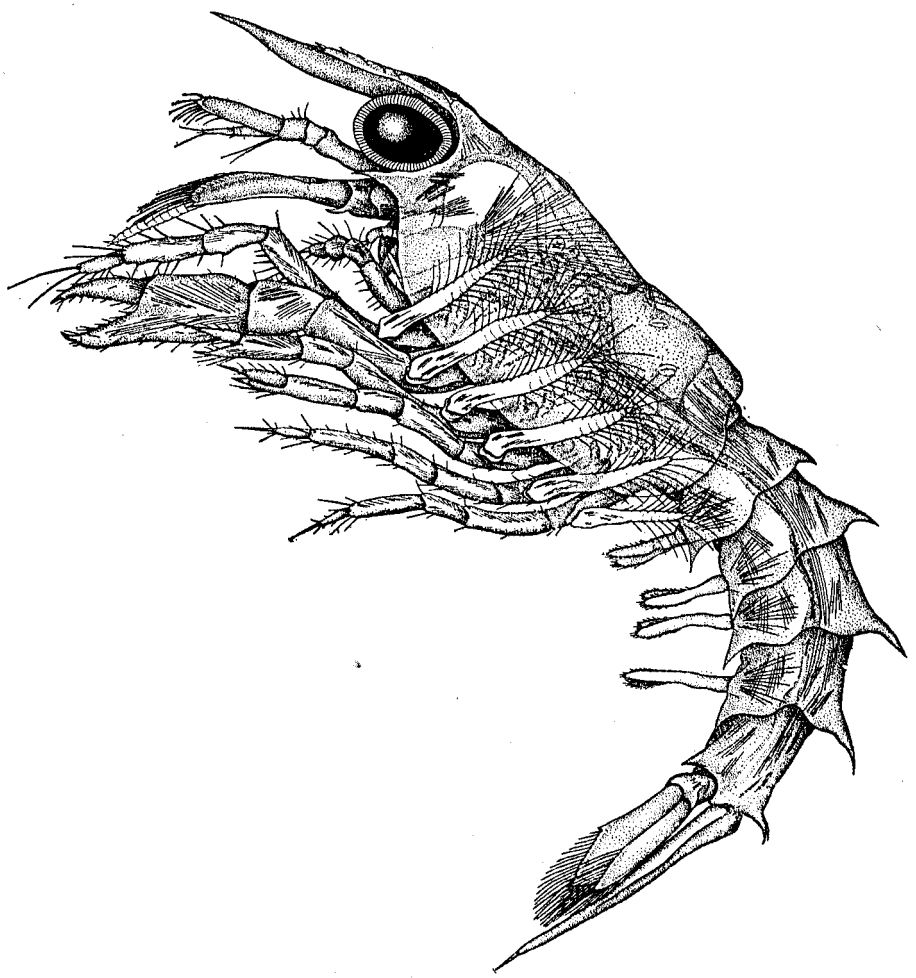


FIG. 42.—Third larva, or third swimming stage of the lobster, drawn to a scale reduced from that of figures 34 and 41. See legend of figure 34. Length 11.1 mm., or 0.44 inch.

are still in an undeveloped state. The swimmerets are now fringed with short rudimentary setæ, but do not come into full play until after the next molt.

As Hadley has pointed out, at birth the larval appendages are less concentrated in the head region than in the adult state, and this is most noticeable in the maxillipeds, the exopodites of the third pair of which are used for swimming. From the first stage

onward there is a gradual forward movement of the appendages—maxillæ, maxillipeds, and pereiopods—until the fourth stage, when they attain essentially their adult condidition. Average length of third larva, Woods Hole, Mass., 11.1 mm.; extremes, 10–12 mm. (79 measurements); Wickford, R. I. (Hadley for 1904), average length, 11.4 mm.; stage period, 5 days.

THE FOURTH OR LOBSTERLING STAGE.

[Plate xxxi.]

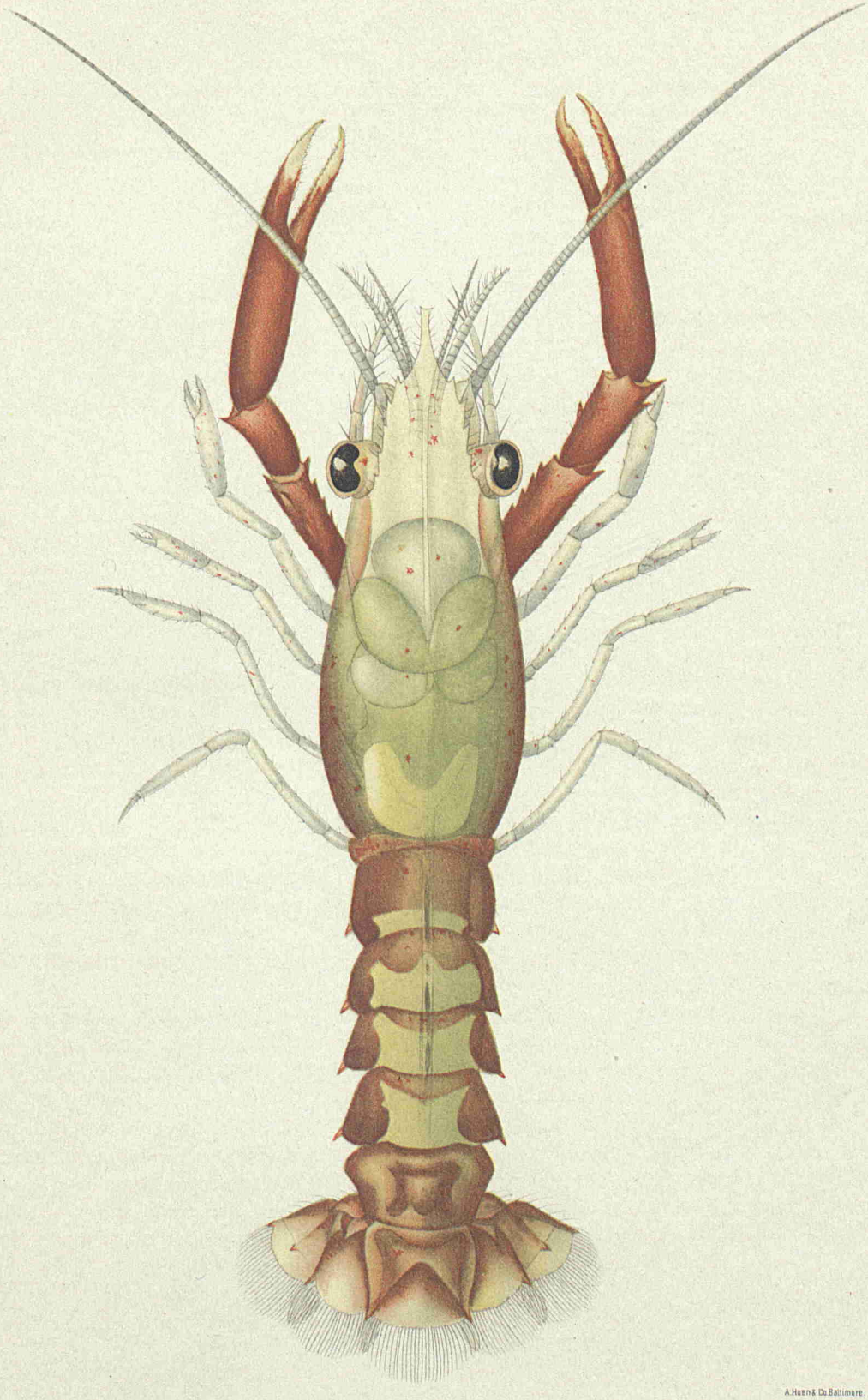
The young lobster makes a surprising leap at the fourth molt, or the third after hatching, when suddenly it seems to undergo a literal metamorphosis and to become a new animal, and when for the first time it truly resembles a diminutive lobster. In form, color, habits, and instincts it differs strikingly from every preceding stage.

The oars or swimming exopodites of its twelve thoracic legs are reduced to functionless stumps, which as a rule are no longer visible to the naked eye. Yet it still swims at the surface with greater agility, precision, and speed than at any former stage. The balancing organs, formerly called the "otolith sacs," at the base of the first pair of antennæ, are fully developed, and the reeling, uncertain gait of earlier stages is no longer observed. Nor is the body bent in swimming, but is straight as an arrow, and as the lobsterling glides swiftly along by the action of its swimmerets, now for the first time in complete working order, the big claws are extended straight in front of the head and held close together. While it uses the same organs in swimming as an adult animal, unlike an adult it swims at the surface and with a relatively much higher rate of speed. As in earlier stages it darts backward by quick jerks of the abdomen, according to one observer even jumping out of the water, a feat which it is never again able to perform, and which is possibly equaled in the higher Crustacea only by certain kinds of surface-feeding shrimp. The great chelipeds are long, slender, and end in symmetrical claws of the toothed type.

The incessant and apparently aimless activity of the young in all their swimming stages has been often remarked. While this activity does not protect them from their enemies or enable them to stem a current of much strength, it is not useless, for it enables them to keep afloat and thus brings them into contact with suspended food, which has been found to be an important requisite in every hatchery. It has been further observed that when at apparent rest the motion of the swimmerets in the third and fourth stages tends to keep the little lobster from sinking.

Like the larvæ, the fourth-stage lobsters continue to feed on copepods and small pelagic organisms of various kinds, even snapping up floating insects, according to Williams (*279*), who saw a swarm of lobsterlings seize, drag under, and devour a full-grown cricket which happened to fall into their tub.

In a number of fasting fourth-stage lobsters, which Williams also examined, the stomachs were found to be empty or to contain only masses of clam cuticle, which they commonly reject, from which it appeared that such lobsters, even when very closely confined in a finger bowl and "hungry enough to eat what they ordinarily refuse, will not attack one another (unless perhaps one or more of their number is newly molted)."



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FOURTH STAGE OF THE LOBSTER
LENGTH 14.6 MM.

Perhaps the most interesting morphological change which appears at the fourth stage, though by no means the most striking, is the torsion of the great chelipeds, described in chapter VII. The differentiation of the big claws, which come in time to equal one half the weight of the entire animal, is preceded by a permanent twist which has chiefly affected the fifth segment. While the lobster in the fourth stage is limber in every joint, the fusion of the second and third podomeres occurs shortly after this molt.

Lobsters after the larval period, and preeminently in the fourth and fifth stages, often exhibit the phenomenon known as "feigning death." When stroked with any object or when water is squirted on them with a pipette they will roll over and straighten out as if paralyzed. Their appearance when in this state is very different, however, from that of a dead animal. The phenomenon appears to be a somewhat sporadic reflex response, but it is interesting to find it appearing for the first time when the animal is about prepared to sink to the bottom, and to assume more fully the habits of an adult animal. (See 149, p. 184.)

Fourth-stage lobsters when approaching the end of their period frequently go to the bottom in shallow aquaria, hide under stones or any accessible objects, and even burrow in mud or sand.

The instinct of fear also appears in this stage and for the first time, associated with the hiding and burrowing tendencies. These are possibly evoked by the development of that contact-irritability which, as Hadley remarks, seems to come suddenly into play toward the close of this period. Burrowing is a kind of behavior in which the lobster frequently indulges from this time onward throughout life. The burrows serve a fourfold purpose—for concealment and therefore for protection, as a point of vantage from which to watch and seize their prey, and probably as a means of avoiding strong light, especially when adult, and particularly when confined in relatively shallow "parks" or pounds.

Digging the hole is an instinctive act; but returning to the same burrow of holding to the same crevice for the purpose of defense, for hiding, or for seizing the prey, so marked in all the later stages of both young and adults, is a distinct mark of intelligence, a habit of returning to the same spot being formed through association.

An interesting phase in the behavior of the fourth-stage lobster, as described by Hadley, is its rheotactic response or tendency to head into the current, which, with its other reactions, will be later discussed.

Color in the fourth stage.—At this period the range of color variation is much greater than at any previous stage, but color change no longer follows so promptly change in temperature, in the illumination, or in the intensity of other effective stimuli. The chromatophores or pigment cells of the skin have so multiplied as to form a continuous screen to the parts below. The former transparency of the larva is thus reduced in the same degree that the depth and brilliancy of its colors are enhanced.

The exoskeleton is now reenforced for the first time with considerable deposits of mineral salts, especially of lime. It is still quite translucent, but of a delicate light-blue tint, as appears at the molt. The body of the lobster, and the cephalo-thorax in particular, is studded with sensory hairs. The hair pores constantly increase in number

up to the adult state, when the shell is finely stippled with them, while the setæ themselves have for the most part disappeared.

Microscopical examination reveals a multitude of minute, closely crowded chromatophores in the skin, containing pigments of various tints, chiefly red and yellow. The color pattern is due mainly to the distribution of these cells; the quality and degree of color which in the same individual is subject to more or less constant variation, especially before and after the molt, is determined by the expansion of the variously colored chromatophores, the contents of the alimentary tract at the moment, and the variable tints of the underlying gastric glands. The bluish tint and slightly diminished translucency of the shell, when preparing to molt, has a considerable influence on the color of the animal as a whole.

The general cast of color may be either (1) yellow and red, (2) red, (3) green, or (4) green and reddish-brown. In the first instance the carapace is light yellow, translucent, and sprinkled with red chromatophores. The abdomen and large chelæ are reddish-brown, and there is a quadrilateral yellowish-green area on the terga of the fourth and fifth abdominal segments. In the red individuals the animal is bright red, especially on the abdomen and large chelæ. The carapace is yellowish, spotted with red, and the abdomen is marked in the way just described. In the green variation the whole animal is bright green. Bright-green areas are noticeable on the abdominal terga as before, and upon the hinder portion of the carapace. There is also some brown pigment on the large chelæ and tail fan. In the fourth variety the abdomen and chelæ are rich reddish-brown, with light peacock-green on the terga of the abdominal rings, as is commonly seen, and on the carapace next to the abdomen. The rest of the carapace is greenish-brown. The characteristic tendon marks on the carapace in this and in all subsequent stages define the areas of attachment of certain tendons or muscles to the shell. They become most conspicuous after the fifth or sixth molt. Average length at fourth stage, Woods Hole, Mass., 12.6 mm.; extremes, 11–14 mm. (64 measurements); stage period, 10–19 days; Wickford, R. I. (Hadley for 1904), average length, 13.5 mm.; stage period 12 days.

THE FIFTH STAGE.

The lobsterling which has not made its descent to the bottom at the close of the fourth stage continues to swim at the surface until the end of its fifth period, but whether pelagic or an inhabitant of the bottom its behavior closely tallies with that manifested in the preceding stage under similar conditions. Hadley has shown, however, that fifth-stage lobsters exhibit a stronger repugnance to light and a greater tendency to seek sanded areas and to burrow.

The structural changes which the lobster undergoes in passing from the fourth to the fifth and again from this to the sixth stage are often so slight as to be unrecognizable by anyone who has not followed each stage under the microscope molt by molt.

The salts of lime and the pigment which begin to appear in the shell at the fourth stage increase, and the carapace is in most cases fairly opaque, excepting immediately

after a molt, when, as often happens in crustaceans, the body for a time becomes quite translucent. From this period onward the color of the lobster is mainly due to shell pigments which are subject to change within certain limits, and are due to the direct activity of the chromatophores of the underlying soft skin. Every chromatophore at the surface of the skin stamps its image and counterpart upon the hard, unyielding shell.

The characteristic colors of the fifth stage are seal brown or maroon, or some combination of brown and green, which bring into strong relief certain snow-white or cream-colored spots on the body and chelipeds. The carapace at this stage presents four and sometimes five prominent white spots, the tendon marks already referred to, two on each side and one crossing the middle line of the back just in front of the cervical groove and in contact with it, marking in part the area of insertion of the posterior gastric muscles. Of the lateral spots the larger is a circular or oval disk-like impression below the cervical groove and in contact with it, while the smaller spot above the groove marks the tendinous insertion of a small muscle. From this time onward it is a constant character of the carapace, although it gradually pales and ceases to be prominent. Another triangular tendon mark which later becomes noticeable and remains throughout adult life lies just above the level of the last, at the intersection of the branchiocardiac lines and the cervical groove, its angles meeting this line and the transverse and lateral divisions of the groove or fold.

The external geography of the carapace, which still remains unexplored territory to a large extent, shows other small spots destitute of hair pores and a great variety of surface marked by depressions and elevations by the varied distribution of hair pores, and by spines many of which bear the ducts of tegumental glands, not to speak of the tendon spots already described, by grooves and larger protective spines, slightly roughened areas of muscle-insertion which are prominent just behind and in front of the transverse division of the cervical fold, as well as by areas of absorption which are essential for the molting process and are developed in correlation with the gradual deposition of mineral salts in the shell, such as the median stripe and the scalloped edges of the gill-covers. (For adult conditions see chapter VI.)

Further, the pleura of the first abdominal somite are snow-white, while the tips of the big claws, the rostrum, and the blades of the propeller or tail fan are washed with dull white or cream color. A light spot is also sometimes seen on the fourth segment of the great chelipeds.

It should be clearly recognized that here, as at every other stage, the color is subject to a considerable range of variation even in the same individual, due in a large measure to periodic changes involved in molting, to the temporary effects of light, and possibly to food and to other causes. At the crisis of the molt the little lobster is capable, as we have seen, of some quite chameleon-like performances.

But slight morphological changes are noticed in the fifth stage; the antennæ are extended in length, the big claws have become somewhat shorter and thicker, and it is common to find that the dactyl is bent so that the edges of the toothed forceps do not

meet. The microscopical rudiments of the swimming exopodites have been further reduced but do not, as a rule, wholly disappear until the sixth stage. Average length at fifth stage, Woods Hole, Mass., 14.2 mm.; extremes, 13.4–15 mm. (15 measurements); stage period, 11–18 days; Wickford, R. I. (Hadley for 1904), average length, 15.5; stage period, 9.5 days.

THE SIXTH STAGE.

[Pl. XXXII.]

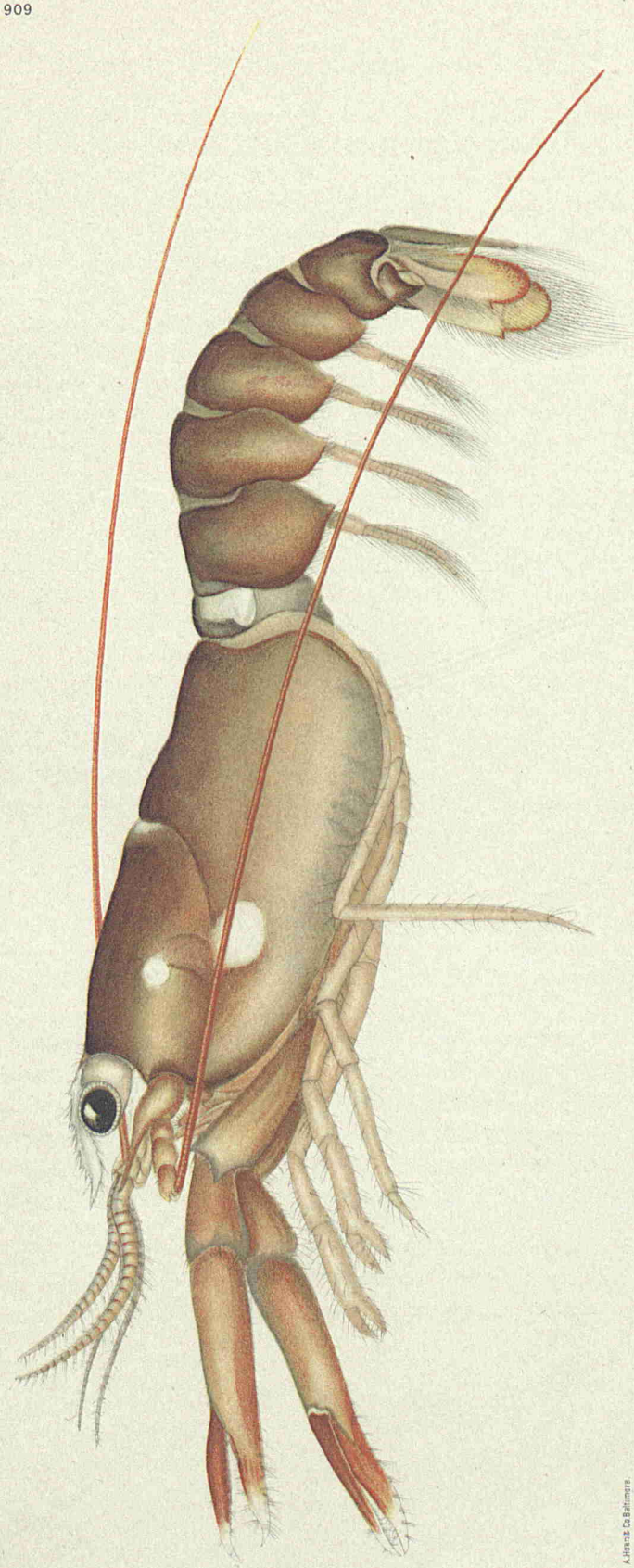
The sixth-stage lobster resembles the preceding stage in all essential respects both in structure and behavior, barring the fact that apparently all or nearly all animals in this period are bottom inhabitants. In color the two stages are nearly identical and subject to a similar range of variation. The tendon marks, and the cream-colored or dull-white spots on the tips of some of the appendages, which begin to show as early as the fourth stage, are even more pronounced than before. There is a prominent light spot at the distal extremity of the fourth podomere of the great chelipeds, as already mentioned for the fifth stage.

The modified abdominal appendages of the first abdominal somite commonly appear in the fifth or sixth stages as minute tubercles or buds, which at first lie upon the sternal surface across the long axis of the body, thus facing each other or pointing toward the middle line. After segmenting into two divisions, which in some cases does not happen until the eighth stage, this appendage becomes bent downward until it stands at nearly right angles with the underside of the tail. I was not able to determine the sex by the abdominal appendages alone until the tenth stage, but Hadley (*124*) maintains that this distinction can be made in the eighth or ninth stages, or even as early as the sixth or seventh stages, by means of the position of the openings of the sexual ducts. My material did not enable me to fix the sex by means of these ducts earlier than the eighth stage, but this was not extensive, and it can not be doubted but that in all such matters considerable individual variation exists.

The development of the crusher type of claw or the transition from the symmetrical to the asymmetrical condition of the great chelipeds begins in the sixth or seventh stage, and is marked by a blunting to be later followed by a fusion of the teeth to form crushing tubercles, but the change proceeds very slowly and is not conspicuous for some time. The future crusher gains at first in girth or breadth rather than in length (see ch. VII, p. 271). Average length at sixth stage, Woods Hole, Mass., 16.1 mm.; extremes, 16–17 mm. (12 measurements); stage periods, 14 days. Wickford, R. I., average length, 18.6 mm. (12 measurements); stage period, 12.7 days.

THE SEVENTH STAGE.

The seventh stage is sometimes distinguished from the sixth period, as already remarked by the first noticeable differentiation of the crushing and toothed claws, but aside from this there are no characteristics in size, form, or function by which this and subsequent stages can be distinguished with certainty unless one has watched and recorded every molt.



SIXTH STAGE OF THE LOBSTER
LENGTH 16 MM.

A. Hoen & Co. Baltimore

The seventh-stage lobsters keep as steadily to the bottom as the adults, and in crawling about make use chiefly of the last three or four pairs of thoracic legs. The large claws and smaller chelate legs are often extended forward in front of the head.

In the case of a lobster which was observed to molt from the sixth to the seventh stage the body was translucent, the general color being reddish brown, with a slight tinge of green on the carapace. The large claws were of a bright terra-cotta color. There was a whitish crescentic spot at the cervical groove on the back, and the characteristic tendon marks on each side of the carapace were as prominent as in the sixth stage. The pleura of the first abdominal somite were also snow white, and the uropods were tipped with cream color.

At the seventh stage pigment has been deposited below the enamel layer of the cuticle in an amount which, though at first very slight, increases with every molt and thus makes the color pattern more and more complex.

According to Hadley (*124*) the color of the seventh stage is usually and characteristically pure slate, becoming darker during the progress of the period, showing further the modifications of blue slate, green slate, and cream slate. The white spottings, as I have frequently observed, show a tendency to become creamy or buff in color in contrast to their porcelain-like whiteness in the fifth and especially in the sixth stage.

I have recorded numerous observations to show that the same animal may undergo no inconsiderable changes of color during the stage period. The color at this time is due to the pigments of the changing cuticle and to the changing pigments of the soft skin beneath it. With the advance of the stage period a new cuticle or shell is gradually formed beneath the old, which is later shed, with the tendency to become darker or more opaque. The color is also affected in some degree by any stimulus or change of the physiological state which affects the more responsive chromatophores of the soft skin.

It is therefore a difficult matter to standardize these ever-changing color effects, and not possible unless the animals are compared in the same stage period, immediately after molting, and under similar physical conditions. It is certain that the activity of the chromatophores is not dependent upon the direction or intensity of the rays of light alone, but rather more, as recent experiments seem to show, upon the physiological states, which follow upon complex and little understood changes.

Further, the act of molting by the stimulus sent into the chromatophores will sometimes bleach a brilliant animal into a pale shadow of its former self, as I have witnessed in the adult shrimp *Alpheus*, as well as in the adolescent lobster. Accordingly I consider it highly probable, if not certain, that the blue-slate or slate color is often due to the advancement of the stage period and to the peculiar opacity which always follows upon the development of a new cuticle beneath the old. It should also be observed that the cast shell, from at least the fourth stage to the present, which veils the brighter colors of the new cuticle, is blue, suffused at this time with green and brown in its pigment layer.

Hadley remarks that the adult structural type is possibly reached in the ninth stage, and the adult color pattern in the eleventh. Inasmuch as single structural characters, such as the differentiation of the big claws, are by no means regular or invariable in their appearance, we should hardly expect to find the sum of such characters expressed at a definite molt, which after all is but an incident of growth. Even at the fourth stage, as Williamson (*282*) has shown in the European lobster, the swimming organs are not shed in the same degree of completeness in all cases. Far less is it possible to fix upon any definite stage when the sexual characters and sexual maturity are reached. The data do not seem to be sufficient to make the determination of averages very precise. Average length at seventh stage, Woods Hole, Mass., 18.6 mm.; extremes, 18–19.5 mm. (4 measurements); stage period, 14–21 days; Wickford, R. I. (Hadley for 1904), average length 22.5 days; stage period, 14.3 days.

THE EIGHTH AND LATER STAGES.

The external structural changes which immediately follow the seventh stage are very slight and concern chiefly the accessory reproductive organs, such as the differentiation of the seminal receptacle of the female and the first pair of pleopods in both sexes.

The eighth stage is similar in color to the seventh, but according to Hadley there is a greater modification of the slate color, with a tendency to develop the blue slate and cream slate, or, in a less marked degree, the green slate and brown slate. According to the same observer, the blue color is more pronounced in the ninth stage, when the prominence of the white or cream colored spots is beginning to wane. It has been further noticed that in the tenth stage the olive green and olive brown combinations become more prominent; the spottings are seldom seen, and the dark mottled character of the coloring of the adult begins to assert itself. This characteristic mottled color pattern was still more pronounced in the eleventh stage, when it was apparently established.

HABITS OF ADOLESCENT LOBSTERS.

From the close of its free-swimming life until the later adolescent period the young lobster drops out of sight so completely that for a long time its habits during this interval were quite unknown (see *149*, ch. XI). After reaching the bottom we know that many of the little lobsters begin to travel toward the shore, in all probability slowly at first, but more rapidly when at the age of about 3 months they have a length of 1¼ inches, more or less.

The instinct of fear, suddenly developed in the fourth stage and present at all later periods, prompts the little animal to display great caution in all its movements, and to hide under stones or in the crevices of any protecting object whenever danger assails it.

Whenever the lobster sinks in very deep water, as must often be the case, it possibly gradually moves shoreward. At all events many adolescent and small lobsters are found along the rocky shores of bays and small inlets, where they apparently remain until driven out by ice. These small lobsters live under stones and submerged rock

piles, the tops or surfaces of which are sometimes laid bare at unusually low tides in fall, when they may be found by digging and turning over the stones, at depths of but a few inches at low water, but where at the flood the sea rises to a height of 5 feet or more. The smallest, from about 1¼ to 3 inches in length, go deep down among the loose stones, where no enemy is likely to reach them. At a later period, when from 3½ to 4½ or 5 inches long, they issue from their retreats more freely and explore the bottom with greater boldness. They also dig caves under stones, from which, as at an earlier period, they stealthily crawl in search of prey, but quickly return when an enemy appears. We have seen that this characteristic burrowing instinct develops as early as the fourth stage.

As the lobster increases in size it becomes bolder and retires farther from the shore, but it never loses its instinct for digging nor abandons the common habit of concealing itself when the necessity arises.

A LOBSTER 413 DAYS OLD.

As is well known, size, whether of lobsters or of mankind, is not a certain criterion of age. In the crustacean it depends upon the number of molts successfully passed, while unfavorable conditions tend to lengthen the molting periods. Some of these conditions will be considered in a later section. This was well illustrated by the young lobster whose history follows. This animal was reared in a small glass aquarium at Woods Hole, Mass., and was fed with minced clams and the eggs of the lobster and cod. It lived from June 20, 1893, until August 6, 1894, when it had attained the length of 36 millimeters (1.44 inches).

In its final stage the colors of the animal had apparently reached the limit of their brilliancy and the mottled color pattern was as complex as in an adult animal. The body was of a light umber color freely speckled and mottled with darker tints. The appendages were reddish brown and slightly translucent. Small light spots or suffusions were found in certain parts of the body; the tendon marks, corresponding to those characteristic of the fifth and later stages, were prominent, the round spot just below the cervical groove being over a millimeter in diameter; the pleura of the first abdominal somite were snowy white, while the free edges of the segments of the body and of the appendages were bright blue; the large chelæ were white tipped. The openings of the oviduct were plainly visible, while the lips of the copulatory pouch or seminal receptacle were not yet closed. The color of the appendages on the under side was light reddish brown, and the tail-fan was of the same hue, edged with deep red; the big claws, which were tufted with setæ at their tips, showed but little differentiation. The compound eyes had acquired the large size and prominence of the later adolescent stages.

WHEN DOES THE YOUNG LOBSTER GO TO THE BOTTOM TO STAY?

Over 15 years ago I raised the question which is now placed at the head of this section, and answered it in a tentative way, but its importance seems to have been underestimated, for it has received little attention from other workers up to the present time.

It was shown that young lobsters did not uniformly make their descent to nether regions during the fourth stage or even at its end, and that the swimming period often lasted to the fifth stage, probably until its close, and possibly into the sixth stage. I have records of young lobsters captured under natural conditions at the surface of the sea (see *149*, table, p. 187), varying in length from 15 to 18 millimeters. The largest, taken 7 miles southwest of No Man's Land, near Marthas Vineyard, 18 millimeters long, was probably in the fifth stage, though possibly in the sixth, as seemed to me very likely at the time. Hadley's measurements for Wickford (R. I.) lobsters, which average much higher than those obtained by me at Woods Hole, Mass., are for the stages in question as follows: Fourth stage, average length, 13.5 millimeters (extreme, 15.5 mm.); fifth stage, average length, 16 millimeters (extreme, 18 mm., two records only); sixth stage, average length, 18.8 millimeters (extreme, 24 mm., one record). (See also later measurements quoted above.) The average length for lobsters raised in aquaria at Woods Hole in the same stages are as follows: 12.6 millimeters (extreme, 14 mm.); 14.2 millimeters (extreme, 15 mm.); 16.1 millimeters (extreme, 17 mm.). Inasmuch as size is a very unsafe criterion of either stage or age, it can not be said that at present there is any satisfactory evidence that the American lobster remains at the surface beyond the fifth stage. It is interesting, however, to notice a record by Meek (*200*) of the capture by surface net of a young specimen of the European lobster, which measured 20.5 millimeters ($\frac{13}{16}$ inch), at Alnmouth Bay, Northumberland, England, in the afternoon of September 7. Its age was estimated at 2 months. Now according to Ehrenbaum (*87*), whose work was conducted at Helgoland, such a lobster should be in either the sixth or seventh stage and upward of 61 or 87 days old, respectively (sixth stage, length, 18–20 mm.; seventh stage, length 21–22 mm.). We should therefore hesitate to affirm that in the American form the swimming life at the surface is never extended to the sixth stage.

The experiments of Hadley and others on the reactions of the larvæ show that the light-shunning, bottom-seeking, and hiding tendencies begin to assert themselves in animals artificially reared toward the close of the fourth or else in the fifth stage.

The bearing of this question upon the artificial propagation of the lobster is very evident, for, if a considerable number of fourth-stage lobsters remain suspended at the surface, the careful rearing to this stage and subsequent liberation in the sea is only feeding the fishes. A small force of predaceous tautog, or cunners, would play havoc with myriads in a short time. As we remarked in 1895, "the problem of the artificial propagation of the lobster will be solved when means are devised by which larvæ, after hatching, can be reared in inclosures until the fifth or sixth stage, when they can take care of themselves." This time limit should have been modified to read "until they go to the bottom." The lack of precision which the lobster displays in his desire to discover the bottom is very disappointing, but it seems evident that liberation of the carefully reared young at the very beginning of the fourth stage is only to court disaster, with the attendant waste of time, money, and labor.

FOOD AND CAUSES OF DEATH IN ARTIFICIALLY REARED LOBSTERS.

The yolk of hard-boiled eggs, crushed crab, boiled liver, minced fish, beef, lobster's liver, the soft parts of clams, and menhaden have all been tried as food for young lobsters by different experimenters in America and Europe with varying degrees of success.

Emmel (*95, a*) in a series of experiments upon the rate of molting of 90 selected lobsterlings which had reached the fourth stage on the same day, and which were divided into lots and were fed on different foods, obtained the following results: Beef-fed lobsters advanced to the fifth stage in an average period of 11.2 days; when fed on minced muscle of soft-shelled clams, in 11.3 days; on shredded lobster muscle, in 11.5 days; on shredded fish, in 11.7 days; on beef liver, in 12.3 days. While his tests showed a slight advantage for the beef fed over those supplied with clams, the lot which received no food other than the natural plankton of the water were twice as long in passing to the fifth stage, or 24.6 days.

In the experiments on the artificial rearing of the lobster conducted at Woods Hole, Mass., by the United States Fish Commission in 1902, the flesh of the menhaden, which is saturated with oil so that it does not readily sink, was found to answer admirably as a food until many of the larvæ began to sicken and die. The fish were shredded in a meat grinding machine, and a teacup full of this finely triturated flesh taken twice daily was found to meet the needs of about 5,000 larvæ. The voracious young can hardly be fed too much, provided the waste is not allowed to accumulate in the rearing tanks or bags, and as they grow older their ration must be increased. In June it was noticed that many of the menhaden-fed fry in the rearing bags were attacked by a fungus, which Gorham (*121*) thought was attributable to the oily fish upon which the young had fed. According to this observer, the mycelial filaments of this fungus spread from the point of infection until all the animal's tissues were destroyed and the lobster's body was reduced to a chitinous shell packed full of the mycelium.

In 1893 I described a case in which a parasitic fungus, probably belonging to the family Chrytridiaceæ, had attacked the late egg embryos of the shrimp *Alpheus*, a relative not far removed of the lobster. In this case the eggs were crammed full of the encysted parasite.[a] No internal egg parasites have yet been reported for the lobster.

The chief causes of death in the artificially reared lobsters are organic sediments, cannibalism, which is caused chiefly by overcrowding or a lack of proper food, and the exceptional fungus growths under the conditions of feeding referred to above. The sediments cling to the hairs of the appendages, interfere with the locomotion of the larva, and send it to the bottom, thus cutting off its supply of food. In this way it becomes crippled, and, being too weak to molt, it usually starves to death. Various algæ, bacteria, stalked protozoa, and diatoms occur in these sediments, but the chief offenders are diatoms.

Gorham (*121*), who has made a careful investigation of the causes of death in artificially hatched fry, names 24 species of diatoms which were found on lobsters reared at

[a] For figures and description, see appendix II, ch. V, of The embryology and metamorphosis of the Macrura, Memoirs National Academy of Sciences. Washington, 1893.

Woods Hole, of which the four most common species were *Licmophora tincta*, *Diatoma hyalinum*, *Rhabdonema arcuatum*, and *Tabellaria unipunctata*, named in the order of their relative abundance.

I have seen the fry almost buried out of sight by diatoms in neglected jars at Woods Hole, especially by *Tabellaria*, which at times was very abundant and destructive.

Other organisms found by Gorham to infest the young lobsters at Woods Hole were a filamentous green alga and a stalked protozoan, *Ephelota coronata*, which was more abundant in the waters of Wickford, R. I.

Cannibalism may be reduced by supplying the young with proper food, by agitating the water and thereby keeping both the young and their food suspended, and by avoiding overcrowding. The growth of diatoms can be checked or prevented, according to Gorham, by filtering the water; by selecting a suitable station for the rearing apparatus where diatoms do not abound, and where the temperature is high or most favorable for hastening growth and molting, by which the little animal escapes for the time being at least from all its troublesome messmates; by frequent cleaning, coating, or renewal of the rearing bags; and by reducing the light and thus hampering the diatoms by cutting down their food supply. (Compare, p. 281.)

THE SIGNIFICANT FACTS OF LARVAL AND LATER DEVELOPMENT.

Some of the most important facts concerning the larval life of the lobster may now be summarized:

(1) The young are hatched in great numbers, 5,000 to 100,000 eggs or young being produced at one time by a single animal according to its size, the number increasing rapidly in proportion to the cube of the body length or to the total volume of the body. This leads us to expect great destruction of the young in nature, an expectation which is unfortunately realized. It is a vulgar error to assume that the abundance of this animal or of any other species is proportional to the number of young born, since it neglects the equally important question of the destruction of the young or their rate of survival. The rapid rise in production beyond the 10-inch size proves that the older the animal the more valuable it becomes for reproductive purposes, barring the question of sexual decline, which is of little importance in an animal so seldom permitted to grow old.

(2) The larvæ are hatched at the bottom of the ocean in relatively shallow water at night or in early morning. A molt occurs at the time of hatching; parental instinct ceases; the larvæ are soon dispersed, and leaving the bottom lead a free-swimming, pelagic existence for a period of from 3 to 6 weeks (see p. 348), according to circumstances. Summer eggs on the coast of Massachusetts are hatched from May 15 to July 15, the majority being extruded in June.

(3) The movements of the larvæ in a natural state are not fully understood. Under certain conditions they rise toward the stronger light at the surface; under other conditions they retreat from the light, sinking to greater depths. They have been taken near the surface in the townet in both strong sunlight and at night, both with and without the aid of artificial light. At the present time they are seldom found at the surface under

any conditions. Since the young feed upon moving or suspended prey, their life can not be spent far from the surface. Their behavior at any given time is the resultant of all the conditions which affect them at that time, and therefore varies with the varying conditions of their life. The rarity of the larval lobsters at the surface in areas where the adults are known to abound may be ascribed to the following causes: (1) Wholesale destruction of the breeding animals, which has caused the present depletion of the fishery; (2) the great destruction of the young, which must take place under natural conditions; (3) the wide dispersal of the young by tides and currents which their swimming habits favor, and (4) the variable character in their reactions or movements, leading to a variable or irregular vertical distribution.

(4) The food of the larval lobster consists of minute pelagic or floating organisms, such as copepods, crustacean larvæ, algæ, and probably to some extent protozoa. The stomachs of young lobsters taken at sea have been found to contain fragments of crustaceans, diatoms, algæ, fine sand grains, and amorphous matter. They seem ready to attack and seize any small moving object, living or dead, which they are able to master. Since they follow moving objects like copepods by sight they discriminate to some extent, but their powers in this direction are slight, and would seem to be unnecessary if they early acquire the adult habit of regurgitating the indigestible residue of their food.

(5) The preying instinct, which is closely associated with that of pugnacity, is very strong in young lobsters from the time of birth. Their disposition to attack and devour one another, as seen in aquaria whenever they are too closely crowded or not supplied with the proper food, is the obvious result of an indiscriminate instinct to seize floating objects which are neither too large nor too active. Another lobster is as good a mark as a floating egg, or as a swimming copepod, which is more apt to elude them. Indeed they often give chase to crustaceans larger than themselves. The fighting instinct, if we may thus describe the tendency referred to, is closely associated with the primary instinct to seize and devour, in accordance with which the character of their activities and the structure of their bodies is distinctly correlated. It is thus evident that the organic food of the young lobster must be finely divided and floating, and that crowding in too close quarters can not be otherwise than destructive.

(6) The body of the larva is covered with a cuticle, which includes the lining of the stomach sac, and at least a part of the intestine. This is continuous with every spine, seta, or hair with which the body is protected or garnished, as well as with the internal skeleton which is produced from folds or pockets of the skin. Active growth entails the shedding of this cuticle, which is cast off in one piece, and the duration of the molting intervals or stage periods depends on the vigor and health of the individual. Each molt is a crisis in the animal's life. If the cuticle is not properly shed, the swimming hairs can not be properly evaginated, and the animal becomes helpless.

A healthy larva is always clean and transparent, while in a weakened or sickly one the hairs tend to gather sediment and parasites. Sea water of normal density in which the plankton or floating population of animal and plant life is properly balanced and an undue amount of sediment is not present, are important conditions for rearing the young, and the warmer the water, within certain limits, the more rapid the growth.

At certain points on the coast it may be possible to rear many marine animals with comparatively little difficulty, or to keep them alive in the adult state for long periods, while at other places every aquarium may become the grave of all but the hardiest species or individuals, and that in a short time. The difficulty seems to arise from the nature of the plankton, and from the tendency of certain prevalent organisms, such as diatoms, parasitic bacteria and fungi, to increase in an inordinate degree. The larvæ become weakened, and can not pass their molts.

(7) In the fourth stage the young lobster, as if in one bound, seems to justify its name, to lose its old swimming organs and acquire new ones, to lose the rolling uncertain gait of the larva and to acquire new strength with greater precision and speed. It loses in large measure its former transparency, and, together with a greater hardness and opacity of its shell, it gains a far greater brilliancy and variety of coloring. The fourth stage also marks the rise of new instincts such as fear, burrowing for concealment, not to speak of far greater pugnacity, and the dawn of intelligence or power of association, displayed in the lobsterling's holding to the same hole or retreat for hiding, to which it will return repeatedly and will defend with spirit. Perhaps more important than any of these characteristics is the fact that many of the fourth-stage lobsters probably go to the bottom and stay there. This at least is their habit when reared in confinement.

The fourth-stage lobsters seem to swim at the surface more regularly and continuously than the larvæ, and accordingly are more often taken in the net, while it is evident that the earlier stages must be thousands of times more numerous.

(8) The rate of growth is greatest during early life, and according to Hadley is 18 per cent at each molt at Wickford, R. I., up to the seventeenth stage, when it begins to slowly decrease. I found the rate to be less in the slightly colder waters at Woods Hole in the case of artificially hatched and reared young. The time interval between successive molts is indeterminate, being subject to every change which affects the physiological vigor of the animal. The advancement of the larva is to be measured by the number of its molts and not by its age. Under favorable conditions the three larval stages are passed in 10 or 12 days; the fourth stage lasts as long, so the swimming period may be over in about three weeks, or may be extended to four weeks or longer when the bottom is not sought until the fifth stage.

The approach of the molt seems to start the lobsterling on its course to the bottom; accordingly when this is delayed until after the fourth stage, it probably does not often occur until the approach of the succeeding molt. (See p. 348.)

Chapter XI.—BEHAVIOR AND RATE OF GROWTH.

BEHAVIOR OF YOUNG LOBSTERS.

Having considered the general habits of the lobster in its successive stages of development, we shall now discuss their behavior in more detail.

In the summer of 1894 I tried a number of simple experiments to test the effect of light upon the movements of the larval lobster. Twenty-five thousand young in the first stage were placed in the observation pool at the Fish Commission station, Woods Hole, Mass., in order that their behavior might be watched. The sun was intermittently obscured by clouds during the greater part of the forenoon. When set free, the larvæ soon swarmed in a large cluster near the surface, where they remained for a short time. Presently all of them went down to a distance of from 1 to 2 feet, and some of them to the bottom to a distance of 3 feet more. A lot of small cunners then appeared on the scene and snapped up the larvæ right and left. Two hours later the remnant were dispersed over the whole pool, a large number remaining close to the surface. At 1 o'clock in the afternoon the surface on the lee side still swarmed with larvæ. Occasionally one could be seen to attack and drag another down. They swam with their usual aimless activity, now rising and falling and changing their direction frequently. The majority of them had now become quite red. Later in the afternoon nearly all of the little lobsters had disappeared, having been swept out by the tide or destroyed by the cunners or other fish in the pool.

Various boxes were then constructed to admit diffuse light from above or direct light through one end, and larvæ in the first stage were found to move toward the source of the light, whatever its intensity. In similar experiments made at another time this reaction, which then seemed characteristic, was reversed, "showing possibly that under certain conditions the larvæ are negatively heliotropic." At this time the subject of animal behavior had hardly emerged as a branch of experimental biology, with its more exact analytical methods and criteria which have since been evolved.

The experimental work of Bohn (*27*) on *Homarus gammarus* and of Hadley (*131*) in particular on the American lobster have illustrated the importance of studying the behavior of such an animal throughout the entire course of its development, and at the same time have revealed the great variety and complexity of the problems involved. The following paragraphs are little more than a summary and running commentary on some of their results.

For the analysis of certain problems in behavior the lobsters are unsurpassed, since with the proper apparatus they may be hatched in unlimited numbers and maintained to any required age or stage during the summer months. The results of studies thus far made show that while the crustacean larvæ may respond promptly and in a definite manner to a certain stimulus, their behavior is complex and essentially variable, and that at any given point of time it is the result of all the influences at work.

It is evident from the preceding chapter, as Hadley has already pointed out, that the life of the lobster may be divided on the basis of behavior into three periods: (1) The three larval stages, when the animals frequently swim with head depressed, upward or downward and forward or backward, according to circumstances, by the use of their thoracic exopodites; (2) the fourth stage, when the animal is a free swimmer at the surface, the abdominal swimmerets being now functional, as in the adult; and (3) the later stages, when the swimming organs are the same, but the animal remains constantly on the bottom after its final descent in the fourth or fifth period.

REACTION TO LIGHT.

The response of the pelagic larvæ of the higher Crustacea to light, as well as the effect of light upon the growth of these animals, are questions not only of great scientific interest, but in the case of the lobster of practical importance in view of the necessity of understanding their behavior in a state of nature and of placing them as far as possible under natural conditions in the hatchery. It has been shown in general that swimming larvæ of crustaceans, in common with many other organisms, exhibit two types of response to the light stimulus, known as phototaxis or reaction to the directive influence of the rays of light and photopathy or response to changes in the intensity of light. The phototactic response is composed of two elements or components—the turning and progressive movements or, as Hadley calls them, the body and progressive orientation; the animal turns so that the long axis of its body coincides with the path of light, and it always heads away from the source; this reaction is primary, constant, and typically reflex. On the other hand, the "progressive" response which follows this stereotyped form of orientation may be positive or negative—that is, the animal may move upward or downward, backward or forward—that is, toward or away from the source of light. The photopathic response is also variable, the animal moving toward or from a more brilliantly illuminated region, according to conditions.

Thus, according to Hadley, apart from the orientation of the body there is no constant type of reaction for the larval lobster. The variable responses vary in accord with changes in the environment of the individual and changes in the individual itself or its physiological state, and are especially marked at the beginning and close of the stage periods. While the phototactic response is eminently variable, the photopathic reaction is usually positive.

In the fourth stage the conditions are somewhat reversed, since in the laboratory lobsters at this period usually give a negative phototactic reaction, while their photopathic response is at first positive and later negative. Light-avoiding reactions of whatever kind are strongly manifested in the fifth stage and may begin at the close of the fourth. So strong indeed was the tendency to shun the light that the little lobsters, as Hadley demonstrated, would even allow themselves to be stranded, with possible fatal results, rather than to approach the light, and thereby gain deeper water. It was further shown that at this time also the thigmotactic reaction, or response to

contact with solid bodies, began to assert itself and thus to modify the previous sensitiveness to light, apparently leading the animal to crawl under shelter and to burrow in the sand or mud at the bottom.

Previous to the fifth stage an increased intensity of light in certain cases may reverse the response, while in others it does not. After the fifth stage no reversal of the response can be effected in this way.

We will now review some of the observations of Bohn on the movements of the larvæ of *Homarus gammarus* of Europe, reported in 1905. He believed that the newly hatched young were immediately attracted to the surface, since they are positively phototactic. At first they approached the light, while later, at the end of some days, they moved toward regions of greater obscurity. Upon the swimming movements and unstable equilibrium of these larvæ this observer remarks as follows: The back of the lobster does not remain constantly directed upward, but is alternately inclined to the right and left, sometimes as much as 90°. It can likewise tip over by turning on the long axis of its body. The displacement of the body is effected not by the position of the longitudinal axis alone, but by that of the vertical axis of the cephalothorax as well. If the carapace is elevated, the animal both advances and rises; if it is inclined to the right, the larva advances by deviating to the right, and the more considerable the rotation the more pronounced the deviation.

In their rolling gait the larvæ tend to keep the back turned upward—that is, toward the surface illuminated by the vast expanse of sky—while the head is bent downward toward the region of shadow. When this position is maintained the eyes are illuminated in a peculiar manner. At their most elevated points, opposite to the illuminated surface, there is a lighted area, while at their most anterior ends, which are directed toward the regions of obscurity, there is an area of shadow.

"All of these observed movements," says Bohn, "such as repulsion and attraction, rolling and other rotations, are made with rapidity and precision and have the character of irresistible movements, according to laws which appear very exact, but which vary with the physiological states." Bohn concludes that the larvæ are guided in their movements mainly by the stimulus of light which enters the eyes, and that the eye acts before the "otocyst" as an organ of orientation.

In regard to the question of any real distinction between the photopathic and phototactic response, or between the intensity as distinguished from the direction of light, Hadley remarks that the direction of the light is effective in determining which eye shall be stimulated most and what parts of both eyes shall be stimulated equally. In the first instance the long axis of the body is swung into line with the rays, so that both eyes are equally affected, while in the latter the body is so placed that the anterior lateral surface of the eyes receive the strongest and the posterior lateral surface the weakest illumination.

Hadley found that when blinded in one eye the larvæ rapidly rotated on its long axis in a definite direction or performed "circus" movements, moving in circles, toward or away from the position of the uninjured eye according as the animal was negatively

or positively phototropic. It was also noticed that these reactions were seldom negative except in the fourth or later stages of the lobster. Each eye is thus apparently connected with a reflex mechanism which controls the movements of a definite side of the body.

If the light which strikes a larval lobster is suddenly blocked, Hadley found that a reorientation of the body was usually effected so that the animal faced the former light source.

Generally speaking the movements of the larval lobsters seemed to Hadley to support the tropism theory, and to represent simple or complex reflexes, in the latter case of serial form, and resolvable, with sufficient data, into a number of simple components.

Both Bohn and Hadley have tested the effects of "screening" upon young lobsters, or their behavior against white and dark backgrounds, brought to bear upon them from any direction, and while the results of the observers are not wholly in accord, Hadley concludes that the larvæ orient themselves to the white and black screens or backgrounds by essentially the identical reflex movements by which they respond to direct illumination and shading.

In the case of red monochromatic light on a white ground the lobster in the first stage was found by Hadley to be negatively phototropic, but on a white ground in blue light positively phototropic. In this respect, moreover, the second and third stage lobsters responded in the same way, while against black the lobsters retreat from both red and blue in all their stages.

The fourth-stage lobsters, on the other hand, were observed to rise from black backgrounds in light of any intensity or color; that is, to display positive phototropism, and the stronger the light, the more marked was the reaction. Against white also the fourth-stage lobsters rise to any light except red, from which they tend to retreat.

The older lobsters of the fourth stage did not respond so promptly in a positive manner, and when preparing to molt they showed a negative reaction; that is, they sought the bottom, a response commonly assumed in the fifth stage, whatever the character of the light or background.

The results of Hadley's experiments were in harmony with observations of the behavior of the larvæ confined in the 12-foot canvas rearing bags, where they showed "at all times a marked tendency to sink to the bottom, except perchance at night, when more active swimming is observed in all the stages. This tendency during the daytime could not be controlled in any way. At night, however, it was possible to evoke a seemingly positive phototactic reaction from any of the young larvæ in the large canvas bags. This was accomplished by means of the acetylene light so directed against a certain area of the white field of canvas that large numbers would at once group themselves thickly about the illuminated area, manifesting in the case of the third and the fourth stages, such an effort to come into the light area that they would often throw themselves out of the water, causing thereby numerous surface ripples" (*131*).

REACTION TO OTHER STIMULI.

The results of galvanic stimulation are particularly interesting, since they apparently represent a fundamental response of living matter, this particular form of energy being unknown under natural conditions. It was noticed by Hadley (*129*) that the young lobsters reacted very definitely to the galvanic current by gathering at the anode. Under the influence of the ascending current a progressive orientation to the anode took place, providing the long axis of the body came into certain relations to the current.

Hadley has also described an interesting rheotactic response in lobsters of the fourth stage, in accordance with which they head to the strong circular current which is maintained in the rearing bags or boxes at the fisheries station at Wickford, R. I. Even within a minute after molting to this stage the lobster would face about and head into the current, swimming so actively as to make some progress if the force was not too strong. "This characteristic manner of swimming, says Hadley," "was evinced in an ever-increasing number of lobsters, until the whole body of them had passed into the fourth stage, and then it was a most interesting sight to observe the young animals, with hardly an exception, heading into the current and as a great phalanx following their circular course—but, because of the force of the current, backward."

This rheotactic response is if anything stronger by night than by day. It may be modified or lost by passing from shadow to full light in the daytime or from darkness to strong light at night, the phototactic response overcoming the influence to swim against the current. Rheotaxis is due in some measure to a stimulus which, as Hadley believes, reaches the nerve centers through the eye. It is gradually lost in the fifth stage.

MOVEMENTS OF THE YOUNG LOBSTER IN A STATE OF NATURE.

We will now review the probable behavior of the young swimming lobsters in their natural state in the sea, in order to ascertain to what extent experimental work in the laboratory has enabled us to understand their complex movements. It must be admitted that comparatively little is definitely known through direct observation upon the subject.

Under natural conditions the young of the lobster, as in many of the higher Crustacea, are presumably hatched at twilight or at night at the sea bottom, their dispersal taking place in the way already described (p. 327). Possibly under some conditions they swim to the surface during the night of their birth, while as a rule they may not make the ascent until stimulated by the light of returning dawn, but remain at the higher levels for a few days only. This is confirmed by captures with the tow net by both day and night (p. 331) and by the experiments of both Bohn and Hadley, already recorded.

Then follows a period of greater fluctuation, embracing the latter part of the first and the two remaining larval stages, during which their movements are variable. Though still coming to the surface and within reach of the net, their capture in this way, at the present time at least, seldom occurs under any conditions. Presumably in shallow waters they even settle at times upon the actual bottom, but their usual beat or range of movement, especially in deeper waters, is not known. Experiment has shown

that while they tend to hold the body constantly with back to the light source they may move up or down, back and forth; that is, toward or away from the source of the stimulus, as a result of a variety of contending and conflicting influences, now one winning the day, or the hour, now another. The issue may indeed vary from hour to hour, and one might almost say from moment to moment.

With the wonderful change registered at the beginning of the fourth stage, the young lobster mounts to the surface and holds more persistently to it than ever before, at times even jumping out of the water like a shrimp, though having discarded its larval swimming organs and having brought into play the permanent swimmerets under the tail. Every observer is agreed that of all the free-swimming stages the fourth is that most commonly taken at the surface of the ocean, and especially in the brightest sunshine. This surface-swimming habit has further been observed by every experimenter who has reared these young or turned them loose into the sea. At this point the experimental testimony seems to conflict with the natural behavior of the lobsterling, since during the early part of its fourth stage it has been observed to avoid the light. The explanation would seem to be that this, like most of its similar reactions, is subject to reversal, under conditions which are not as yet fully understood, but which, as Hadley suggests, may be due to an increased intensity of the light stimulus or to an impulse which leads it to seek its food at the upper levels of the water.

At the close of the fourth, or at some time probably near the end of the fifth period, the little lobster makes its complete and final descent to lower regions. (Compare p. 348.) Thereafter the bottom of the sea becomes its fixed abode, which it seldom or never leaves unless snapped up by an enemy, or in after years it is hauled to the surface in a lobster pot.

In the fifth and all later stages the light-shunning tendency becomes more and more pronounced, but it can not be said that it is never subject to change, for more than once I have seen adult lobsters exploring the bottom in shallow water on sunny days. Yet their avoidance of strong light and their impulse to hide and to burrow after the fifth stage is fairly constant. In a word, their behavior is no longer essentially variable, but is in a measure stereotyped.

VARIATION IN THE RATE OF GROWTH AND DURATION OF THE STAGE RERIODS.

The following table shows the size and age of lobsters during the first eleven stages, and is based upon data obtained at different points on the coast under different conditions of temperature upon a varying number of individuals and by different observers. New measurements of any number of individuals made under approximately similar conditions would possibly give a different result, but this difference would not be great.

I found that the fourth stage was reached at Woods Hole on the average in 14 days, while Mead has determined this period for Wickford, R. I., to be a little over 12 days, the average duration of the first three periods varying from 9 to 16 days, with an individual variation of 3 to 7 days, according to the temperature and other conditions.

Assuming that the lobster goes to the bottom to stay at the close of its fourth stage, the pelagic life of the Woods Hole lobsters would be about 30 days, while at Wickford

it would last 23 days, or a little over 3 weeks. Assuming that the bottom is not definitively sought until the close of the fifth stage, the free swimming life at Woods Hole would last 46 days, or a little over 6 weeks, and at Wickford about 30 days.

TABLE 11.—AVERAGE SIZE AND DURATION OF STAGE PERIOD IN THE FIRST ELEVEN STAGES.

Stage.	Wickford, R. I. (Hadley).		Woods Hole, Mass.	
	Average length (millimeters).	Stage period (days).	Average length (millimeters).	Stage period (days).
1	8.2	2.0	7.8	1–5
2	9.6	4.0	9.2	2–5
3	11.4	5.0	11.1	2–8
4	13.5	12.0	12.6	10–19
5	15.5	9.5	14.2	11–18
6	18.6	12.7	16.1	14
7	22.5	14.3	18.6	.....
8	26.5	16.0	21.03	.....
9	32.1	.....	24.5	.....
10	37.9	.....	28.23	.....
11	42.9	.....	.....	.....

Assuming, further, that under natural conditions the molts are passed more rapidly, and that the bottom is sought some time between the close of the fourth and of the fifth stages, the pelagic life will be found to cover a period of from 3 to 4 weeks.

CONDITIONS WHICH DETERMINE THE RATE OF GROWTH AND THE DURATION OF STAGES.

The length of the stage period or the period between molts from first to last depends upon (1) intrinsic and (2) extrinsic causes. Among the intrinsic causes the following must be considered: (*a*) Inherited characters or the individual constitution, which gives a certain bent or direction to activities and limits their scope, and (*b*) acquired characters, such as the loss of limbs, which is certain to retard the rate of growth of the body as a whole by diverting energy to the regeneration of the lost parts.

Thus if the fighting and preying instincts, due to inheritance, are stronger in larva A than in larva B, A will get more food, grow faster, molt sooner, and, its inherited capital being equal in all other respects, it will distance B in the race from the start and, barring mishaps, forge ahead at every step of the way. The early advantages gained by A are cumulative in their effects. The parable of the talents is applicable even to the lobsters, and the laggard in the race, though of the same age, may not attain one-half, or even one-quarter, of the strength of its more strenuous rival, and will be fortunate if it is not cut into pieces and devoured, a contingency quite likely to happen when its running mates are crowded or underfed.

Among the acquired characters are to be reckoned any weakness which may be due in the first instance to congenital defects, such as imperfect or undersized eggs, accidents like the loss of a limb, mutilations of any kind, which, as Emmel (*90*) has shown, increase the stage period and therefore diminish the rate of growth, or parasitism which may be encouraged by a lowered vitality or improper food.

Of extrinsic causes the most important are (*a*) food of the proper sorts, (*b*) changes in temperature, a powerful factor under ordinary conditions, and (*c*) changes in light, to which the lobster, whether as larva, adolescent, or adult, is very sensitive from infancy to old age.

Every stage period culminates in molting, a result and expression of growth which is subject to the causes above enumerated and therefore indeterminate. Consequently the rate of growth in lobsters is subject to wide variation. Every individual has its own rate, which may vary from that of others or from its own rate at a later period of life by 100 per cent, and which may be different at different times of the year and at different places, as well as different at corresponding times in different years at the same place. Moreover, beyond a certain stage the rate of growth varies in the sexes. Variation in the rate of growth is far from uniform in man and the higher animals, but it is not subject to such rapid changes and wide fluctuations.

Notwithstanding the drawbacks and difficulties of the problem, it is possible to determine the average rate of growth and age of maturity, provided our statistics are ample, which is not the case at present except for one or two points on the coast.

RATE OF GROWTH AND AGE AT SEXUAL MATURITY.

In 1895 I made the first systematic attempt to determine how long it takes an adult marketable lobster to grow, and remarked: "It is impossible to answer the question with certainty, since complete data for solving the problem have not been gathered. We can, however, give a tentative answer which is probably not far from the truth."

It was further pointed out that in order to ascertain the average age of a lobster 10½ inches long (weight 1¾ pounds) it would be necessary to know, first, the number of molts which the animal had passed through, and, secondly, the time interval between each molt. We showed that the number of molts could be approximately determined by certain means discussed. The time interval could only be ascertained by keeping the animals alive for a period of years and carefully recording their growth. Both of these factors, as we have already seen, are highly variable quantities. Thus, to give further examples, the length of a certain yearling lobster which was raised from the egg was only 36 millimeters, while three other lobsters measured from 35 millimeters to 51.8 millimeters when only 5 months old. Even more striking individual differences have been given by Mead (*195*) and Hadley (*126*); two of Professor Mead's lobsters each 4½ months old (June 1 to October 7) measured about 55 millimeters and 30 millimeters, respectively, the smaller being not much larger than one of the big claws of the former. Of three lobsters figured by Hadley, each having attained an age of 1 year and 4 months on October 23, 1902, the larger had reached a length of about 120 millimeters (nearly 5 inches), the smaller but 58 millimeters (about 2⅓ inches). Lobsters that live in harbors where they find abundant food undoubtedly grow much faster than those farther from shore and on poor feeding grounds. It could hardly be expected, moreover, that lobsters kept under artificial conditions would grow as rapidly as when free in the ocean.

I also gave a record of the molts of eight lobsters varying in length from 5½ to 11¼ inches, and found the average percentage of increase (ratio of increase to total length before molting) to be 12.01. Then using the records of the lengths of lobsters reared from the first to the tenth stages at the laboratory of the United States Bureau of Fisheries at Woods Hole, Mass., the percentage of increase for a total of 246 young individuals gave the percentage of increase as 15.3 for each molt. The table follows:

TABLE 12.—ACTUAL LENGTH OF LOBSTERS DURING THE FIRST TEN MOLTS.

Number of molt or stage.	Average length.	Extremes in length.	Number of lobsters examined.
	mm.	*mm.*	
1	7.84	7.50 to 8.03	15
2	9.20	8.3 10.2	47
3	11.1	10 12	79
4	12.6	11 14	64
5	14.2	13.4 15	15
6	16.1	15 17	12
7	18.6	18 19.5	4
8	21.03	19.75 22	5
9	24.5	24 25	2
10	28.03	26.6 29.5	3

It should be added that the measurements here recorded were not made with this problem definitely in view, and are therefore uneven in number, and further that the number of young considered in the last four stages are too small to give satisfactory results.

Assuming the average length of the first larva at Woods Hole to be 7.8 millimeters, a table was drawn up giving the estimated length of lobsters during the first 30 molts as follows:

TABLE 13.—ESTIMATED LENGTH OF LOBSTERS DURING THE FIRST 30 MOLTS.

Stage.	Length.	Stage.	Length.	Stage.	Length.
	mm.		*mm.*		*mm.*
1	7.84	11	32.55	21	135.17
2	9.04	12	37.54	22	155.86
3	10.42	13	43.28	23	179.70
4	12.02	14	49.90	24	207.20
5	13.86	15	57.53	25	[a] 238.90
6	15.98	16	66.34	26	[b] 275.45
7	18.42	17	76.49	27	317.59
8	21.24	18	88.19	28	366.16
9	24.49	19	101.68	29	422.21
10	28.23	20	117.24	30	[c] 486.81

[a] 9.5 inches. [b] 11 inches. [c] 10.1 inches.

We called attention to the fact, which has since been verified, that the increase is similar from period to period during the larval and early adolescent stages. According to Hadley (*126*), during the first 17 stages, when the young have reached an age of 2 years and 3 months, the increase per cent is 18.

The frequency of molting or the stage period was next considered with the following result: We concluded that during their first year, lobsters as a rule molted from 14

to 17 times, and attained a length of from 2 to 3 inches, with the probability that this limit was often extended. Examining all the data available at the time we further concluded that the 10-inch lobster was between 4½ and 5 years old, the higher degree of probability favoring the smaller number, and had molted from 25 to 26 times. "The reader is reminded," we then added, "that this is only an estimate, based, it is true, upon rather slender data, but upon the only facts which we possess. In future years some experiments will be made by which this result can be tested."

The words just quoted were written in 1894; twelve years later the problem of the rate of growth in the lobster was taken up by Hadley (*126*), who has given an excellent discussion of the question in all its bearings and has supplied many of the data which were then lacking. His work was conducted at the Wickford hatchery of the Rhode Island Commission of Inland Fisheries under conditions which the experience of many years and of many workers has brought to a high degree of perfection. His results are therefore more complete and more valuable than those of any previous students.

Hadley's final conclusions (see *126*) so far as general results are concerned do not differ greatly from those reached by me in 1895, as may be seen by the following comparisons: Thus, I estimated that a lobster in the first year of life molted from 14 to 17 times, and reached a length of from 2 to 3 inches; Hadley determines that the yearling molts 12 times and attains a length of 2⅛ inches. According to the table (here reproduced as table 13) the 10-inch lobster has molted from 24 to 25 times and was estimated to have reached the age of 4½ to 5 years; according to Hadley a male 9⅞ inches long has molted 23 times and is 5 years old, while the female of the same length is 1 year and 5 months older. Thus at this juncture the estimates are from one to two molts apart, and for the male in essential agreement as to age.

TABLE 14 (AFTER HADLEY).—AN ESTIMATE OF THE RATE OF GROWTH OF THE AMERICAN LOBSTER FROM TIME OF HATCHING TO ATTAINMENT OF A LENGTH OF 22¾ INCHES.

Stage.	Approximate age.	Length.		Increase.			Approximate time of molt.	Stage period.	Sex.
		Millimeters.	Inches.	Millimeters.	Inches.	Per cent.			
No. 1	0	8.2					June	2 days	M. F.
No. 2	3 days	9.6		1.4		18	do	4 days	M. F.
No. 3	7 days	11.4		1.8		18	do	5 days	M. F.
No. 4	12 days	13.5		2.1		18	do	12 days	M. F.
No. 5	24 days	16.0	5/8	2.5		18	July	11 days [a]	M. F.
No. 6	35 days	18.8	¾	2.8		18	do	12.5 days	M. F.
No. 7	7 weeks	22.5	⅞	3.7		18	August	14 days	M. F.
No. 8	9 weeks	26.5	1 1/16	4.0		18	do	15.5 days	M. F.
No. 9	3 months	32.0	1¼	5.5		[b] 18	September	21 days	M. F.
No. 10	5 months	37.9	1½	5.9		18	October or November	25 days	M. F.
No. 11	9 months	45.0	1¾	7.1		18	April	5 months	M. F.
No. 12	1 year	53.0	2⅛	8.0		18	June	1½ months	M. F.
No. 13	1 year 1 month	62.0	2½	9.0		18	July	33 days [c]	M. F.
No. 14	1 year 3 months	73.0	2⅞	11.0		18	August or September	51 days	M. F.
No. 15	1 year 6 months	86.0	3⅜	13.0		18	October or November		M. F.
No. 16	2 years	102.0	4 1/16	16.0		18	April or May		M. F.

[a] The fifth stage period is generally shorter than the fourth.

[b] For female lobsters bearing eggs, there can naturally be no molt during the period that the external eggs are carried; this is at least for 11 or 12 months.

[c] The midsummer stage period is usually the shortest.

TABLE 14 (AFTER HADLEY).—AN ESTIMATE OF THE RATE OF GROWTH OF THE AMERICAN LOBSTER FROM TIME OF HATCHING TO ATTAINMENT OF A LENGTH OF 22¾ INCHES—Continued.

Stage.	Approximate age.	Length.		Increase.			Approximate time of molt.	Stage period.	Sex.
		Millimeters.	Inches.	Millimeters.	Inches.	Per cent.			
No. 17.....	2 years 3 months.	121.0	4¾	19.0	.....	18	August.....	.....	M. F.
No. 18.....	2 years 6 months.	141.0	5⅝	20.0	.....	16	November.....	.....	M. F.
No. 19.....	3 years.....	162.0	6⅜	22.0	.....	15	May.....	.....	M. F.
No. 20.....	3 years 6 months.	180.0	7¼	18.0	.....	11	Autumn [a].....	.....	M. F.
No. 21.....	4 years.....	200.0	8	20.0	.....	11	Late spring.....	.....	M. F.
No. 22.....	4 years 6 months.	222.0	8⅞	22.0	.....	11	Autumn.....	.....	M.
	4 years 6 months.	222.0	8⅞	22.0	.....	11	Late summer or autumn	.....	F.
No. 23.....	5 years.....	247.0	9⅞	25.0	.....	11	Summer.....	.....	M.
	6 years 5 months. [b]	247.0	9⅞	25.0	.....	11	Late summer or autumn	.....	F.
No. 24.....	6 years.....	275.0	11	28.0	.....	11	Summer.....	.....	M.
	8 years 4 months.	275.0	11	28.0	.....	11	Autumn.....	.....	F.
No. 25.....	7 years.....	300.0	12	25.0	.....	9	Summer.....	.....	M.
	10 years 4 months.	300.0	12	25.0	.....	9	Autumn.....	.....	F.
No. 26.....	8 years.....	327.0	13⅛	27.0	.....	9	Summer.....	.....	M.
	12 years 4 months.	327.0	13⅛	27.0	.....	9	Autumn.....	.....	F.
No. 27.....	9 years.....	356.0	14¼	29.0	.....	9	Summer.....	.....	M.
	14 years 4 months.	356.0	14¼	29.0	.....	9	Autumn.....	.....	F.
No. 28.....	10 years.....	380.0	15¼	24.0	.....	7	Summer.....	.....	M.
	16 years 4 months.	380.0	15¼	24.0	.....	7	Autumn.....	.....	F.
No. 29.....	12 years.....	406.0	16¼	26.0	.....	7	Summer.....	.....	M.
	18 years 4 months.	406.0	16¼	26.0	.....	7	Autumn.....	.....	F.
No. 30.....	14 years.....	431.0	17¼	25.0	.....	6	Summer.....	.....	M.
	20 years 4 months.	431.0	17¼	25.0	.....	6	Autumn.....	.....	F.
No. 31.....	17 years.....	457.0	18¼	26.0	.....	6	Summer.....	.....	M.
No. 32.....	20 years.....	480.0	19¼	23.0	.....	5	.....do.....	.....	M.
No. 33.....	23 years.....	505.0	20¼	25.0	.....	5	.....do.....	.....	M.
No. 34.....	26 years.....	525.0	21	20.0	.....	4	.....do.....	.....	M.
No. 35.....	29 years.....	546.0	21⅞	21.0	.....	4	.....do.....	.....	M.
No. 36.....	33 years.....	568.0	22¾	21.0	.....	4	.... do.....	.....	M.

[a] After the eighteenth stage it is very doubtful whether the lobster molts oftener than twice in a year.
[b] It is uncertain at just what time the spring or early summer molt for female lobsters not bearing external eggs is first omitted, but it is probably near this stage.

It is shown, however, by Hadley, that the rate of growth is more rapid in the young Wickford lobsters (stages 1 to 17), that it begins to fall at the age of about 2½ years (stage 18), becomes differentiated in the sexes in favor of the more rapid growth of the male at the twenty-third stage, and continues to decrease, the stage period becoming longer and longer with age, especially in the female, where the production of eggs proceeds at a very rapid rate. Thus, according to Hadley, the increase in the 12-inch lobster has dropped to 9 per cent, or about one-half that in the first 17 stages, and while both sexes have molted 25 times, the male is but 7 years old, while the female is 10 years and 4 months. Thus he thinks that the female is outstripped in the race with the other sex on account of the drain upon her vitality due to the periodic production of a rapidly increasing egg supply, and that this accounts for the fact that so far as observed giant lobsters beyond 18 or 20 inches in length are invariably of the male sex.

Following Hadley's estimate still further, for the larger lobsters, upon the age or rate of growth of which no data are yet available, a male lobster 19½ inches long is 20 years old and has passed successfully 32 molts, while a mammoth measuring 22¾ inches from beak to telson has entered upon his thirty-sixth stage, and attained to the green old age, for a lobster, of 33 years. According to my earlier estimate a lobster at the thirtieth molt had attained a length of 19.1 inches.

That the stage periods increase with age no one can deny, for this is only another way of saying that youth is the period of most active growth. There is no theoretical limit to the growth of such a crustacean, although there is a practical limit. Thus lobsters do not attain a weight of 100 pounds, but they have tipped the scales at 34 pounds. Again, there is no *a priori* reason for assuming that the percentage increase in weight in the adult lobster at each molt may not be fairly uniform up to the period of decline. But since molting is not only the prelude to expansion in size, but also of the greatest use to the animal in freeing it from troublesome parasites and messmates and at the same time keeping its cuticular glandular system in order, as well as in the repair of injuries through the restoration of appendages and other lost parts, we should surely expect to find so useful and necessary a process limited only by the duration of life itself. This is apparently the case, and since the tendency, in all the higher organisms, at least, is to lose vitality with age we might expect the percentage of increase in weight or in the expansion of the body to decrease gradually in old age until it was practically nil, or reduced to the ability of renewing the shell or exoskeleton only. This would seem to be actually the case, although we have no direct observations upon which to found the opinion, and it is possible that death from old age in the lobster, if it come at all, would follow from final failure to cast the heavy armor, rusty with age, and scarred in many a conflict.

As has already been noticed in considering the rate of growth of the ovary (p. 299) the volume of any part or of the body as a whole does not increase proportionately with the length but more nearly with the cube of the length. In other words the percentage increase in the length of the body at each molt does not accurately express the true rate of growth, which concerns the entire volume of the body. Therefore it may be found that after a period is reached corresponding to the length of from 8 to 10 inches, the lobster, and more particularly the male, may increase more rapidly in volume and become stockier, especially to be noticed in the enlargement of the big claws, while increase in total length of the body may be relatively less.

I have shown that the male, length for length, weighs more than the female, and that a female with external eggs is lighter than one of the same length without eggs (*149*, p. 118–120, table 31); it is therefore only natural to expect to find the female handicapped by the male after reaching sexual age (7¼ to 12 inches).

We will now briefly consider the rate of growth of Woods Hole lobsters, average increase per cent 15.3, and that of Wickford lobsters with average of 18 per cent for the first seventeen stages, or 18.4 per cent as given in another place. Hadley in attempting to account for this discrepancy concludes that the former figure is too low and that it does not represent the growth of young lobsters under natural conditions at Woods Hole.

I think it highly probable now, as I did in 1892–1894, that lobsters grow more rapidly in nature than when confined in glass jars in a hatchery, but that the measurements of the early stages of the lobster which were then made were correct for the place and time there can be no doubt. They were taken upon a standardized scale, and made with care under a hand lens or dissecting microscope.

The lobster in the first stage, according to our table, was found in fifteen measured individuals taken from the hatching jars to have an average length of 7.84 millimeters (extremes 7.50 to 8.03 mm.), against an average length of 8.2 millimeters as given by Hadley for Wickford, R. I. The eggs from which these young were hatched at Woods Hole were stripped from old lobsters, taken in June to July, and placed in the McDonald type of jar then in use. The mean average temperature of the sea water at the U. S. Fish Commission wharf for a period of five years from 1889 to 1893 was for June 62.1° F., and for July 69.1° F. The water in the hatching jars was found to average one degree higher than that outside. Since I could not begin operations until the latter part of June, the eggs with which I had to deal directly or indirectly had reached a late stage of development under natural conditions, and were near the hatching point when taken. Accordingly these eggs were probably not undersized and the larvæ may be regarded as normal for Woods Hole for the period in question.

What is the average length of first-stage lobsters hatched in the waters of Vineyard Sound? Although during six consecutive seasons (1889–1894) I never succeeded in taking, with the net at the surface of the sea, under natural conditions, a single larva of the first stage, and but one of the third stage, this question can be partially answered by the earlier observations of Smith (*256*) made in 1871, who says that "the lobsters in the first stage were first taken July 1, when they were seen swimming rapidly about at the surface of the water among great numbers of zoeæ, megalops, and copepods." * * * "They were frequently taken at the surface in different parts of Vineyard Sound from the 1st to the 7th of July, and several were taken off Newport, R. I., as late as July 15, and they would very likely be found also in June, judging from the stage of development to which the embryos had advanced early in May in Long Island Sound. These young lobsters with two exceptions were taken at the surface in the daytime (forenoon) from July 1 onward, but not so commonly as young in the fourth stage." Smith gives the measurement of the first stage as 7.8 to 8 millimeters. It therefore seems probable that the average length of Woods Hole lobsters in the first stage is under 8 millimeters, and not above this measure as found by Hadley for the same stage at Wickford, but probably above 7.84, the average found for the artificially hatched young. If this be the case, it is quite certain that the rate of growth up to at least the tenth stage is slower than at Wickford, as is further indicated by the longer stage periods.

Hadley concluded that a 11-inch male lobster from Wickford was 6 years old, while a female of the same length was 8 years of age, whereas upon the Massachusetts coast this length is not attained in less than 7 and 9 years, respectively. Accordingly a 10-inch Wickford male would be about 6 years old, and a female of the same length somewhat over 7 years. I am inclined to doubt whether the difference is really as great as is here implied.

While we can not make direct comparisons with confidence without knowing the number of individuals in each case concerned, figures which neither Smith nor Hadley give, I am inclined to believe that while the rate of growth for Woods Hole lobsters during their earlier stages may be greater than 15.3 it is less than 18 per cent, and that while my former estimate of the age of a 10-inch marketable lobster to be from 4½ to 5 years may need the addition of a plus mark, especially in the female, it is probably not far from the truth.

Female lobsters are found bearing eggs for the first time when measuring from 7¼ to 12 inches (18.5 to 30.5 cm.). Amid limits so wide it is impossible to say at what time the average female lobster reaches the reproductive age, but it is probably not far from the 10-inch length, which according to Hadley would represent the twenty-third molt and an age of about 6½ years. We have no data upon the time of sexual maturity in the male, but should expect that it would be reached at the same or at a slightly earlier period.

Regarding the questions of rate of growth in *Homarus gammarus* of Europe, I shall give the general conclusions of Ehrenbaum (*87*), whose studies at the Helgoland laboratory are well known:

> It is possibly not superfluous at the end of these observations to state again clearly that the results which the American naturalists and we in reliance upon them have reached in regard to growth and the relations between size, age, and life-stage cannot be regarded as completely reliable.
>
> The numerical results which are given in the works referred to and which have been partly reproduced, can in the most favourable cases be regarded as of only average value, especially when we reflect that all biological relations possess a certain variability and cannot be expressed in absolute figures.
>
> If, moreover, we reach the result that the Helgoland lobster lays her eggs for the first time in her seventh year of life, it by no means contradicts the idea that in many individuals this may happen in the sixth year, while occasionally females of only 23 centimeters (9⅛ in.) in size have been observed with extruded eggs, and moreover it may happen that in single cases the first egg-laying is delayed until the eighth year of life.
>
> But even disregarding this natural and anticipated variability, it cannot be denied that our figures, even as averages, possess a certain untrustworthiness, since only one element rests upon direct observation, while another is based upon combinations. This uncertainty is sufficiently reflected in my earlier contributions (see communication of 1903, p. 154), wherein I came to the conclusion that female lobsters were in their sixth year of age when for the first time they carry eggs, while now, standing upon a basis not much more extended, I have accepted the seventh year in preference.
>
> Moreover the American authors waver between the sixth and seventh year as regards the period in question, and find a way out on the supposition that the period is six years for the southerly state of Rhode Island, and seven years for more northerly Massachusetts and Maine. Accordingly it is well to lay it down as a general rule that the first egg-laying takes place in the sixth or seventh year of life, with the higher probability favoring the longer period. This statement would then hold good for both American and European lobsters throughout their areas of distribution. Moreover, it can be accepted as fixed that this egg-laying takes place in from the twenty-third to the twenty-fourth stage of life.

Chapter XII.—THE PRESERVATION AND PROPAGATION OF THE LOBSTER.

The lobster is easily the king of the crustacean class, and though neither "fish, flesh, fowl, nor good red herring," he is excellent eating, and that his race may increase is a wish generally felt and often expressed. Unfortunately, for many years past we have watched this race decline until some have even thought that commercial extinction, and that not far remote, awaited the entire fishery. What is the matter with the lobster?

If this is primarily a scientific question, the zoological history of the animal should give us the answer. The lobster has attracted many naturalists and other observers, both in this country and in Europe, especially during the past 15 years, until it has become the focus of a wide literature, as a glance at the bibliography at the close of this work will show. Indeed, few marine animals are now so well known. The main biological facts concerning this classical type are well in hand, and excuse can no longer be offered on the ground of ignorance.

If the question is only an illustration of "many men, many minds," we may as well give it up and let the process of extermination take its usual course. However, we consider that this problem is primarily a scientific and not a social one. When the causes of the evil are definitely known, it becomes necessary to evoke the law. If ideal legislation can not be secured, we must then strive for the best within reach. It is obviously useless or even worse to enact laws which can not be enforced, and statutes which are a dead letter and have no moral effect had better be expunged.

We have already given a brief history of this valuable fishery (p. 170), and shall now consider in a little more detail the evidences of its decline and what we consider the most effective remedies for its restoration.

THE FACT AND CAUSE OF DECLINE.

It is no exaggeration to say that in practically every known natural region of the North Atlantic coast the lobster fishery is either depleted or in a state of decline. The evidences of this condition are to be found in steadily increasing prices and in the statistics of the fisheries.

The market price, or cost to the consumer, has steadily advanced in direct ratio to the steady decrease in the market supply. Thus, in 1889 the annual catch of lobsters in the United States was somewhat over 30,000,000 pounds, valued at over $800,000; in the course of a decade, or in 1899, the annual crop was reduced by one-half, while its value had more than doubled. Since 1899 the failing supply has not been sensibly checked. Statistics of the fisheries of the two New England States—Maine and Massachusetts—which are most interested in the lobster question, have the same story to tell. In Maine, which in some years has produced two-thirds of the entire output of

this fishery, the catch amounted to 14,234,182 pounds, with a market value of $268,739. Twenty years later the product had fallen to 12,346,450 pounds, a decline of over 2,000,000 pounds, while its value ($1,062,206) had advanced fourfold. The product of the fishery for 1880 in Massachusetts was 4,315,416 pounds, which sold for $158,229, while the catch of 1900, though only half as great, was worth more than that of 10 years before.

The average price per pound in the shell in Canada was 9.12 cents in 1883, 14.10 cents in 1893, while in 1898 it had risen to 18.72 cents (*187*). Large lobsters which 25 or 30 years ago could often be bought at 5 cents apiece are now sold in the shell at 20 to 30 cents a pound,[a] which at the latter figure represents a cost of about 55 cents a pound for all the edible parts, and over a dollar a pound for the clear meat of the tail and claws alone. (See table 3, p. 214). Thus, from being one of the cheapest food products of the ocean, this delicious crustacean has become one of the dearest luxuries. Once the regular summer visitor to the country villages throughout the New England States, it has now practically disappeared from the markets of all but the larger centers, and is there to be had only at many times the former cost. The fame of the live broiled lobster has spread over the Eastern and Western States, but, regardless of size or quality, the consumer must pay from 60 cents to a dollar or more for a single lobster.[b]

The former abundance of these animals on the Atlantic coast of Canada and New England was incredible, and probably for many years in succession more than 100,000,000 have been marketed, representing a cost to consumers at present prices of upward of $40,000,000. The shores on certain sections of the coast have been often described as strewn with lobsters in "windrows" after a storm. (See p. 218.) The animals were so common it is not surprising that their value was not appreciated.

A fisherman at Southwest Harbor, Maine, who had trapped lobsters for half a century, gave me the following account of his experience: About the year 1875, when the annual shrinkage in the wild crop had already been felt in many places, he took at one haul from 100 traps, which had been down 2 days, 1,985 pounds of lobsters. All but 15 of his pots contained lobsters, and from one, which was filled to the spindle, 35 animals were taken. As a contrast to past conditions, few of marketable size were at this time to be caught (July 27, 1902). The day before our interview this fisherman's son pulled 60 traps, set off Bunkers ledge, between that point and the Duck Islands, once a famous fishing region for this crustacean, and took only 9 lobsters of marketable size. Illustrations of this kind could be extended indefinitely, but the fact of decline is the one subject upon which all are agreed. It is the burden of nearly every report on the fishery which has been issued for a score of years.

The causes of the decline of the fishery are plainly evident. More lobsters have been taken from the sea than nature has been able to replace by the slow process of reproduc-

[a] Thirty cents a pound at Cleveland, Ohio, April, 29, 1907. Wholesale prices at T Wharf, Boston: Large live lobsters, 24 cents per pound; boiled, at 28 cents; chicken, live, at 18 and 20 cents; boiled, 20 and 22 cents.—(The Boston Globe, August 4, 1910.) Retail prices at the same time, 30 cents per pound; earlier in season, 25 cents.

[b] Lobsters are not cheap in the restaurants of London, where boiled lobsters are sold for 8 pence to 2 shillings or more each, according to size. One and six is a common price for the half of a boiled lobster. (1903.) (Compare p. 173.)

tion and growth. In other words, man has been continually gathering in the wild crop, but has bestowed no effective care upon the seed. The demands of a continent steadily increasing in wealth and in population have stimulated the efforts of the dealers and fishermen, who must work harder each year for what they receive in order to keep up the waning supply. The natural result has followed, namely, a scarcity of numbers and a decrease in the size of the animals caught, with steadily advancing prices paid for the product. This is precisely what we should have been led to expect, had we based our judgment upon any sound principles of common sense and human economy, not to speak of a knowledge of the mode of life and general natural history of the animal in question.

THE PROBLEM.

The problem before us is how to aid nature in restoring and maintaining an equilibrium of numbers in the species, or how to increase the number of adult animals raised from the eggs. It concerns not only the fisherman who earns a livelihood through the fishery, or the dealer who has capital at stake, but the public of many lands; in fact, everyone in the Western Hemisphere at least who likes the lobster for food. When the decline of the already depleted fisheries became a serious menace protection was sought in legislation, but since the lobster supply of this country is drawn from several States and from Canada and the maritime provinces as well, no uniformity of laws or methods was to be expected. Each state enacted its own laws, which were often widely at variance, unscientific, and subject to continuous change. Up to the present time every effort to check the constant and ever-increasing drain upon this fishery has signally failed, which shows that either the laws are defective or that the means of enforcing them are insufficient.

A sound and essentially uniform code of laws for the entire fishery is plainly demanded if legal restrictions are to be of much avail.

HOW THE PROBLEM HAS BEEN MET.

What means have been adopted in this country and in other parts to check the decline of this fishery so general and so universally acknowledged? The more important restrictive measures enacted at sundry times and in divers places have been as follows:

(1) Closed seasons of various periods in different localities.

(2) A legal gauge or length limit—namely, 9 inches in New York, Rhode Island, and Connecticut; 10½ inches in Maine, New Hampshire, and also in Massachusetts, until reduced to 9 inches in 1907; 8 inches in Norway and England; and 8, 9, and 10½ inches in different districts of Canada; in all cases penalizing the capture and sale of all lobsters under these limits, and legalizing the destruction of all adults above the gauge.

(3) "Egg-lobster" laws,[a] or the prohibition of the destruction of female lobsters carrying their external eggs. In addition to such legislative enactments, efforts of a constructive character have been made as follows:

[a] The phrases "egg lobster," "berried lobster," or "lobster in berry," or "lobster with external eggs," are all synonymous, and always mean a female with her cargo of eggs, new or old, attached to the swimming feet under the tail.

(4) To increase the supply of lobsters in the sea by fry or larvæ artificially hatched and immediately liberated, and as practiced chiefly in Canada, by holding the berried lobsters in large inclosures, called lobster pounds, ponds, preserves, or parks, and later setting them free when the young are ready to hatch.

(5) By the rearing method later introduced of holding the fry artificially hatched and rearing them until the fourth or fifth stages, when they go to the bottom and are able to take care of themselves. We need not enter here into other legislative channels, such as laws prohibiting the sale of broken or picked-out lobster meat, the operation of canneries, and the construction of gear, however necessary they may be for this fishery. We shall devote our attention mainly to those questions of most vital concern to the fishery as a whole.

CLOSED SEASONS.

A closed season for any animal, during which it is made illegal to hunt or fish for it, can only be completely justified and placed upon a scientific basis when it is made to correspond to the breeding season of the species as a whole, and when this season is limited to a relatively small part of the year. Neither of these things is possible in the lobster, since the question is complicated by the fact that this animal spawns but once in two years, so that not more than one-half of the adult females reproduce annually, and the eggs when laid are carried about by the lobsters through nearly an entire year. Closed seasons of this character are therefore not to be recommended, since they serve merely to restrict the total amount of fishing done in the year, and do not touch the root of the difficulty.

There is a closed season in the maritime provinces from June 30 to January 14, and in 1889 the Norwegian fisheries laws prohibited the taking and sale of lobsters from July to November. The apparent aim in these cases is to protect the lobsters during the spawning season and for a longer or shorter period after it, but the females only can receive much benefit, and then only provided the law against the destruction of their eggs is observed. Closed seasons set a limit to the period of destruction and may help to preserve the females by taking them into the protected class, after they have emitted their eggs.

As we have already shown, the lobster is a very sedentary animal, so far as any extended coastwise migration is concerned, and many which escape the traps in the fall will undoubtedly enter them again in the spring and upon the very same grounds.

PROTECTION OF BERRIED LOBSTERS.

A certain percentage of lobsters captured at all times of the year bear spawn, and how best to save these animals and their eggs is a serious question. The Maine laws impose a fine of $10 for every berried lobster destroyed or offered for sale. It is an easy matter to brush or comb off the eggs, however, and thus evade the law, which it is impossible to enforce completely; but however difficult of enforcement it is not wise to invite the destruction of the seed, upon which we depend for every future crop.

To save the precious spawn thus inevitably lost two plans have been tried or suggested: (1) Collecting the egg lobsters from the canneries and fishermen and subsequently hatching and liberating the fry, and (2), placing the berried females thus obtained in suitable inclosures and allowing the young to hatch under more natural conditions. The former plan has been adopted and carried out on a rather large scale in Canada and less extensively in the United States. As a means of saving the eggs which might be otherwise totally lost, both methods are to be commended, but for the preservation of the fishery neither is adequate.

By use of the second method more eggs would doubtless be hatched and more vigorous larvæ produced, while, on the other hand, an unnatural concentration of the young at a few points near shore would lead to a greater destruction. The hatching and immediate liberation of the young, which is far less commendable, will be later discussed.

The most important things to consider first are (2) the legal length limit, and (4) the hatching and immediate liberation of the young, because they are fundamentally related, have been long on trial, and have entailed great expense. That they have had a fair trial and that they have signally failed all must admit.

THE GAUGE LAW.

No doubt there are many who are ready to affirm that the present laws would be good enough if enforced. Most people are aware that the gauge law has not been rigidly carried out, and that the illegal sale of short lobsters has become a trade of big proportions. I know very well that at many times of the year it is possible to buy short lobsters (said to come from Baltimore) in the markets of Cleveland and of other towns in the great Middle West. Nevertheless I can not share this idea. Both of these measures were bound to fail, and would have failed whether the short lobsters were destroyed or not.

To come back to our question, What is the matter with the lobster, or with our means of fostering it? We have committed a series of grave errors in dealing with this fishery, to the chief of which, the gauge law, the others have been contributory.

First, by legalizing the capture of the large adult animals, above 10½ inches in length, we have destroyed the chief egg-producers, upon which the race in this animal, as in every other, must depend. Second, as supporting or contributory causes, some of us now, like others in the past, have entertained false ideas upon the biology of this animal, especially (*a*) upon the value of the eggs or their rate of survival, that is, the ratio between the eggs and the adults which come from them, and (*b*) of the true significance to the fisheries of the breeding habits, especially in regard to the time and frequency of spawning and the fosterage or carriage of the eggs. Our practices have been neither logical nor consistent, for, while we have overestimated the amount of gold in the egg, we have killed the "goose" which lays it. We have thought the eggs so valuable that we have been to great trouble and expense in collecting and afterwards hatching them and committing the young to the mercy of the sea, while we have legalized the destruction of the great source of the eggs themselves—the large producing adults.

This fundamental error of destroying the adult lobster was first clearly pointed out in 1902 by Dr. George W. Field, chairman of the Commissioners on Fisheries and Game in Massachusetts, who in various reports since has ably advocated a sounder policy, based both on science and common sense, as will appear later in this chapter.

At first sight this question seems to be about as broad as long and suggests the problem of how to eat your bread and butter and save enough for another meal when the demands of hunger are strong. While we are dependent on the adult lobsters to yield a continuous supply of eggs, and let us say we will reserve them for that purpose, we also depend upon a continuous supply of the young to yield the adults; moreover, the young at 6 inches long are many thousand fold more useful to the fishery than the eggs.

In dealing with such questions comparisons are often made with the flocks or herds of domesticated animals, and are almost certain to be misleading. The shepherd knows his flock and its resources; every member of it is numbered and under his control, and he is able to select the young or the old for slaughter, as his interest or that of his flock may demand. Among wild animals the conditions are entirely changed, and especially in those that are aquatic like the lobster, which lives at the bottom of the sea and is seldom seen, except when caught and brought up in a trap. We can select or reject among the captured only and have no definite knowledge of the proportion of young to the adults, of the various sizes, or of their distribution at any given time. If the wild flock could be brought under our knowledge and control, the comparison sought would be of real value.

We might form a comparison, however, which would be parallel in every respect by assuming that the animals of a domestic herd became more valuable for breeding purposes with each added year of life. If instead of producing 1 young at each reproductive period, they were to give birth to 2 in the second year, 4 in the third, 8 in the fourth, and so on for a considerable time, would the ranchman sacrifice his old or his young breeders for the market?

In dealing with the problem we are reminded of the proceedings of a fisheries committee in Great Britain, quoted by Mr. Allen (*2*), and the answers of a stubborn witness on the proper legal size limit of crabs: "If they do not breed till they are much larger than 4¼ inches, do you not by killing all the crabs that are under the breeding size, stop the supply of crabs from those fish?" This fisherman thought not. "Then," said his questioner, "how is the supply to be kept up if you kill the crab before sufficient time is allowed for it to spawn once?" The witness was obdurate, and answered that they did not kill them all. "Then," said another member, "suppose all girls are killed when they are twelve years of age; there would be no young women or children. I think you understand that, and if young crabs under the age at which they can spawn be killed, it follows that there can be no crabs from them." "But crabs," replied the fisherman, "breed a deal different from what girls do; crabs when they spawn, spawn many thousand at a time."

While it is essential to recognize that the older the female lobster the more useful as an egg producer she becomes, we must also remember that nature kills far more of

the young than of the adults. If man's almost unlimited power of destruction is allowed to supplement the destructive forces of nature, will the depleted stream of young be adequate to maintain a steady current of adults? We think that it would, since under Dr. Field's plan the number of breeding animals should tend to increase year by year.

Our lobster-fishery laws, which date in the main from 1873, are in principle like those which prevail elsewhere, and taken as a whole they illustrate the force of example and tradition, which were established long before the biology of this animal was even approximately understood. The past literature of this crustacean bristles everywhere with these false notions, which are more or less directly and mainly responsible for the enactment and maintenance of the present laws and practices of this fishery.

The legal length limits of 9 and 10½ inches, which sanction the destruction of the big egg-producers, but for these supporting causes would probably never have been retained, for these causes have led to a diversion of energy in various directions, such as the enactment of closed seasons and the practice of hatching and immediate liberation of the fry.

The reasoning which has led to the establishment of the gauge limit has been somewhat as follows: Lobsters come to breeding age when 9, 10, or 10½ inches long, and when they spawn they spawn many thousands at a time, which is true. Therefore, by placing the legal gauge at 9 or 10½ inches we allow this animal to breed at least once before it is sacrificed, which is also true in the main. Ten-inch lobsters lay on an average 10,000 eggs; the lobster, being a good mother to her unhatched progeny, and the best incubator known, will bring most of these eggs to term, and will emit to the sea her young by the tens of thousands. What more is needed to maintain this fishery? The answer is, Vastly more. This race needs eggs not by the tens of thousands merely, but by the tens of billions, and it must have them or perish. Moreover, it can get them only or mainly through the big producers, the destruction of which the present gauge laws have legalized. If the lobster is a good "incubator," the sea is a very poor nursery. We have put a false value upon the egg.

Before proceeding farther in this analysis, we shall review some of the most pertinent facts in the biology of the lobster, most of which have been fully discussed in earlier chapters. These facts concern chiefly (*a*) the period of maturity of adult lobsters; (*b*) the number of eggs borne by the females, or the size of the broods; (*c*) the frequency of spawning; (*d*) the treatment which these eggs receive, or the habits of spawning lobsters; (*e*) the habits of the fry or larvæ; and (*f*) possibly more important than all else, the death rate or the law of survival in the young.

(*a*) Lobsters do not mature at a uniform age or size, but females produce their first broods when from 7 to 11 inches long, approximately, the difference between these limits representing a period of from 4 to 5 years (age of female lobsters at these limits about 3 and 8 years, according to Hadley). Very rarely are eggs laid before the 8-inch stage is reached, and the majority are mature at 10 or 10½ inches, when some have reared more than one brood. Accordingly, by merely reducing the 10½-inch gauge to 9 or 8 inches we rob the animal of the very meager protection which it now enjoys.

(*b*) The number of eggs produced increases with surprising rapidity in proportion to the cube of the length or the total volume of the body, from the very beginning of sexual maturity. The approximate number of eggs at 8 inches is 5,000; at 10 inches, 10,000; at 12 inches, 20,000; at 14 inches, 40,000; at 16 inches, nearly 60,000; and at 18 inches, nearly 80,000. In the case of 532 10½-inch berried lobsters taken from the waters of Massachusetts, the smallest, average, and largest number of eggs borne were 5,000, 13,000, and 36,000. The smallest number probably represents a first brood, so that the average berried lobster at this size is probably carrying eggs for the second time. The maximum of production is reached at the 15 to 16 inch stage, when some individuals produce nearly 100,000 eggs at one time.

The average 10½-inch berried lobster is from 5 to 7 years old; and assuming that it has borne eggs once before, it has lived to produce 23,000 eggs. On the other hand, an egg-bearer 16 inches in length, which according to Hadley's estimate is nearly 18 years old, has had a succession of eight broods and has produced 210,000 eggs. The larger animal is thus worth nine times as much as the smaller; in other words, in the course of twelve years its value to the fishery has been increased 800 per cent.

Again, it should be noted that it is the class of small adults up to, but not including the 9 or 10½-inch animals, those which produce by the fives or tens of thousands, upon which we have relied to maintain the race, while it is the class of big lobsters, which produce the fifty and the hundred thousands, that has been nearly wiped out.

(*c*) There is a definite spawning period for the majority of adults, ranging on the coast of Massachusetts from July 15 to August 15, and averaging two weeks later in northern Maine. A relatively small per cent lay their eggs in fall and winter.

(*d*) It is a fact, though frequently denied, that the American lobster lays its eggs, as already stated, but once in two years (though rare exceptions to this rule may be looked for), and not annually, as was formerly supposed.

(*e*) The eggs are carried attached to the underside of the tail, and admirably guarded by parental instinct for nearly a year, or until they are hatched 10 or 11 months after deposition.

Ignorance of the fact that there is a definite spawning period, that the eggs are laid but once in 2 years, and that they are subsequently carried from 10 to 11 months, to hatch in June or July following the summer when laid, is responsible, in considerable measure, for erroneous ideas regarding the efficacy of closed seasons, laws protecting the berried lobster, and other matters of legislation, the effects of which have not yet worn away.

(*f*) The fry or young, when hatched, rise to the surface or toward it, and lead a free-swimming life for 3 weeks, hardly larger than a mosquito and infinitely more harmless, translucent, brilliant in reds and blues, and quite helpless in the presence of all but the minute animals upon which they prey. They perish quickly by the thousands before the storm and the countless fish and other enemies which they meet in their varied movements, and which do not disdain small fry.

At the third molt, or the fourth, counting that passed at the time of hatching, with what seems like a sudden leap and bound, they are transformed into the fourth or the

lobsterling stage, which really looks like a little lobster. Either in this stage or in the fifth, which follows, they go to the bottom, hide under stones, burrow in the sand, and show an ability to protect themselves. The most critical period of infancy being now past, one lobster at this stage is worth many thousands in the first. Therefore, our efforts, to be of real avail, should not end with the hatching and immediate liberation of the fry; we should rear them to the bottom-seeking stage.

THE LIFE RATE OR LAW OF SURVIVAL.

What is the death rate or the rate of survival in the lobster? Upon the answer to this question hinges the gauge or legal-length law, as well as the expensive practice of hatching and turning loose the young, which has been pursued in this country and Canada for many years (since 1886 in the United States and since 1891 in Canada).

As was pointed out 10 years ago, too many fish culturists have been content to turn out so many thousands or millions of eggs of lobsters and fish, and confidently expect results, to the neglect of the most important question of the whole matter—the rate of survival in the young set free, or the number of adults which can be raised from them—the very end for which all the time, trouble, and money have been expended.

In the popular mind an egg is an egg, like that of the fowl which we eat for breakfast. An egg really represents opportunity or chance to survive, and its biological value to the race depends upon the law or rate of survival, which was definitely fixed in nature before the advent of man with his traps and hatching jars, and differs in every species of animal and plant known. When the gantlet of life is long and hazardous, especially in infancy, nature, as in the present case, multiplies the chances or multiplies the eggs. Many eggs always means death, under natural conditions, to all but a remnant of the host. The number of eggs alone serves as a rough gauge to determine the rate of survival.

At one end of the scale stand the birds and mammals, with few eggs and the highest life rate known, secured by guarding and parental instincts, with big yolks and rapid development in one case and the special conditions of fetal life in the other. At the other extreme we find a parasite like the tapeworm, where the conditions of early life are so unpromising—since it must run a long hazard of chances and be eaten by two distinct vertebrates—that its eggs are required by the hundreds of millions or even billions. The lobster needs more eggs than the trout, and of smaller size, but far less than the edible blue crab, which carries nearly five millions of eggs attached to its body. Each one of these is barely visible to the unaided eye and the young which issues from it must pass a long and dangerous larval period before reaching maturity.

What, then, is the life rate or rate of survival in the lobster? Probably not more than 2 in 30,000, and certainly not more than 2 in 10,000. This number would be exactly known, provided we knew the exact proportion of the sexes or the proportion of the total number of males to the total number of females and the average number of eggs laid by mature females during their entire life. The life rate accordingly would be expressed by the proportion $2 : x$, in which x represents the average number of eggs laid by mature females during the whole of life.

Since the sexes are about equal numerically, to maintain the species at an equilibrium it is only necessary for each pair of adults, or for each adult female to leave two children which attain adult age, whatever the actual length of life in either generation. If the adult progeny exceeds two, the race will increase; if less than two, it will diminish. Since under present conditions the race of this animal is falling off, the actual rate of survival for the individual having remained the same, the total number of survivals only has changed. In other words, there is at present a deficiency of eggs.

What is the average number of eggs for the entire life of this animal? We know the minimal and maximal limits of egg production in individuals (roughly, 3,000 and 100,000); we know the average number of eggs borne at the average age of maturity (at the 10-inch size, 10,000 eggs); but, as Allen (*3*) in discussing this question points out, we do not know the number of female lobsters destroyed at different ages. Many after laying their first eggs are killed before any young are allowed to hatch, and the number which survive to produce successive broods is a constantly diminishing one; but this is made good in part by the rapid increase in the number of eggs.

The average number of eggs borne by all the berried lobsters captured should give us an indication of the average number of eggs borne by all female lobsters during life—the number sought. In 4,645 egg lobsters from the Woods Hole region, Massachusetts, the average number of eggs was 32,000, which would correspond to a 13 or 13½ inch lobster which had produced three or more broods. Allen found the number of eggs borne by 96,098 lobsters caught in Newfoundland to be 2,247,908,000, which would give an average of 23,000 to each female. This number corresponds to an animal 12 or 12½ inches long, which, as he remarks, from the known average age at which female lobsters mature (10–10½ inches), would be carrying at least a second brood. Such a lobster must therefore have produced 13,000 eggs (the average product at 10½ inches) plus 23,000, or at least 36,000 in all. We are therefore right in concluding that the maximum rate of survival of 2 in 10,000, formerly given, was much too high, as it was known to be at the time, and that the proportion of 2 to 30,000 is much nearer the truth. Another estimate, by Meek (*200*), based upon the statistics of the fisheries of Northumberland, England, gives a life rate of 1 in 38,000.

If, then, it is true, as we are thoroughly convinced it is, that the normal rate of survival in the lobster is not greater than 2 in 30,000 or 1 in 15,000 (and it can not be greater than 2 in 10,000), the fact is big for the lobster fishery, and the sooner it is faced the better. It has a direct bearing upon our laws and fishery operations. It enables us to evaluate the egg and the egg lobster truly. It shows in a conclusive manner that the present gauge laws are indefensible, because they rob the fishery of the billions of eggs necessary to maintain it. It further shows that the method of hatching the eggs of this animal and immediately liberating its young is ineffective, because of the meager results which can come from it. On the other hand, it speaks loudly in favor of a law to protect the large egg producers, and of the newer plan of rearing the young to the bottom-seeking stage, as the only means by which pisciculture can hope to aid this fishery materially.

The importance of the law of survival to the operations of the fisheries, and especially in its bearing upon some of our present illogical laws, is the only excuse for dwelling upon it at this length. To illustrate further: With respect to period of maturity and value to the fishery, all lobsters in the sea may be divided into three classes—(1) the young and adolescents, mainly from egg or larva, to the 8-inch stage; (2) intermediate class of adolescents and adults, 8 or 9 to 10½ inches in length; and (3) large adults, mainly above 10½ inches long. The biological value of the individual increases with every stage from egg to adult of largest size, and therefore is greatest in class 3. The present laws sanction the destruction of class 3, but class 1, the beginning of the series, must, as we have seen, be mainly recruited from this class or from those animals which under present conditions are being wiped out. In other words, our policy shifts the duty of maintaining the race upon the small producers, which the law of survival plainly tells us it is unable to bear. There is no way of getting over this grave defect.

We speak of the "living chain" from egg to adult, but the metaphor is not a happy one. There is no "chain" relation in living nature, only a succession of individuals, of individual eggs, united in origin but discrete in each generation. The embryologist begins with the egg, but the fish culturist with the egg producer. Spare the egg producer, then, and nature will save the race. We can not wholly take the place of nature in dealing with the eggs, but we can defeat the ends of nature by killing the "bird" which lays them.

But, do you say, "We have the egg lobster law, and the protection of lobsters in spawn should remedy our difficulties?" In reply we have but to recall the fact that adults lay their eggs but once in two years, and consequently we should not expect to find more than one-half of this class with spawn attached to the body at any given time. This at once reduces the protection aimed at in the egg lobster law by one-half. The other half shrinks to small proportions when we consider that there is an overlap of four weeks in July between the climax of the periods of hatching and spawning, when the majority of all adult female lobsters are without eggs of any kind, and also when we further consider the ease with which a fisherman by a few strokes of the hand can make a berried lobster eggless.

When analyzed in the light of the law of survival, the showing of the lobster hatcheries is not very encouraging. The hatching and immediate liberation of the fry has been practiced for many years in Europe, where experiments were made in Norway as early as 1873, as well as in Canada and the United States. The whole number of fry hatched and liberated on the Atlantic coast for a period of ten years, according to official returns from the hatcheries of the United States, Canada, and Newfoundland, reached a grand total of 4,214,778,200. Detailed statistics are given in the following table.[a]

[a] H. F. Moore, of the United States Bureau of Fisheries, to whom we are indebted for collating these statistics, says that no definite annual records appear in the official reports of Newfoundland for 1896 and 1897. The number of fry for each of these years is stated to be an average of the output for the seven preceding years.

TABLE 15.

Fiscal year.	United States.	Canada.	Newfoundland.
1893	8,818,000	153,600,000	517,353,000
1894	78,398,000	160,000,000	463,890,000
1895	72,253,000	168,200,000	174,840,000
1896	97,079,000	100,000,000	435,079,200
1897	115,606,000	90,000,000	450,000,000
1898	95,234,000	85,000,000	171,900,000
1899	108,463,000	100,000,000	.....
1900	77,166,000	120,000,000	.....
1901	60,879,000	110,000,000	.....
1902	81,020,000	120,000,000	.....
Total for 10 years..	794,916,000	1,206,800,000	2,213,062,200

In addition to the number of lobster fry planted by the United States Fish Commission in 1900, there were sent to Dr. H. C. Bumpus 3,767,000 for experimental use. In 1902 also, in addition to the plant recorded by the commission, 6,178,000 fry were used for the same purpose.

Applying the law of survival, with life rate of 2 in 30,000, which has been shown to be a fair allowance, this number of young would yield only 280,985, while there must have been captured on this coast in the same period nearly 1,000,000,000 lobsters. By applying the maximum rate of 2 in 10,000, which we are assured is far too large, the yield would be 842,955. To have held the fishery at an equilibrium by this means, there should have been hatched 5,000,000,000,000 young, or 1,250 times as many as were actually liberated.

To take another example, the total output of all the Canadian lobster hatcheries for the entire history of this fishery, 1880 to 1906, was as follows:

Bay View, Nova Scotia, 1891–1906	1,889,300,000
Canso, Nova Scotia, 1905–6	79,000,000
Shemogue, New Brunswick, 1903–1906	291,000,000
Shippegan, New Brunswick, 1904–1906	220,000,000
Charlottetown and Dunk River, Prince Edward Island, 1880–1906	256,085,000
	2,735,385,000

Again, allowing the too generous rate of 1 in 5,000, this product of the activity of 24 years would yield only 547,077 lobsters, or but little over the two-hundredth part of the numbers caught in certain years in Canada alone.

In cases of this kind it is as detrimental to overestimate the value of the egg as to undervalue it. The eggs are true gold, although the amount which each weighs is infinitesimal. Like drops of water and grains of sand, these eggs count for but little singly, but in mass the inanimate particles can make the oceans and the continents, while the living germs can fill them with teeming inhabitants.

We can not work on the colossal scale of nature in dealing with egg or larva, but we may frustrate nature by destroying the egg producers. Nature long ago provided for the cod and hundreds of other predaceous fishes; she took into account the tides,

the storm, and the rock-ribbed coast also, by giving to this race billions of eggs each year; but no provision was made for millions of traps working night and day at the bottom of the sea to destroy the producers of these eggs.

THE PROPAGATION OF THE LOBSTER.

The method of rearing the young through their critical larval or pelagic period, until they finally go to the bottom in the fourth or fifth stages, promises material aid to this fishery. While opinions may differ upon most of the questions which have been hitherto discussed, here is a subject upon which all should be agreed, and we believe that the method can not be extended too far or adopted too widely. Accordingly we shall briefly review the history of lobster rearing.

The first successful attempts at the artificial breeding of fish in America were made upon the speckled trout by Dr. Theodatus Garlick and Prof. H. A. Ackley, of Cleveland, Ohio, in 1853, the eggs and sperm being forcibly removed from the bodies of the ripe animals, brought into contact, and young trout subsequently reared from the eggs thus artificially impregnated.

No such results have ever been obtained in the Crustacea, nor is such a procedure possible in an animal like the lobster, owing to the unyielding nature of its body, due to a hard external skeleton. In the case of this animal we can only remove the already naturally fertilized and developing eggs from the underside of the abdomen, to which they are attached by the female herself at the time of egg laying, and afterwards give them such favorable conditions that the processes of development will proceed in a normal course to the time of hatching, as in the case of the artificial incubation of the eggs of fowls.

Messrs. Guillon and Coste were apparently the first to rear lobsters in Europe in considerable numbers, and an account of their experiments, which were conducted at the laboratory of Concarneau on the coast of France, was published in 1865 by Moquin-Tandon and Soubeiron (*202*).

How sanguine were these pioneers of the success of their experiments is shown by the following extracts:

> The ease with which young lobsters are reproduced and developed in the basins of Concarneau is a sure token that upon our coasts suitable places should be readily found for establishing vivaria where one may obtain myriads of the young, but these should not be permitted to enter the sea until they are sufficiently advanced to resist most of the causes of destruction which constantly menace them. What we have seen since our first visit to Concarneau, namely, basins literally black with little lobsters hatched in a vivarium, and from what we know of the habits of a great number of fishes in coming in immense numbers to stock particular regions of the coast, we may hope that it will be possible to regenerate the fishery on parts of our shores. By means of reservoirs we should be able to create an abundant food supply.

It was also stated that at the island of Tudy, M. de Cresoles had designed aquaria for preserving, hatching, and feeding lobsters and the *Palinurus* or langouste, some of the compartments being shaded or otherwise adapted to the animals in different stages of growth.

The writers quoted above further add:

To surprise nature with the accomplishment, to see life develop down to the smallest details, to possess a world of the sea in miniature in a transparent house, where nothing could escape investigation, such are really the promises of the establishment at Concarneau. These promises, gentlemen, are to-day realized.

It is pleasant to read of this enthusiasm at the dawn of the period of marine laboratories, and so far as the lobster is concerned we can only regret that the difficult problems of its successful culture, which were then hardly appreciated, should have had to wait nearly 40 years for their solution.

According to Roché (*237*), Mr. S. H. Ditten, a pharmacist to the court at Christiania, proposed to collect the egg-bearing lobsters in large floating cars and keep them until the young hatched out and were set at liberty naturally.

In the years 1873 to 1875 experiments in the hatching and rearing of lobsters were again undertaken by several gentlemen at Stavanger, Norway (*227*), both independently and with the aid of the Kongeligt Selskab for Norges Vel. According to the reports of Professors Rasch and G. O. Sars they were eminently successful; many young lobsters were carried to the ambulatory or bottom-seeking stage, the necessity of which was duly emphasized, and incidentally important facts on the natural history of the lobster were brought to light. Again, whatever progress was made at the time, the work was not systematically continued.

In 1883 Saville Kent (*245*) contributed a paper on "The Artificial Culture of Lobsters," which later appeared in the proceedings of the International Fisheries Exhibition at London for that year. He stated that in 1877 1,000,000 lobsters, valued at £22,500, were imported from Norway into Great Britain; that the catch in both countries was falling off; and that the decadence of the fisheries was due to three main causes, as follows: (1) Overfishing of the inshore districts; (2) destruction of undersized lobsters, and (3) destruction of the spawn for culinary purposes; the destruction of the eggs being the chief cause, which should be combated by artificial propagation.

By feeding lobsters hatched in aquaria on minced fish he reared them to the 1-inch length, when they would go to the bottom and hide. As a result of his experience he made the following significant remarks:

The rearing of lobsters in thousands instead of in tens or units would, it is needless to assert, be but a matter of augmented apparatus, and what the results would be upon our depopulated lobster grounds if several thousands, or rather millions, of such young animals could be turned out upon them annually, those are best qualified to record a verdict who have already had practical experience in the cultivation of the Salmonidæ.

He would pay a bounty for the egg lobster in order to divert the supply of eggs, "at present only flowing to the saucepans of the cooks," into the hatcheries of the cultivator, advises the use of hatching jars, feeding upon minced fish and mussels, rearing to the ambulatory stage, and liberating on rocky ground.

Still later, in 1885, Captain Dannevig (*69*) also succeeded in hatching the eggs of the lobster and in rearing the young through the first three earliest stages, at Flödevig, Norway. He did not consider it of much service to hatch the eggs and set free the

young immediately; and he rightly said that so great was the destruction in nature from storms and other causes that out of the 25,000 or 30,000 eggs which a lobster might produce not a single one might reach its full development.

This work gave the first impetus to lobster culture in this country, where the hatching of eggs was accomplished in the summer of the same year (1885) at the newly opened laboratory of the United States Fish Commission at Woods Hole, Mass., as reported by Doctor Rathbun (*229*).

In 1894 we urged the importance of finding a means of rearing the young through the free-swimming stages, and thereby reducing the terrible death rate which inevitably occurs under natural conditions. As we then remarked, "If we could save 100 instead of 2 out of every 10,000 hatched, every million young would produce 10,000 adults and every billion would yield 10,000,000 lobsters capable of reproduction" (*143*).

While results somewhat similar to those outlined above have been obtained in England and in other parts of Europe, signal success in providing the young with a proper food supply and in maintaining them in a healthy condition up to the lobsterling stage has only been obtained in recent years in this country through the admirable work of Messrs. Bumpus and Mead and their associates. These experiments were begun under the auspices of the U. S. Fish Commission, at Woods Hole, Mass., in 1900, and were continued at other points on the coast, and especially at Wickford, R. I., where, under the direction of Professor Mead and of the Commissioners of Inland Fisheries of Rhode Island, the most efficient apparatus yet devised for the culture of lobsters has been gradually perfected and installed. All who are interested in the problems of lobster rearing should consult Professor Mead's original papers. (See, especially, *198*.)

Given a water supply which has been found by experiment to offer favorable conditions for the growth of lobster larvæ, and a suitable food supply, such as minced clams, beef, or "scrambled" eggs, the apparatus mechanically aerates the water and at the same time holds both the lobsters and their food in suspension with little detriment to the larvæ themselves.

At an early stage in his work Professor Mead found that in no case was the number of lobsters reared to the fourth stage less than 16 per cent of the total number of fry placed in the brood chambers (scrim bags, or wooden boxes, as now in use). The ratio of survival may even exceed 50 per cent. In 1901, between 9,000 and 10,000 lobsterlings were thus reared at the Wickford station to the bottom-seeking stage; in 1908, between 300,000 and 400,000 fourth or fifth stage lobsters were reared and distributed on the coast.

The rate of survival of the young in the early ambulatory stage is not known, but it is probably not less than 1 in several hundred, or a fraction of 1 per cent.

Instead of striving to work on the vast scale of nature in dealing with the egg, this is an attempt to improve upon nature by lowering the death rate in the most critical period. Great care, however, is needed at every stage of the process, and especially at the last, since the young do not seek the bottom at a uniform time.

Had it been our attempt to destroy this animal, could we have acted more effectively than by destroying its great egg-producing class? When we attempt to rid this country

of the English or house sparrow, will it help greatly to break its eggs and destroy its young ones, though so relatively few and with a far higher life rate than in the crustacean? Must we not eventually kill the producers of the eggs if we would be rid of the pest? This is the nature of the treatment which the lobster has received. If we would preserve this fishery, we must reverse our laws, as Doctor Field has ably pointed out, and follow the principles and practice of breeders of domestic animals everywhere—use the smaller and better animals for food, and keep the older, and in this case by far the most valuable, for propagation.

RECOMMENDATIONS.

In applying the principles already discussed the following suggestions are offered:

1. Adopt a double gauge or length limit, placing in a perpetual close season or protected class all below and all above these limits. Place the legal bar so as to embrace the average period of sexual maturity, and thus to include what we have called the intermediate class of adolescents, or smaller adults. These limits should be approximately 9 inches and 11 inches, inclusive, thus legalizing the destruction of lobsters from 9 to 11 inches long only when measured alive. In this way we protect the young as well as the larger adults, upon which we depend for a continuous supply of eggs. The precise terms of these limits are not so vital, provided we preserve the principle of protecting the larger adults.

2. Protect the "berried" lobster on principle, and pay a bounty for it, as is now done, whether the law is evaded or not, and use its eggs for constructive work, or for experimental purposes with such work in view.

3. Abolish the closed season if it still exists; let the fishing extend throughout the year.

4. Wherever possible, adopt the plan of rearing the young to the bottom-seeking stage before liberation, or cooperate with the United States Bureau of Fisheries or with sister states to this end.

5. License every lobster fisherman, and adopt a standard trap or pot which shall work automatically, so far as possible, in favor of the double gauge, the entrance rings being of such a diameter as to exclude all lobsters above the gauge, and the slats of the trap of such a distance apart as to permit the undersized animals to escape.

Many objections can be raised, but this plan is defensible on scientific grounds, while the older methods are not. The best thing which can be said of it is that it would eventually give us more eggs, and in an ever-increasing quantity—the greatest need of this fishery, both now and in the future. Under present conditions, the supply of eggs is yearly diminishing and at a tremendous rate.

The most striking objection to the proposed changes would be that if class 3, that of the big producers, has been nearly exterminated, and we proceed to wipe out class 2, the smaller adults, there will soon be no more lobsters; but this is not valid. No doubt if this change were made, the supply of smaller lobsters would be temporarily increased where the 10½-inch gauge law still prevails, as was the case in Massachusetts in 1907

when the 9-inch law went into effect; and this might be followed by a temporary stringency. No one can speak with positive assurance upon this subject, but the important point to bear in mind is that under such an arrangement we would have a perpetually protected class constantly growing and at work all the time.

Again, it may be asked, Will enough lobsters survive to enter the exempt class? We believe that there would, and that the answer to this question is to be found in the records of catches for every locality where lobsters are now trapped. Even in places where the average size is small, larger lobsters occasionally appear, and in sizes showing more than one year's growth. Why were not all such animals weeded out the previous year? Instead of waiting to be caught up in the end, these "escapes" would all enter the protected growing class, to enjoy a green old age of 50 years and possibly more, though we have no positive knowledge of the life span in this interesting race.

The trouble of a double gauge, such expense as would be needed in adjusting traps to admit and hold lobsters of the legal size, would have to be met, but it would be well worth while. In our opinion, the markets would not be seriously disturbed. Protect the big egg producers and nature will preserve the race.

Without doubt there are many who would consider any legal measure involving a double gauge impracticable because of the difficulty of carrying it out, for to be effective it must be uniformly adopted and enforced. If the present laws are to be maintained in principle, the following steps should be taken:

(1) Raise the legal gauge to 10½ inches wherever it now stands below this limit.

(2) License every lobster fisherman, and adopt a standard trap, with slats of sufficient distance apart to permit the undersized lobsters to escape.

(3) Destroy the present enormously destructive interstate commerce in short lobsters.

(4) Do not turn another larval lobster into the sea, but devote the energy expended in lobster hatcheries to rearing these young to the bottom-seeking stage after the methods now successfully practiced at Wickford, R. I.

BIBLIOGRAPHY OF THE LOBSTER—HOMARUS.

In the following bibliography we endeavor to give a record of the scientific literature of the lobsters (*Homarus gammarus* and *H. americanus*), embracing their anatomy, physiology, development, general habits, behavior, and habitat, as well as the lobster fisheries, and the preservation, artificial propagation, and economy of the species in general. In order to reflect the history of our knowledge of the subject, we have endeavored to include all papers, which were once, or are now, of any interest or value, from an early period to the present time. While keeping, in the main, within the limits of original research, we have given place to some minor works in which the knowledge of the day or period was reflected more or less clearly. The statistical records of the fisheries, however, are so widely scattered, and in some respects so unsatisfactory, that we have attempted to give only the most important references.

The voluminous literature of the related crayfishes, of the Norway lobster (*Nephrops norvegicus*), the spiny, thorny, or rock lobsters, "la langouste" of the French (*Palinurus*), and the Spanish lobsters (*Galathea*) is not generally included in this survey, and when referred to is noticed in the text. While we have endeavored to secure accuracy in giving titles, a few have been necessarily taken at second hand; further, we have not hesitated to add an occasional note, when in our opinion the use of this list to future students could thus be enhanced.

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Coste's original account of the reproduction and development of the European lobster, thus buried in an appendix to a public document, seems to have successfully escaped bibliographers up to the present. We are indebted to Dr. Richard Rathbun, who gave a summary of the paper in 1884 (see *226*, p. 803), for unearthing it at the present time. An indication of the accuracy of Coste's statements is given at page 190 of the present work.

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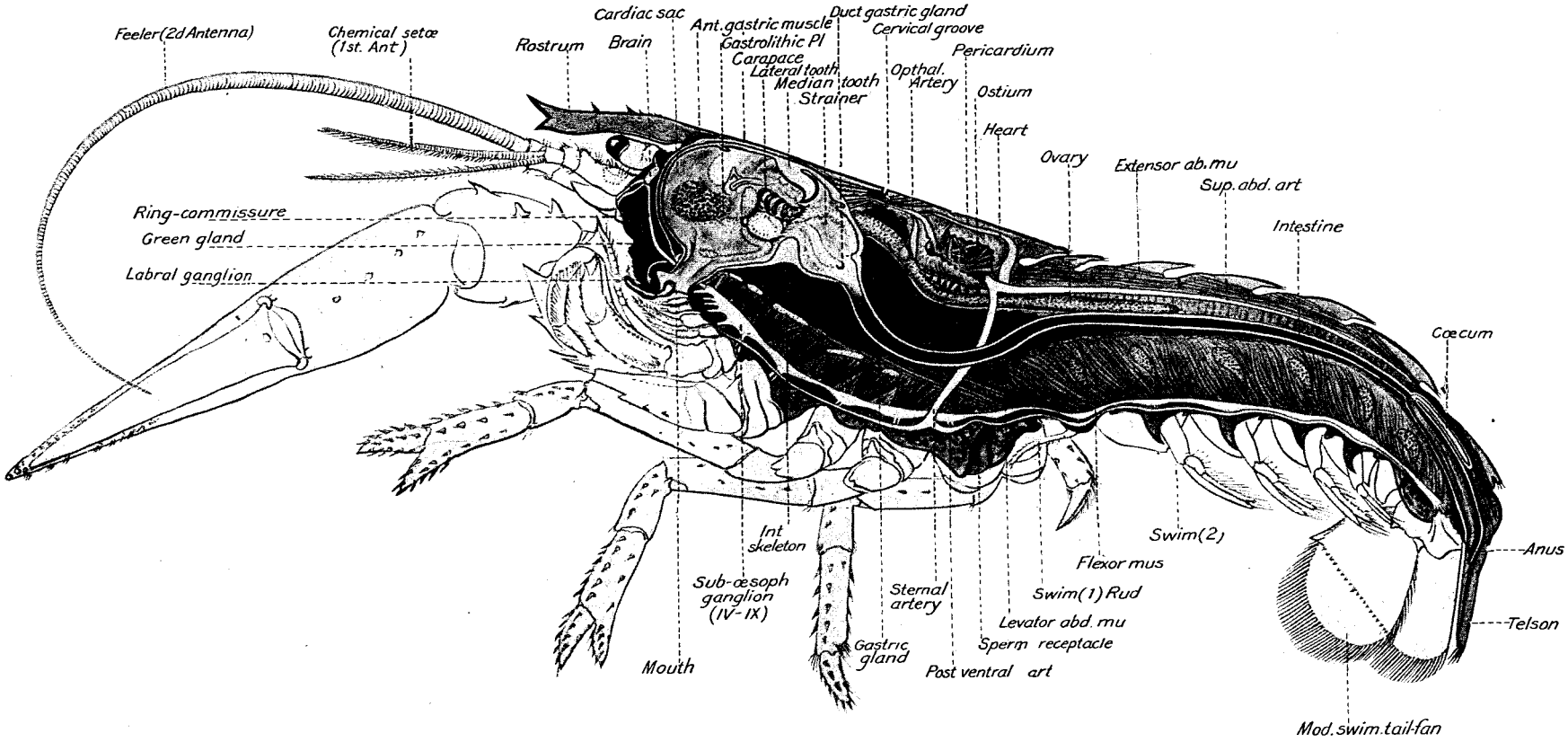
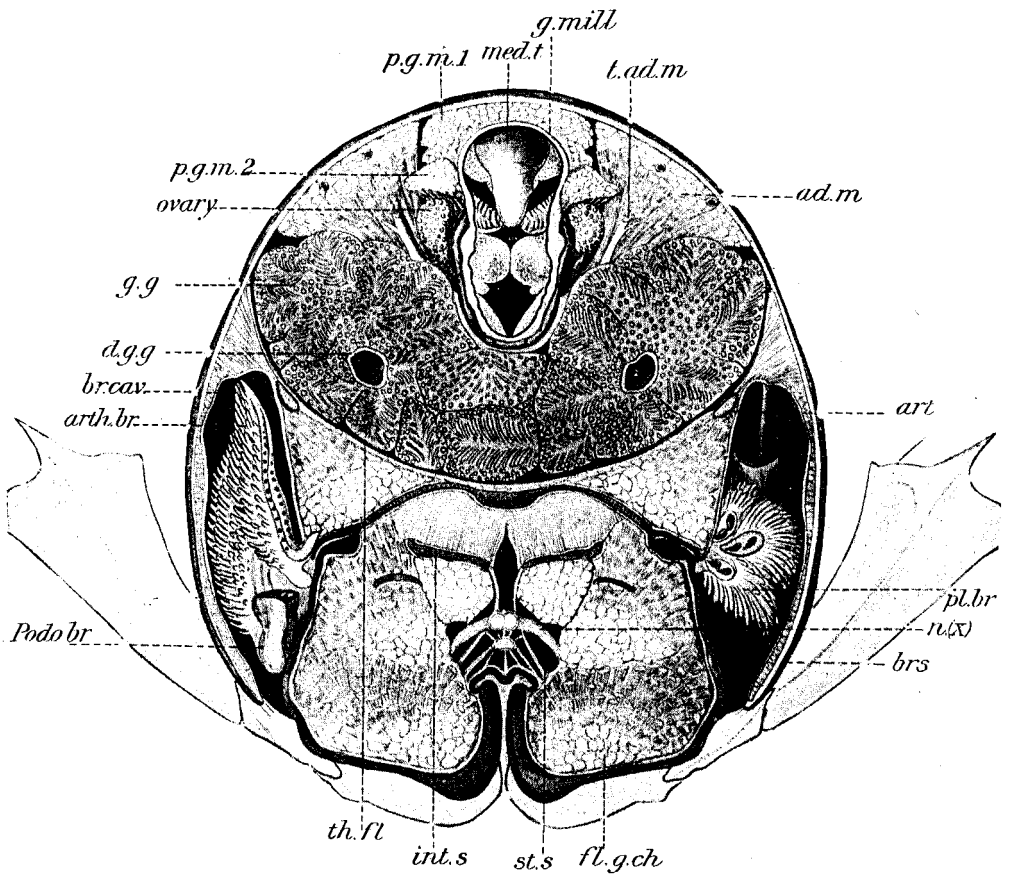


Half section of lobster cut in median plane to illustrate general anatomy. From soft shell female, 6½ inches long, slightly favored in head to show nervous system. Esophageal and gastric ganglion (the latter below reference line to anterior gastric muscle) and anterior visceral and median nerves are shown. Muscle marked levator abdominis (thoracico-abdominis) originates far forward in the thorax and joins enveloping muscles of the flexor system of abdomen. Note that abdominal sternal spines are much longer than in sexually mature animals.



Transverse section of body of female lobster in plane of gastric mill (see pl. XXXIII). *ad. m*, adductor mandibuli muscle; *art*, branchio-cardiac vessel; *arth. br*, arthrobranch; *br. cav*, branchial cavity; *brs*, branchiostegite; *d. g. g*, duct of gastric gland; *fl. g. ch*, basal flexor of great cheliped; *g. g*, gastric gland; *int. s*, internal skeleton, in roof of sternal sinus; *n.*(X), main nerve of great cheliped; *p.g.m.1*, first division of posterior gastric muscle; *pl. br*, pleurobranch; *Podo br*, podobranch; *t. ad. m*, tendon of adductor mandibuli muscle; *th. fl*, floor of thoracic cavity.

Fig. 1.

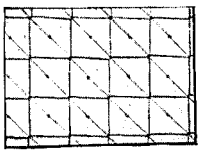


Fig. 2.

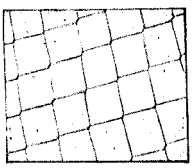


Fig. 3.

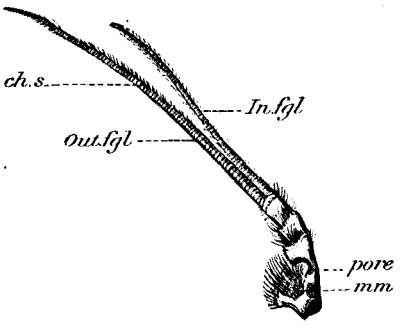


Fig. 4.

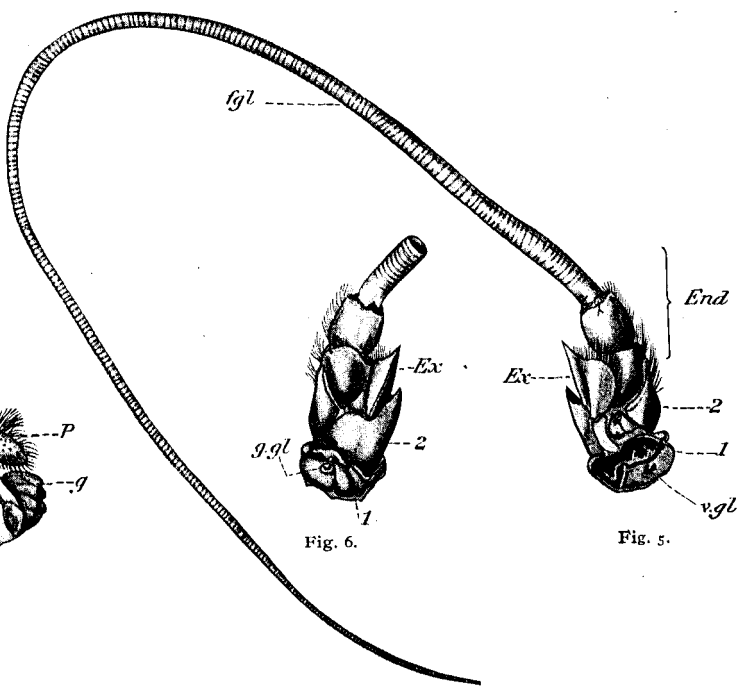


Fig. 6.

Fig. 5.

Fig. 7.

FIG. 1.—Left eyestalk, from above, or from what was originally the anterior side. *cor*, transparent cornea, parts of which are shown in figures 2 and 3; *1* and *2*, segments of stalk, the homologies of which are doubtful.

FIGS. 2 and 3.—Parts of corneal membrane of compound eye, composed of modified hexagonal facets of individual eyelets, each being secreted by two corneal cells, the boundaries of which are indicated in figure 2. Enlarged about 110 times.

FIG. 4.—Left first antenna from above. *ch. s*, chemical or "olfactory" setæ of primary outer flagellum (*Out. fgl*); *mm*, modified membrane over statocyst, which opens to outside by *pore*.

FIGS. 5 and 6.—Left second antenna from upper and under sides. *Ex*, exopodital scale; *End*, long multiarticulate "feeler"; *v. gl*, position of valve of green gland, which opens on under side of coxa (*g. gl*).

FIG. 7.—Left mandible from inner side; *ab. m*, opening muscle; *t. ad. m.*, tendon of closing muscle; *g*, groove in which palp (*p*) and upper lip work. Figures on plates XXXV–XXXIX, unless otherwise designated, represent the serial appendages from left side of a female lobster about 10½ inches long and in hard shell, drawn to same scale, as seen from anterior side, and but little under natural size. The segments of the permanent limb are numbered from base to apex.

Fig. 1.

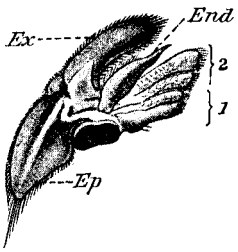


Fig. 2.

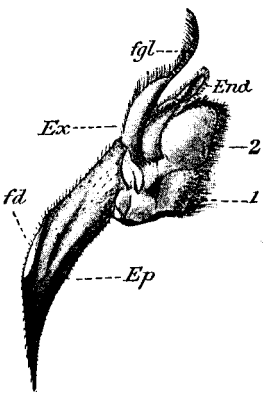


Fig. 3.

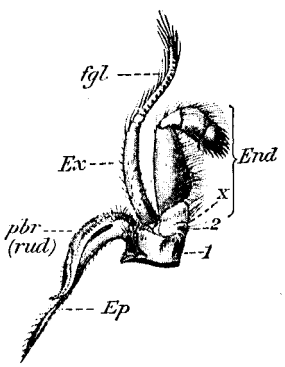


Fig. 4.

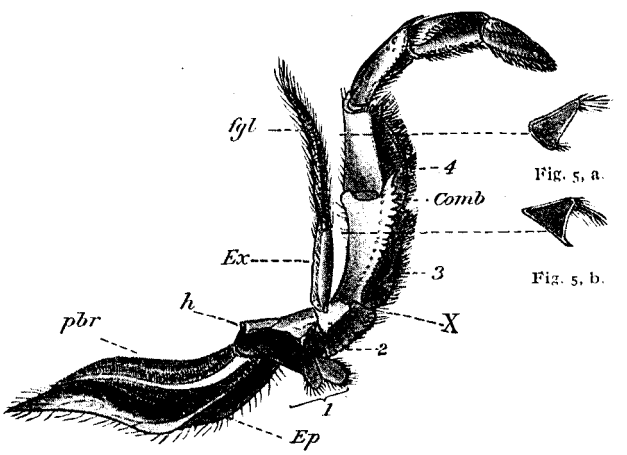


Fig. 5.

Fig. 5, a.

Fig. 5, b.

FIG. 1.—Left first maxilla of adult, from inner side.

FIG. 2.—Left second maxilla. *Ex*, *Ep*, exopodital and epipodital divisions of respiratory fan or scaphognathite. *1*, *2*, partially divided plates of protopodite modified for mastication.

FIG. 3.—First maxilliped. *fd*, fold of epipodite, which forms trough in which inner blade of fan (fig. 2, *Ep*) works.

FIG. 4.—Left second maxilliped, showing fused third joint (*x*) and rudimentary podobranch.

FIG. 5.—Left third maxilliped, illustrating type of primitive two-branched limb, with functional podobranch, but fused third joint (*x*), and *Comb* and cleaning brushes of third and following segments.

FIGS. 5, a and 5, b.—Transverse sectional views of three-sided meros and ischium, to show comb and brush, in planes indicated. In preceding and following plates, *End* represents the permanent inner branch of the limb; *Ex*, the outer branch or exopodite; *pro*, the protopodite; *ep*, the epipodite; and *pbr*, the podobranch. See legend of figure 7, plate XXXV.

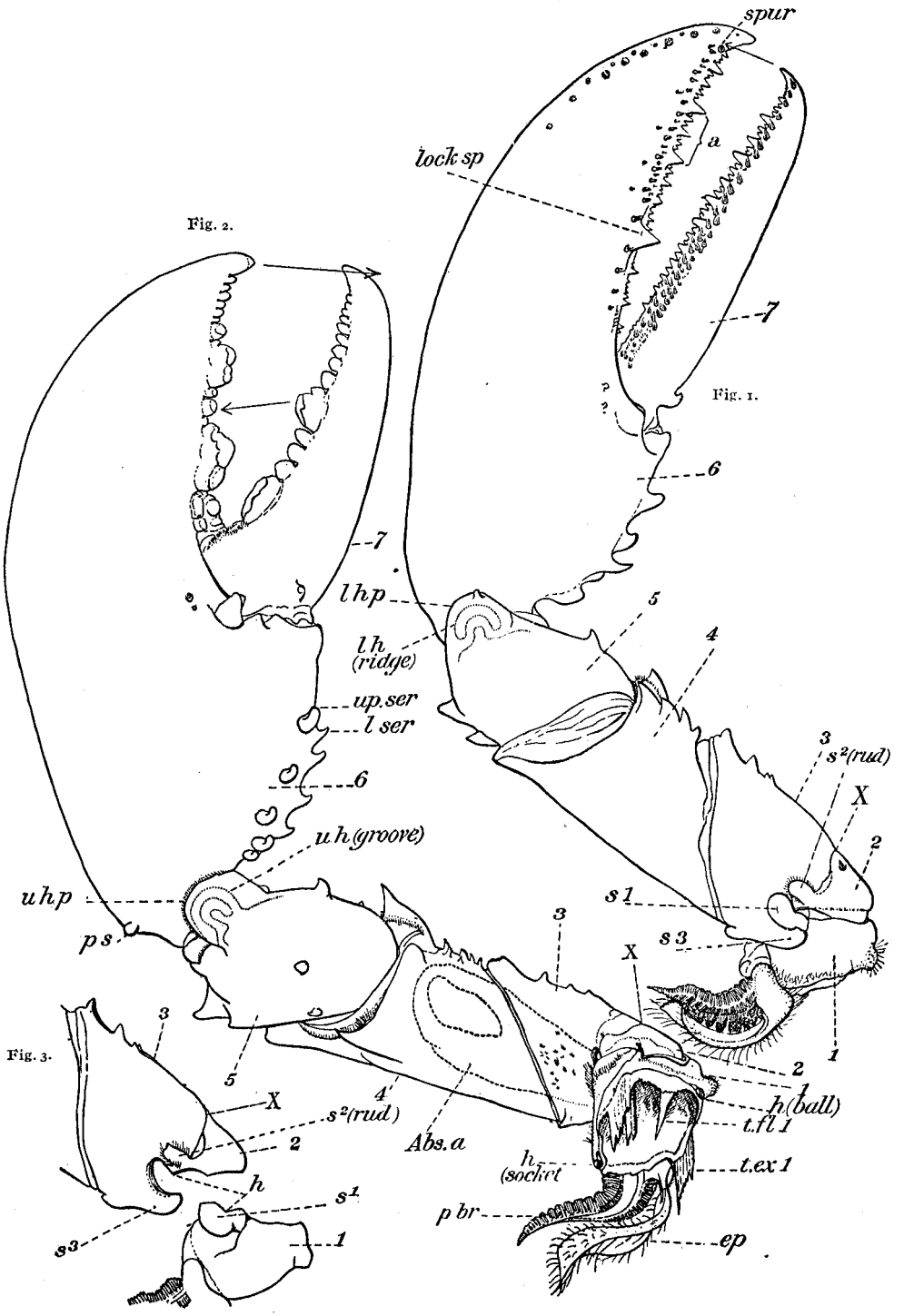
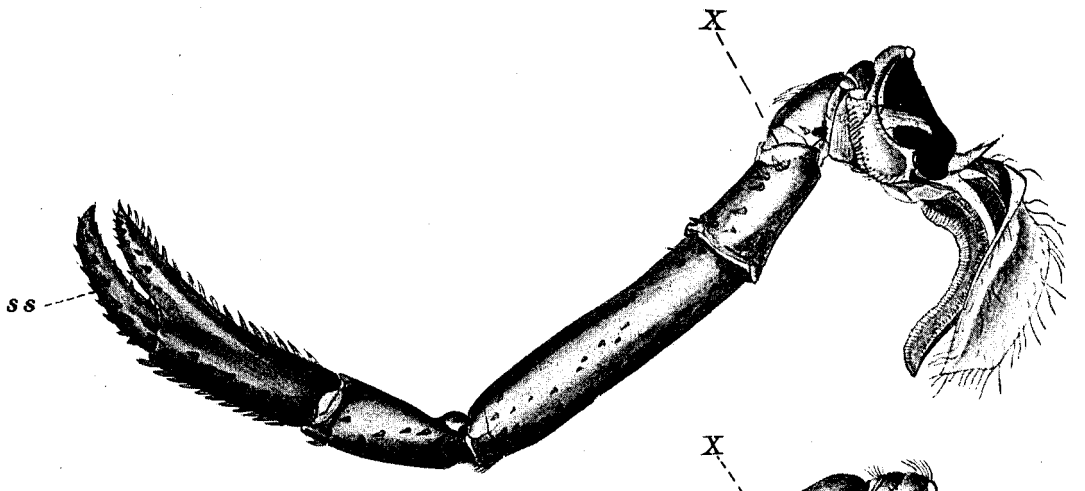


FIG. 1.—Right toothed forceps and cheliped of female lobster from lower side, showing periodic teeth, carpal ridge of lower lock hinge, represented as if seen through hinge-process (*l h p*), breaking joint (x), and interlock (*s 1* and *s 3*) between first and third podomeres. This claw is locked when closed by means of the underlapping lock spine (*lock sp*) and underlapping tip of dactyl, indicated by arrow.

FIG. 2.—Left cracker claw and cheliped of female from above, showing crushing tubercles, serial displaced teeth on margin of "hand" (*up. ser* and *l. ser*), carpal groove of upper lock hinge (*u h groove*), absorption area of fourth segment (*Abs. a*), breaking plane (at x), reversed basal hinges, or inner ball (*h ball*), and outer cup (*h socket*); tendons (*t. fl* 1 and *t. ex* 1) of first joint, podobranchia (*pbr*), gill separator (*ep*), and proximal spur (*ps*) of claw.

FIGS. 3 and 4.—Base of great cheliped from below, disarticulated at second joint to show interlocking mechanism or spines (s^1, and s^3) of first and third podomeres.



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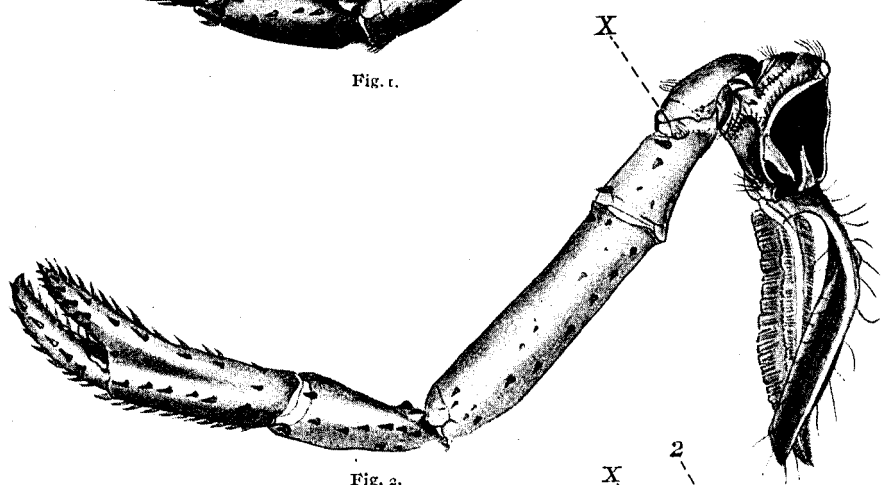

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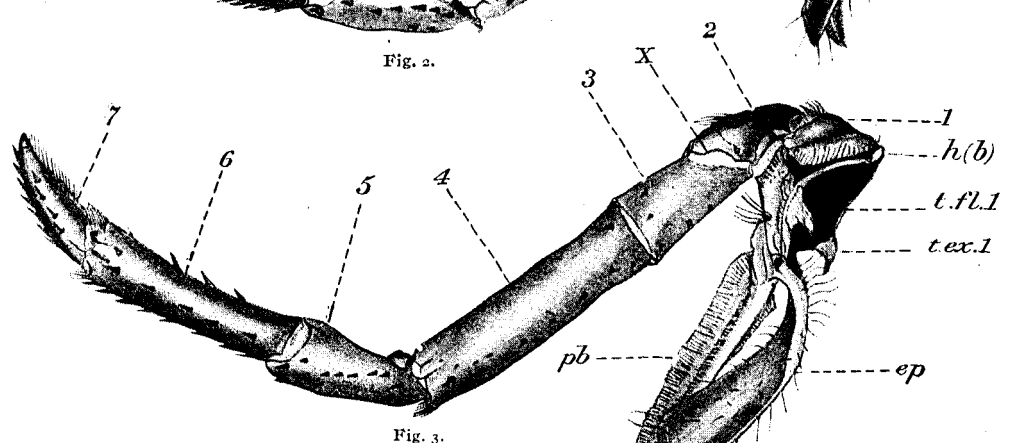

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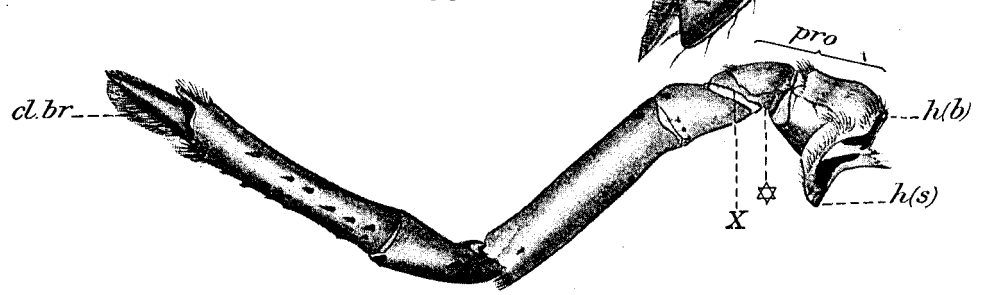
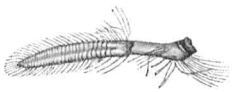


Fig. 4.

FIGS. 1–4.—Left second to fifth pereiopods or slender legs of adult lobster from anterior side, showing numbered segments of permanent limb, distribution of sensory tufts (*s s*), gills (*pb*, in fig. 1–3), and gill separators (*ep*), arrangement of ball-and-socket basal hinges, median ball (*h*, *b*), and peripheral socket (*h*, *s*), tendons of basal joints (*t. fl. 1*, and *t. ex. 1*), and cleaning pick and brush (*cl. br*) of last leg. Star in figure 4 marks position of exopodite or outer swimming branch of thoracic limb, shed at fourth stage.



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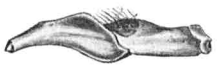

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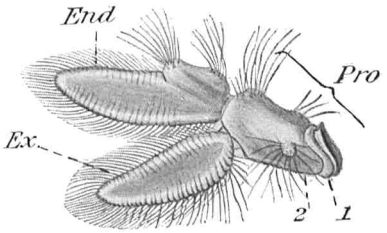

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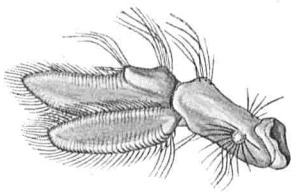

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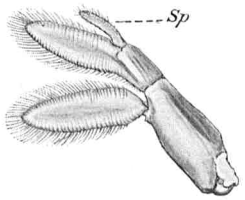
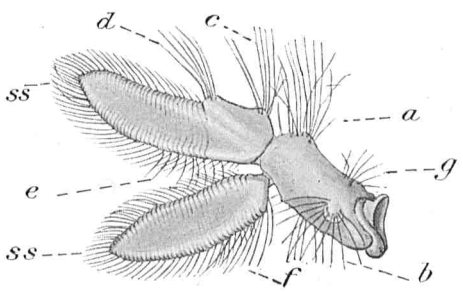


Fig. 2a.



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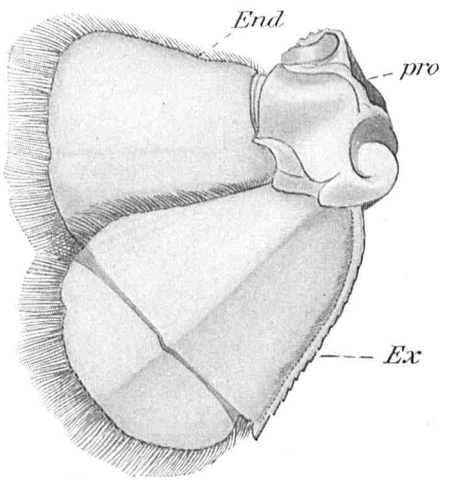

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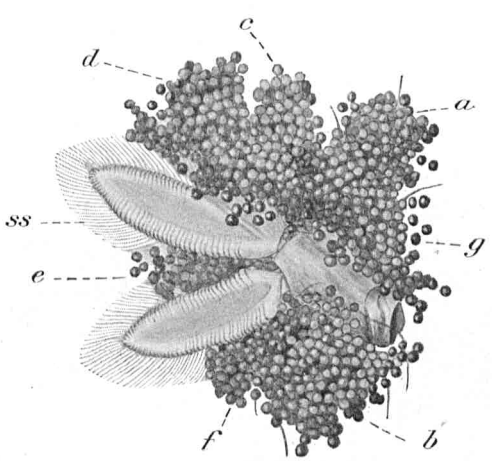

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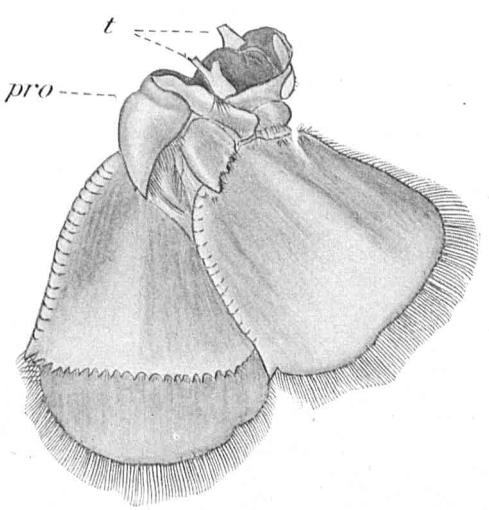


Fig. 7.

FIGS. 1 and 1a.—Left first pleopod of female and male respectively, in the former representing a rudimentary endopodite, and in the latter a styliform process modified for copulation.

FIG. 2 and 2a.—Left second swimmeret of female and male lobster, respectively, the endopodite in the latter bearing a short spur.

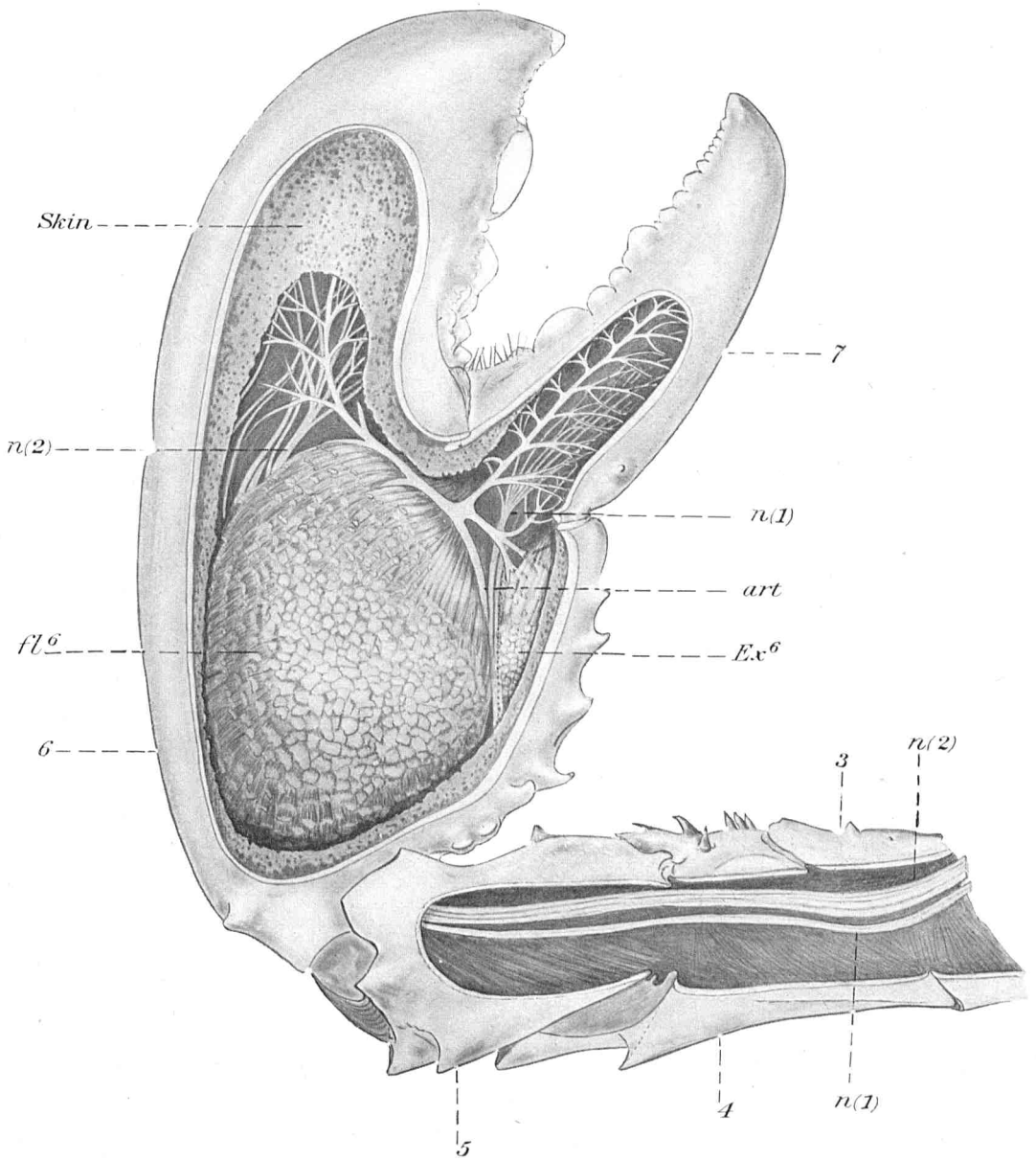
FIG. 3.—Left third swimmeret, showing swimming setæ (*ss*), and long, nonplumose hairs, modified for bearing the eggs, and distributed in 7 groups, marked *a g*.

FIG. 4.—Left fourth swimmeret from egg-bearing female of approximately the same size as represented in preceding figure, and drawn to same scale. Hair clusters *a*, *b*, *c*, and *d* catch the greatest number of eggs.

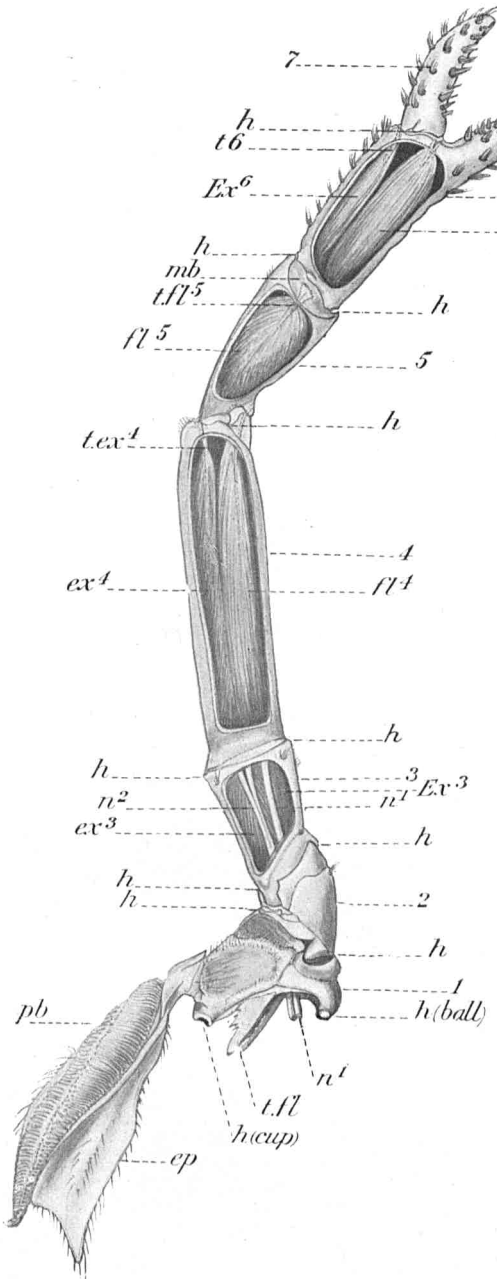
FIG. 5.—Left fifth swimmeret of series 1–3.

FIG. 6.—Left uropod, or modified swimmeret of tail fan, seen from the under or anterior side, in position corresponding to that of preceding, showing 2-jointed exopodite (*Ex*) and marginal fringe.

FIG. 7.—The same appendage reversed, and seen from the upper side.



Left crusher claw of lobster, partly dissected from upper side, to show relations of muscles, nerves, blood vessels, and skin, with principal branches of claw arteries and nerves laid bare. *art*, large artery which supplies both muscles of claw, and breaks into a regular system of branches in fine meat of tips; *n* (1), *n* (2), posterior and anterior nerve trunks supplying, respectively, the extensor (Ex^6) and thumb, and the flexor (fl^6) and index.



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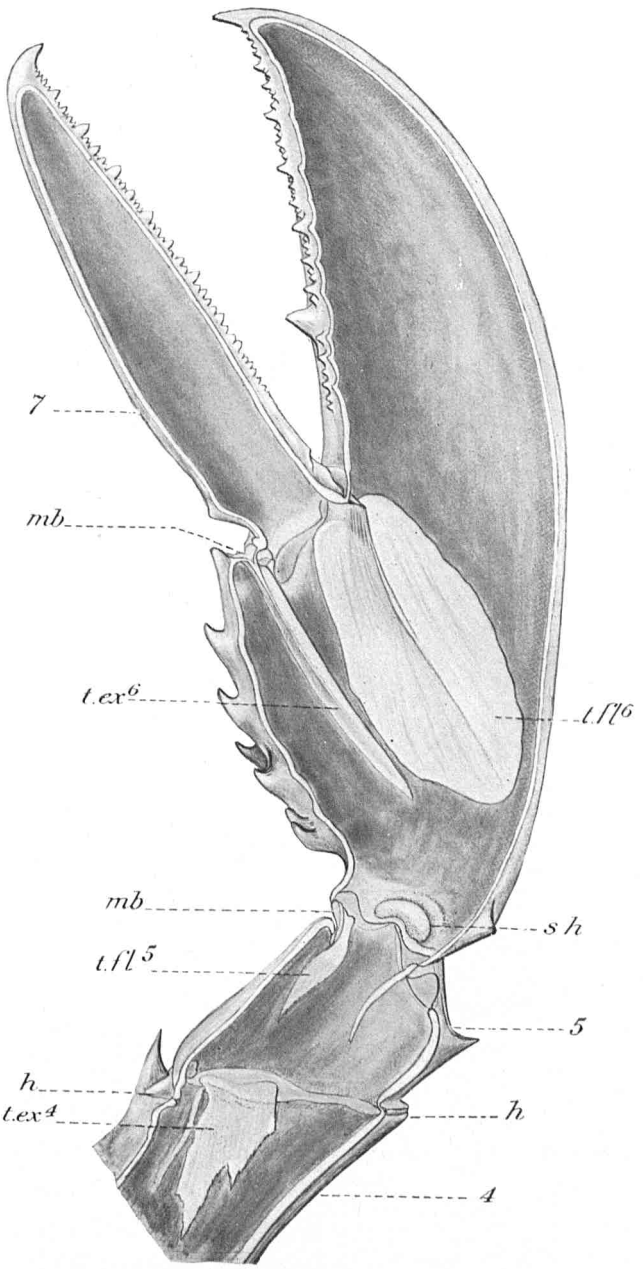
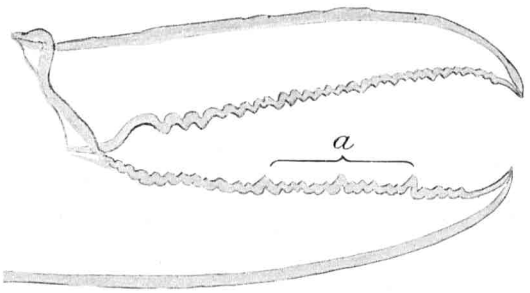


Fig. 2.

FIG. 1.—Left second pereiopod from anterior or upper side, partly dissected to show the relations of muscles and tendons in the principal segments; hinges (*h*) and nerves (n^1 and n^2) are indicated; and extensor and flexor muscles (*ex*, *fl*) are numbered to correspond to segments of origin.

FIG. 2.—Shell of right toothed forceps in sectional view from above, to show tendons crossing distal joints. *s h*, lower sliding hinge, from inside; *mb*, interarticular membrane (dotted line marking position of former tendon pocket).



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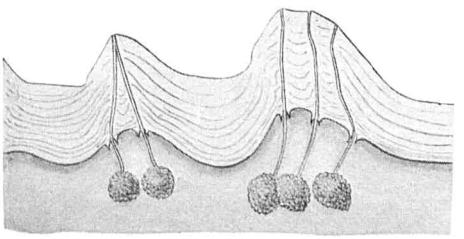

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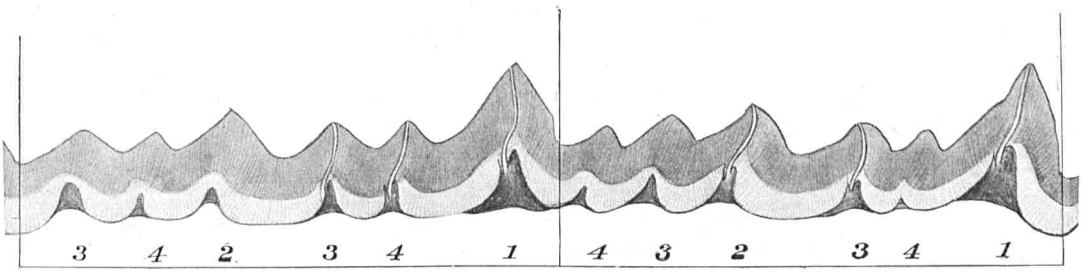

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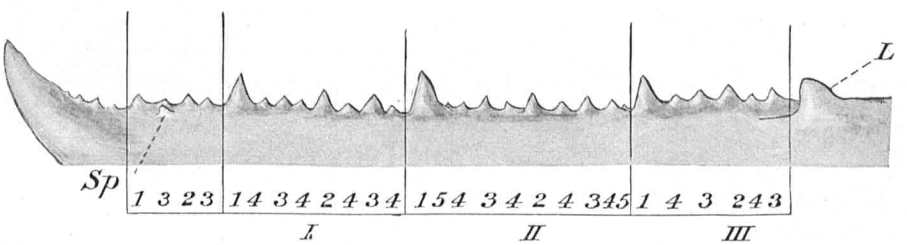

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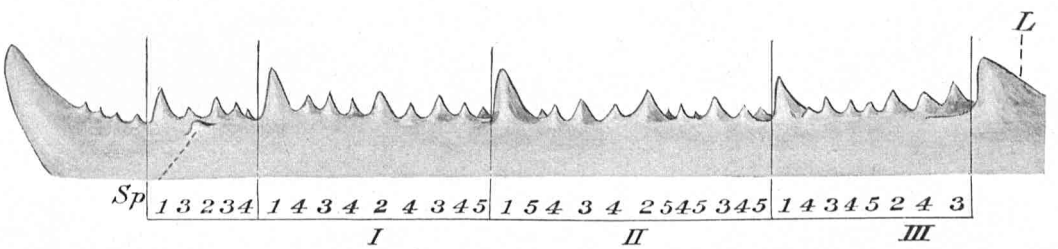


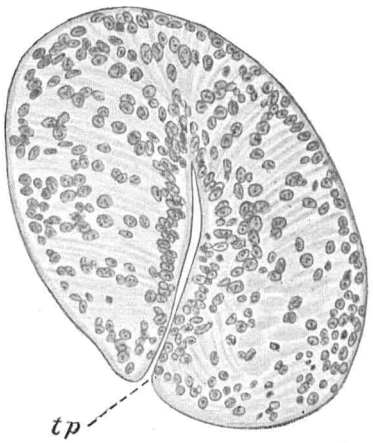
Fig. 5.

FIG. 1.—Right toothed forceps of lobster in seventh stage, seen from above, and drawn from molted shell. Dental armature of jaw, marked *a*, shown greatly enlarged in figure 3.

FIG. 2.—Teeth from dactyl of lobster in fifth stage, showing multiple or bifurcate ducts of tegumental glands.

FIG. 3.—Serrate margin of jaw in area marked *a*, figure 1, embracing series i–ii, and showing spines pierced by the ducts of tegumental glands. Cuticle only represented; enlarged about 170 times. Figures 1–3, from glycerine preparations and represented in optical section.

FIGS. 4 and 5.—Armature of index or propodus of right toothed forceps of lobster in seventh stage, and after molting to the eighth, as seen from under side, showing changes in spines of each period introduced at this molt. *L*, lock spine, and *Sp*, spur.



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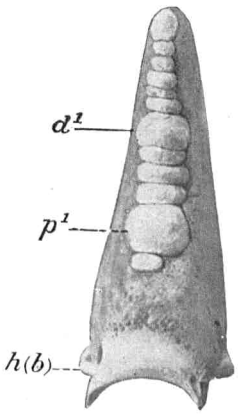

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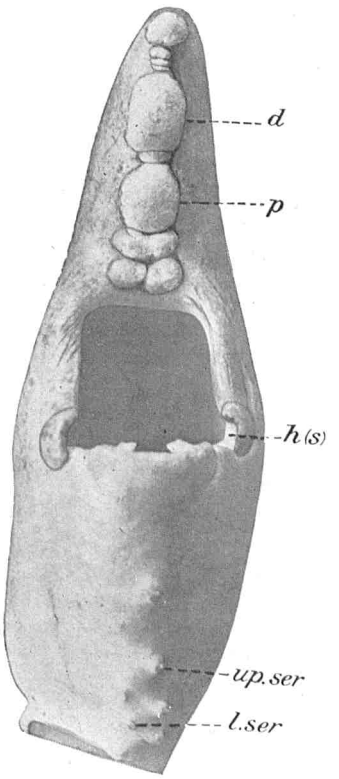

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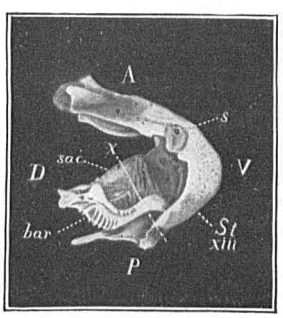

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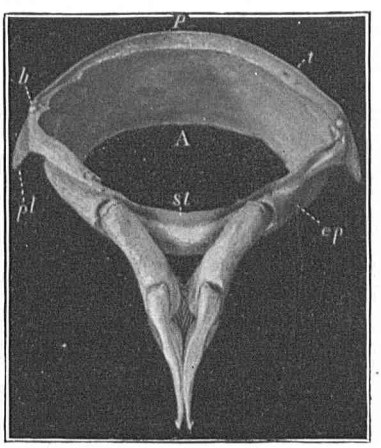

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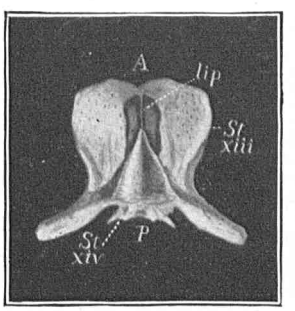


Fig. 6.

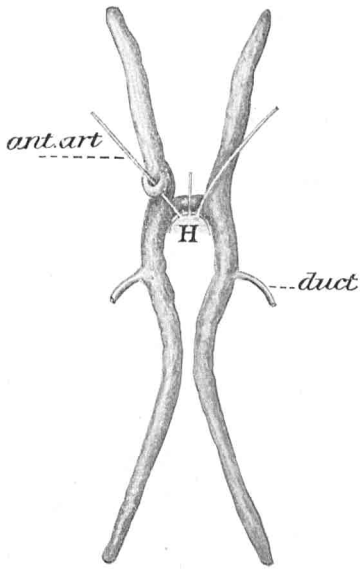
FIG. 1.—Oblique section through large claw of lobster in first larval stage, showing open tendon pocket (*t p*) of adductor muscle; before fusion of flattened cuticular walls has taken place.

FIGS. 2 and 3.—Jaws of cracker claw of lobster weighing about 12 pounds, disarticulated and placed to show correspondence of "molars" when jaws are closed. Proximal and distal tubercles of index (*p*, *d*) alternate with larger "crushers" of thumb (p^1, d^1); *h(s)*, socket, and *h(b)*, ball, of terminal hinge joint; *up.* and *l. ser*, upper and lower series of alternately displaced protective spines of propodus.

FIG. 4.—Profile of seminal receptacle of female, from molted shell. *A*, anterior; *D*, dorsal; *St. xiii*, modified sternum of somite XIII; *bar*, sternal bar, supporting seminal sac; *x* with dotted line marks plane of section of seminal sac shown in figure 3, plate XLIV; *s*, proximal socket of first joint of fourth pereiopod.

FIG. 5.—Skeleton of first abdominal somite of male from behind, showing stylets directed forward and meeting on mid-line, their probable position for conveyance of spermatophore to seminal receptacle in impregnation. *A*, anterior, and *p*, posterior margin of somite; *b*, posterior ball of hinge joint; *t*, tergum; *ep*, epimeron; *st*, sternum; *pl*, reduced pleuron, which forms "button" to carapace.

FIG. 6.—Seminal receptacle shown in profile in figure 4, as seen from under side, presenting median elastic lips of pouch into which nibs of stylets are supposed to be pressed in copulation. Figures 4–6, nearly natural size.



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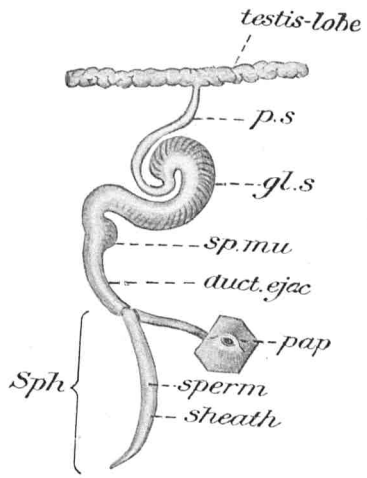

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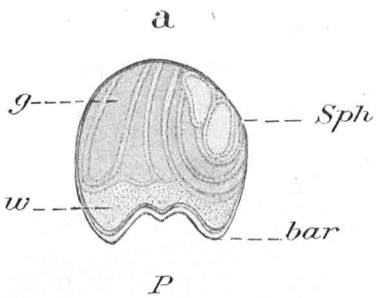

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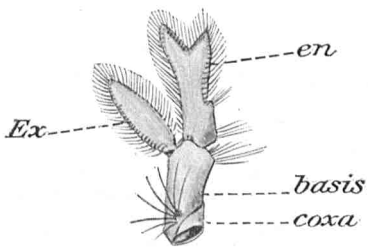

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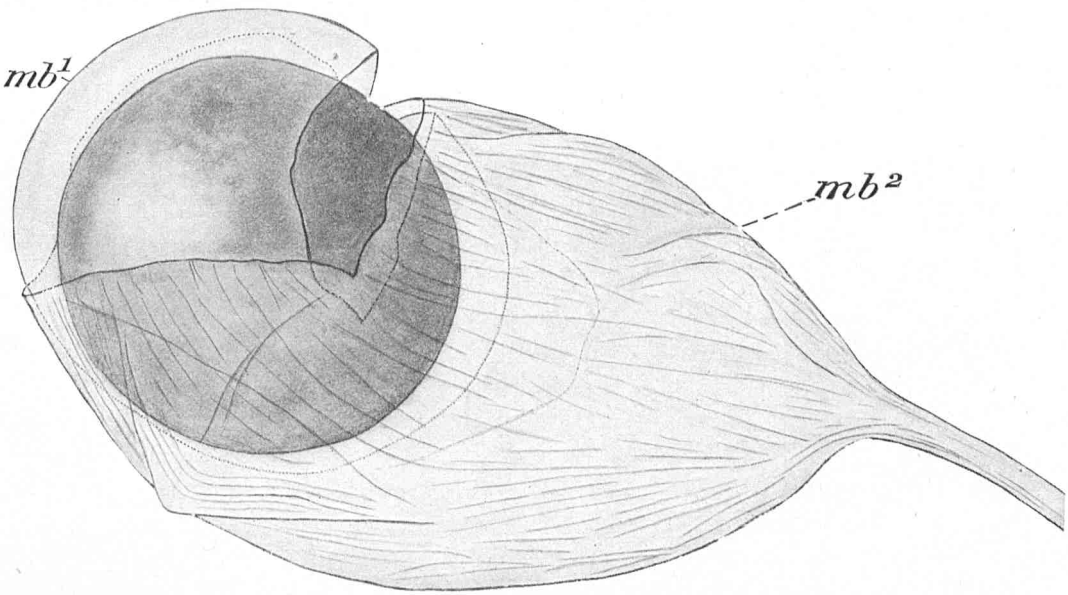


Fig. 5.

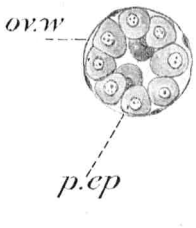
FIG. 1.—Immature ovary of lobster with abnormal ring on left anterior lobe for transmission of left antennal artery (*ant. art*) *H*, heart.

FIG. 2.—Reproductive organs from right side of male, dissected to show sperm duct, and spermatophore (*Sph*) pressed from slit made in its side. *p. s, gl. s, sp. mu, duct. ejac*, proximal segment, glandular segment, sphincter muscle, and ductus ejaculatorius of vas deferens; *pap*, papilla for opening of duct on coxa of fifth pereiopod.

FIG. 3.—Transverse section (in plane *x*, fig. 4, pl. XLIII) of horny pouch of seminal receptacle of female lobster, showing contained spermatophore (*Sph*), gelatinous coats (*g*), and soft substance on lower side (*w*) over sternal bar. *a*, Anterior; *p*, posterior.

FIG. 4.—Left third swimmeret of female, 9½ inches long, with bifurcated endopodite; anterior side.

FIG. 5.—Lobster's egg, showing its two membranes ruptured and greatly distended by reagents; mb^1, primary membrane or chorion; mb^2, cement membrane of attachment, forming bag continued into basal stalk.



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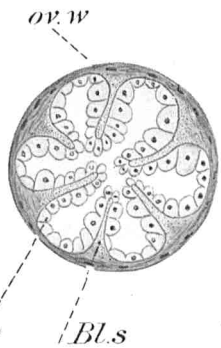

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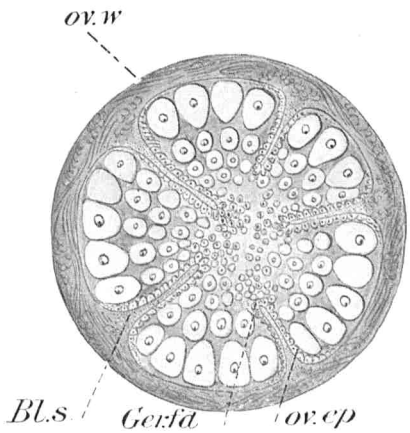

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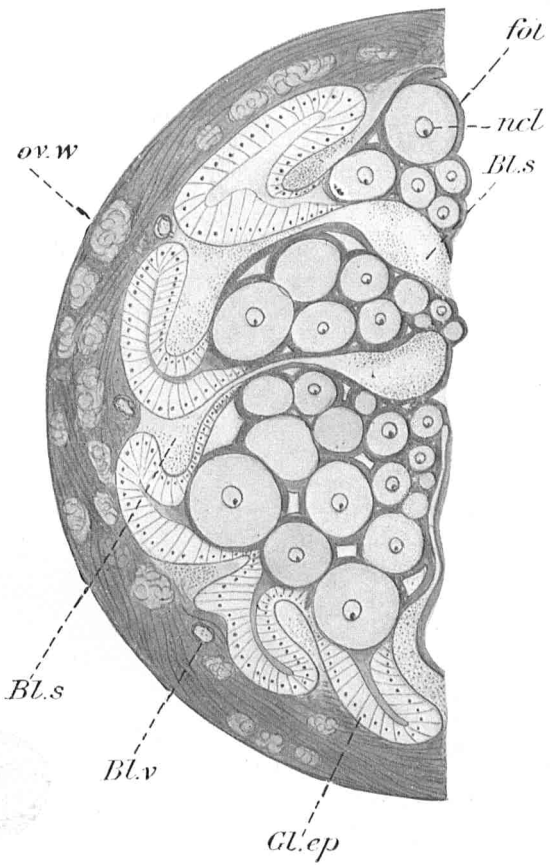

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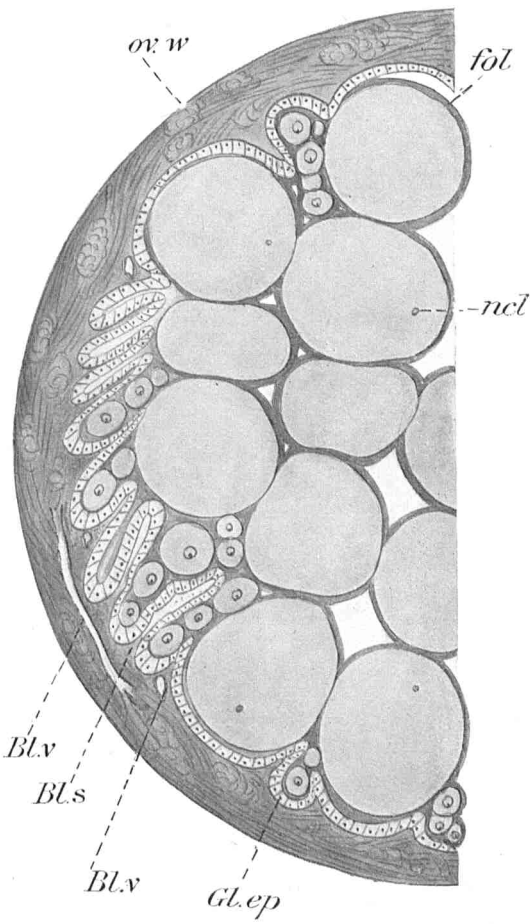
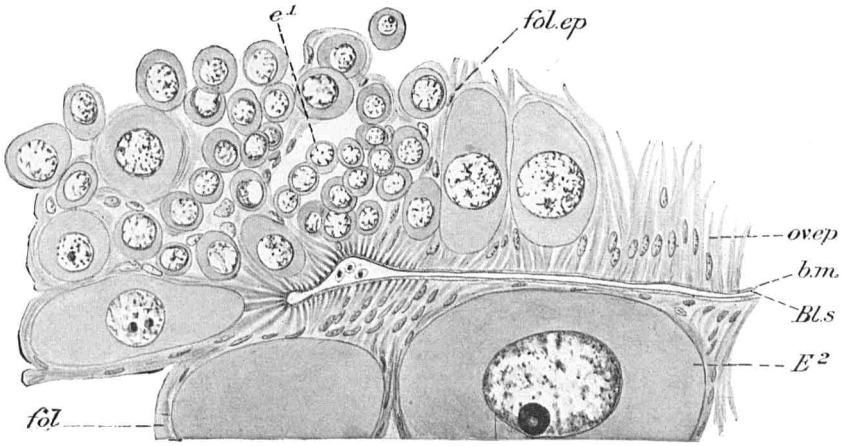


Fig. 5.

FIGS. 1–5.—Diagrams to illustrate structure and growth of ovary of the lobster from first larval stage to maturity. Note the primordial epithelium in larva (*p. ep*, fig. 1), the germogenal folds (*Ger. fd*, fig. 3), and reentrant blood sinuses (*Bl. s*) formed by foldings of this layer, the multiplication of epithelial cells along the crests of these folds, and their differentiation into ova and follicle cells (see fig. 1, pl. XLVI), the development of glandular pouches after eggs are laid (fig. 4), and their recession when the latter are ripe. Figure 1, from larva; figures 2 and 3, from early and late adolescent stages; figure 4, from adult with ovary nearly ripe; figure 5, from adult, 36 hours after extrusion of ripe eggs. *Bl. v*, blood vessel; *fol*, egg-follicle; *Gl. ep*, glandular epithelium; *ov. ep*, ovarian epithelium; *ov. w*, ovarian wall.



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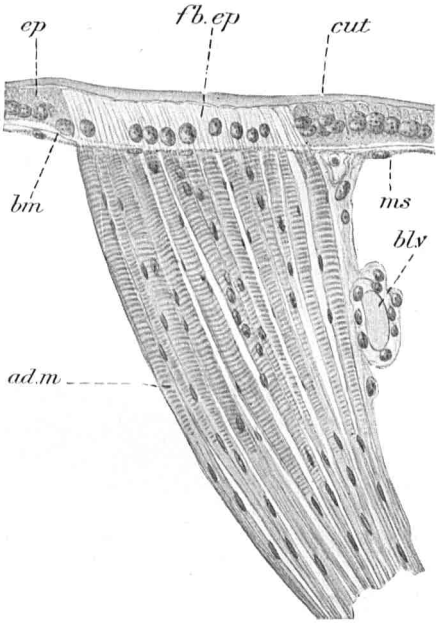

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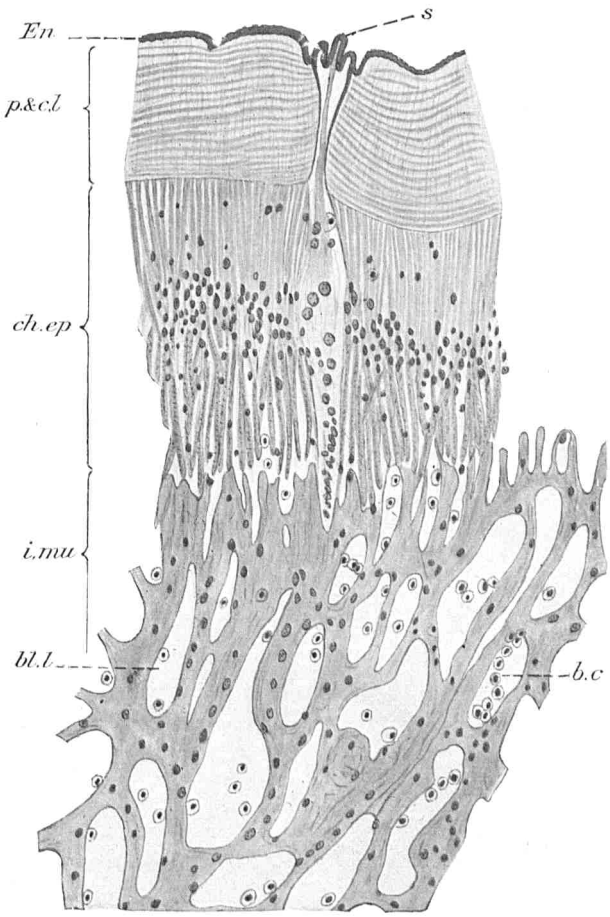

Fig. 3.

FIG. 1.—From transverse section of ovary of lobster 8¼ inches long, July 25, showing cluster of epithelial cells on crest of fold, and their differentiation into primordial ova (e^1) and follicle cells (*fol. ep*), with formation of egg-sacs (*fol*); *b. m*, basement membrane; *Bl. s*, blood sinus; *ov. ep*, epithelium of ovary. Enlarged about 230 times.

FIG. 2.—Part of longitudinal section of first larva, at point of attachment of adductor mandibuli muscle (*ad. m*), showing fibillar modification of epithelium (*fb. ep*), and basement lamella (*bm*); *bl. v*, blood vessel; *cut*, cuticle; *ms*, mesoblast. Enlarged about 230 times.

FIG. 3.—Part of transverse section of dactyl of soft lobster, close to spines of dentate margin, showing the enamel (*En*), pigmented and calcified layers of shell (*p.* and *c. l*), chitogenous epithelium (*ch. ep.*), and involuntary muscle spongework (*i. mu*), with blood lacunæ (*bl. l*), in "fine meat" of claw tip; *b. c*, blood corpuscles; *s*, seta. Enlarged about 115 times.

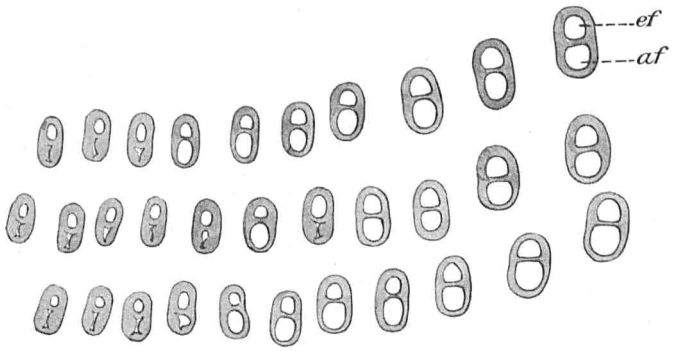

Fig. 1.

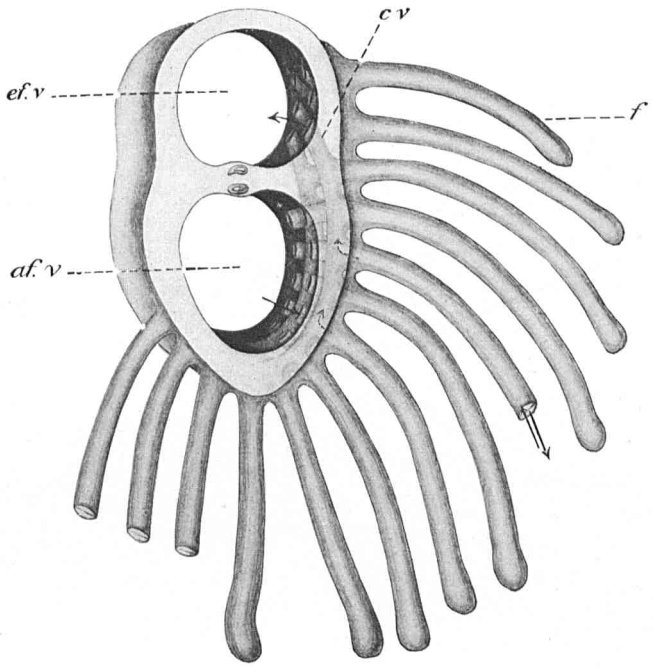

Fig. 2.

Fig. 3.

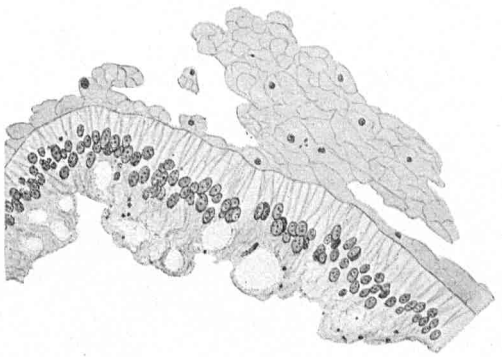

Fig. 4.

FIG. 1.—Part of section parallel to long axis of gill, showing three transverse rows of filaments, cut crosswise, and their double tubular character; *af* and *ef*, afferent and efferent division of filament. Enlarged 27 times.

FIG. 2.—Diagram of transverse section of lobster's gill, viewed as a transparency, to show probable course of circulating blood as indicated by arrows; *af. v*, branchial stem afferent; *ef. v*, branchial stem efferent; *c v*, circular vessel; *f*, gill filament. The relations of the two divisions of the filament to the two divisions of the stem are shown in but few cases only. All filaments communicate with the stem afferent on the one hand and with the stem efferent on the other.

FIG. 3.—Transverse section of oviduct of adult lobster immediately before egg-laying, showing its glandular lining epithelium greatly distended.

FIG. 4.—Transverse section of oviduct of adult lobster taken immediately after egg-laying, showing the shrunken and vesiculated character of its epithelium.

ANATOMY AND PHYSIOLOGY OF THE WING-SHELL ATRINA RIGIDA

By Benjamin H. Grave

Assistant Professor of Zoology, University of Wyoming

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ANATOMY AND PHYSIOLOGY OF THE WING-SHELL ATRINA RIGIDA.[a]

By BENJAMIN H. GRAVE,
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INTRODUCTORY.

Atrina rigida (Dillwyn) occurs along the eastern coast of America from the northern shore of South America as far north as Cape Hatteras. At Beaufort, N. C., where most of the observations reported in this paper were made, this species is confined to shallow water near low-tide mark, occasionally being exposed during unusually low tides. Another species, *Atrina serrata* (Sowerby), is found in the deeper water of the inlet. The largest specimen found measured 14 by 9 by 3 inches, but the average size is only about 11 by 8 by 2½ inches.

This mollusk is not without an economic interest and value. The black pearls formed in *Atrina* and *Pinna*, and produced in considerable numbers, have been used in the manufacture of brooches and other articles of jewelry, and there is no reason why they should not be used more extensively. They are usually spherical in shape and quite smooth.

The pearls are not found in all specimens, but as many as ten have sometimes been found in a single individual. At a rough estimate I should think pearls would be found in about one-fifth of the individuals. This was about the proportion as regards those examined during the preparation of this paper.

The byssus has been used extensively in the manufacture of various articles, such as shawls, caps, waistcoats, gloves, purses, etc. The following quotation from Simmonds's Commercial Products of the Sea gives in a few words the extent to which the byssus has been used in the past, as well as its present standing as a commercial product:

> The ancients made this [the byssus] an article of commerce, greatly sought after, and the robes formed of it, called "tarentine," were very much in esteem. * * * * *

---

[a] Dissertation submitted to the Board of University Studies of the Johns Hopkins University in conformity with the requirements for the degree of doctor of philosophy.

I am indebted to Prof. W. K. Brooks for the suggestion that I undertake the study of the anatomy of *Atrina*. My thanks also are due especially to Prof. E. A. Andrews, under whose direction this work has been done and who has offered many helpful suggestions and stimulated my interest in biological study. I am indebted to the Commissioner of Fisheries for the use of a table at the fisheries laboratory at Beaufort, N. C., during the summers of 1908 and 1909; to H. D. Aller, director of the laboratory, for many conveniences while there and for assistance in procuring material; to Prof. G. A. Drew for counsel and suggestions; and to Prof. William H. Dall, of the Smithsonian Institution, for the determination of the species and the free use of his library.

Even in the present day the fiber is utilized, but more for its rarity than anything else. The women comb the *lana* [byssus] with very delicate cards, spin it, and make from it articles which are much esteemed for the suppleness of the fiber and their brilliant burnished gold luster.

A considerable manufactory is established at Palermo; the fabrics made are extremely elegant and vie in appearance with the finest silk. The best products of this material are, however, said to be made in the Orphan Hospital of St. Philomel, at Lucca.

This byssus forms an important article of commerce among the Sicilians, for which purpose considerable numbers of *Pinna* are annually fished up in the Mediterranean from the depth of 20 to 30 feet.

Under normal conditions *Atrina* occupies one position during its entire life—nearly buried in the mud, with its anterior end downward. The enormous byssus extends deep into the mud and attaches to shells and coarse pebbles. Specimens are most easily collected in calm weather at low tide, when they can be seen extending an inch or less above the surface of the mud.

In the following discussion, although the continuity is thereby interrupted, it seems advisable to treat the organs under separate headings, passing briefly over those which have yielded nothing of particular interest. To avoid repetition the anatomy and physiology of the organs will be treated together. The general anatomy is shown in figures 16 and 20.

Since every species is adapted to its peculiar mode of life certain anatomical features are better understood when their function is known. It has therefore been my purpose to study habits and function as well as anatomy.

SHELL.

The shell valves are large in comparison with the size of the body, and they are united to each other along one side by a hinge ligament which extends in a straight line from their anterior to their posterior ends. The hinge ligament is more or less calcified, so that it is not greatly different from the other parts of the shell. The outer surface of each shell is studied with spines, which are distributed in rows radiating from the anterior pointed end as a center to the posterior end. Primary, secondary, and tertiary rows of spines may be distinguished in the shell of a large specimen. The portion of the shell which lies posterior to the adductor [a] consists of a single layer in contrast to the typical lamellibranch shell, which has three layers, easily distinguishable by difference in structure or material. It apparently corresponds to the middle or prismatic layer of the typical lamellibranch shell, being composed of prisms which lie at right angles to the surface. When the surface is examined with a compound microscope it appears honey-combed, while a transverse section, obtained by grinding, looks not unlike a lot of quartz crystals corded like wood. (See fig. 1.) It is possible to dissolve out the lime salts with acid, leaving behind only the organic matrix. This matrix resembles cork in many respects, but when examined histologically it is seen to have the same gross structure as the shell before treatment with acid, except that the chambers formed by the organic matrix are now empty.

[a] I refer here to the posterior adductor muscle, and unless otherwise stated further references to the adductor may be taken to mean the posterior adductor.

The portion of the shell in the region of, and anterior to, the adductor is composed of two layers, there being a second or nacreous layer of the ordinary type deposited upon the inner surface of the prismatic. This layer is secreted by the general surface of that part of the mantle which lines the shell in these regions. The outer layer frequently wears through, or becomes brittle and broken, on the older portions of the shell, leaving the nacreous layer exposed. A discussion of experiments on the growth and regeneration of the shell will be found at the end of the next section.

MANTLE.

The mantle is a muscular membrane, the folds of which adhere closely to the shell, but are attached to it only at a single point just ventral to the adductor muscle. The muscles which control the ventral and posterior portions of the mantle are attached here and radiate from this point as divisions and subdivisions of a single bundle. Another bundle of muscle fibers is located near the dorsal part of the body. It is not attached to the shell at any point, but is inserted into the mantle itself. This bundle of mantle muscles also divides and subdivides into smaller and smaller bundles and is distributed to a portion of the posterior part of the mantle. (Fig. 16, pl. XLVIII.) It is thus seen that there is no pallial line in the shell for the attachment of the mantle muscles, though that is so common among lamellibranchs. Since the muscles are attached so high up, the mantle margin can be withdrawn a considerable distance from the edge of the shell; in fact, it can be withdrawn nearly to the adductor. After being contracted the mantle again expands by creeping outward upon the shell, to which it adheres closely. This result can not be brought about at once. At least half an hour is required for the mantle to again reach the edge of the shell after having been fully contracted. There are no siphons, but the two lobes of the mantle are united posteriorly by an intermantle septum at the place where siphons might be expected to occur. This structure consists of two prominent ridges, one on each mantle lobe, which stretch across posterior to the gills to meet each other in the mid line. Each mantle ridge is continued anteriorly, though reduced in size, and forms the place of attachment for the upper borders of the reflexed lamellæ of the outer gills.

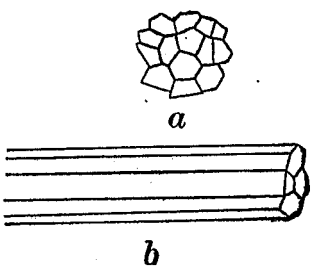

FIG. 1.—The shell. *a*, Surface view; *b*, transverse section showing prismatic structure.

On account of the position assumed by *Atrina*, only the posterior portion of the mantle is exposed to frequent sensory stimulation. Connected with this fact we find that the edge of each mantle lobe has a row of short sensory tentacles, which decrease in size and gradually disappear toward the anterior end. This part of the mantle is thick and muscular, as an adaptation to burrowing. A deep narrow passage or groove, formed by the development of two tall ridges on the inner surface of the mantle, is also correlated with burrowing. (Fig. 16, D, pl. XLVIII.) This groove lies parallel to the edge of the mantle and extends from the region of the foot to the intermantle septum,

where it approaches the edge of the mantle. The cilia within this groove beat toward the posterior to produce currents that continually remove foreign bodies from the mantle chamber. Any large particle of dirt or sand which enters the mantle chamber soon finds its way into this ciliated passage and is carried forthwith to the exterior.

BURROWING.

In order that *Atrina* may maintain its position in the mud throughout life, it must burrow more or less. The bottom about it is sure to be shifted considerably by the tides, thus tending to uproot or cover up fixed objects on its surface. This shifting of the bottom was observed last year on the very beds where *Atrina* was found most abundant. During the summer of 1908 these beds were covered by eel grass, while a year later this grass had entirely disappeared and the character and depth of the bottom had changed to a noticeable extent. *Atrina* while undisturbed in its natural surroundings was never seen to burrow. But the method of burrowing was frequently observed when the animal was removed and again partially buried with the anterior end downward. The shell valves were opened wide by the relaxation of the adductor muscle, and the edges of the posterior part of the mantle lobes were brought together firmly to prevent the escape of water in this direction. Then followed the contraction of the adductor, forcing water from the mantle chamber at the anterior end. The force of the expelled current makes the water fairly boil, washing up quantities of sand and mud from beneath. This process was usually repeated several times at intervals of four or five seconds and then there followed a period of rest during which the sand and mud which had entered the mantle chamber during the burrowing movements was removed through the ciliated groove. This heavy material was expelled over the posterior edge of the shell in surprisingly large quantities in a short time. This accomplished, the burrowing movements were resumed. The settling of the specimen was very gradual, but in the course of an hour one could see that it had sunk 3 or 4 inches. Although the ciliated groove is of service in removing solid particles which enter the mantle chamber with the respiratory current, I think it is an especial adaptation for removing the heavier bodies which enter the mantle chamber during burrowing movements.

A number of *Atrina* individuals were laid upon their sides to see if they would bury themselves. The results were practically negative, for although they were left for weeks in this position not one made any attempt to bury itself. They seemed to thrive as well in this position as in any other, and none were seen to make movements which could be construed as an attempt to assume the normal position. Mr. Charles Hatsel, official collector at Beaufort, in whose charge certain experiments were left during the winter, reported that one specimen buried itself as far as the box in which it was kept would permit.

REGENERATION AND GROWTH OF SHELL.

Atrina is a particularly good subject for experiments upon the growth and regeneration of the shell because of the great rapidity with which this is produced. When one breaks a piece from the posterior or ventral edge of the shell, the mantle in this region becomes particularly active in mending the breach, a strip one-tenth of an inch in width

often being produced in twenty-four hours, the amount varying in different specimens between one-eighth and one-twelfth. In one instance a hole which measured approximately one-half by three-fourths of an inch was cut in the shell of a vigorous young *Atrina* with the result that it was repaired in three days. Experiments performed to determine what parts of the mantle are capable of producing shell go to show that this power belongs only to the very edge and is probably confined to a small portion of modified epithelium located in a groove in the edge of the mantle.[a] (Fig. 2, *a*.) When a notch was formed in the shell by breaking out a piece, the edge of the mantle was quickly applied to the bottom of it with the result that it was soon built up even with the general level of the edge of the shell. When holes were cut in the shell at a great distance from the edge to see if other portions of the mantle could produce shell, it was found that the mantle edge was drawn back to these places and remained there until they were repaired. Although conclusive proof that only the edge of the mantle can produce shell is lacking, there is abundant evidence that *Atrina* generally repairs all injuries to the shell with this part of the mantle, and it seems safe to assume that shell formation is confined to this portion.[a]

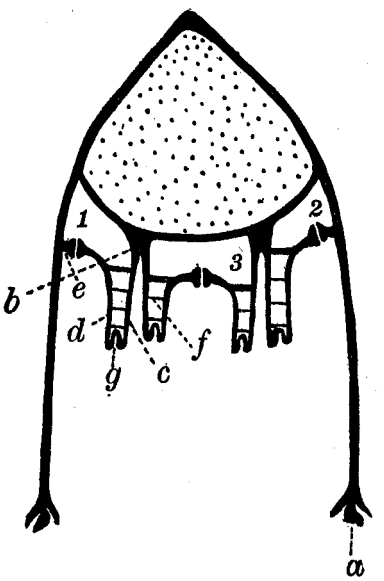

FIG. 2.—Diagrammatic cross section of the body anterior to the adductor muscle. *a*, Modified epithelium which secretes shell; *b*, suspensory membrane; *c*, descending lamella of outer gill; *d*, reflected lamella; *e*, longitudinal ridge on the mantle to which the gill is attached by means of interlocking cilia; *f*, vascular interlamellar septum; *g*, longitudinal groove in edge of gill. *1*, *2*, and *3*, suprabranchial chambers.

As stated in a previous section, the outer surface of the shell bristles with spines, which are distributed in rows. They have the same prismatic structure as the shell and like it they are secreted by the edge of the mantle. When fully formed, they are between one-half and three-fourths of an inch in length, and, except that they are slightly broader at the base than at the top, have the shape of a half tube, the hollow side of which faces the edge of the shell. During the growth period of one of these spines a little fold or tongue of the mantle edge extends beyond the shell and fits into the hollow surface of the spine. In time the shell, by its growth at the edge, extends beyond the spine so that the mantle no longer comes into contact with it. This mode of formation accounts for the fact that the spines are hollow and open toward the growing edge of the shell. There is no visible differentiation of the mantle edge in the form of permanent folds to which the formation of the spines is due. The edge of the mantle opposite a row of spines does not seem to differ from that located between two rows. The tongues which creep out into the spines are not permanent structures, but are formed by a local expansion of the mantle.

[a] This refers only to the prismatic layer. The second layer, which is laid upon the inner surface of the shell at the anterior end, is secreted by the whole of the epithelium of the mantle of this region.

Measurements to determine the rate of growth of *Pinna* under natural conditions revealed slower growth than had been anticipated. In seven weeks' time some specimens increased one-half inch in length with corresponding increase in breadth. The greater number grew only about one-fourth of an inch in this time and the oldest specimens showed no growth. It is impossible to estimate from these figures the time required for an individual to reach maturity, but the fact is revealed that when they reach a certain age growth ceases.

At the suggestion of Professor Andrews I endeavored to discover whether the calcium salts used in shell formation are taken directly from the sea water or whether they are taken from the blood. The results are not satisfactory, but I give them for what they are worth: A notch was cut in the shell of a young specimen and the broken edges were filed until they were quite smooth. The specimen was then placed in artificial sea water which lacked only the calcium salts. This water was kept aerated by compressed air. The specimen applied the mantle edge to the broken place in the shell and kept at work for several hours without accomplishing much. During the first experiment, which was continued for twenty-four hours, only about one-tenth as much shell was produced as would have been formed under normal conditions. However, enough was produced to be plainly visible and when it was removed and examined under the microscope it showed normal structure and effervesced when hydrochloric acid was added.

Several similar experiments were tried, but no perceptible growth of shell was obtained. In the first experiment the chemicals used were not "C. P." and may have had some calcium in them, and this may account for the lack of uniformity in the results. It was impossible to keep the specimens in good condition for twenty-four hours in this artificial sea water and on this account I think it unwise to draw hard and fast conclusions from the experiments. The method seems worth trying under more favorable conditions. Recently the question has been raised as to whether animals which live in a water medium can take nourishment from it through the general body surface. It seems quite possible that lamellibranchs take the lime salts from the water directly rather than indirectly from the digestive tract. If lamellibranchs elaborate shell from calcium salts in the blood, their supply must be continually replenished, judging from the above experiments, which indicate that these specimens could not make much headway from stores already present in the body.

MANTLE GLAND.

A large muscular structure, which appears from its connections to have been developed from the mantle, lies in the cloacal chamber. It resembles the foot in many respects and, like it, can be extended by blood pressure. When extended it becomes slender and may reach a length of nearly 6 inches, but when contracted it is short and thick. Upon its tip it bears a large mucous gland. (Fig. 16, M, pl. XLVIII.) This peculiar organ is not commonly found in lamellibranchs, being confined to the Pinnidæ. Many specimens were examined in their natural habitat and in the laboratory for the purpose of learning

its function. So long as a specimen is undisturbed this glandular structure is likely to lie quietly in the cloacal chamber, but when the mantle is irritated, for example by breaking off part of the shell, it becomes active and moves about in every conceivable direction. It was frequently pushed far down into the branchial chamber toward the point of irritation. When grains of sand were put upon the mantle this muscular gland sometimes succeeded in brushing them off after several trials and much aimless maneuvering. While this organ is moving about the glandular tip is usually kept pressed against the mantle and appears to be sweeping its surface. It seems to be a "swab" for the purpose of freeing the mantle of any foreign body which may lodge upon it.

Just why the Pinnidæ need such a structure is difficult to determine, since other lamellibranchs get on without it, the cilia on the inner surface of the mantle being equal to the task of keeping it clean. The position assumed by *Atrina* is one of disadvantage for removing débris. It has been pointed out that great quantities of dirt and sand do enter the mantle chamber, and this must all be raised vertically to the edge of the shell for expulsion, so that structures especially adapted to this purpose are to be expected. The mantle gland is probably such a structure.

The mantle gland is much less compact in structure than the foot. On the outside there is an epithelial covering which is glandular only at the tip of the organ. Here the cells are very much elongated and they contain a large amount of secretion in the form of granules. Immediately beneath the epithelium there is a band, or cylinder, of longitudinal muscle fibers. They are attached to the organs at the base of the gland for support. Many of them spread out over the adductor, into which they are inserted. They are so distributed in the gland that they can control the direction of its movement provided that they do not all contract at the same time. The shortening of the gland is also brought about by the contraction of these muscles. The central part of the gland is composed of very open connective tissue and a few transverse muscle fibers.

LABIAL PALPS.

The palps consist of two thin muscular lamellæ which extend across the anterior end of the body, one above and the other below the mouth. Their outer ends are roughly triangular in shape and lie alongside the body. The epithelium lining the palps is continuous with that of the mouth and Drew (2) has aptly likened these structures to a pair of drawn-out lips. They are essentially alike in many lamellibranchs but vary greatly in size and shape in different species. In *Atrina* they are comparatively large and consist of two well-defined portions. That part which lies near the mouth is narrow and is lined by a smooth ciliated epithelium, while the outer triangular portion is broad and is lined by an epithelium that is thrown into a series of prominent ridges and grooves large enough to be plainly seen without magnification. Posteriorly the palps inclose the anterior ends of the gills, and it is their function to transport the food collected by these organs to the mouth. An extra projecting membrane is present on the ventral border of the inner palp, which folds up over the outer. (Fig. 16, pl. XLVIII.)

GILLS.

There are two large gills on each side of the body which extend parallel to its longitudinal axis from the neighborhood of the mouth almost to the posterior extremity of the mantle. (Fig. 16, pl. XLVIII.) They are attached to the body by a suspensory membrane in the usual manner. The gills are much alike except that the inner one of each pair is somewhat broader than the outer and hence reaches below its fellow. They are pointed at the extremities and anteriorly are inclosed by the palps. Each gill consists of two lamellæ which lie close together; or perhaps it is more correct to think of it as being composed of a single lamella which has been folded upon itself. According to this conception, the gill consists of a direct and a reflexed lamella, the two being continuous at the free edge of the gill. Various anatomical and embryological studies, especially those of Lacaze-Duthiers (8) and Peck (12), show this to be the correct interpretation. The two lamellæ are united to each other merely by blood vessels which pass from the one to the other. The interlamellar space is not partitioned off into definite parallel water tubes by continuous septa, but is undivided except for the scattered blood vessels which traverse it. The only place where there is anything resembling true interlamellar septa is at the upper borders of the gills where nonvascular, or only partially vascular, strands bind the two lamellæ together. At the outer free edge of the gill they are bound firmly together by lacunar connective tissue and by a continuous plate or cord of muscle whose fibers run longitudinal to rather than transverse to the gill. By its contraction the gill is shortened and folded. A large nerve lies immediately above this muscle, but I have made no attempt to study its distribution.

Each gill is attached to the suspensory membrane by one lamella only, as is common among lamellibranches. The inner lamella of the outer gill and the outer lamella of the inner gill are attached to the suspensory membrane as far back as the adductor muscle. From this point they are attached to each other. The outer lamella of the outer gill is attached to a ridge on the mantle (the same as that mentioned above). The inner lamellæ of the inner gills of the two sides are united to each other, except at the extreme anterior, where for a space of half an inch or so they are attached to the sides of the byssal apparatus which with the foot extends ventrally at this point. The attachments of the gills, together with the intermantle septum, thus cut off a system of supra-branchial passages from the general mantle cavity. A section across the body shows that there are three of these, which are diagrammatically represented in figure 2 (*1*, *2*, and *3*). A section taken posterior to the visceral mass would show only a single suprabranchial passage, the three having been thrown together at the termination of the suspensory membranes. This single suprabranchial passage lies below and posterior to the adductor muscle, and for distinction might be called the cloacal chamber.

The direct lamellæ are outgrowths from the suspensory membrane, and hence there is a firm organic union between them. On the other hand, the attachment of the upper borders of the reflexed lamellæ to the neighboring parts and of the ridges on the mantle to each other, to form the intermantle septum, is merely an interlocking of cilia so that they can be torn apart without doing the slightest injury to the animal. Only

a slight pull is necessary to separate them. In this way the branchial and suprabranchial chambers can be thrown together. In fact, the animal can maintain them separate or throw them together apparently at will. These unions commonly show an interlocking of the epithelial cells as well as the cilia, and sometimes the epithelium of the opposed surfaces is thrown into a series of ridges and grooves, thus producing a firmer union. Although Lacaze-Duthiers (8) and Peck (12) have described forms in which there is a weak union between the upper borders of the reflexed lamellæ and the mantle, they did not describe the actual mode of union. Their purpose in the description was to show the transition between those forms which have the mantle edge free and those which have it permanently united to the neighboring parts. Grobben (5) has shown that this weak union is by means of interlocking cilia, and he considers it to be universal among the Aviculidæ. He states also that when the opposed surfaces are forcibly separated they will reunite in a short time if undisturbed. The evidence upon which this assumption was based was his observations on the gill of *Mytilus*. Here he found, what Lacaze-Duthiers had already described, that the ciliary interfilamentar connectives would reform after being separated. Stenta (14) demonstrated that the reflexed lamellæ of the gills of *Pinna* and *Solen* would reunite to adjacent parts after being separated from them, and I have confirmed the same for *Atrina*. I separated the gill from its attachment to the mantle for a distance of 2 inches. When examined several hours later it had effected a union. Stenta thinks that this type of union between the gills and mantle is of much more general occurrence than has been supposed, suggesting that it may occur in those forms in which the gills have been described as free. He maintains that in life they are never separated unless by accident, but he is probably in error, because I observed the mantle gland, which normally lies in the cloacal chamber, extending far down into the branchial chamber. This could not take place so long as the gills retained their connection with each other.

When magnified sufficiently each lamella is seen to be thrown into a series of folds (grooves and ridges). These structures are barely visible to the unaided eye as a series of parallel lines running across the gill perpendicular to its base. Each ridge (fig. 3) is composed of from 10 to 12 hollow filaments which are slightly separated from each other. The latter are bound together at regular intervals by tubular interfilamentar connectives which are somewhat larger than the filaments and run at right angles to them. These two sets of tubules thus form a trelliswork in which the spaces between are the ostea through which water enters the gill from the branchial chamber. (Fig. 4.) The one or two filaments which occupy the summit of the ridge differ somewhat from the others in that they contain numerous goblet cells whose sticky secretion entangles minute organisms as they are carried over the gills in the respiratory current. The filaments and ridges of one lamella do not pass directly over into those of the other, but gradually decrease in size and disappear as they approach the edge of the gill. There is a deep groove with smooth walls in the edge of each gill which is lined by ciliated epithelium. (Fig. 2, *g*.) There is no fusion of filaments due to crowding as has been described by Rice for *Cardium* and other forms (13).

The grooves which lie between the ridges just described are not filamentous in structure but are lined by a continuous finely ciliated epithelium, below which there is a large crescent shaped rod of chitinous material for giving rigidity and elastisity to the gill. (Fig. 3, *c*.) Running along the floor of each groove within the cavity of the gill there is a large blood vessel. Each is connected with the similar vessels which lie next

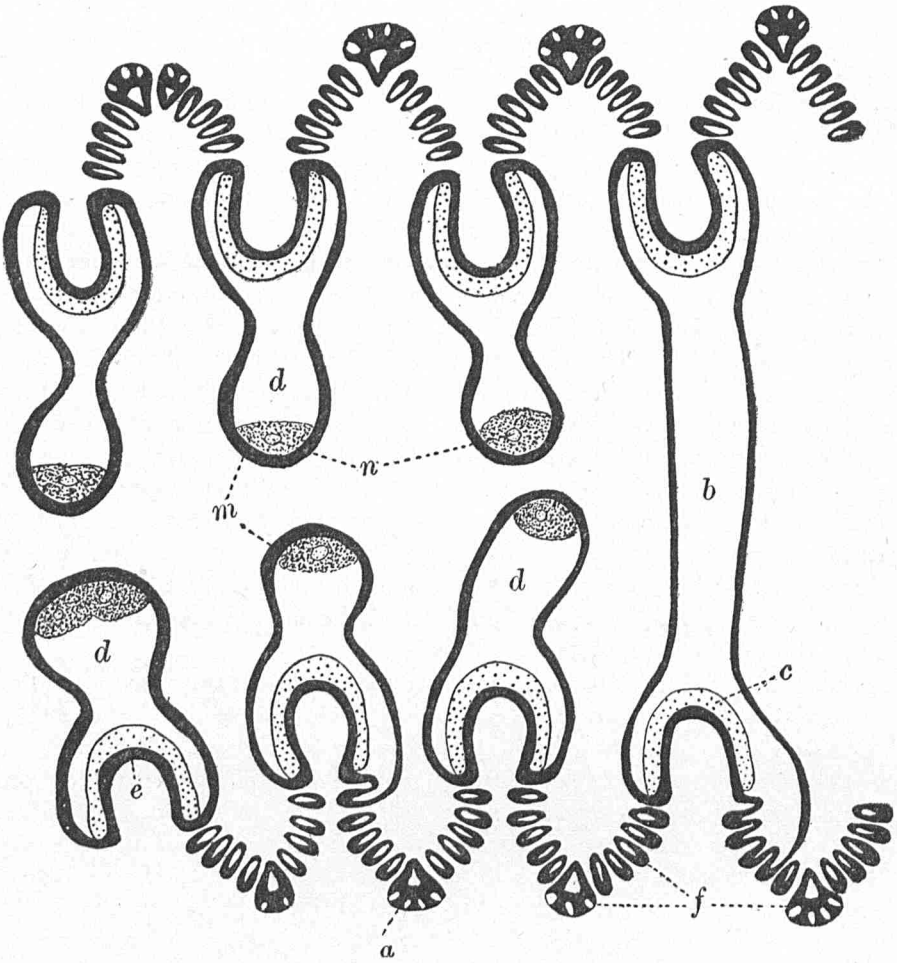

FIG. 3.—Transverse section of gill highly magnified. *a*, Modified filament containing glands; *b*, vascular interlamellar connective; *c*, chitinous supporting rod; *d*, large blood vessel; *e*, epithelium; *f*, filaments; *m*, muscles; *n*, nerves.

to it, at regular intervals, by smaller tubes which are the interfilamentar connectives already described as binding the filaments together. All of these structures are hollow and the cavities of all are in open communication. Thus when blood enters the gill it penetrates every part, including the filaments and interfilamentar connectives. (Fig. 4.) It is common to regard the structures which occur between two folds of the lamella as

a large modified filament, or as a single filament with its subsequent development of subfilamentar lacunar tissue, and there is some evidence that this is correct, viz, the epithelium lining the ciliated groove is continuous with that of the blood vessel. (Fig. 3, *e*.) At the edge of the gill also the resemblance becomes much more striking where it assumes clearly the appearance of a filament.

STRUCTURE OF THE FILAMENTS.

The structure of the individual filaments is best made out in cross sections such as that represented in figure 5. Each is composed of a simple epithelium which is lined by a very thin layer of chitinous material resembling a cuticle. (Fig. 5, *c*). Peck (12) considers this lining cuticle to be modified lacunar tissue. Sometimes protoplasmic

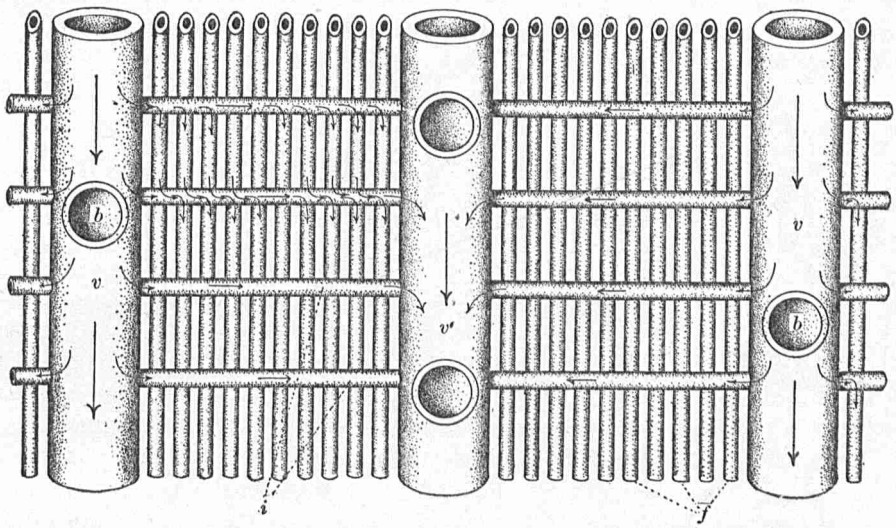

FIG. 4.—Diagrammatic drawing of a bit of the gill. *b*, Interlamellar connectives; *f* filaments; *i*, interfilamentar connectives; *v* and *v'*, large blood vessels. The arrows indicate the direction of the flow of the blood.

corpuscles can be seen lying upon its inner surface but none have been detected within it. There are no transverse bridges of this material such as are uniformly present in the filaments of the lower forms (*Arca*, *Mytilus*, and *Pecten*). It has commonly been supposed that the septum in these forms divides the cavity of the filament into two blood channels—the one afferent the other efferent—and this view seems well founded. Drew (2) by use of injections found that in *Pecten* this bridge had no such physiological significance. He has therefore suggested that it may serve to prevent the walls of the filament from spreading under the pressure of the inclosed blood which might close the incurrent ostea of the gill. He thinks that further study of gills of similar structure might throw light upon this interesting point. The gill of *Atrina* is made up on exactly the same plan as regards the shape of the filaments and amount and kind of interfilamentar connectives and yet there is no septum dividing the blood channel

into two parts. It seems better to regard this structure as a partition which divides the blood space of the filament into two blood channels because it is known to serve this purpose in *Arca* (1). In *Pecten*, where the circulation of the blood has been changed from the original type, it no longer serves this function but remains as a functionless membrane.

The outer surface of each filament is ciliated and three cells on each side have a tuft of long cilia. (Fig. 5). The latter point outward and are usually regarded as having a straining function, preventing food particles from entering the interlamellar cavity with the water currents. If the usual interpretation be correct they have nothing to do with the production of water currents.

The larger blood channels of the gill (fig. 3, *d*) show a structure similar to that of the filaments. There is a one-layered epithelium on the outside which is ciliated for the most part and contains numerous goblet cells (probably mucous secreting cells). Lining the epithelium inside the vessel there is more or less of lacunar tissue which has retained its primitive character. It contains scattered nuclei and its lacunar nature is easily made out. I find no evidence of an endothelium, which has been described by Bonnet (1) and Menegaux (9). The vessels frequently contain bundles of muscle fibers and nerves which run from the attached border to the free border of the gills. Their distribution has not been studied, but figure 3 shows their position.

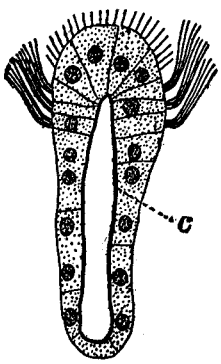

FIG. 5.—Transverse section of a filament highly magnified. *c*, Cuticle lining the blood space.

COURSE OF THE CIRCULATION IN THE GILLS.

Before giving the course of the circulation in the gills it will be necessary to describe certain vessels which carry the blood to and from these organs, and since the circulation is the same for the two sides it will be necessary to describe it in but one. A very large vessel, which we will call X, arising from the kidney, passes posteriorly along the line of junction of the two gills as far as their extremities. (Fig. 20, X, pl. L). It gives off numerous branches, to the right and left, which pass through the interlamellar septa to the upper borders of the reflexed lamellæ. These lateral vessels open into one which runs along the upper broder of the lamella. The latter which will be called vessel Y in further descriptions, is a distributing vessel made necessary, it would seem, because the main vessel from the kidney takes its origin near the middle of the gills, and hence no blood could pass from it to their anterior portions except through some such arrangement. Every other one of the larger vessels of the reflexed lamella (fig. 4, *v*), which lie at the reentrant angles of the folds, connects directly with vessel Y. Every alternate one (fig. 4, *v'*) ends blindly at the upper border of the lamella. This was proved not only by the study of sections but by injections as well. In the same way one-half of the larger vessels of the direct lamella end blindly while the other half connect with an efferent vessel which runs along its upper border carrying the blood back to the heart

after being aerated in the gills. The latter is a T-shaped vessel, one arm of which lies in the suspensory membrane and carries blood from the anterior half of the gills, while the other arm lies immediately below the vessel X and collects the blood from the posterior portions of the gills. The two arms of the vessel flow together just anterior to the kidney and form a rather wide tube disposed at right angles to them. (Fig. 9, *a*.) This tube is perhaps an inch and a half in length and connects directly with the auricle.

From these connections it is clear that the blood enters the gills through the reflexed lamellæ and leaves them through the direct. When a starch mass was injected into the vessel X the afferent vessels of this gill were injected and the course of the blood was made out with certainty. The mass first distends vessel X and then passes to Y, through the interlamellar septa, filling it from end to end. The mass now enters the vessels of the gill which communicate with vessel Y and passes toward the gill's free margin. (See fig. 20, pl. L.) Half of the vessels of this reflexed lamella are thus filled. Some of the mass flows across to the opposite lamella through the interlamellar connections and fills half of its vessels. (Figs. 3 and 4, *b*.) Examination shows that only those which end blindly above are filled with the mass, so that none of the injection mass finds its way into the efferent vessels of the gills. By injecting through the auricle, or the T-shaped vein which carries the blood from the gills, it is possible to fill all the vessels of the gills not already filled by injecting from the kidney. The mass first enters the direct lamellæ and spreads across to the other. I have a preparation in which the afferent vessels are injected with a black mass and the efferent with a yellow one, which brings out the relationship between them quite clearly. It is evident that provision is made for making the blood pass through the smaller vessels of the gill before returning to the heart.

We may conclude from evidence obtained from the injections and anatomical studies that the blood enters the gill through every alternate vessel of the reflexed lamellæ, from which part of it spreads to the right and left in the interfilamentar connectives and filaments (fig. 4, *i* and *f*), finally finding its way into the neighboring vessels of the same lamella. These vessels (fig. 4, *v'*) end blindly above so that it must yet pass across to the opposite lamella through the interlamellar connectives before finding its way out of the gill to the heart. On the other hand part of the blood on entering the gill passes at once across to the opposite lamella through the interlamellar connectives into vessels which end blindly above. From these it spreads laterally, right and left, in the interfilamentar connectives and filaments of this lamella and finally into the neighboring vessels which open freely above into the vein which leads back to the heart. The general course of the blood in the gill is therefore outward in the reflexed lamella and the opposite in the direct, and the vessels are so connected that it must pass through a capillary system in one lamella or the other before leaving the gills.

The relationship of vessels just described holds good for all parts of the gills, except a narrow strip at their outer free margin. Here it is different and for completeness must be briefly described. Here the transverse vessels (interlamellar connectives), are very numerous and lie side by side. In the mid-line between the lamellæ they

fuse and their cavities intercommunicate, forming a sort of irregular sinus. Here all the vessels of the two lamellæ seem to be in open communication, but the starch mass was not forced into them sufficiently to show this. If one can rely upon sections, this is true. Blood which does not find its way across to the direct lamella before reaching the edge of the gill does so here by passing through one of the very numerous transverse vessels which are present in this region. As has already been said, these intercommunicate, and this may be an adaptation to take care of the extra amount of blood which flows through the gills during muscular activity or when the heart beats rapidly from any cause, supposing that the capillaries are not sufficient to accommodate it at such times. Only a very small part of the blood passes around the edge of the gill. As has been stated already, the filaments disappear at the edge of the gill, but it is possible to trace vessels to the edge where they communicate with irregular spaces which pass around to the opposite lamella.

It is clear that the blood does not pass, as a whole, down one lamella and up the other, as is the case in *Pecten tenuicostatus*, as described by Drew (2). All the vessels of the outer lamella of this form are afferent, and all of those of the inner lamella are efferent. He found none ending blindly and no cross connections. On the other hand, Johnstone (6), studying *Cardium edule*, found that half of the vessels of each lamella are afferent and half are efferent. He implies that the efferent vessels of each lamella open separately into the main efferent vein, but he does not make this plain, and his figures 24 and 30 are inconsistent. If we imagine the efferent vessels of the outer lamella as ending blindly above, and give them many cross connections with those of the opposite lamella, we have practically the arrangement found in *Atrina*, although the gills of the two forms differ considerably in other respects. As regards circulation the gill of *Atrina* is therefore intermediate between those of *Cardium* and *Pecten*, but is more nearly like *Cardium*.[a]

RESPIRATORY CURRENT.

The respiratory current in *Atrina* is remarkably strong. When specimens are as much as 6 inches below the surface a very considerable agitation of the water directly above them is perceptible when the respiratory current is running full force. In fact, the water fairly boils. The mantle, being open, may admit water at any point ventral to the inter mantle septum and it is expelled dorsal to this structure. While the respiratory current is flowing the edges of the mantle are brought quite close together, so that objects of any considerable size are prevented from entering the mantle chamber. It was found difficult to get admission even for powdered carmine. The sensory tentacles detect solid objects in the water and the mantle closes, preventing their entrance. When one shell is partially removed and the mantle lobe folded back the respiratory current within the mantle chamber can sometimes be seen. Powdered carmine shows strong

[a] Bonnet describes a different circulation for the gill of *Pinna nobilis*, a form so closely related to *Atrina* that one would expect to find no fundamental differences in the circulation. Menegaux finds the work of Bonnet incorrect. His description of the anatomy of the gill for *Pinna* agrees very closely with mine for *Atrina*. but he gives a different description of the course of the circulation through it. I am inclined to think they are the same.

currents sweeping anteriorly in the ventral part of the mantle chamber, turning dorsally between and over the outer surface of the gills. The inflow of the water seems to be due in part to the action of the fine cilia of the inner surface of the mantle, but the gills, much of whose inner and outer surfaces are ciliated, are evidently the seat of the great pulling force.

FOOD-BEARING CURRENTS.

The respiratory current entering the mantle chamber carries with it many small objects in suspension, including minute living organisms. These are not allowed to pass through the gills, but are filtered out and passed in slow moving currents toward the mouth. These food-bearing currents are easily followed when powdered carmine, suspended in water, is dropped upon the gills. The particles of carmine are seen to move outward to the free border of the gill, where they enter the longitudinal groove in its edge and pass toward the anterior, finally reaching the palps, between which they continue to the mouth. These respiratory currents and food-bearing currents have long been known, and they seem to be much the same in all lamellibranchs. It was thought until recently that so long as water was flowing into the mantle chamber the lamellibranch had no choice but to receive the food, strained from it, into its digestive tract. In 1900 J. L. Kellogg (7) showed that when food was not desired it could be turned aside in the palps and deposited by them into backward-moving currents in the mantle, through which it was carried directly or indirectly to the exterior. Stenta (14), working independently upon many forms, including *Pinna*, came to the same conclusions. In *Atrina* I found the food-bearing currents turned aside at about the middle point of the palps at the anterior end of the corrugated portion. Here it moves outward to the edge of the palps and then posteriorly to their tips, where it leaves them to enter the ciliated canal of the mantle, which transports it to the exterior. Whether lamellibranchs can exercise choice in their food, accepting only the part which is desirable, is not known. C. Grave (3) compared the contents of the digestive tract of oysters with diatoms found in the water above their beds and came to the conclusion that they have the ability to choose. J. L. Kellogg read a paper before the American Society of Zoologists in December, 1909, in which he stated that it is not the nature of the food but the quantity of it which causes lamellibranchs at times to reject it. When great quantities of food material are carried to the palps by the gills they reject it. In this case it passes outward in the grooves of the corrugated portion of the palps to their outer borders and then posteriorly to their tips. It then enters the backward-moving currents in the mantle chamber and is expelled.

CIRCULATORY SYSTEM.

In order to get a good injection of the blood vessels it was necessary to narcotize the specimens. Otherwise they would contract to such an extent as to make the relation of the parts unintelligible. This was done by placing them in a large pan of sea water and adding alcohol slowly until dead, which required from six to eight hours. By this means they remained expanded and the vessels were relaxed sufficiently to allow easy penetration of the injecting fluid.

ARTERIAL SYSTEM.

The arterial system is not bilaterally symmetrical, so that a description of the arteries of each side will be necessary.

The heart lies in the pericardium just anterior to the adductor muscle and mantle gland. It consists of a heavy walled ventricle and two thin walled auricles. (Fig. 17, *h*, pl. XLIX.) The latter are elongated in the direction of the longitudinal axis of the body and are attached at one extremity to the tissue covering the retractor muscle and at the other to the adductor. They receive the blood from the gills through a short tube which lies external to the retractor muscle. (Fig. 17, *t*, pl. XLIX, and text fig. 9, *a*.)

The ventricle is a saddle-shaped structure into which the auricles open on either side. It gives off an anterior and a posterior aorta. The latter soon gives rise to a large branch which passes dorsally to the right of the rectum and enters the mantle. This artery divides into two equal branches at the posterior dorsal angle of the mantle, one branch going to the right mantle lobe, while the other goes to the left.

The arteries of the left mantle are represented in figure 17, plate XLIX, the right mantle lobe having been removed and its artery being therefore shown cut off. The mantle artery branches very profusely. It will be noted that there are two parallel arteries connected by numerous anastomoses. The outer and smaller of the two is distributed to the edge of the mantle, the other branches mostly in the opposite direction, and supplies the greater part of the mantle. This posterior mantle artery meets and joins with a similar one from the anterior end of the body.

The posterior aorta gives rise to a second branch, which is distributed to the rectum and mantle gland, then, bending abruptly ventrally, it enters the adductor muscle. A small branch continues over the anterior face of the adductor and goes to the region of the visceral ganglia and kidneys. (Fig. 18, pl. XLIX.)

The anterior aorta is much the larger of the two. On the right side (fig. 17, pl. XLIX) it gives rise to five branches which go to the reproductive organ and liver. Three small branches go to the dorsal part of the mantle where they spread anteriorly and posteriorly in the midline. At the anterior end of the visceral mass the aorta gives off a branch which passes forward over the anterior retractor muscle. Three arteries arise from this branch; one to the outer palps, one to the middorsal line of the mantle, and one to the anterior adductor muscle. It then passes over the anterior adductor and at the extreme anterior end of the body divides into two equal branches, one of which goes to the right mantle lobe and the other to the left. These two branches join with the similar mantle arteries which arise from the posterior aorta.

The aorta after giving off the artery, which has just been described as passing above the anterior retractor muscle, bends ventrally and divides into a number of arteries which are distributed to the inner palps and byssal apparatus and foot. Those which go to the byssus are paired, right and left; but those to the left side are not represented in the figure.

The arteries given off from the aorta on the left side of the body are represented in figure 18, plate XLIX, and are three in number. All three are distributed to the digestive

tract, to some extent, as well as to the reproductive organ and liver. The middle one lies deep within the visceral mass and follows closely the coils of the intestine. The most anterior one, besides giving branches to the stomach and liver, gives one to the byssal apparatus and posterior retractor muscles of the foot (fig. 18, *a*, pl. XLIX). Other arteries shown in this figure have already been described as belonging to the right side of the body. The main branches of the arteries are constant in number and portion, but the smaller ones are not so constant. There is so much variation in these as to be confusing to one who is studying them. The figures were drawn after dissecting several specimens, so that they may fairly be considered typical.

VENOUS SYSTEM.

The venous system, unlike the arterial, seems to be absolutely symmetrical, so that a description of one side will suffice for both. The venous blood enters the kidney from the visceral mass through a large vein which runs diagonally over the surface of the posterior retractor muscle of the foot. This vein brings blood from nearly all parts of the body, including the foot, byssus, liver, reproductive organ, and digestive tract. (Fig. 19, *v*, pl. XLIX.) There is no venous sinus below the pericardium into which the blood collects previous to entering the kidney. The blood enters the kidney, as stated above, through a large vessel which breaks up into a closed capillary system. After bathing the glandular cells of the kidney the blood is collected into a large vein which transports it to the gills to be aerated.

The blood from the adductor muscle, and probably also the mantle gland, drains into a sinus located on the ventral surface of the adductor. This sinus communicates with the vein to the gills on each side just as it emerges from the kidney, and hence the blood from the adductor and mantle gland does not enter the kidney, but goes directly to the gills. Since this sinus communicates with both sides it is possible to inject the veins of both sides from one point.

Besides the sinus just mentioned there is another at the base of the foot. Those organs which are extended by blood pressure therefore have sinuses in their immediate vicinity.

After traversing the gills the blood is returned to the heart by two vessels, one of which lies in the suspensory membrane and carries the blood from the anterior half of the gills, the other bears the same relation to the posterior half of the gills as the first to their anterior portion. These two vessels flow together to form a single short wide tube which runs at right angles to them and communicates with the auricle. This tube lies just anterior to the adductor muscle and runs over the outer surface of the retractor muscle. (Text fig. 9, and fig. 16, pl. XLVIII.) Just before entering the auricle it receives a vein from the mantle. The latter is formed by the union of two mantle veins, one from their anterior and the other from their posterior portions.[a]

[a] A number of small vessels from the palps enter the distributing vessel of the gills. The direction of the flow of the blood in these vessels was not determined, but it is probably toward the gills. They may therefore be considered as part of the venous system.

It will be noted that the blood which goes to the mantle passes through one capillary system before returning to the heart, that to the adductor and mantle gland passes through two, while that to the body proper passes through three, viz, those of the body, kidney, and gill. In this respect as well as in general plan the circulation seems to be similar in many lamellibranchs. The walls of the veins in general are not so well defined as those of the arteries. When a starch mass which had been strained through fine bolting cloth was injected into the veins, it soon spread out among the tissues, showing that the blood is not confined in a closed system of vessels. The arteries, however, divide into extremely small branches, so that it was impossible to force the injection mass to their ends.

ADDUCTOR MUSCLES.

There are two adductor muscles, the anterior of which is small and practically useless so far as could be made out. The posterior adductor is large and powerful and is situated near the middle of the shell. It is composed of two distinct kinds of fibers as indicated by a difference in color. The ventral two-thirds is darker than the dorsal one-third. No attempt was made to distinguish physiological differences in these parts, but various opinions have been given. Von Jhering (15) experimented upon *Pecten* to determine the difference in function of the two kinds of fibers. He cut the dark portion and found that the remaining white portion contracted only very slowly, but it prevented the valves from opening widely under the influence of the hinge ligament. He next cut the white portion of another specimen and found that the remaining dark portion was capable of very rapid contraction, but it could not hold the valves closed for any considerable time. It also allowed the valves to gape widely. He therefore concluded that it is the function of the white portion to keep the valves from gaping widely and to hold them closed for a long time when occasion demands. The dark portion, according to his view, is the real muscle to which the contractions are due. J. L. Kellogg (7) holds the opposite opinion, that it is the white portion which is contractile, and that the dark part is for the purpose of keeping the valves tightly closed.

In *Atrina* the mantle muscles are white and are capable of rapid contraction, while the anterior adductor and foot retractor muscles, which are also white, scarcely contract at all. The white muscle fibers of lamellibranchs may therefore be quick or sluggish in their contractions. Von Jhering is the only investigator who has isolated the two kinds of fibers to test them, and his results seem conclusive, although Pelseneer (11) and Kellogg have opposed his view.

RETRACTOR MUSCLES OF THE FOOT.

There are two pairs of foot retractors, one posterior and the other anterior. The latter is so situated that the foot would be extended by its contraction rather than retracted, but it is customary to call this pair of muscles retractors. As a matter of fact none of these muscles has any considerable power of contraction. Their function seems rather to be to support the body. They suspend it in the manner of a hammock.

(Fig. 19, pl. XLIX.) The anterior retractors are cylindrical and composed of white fibers. At one end they are inserted into the anterior surface of the foot, while at the other they are attached to the shell just posterior to the anterior adductor muscle. (Fig. 19, *ar*, pl. XLIX.) The posterior retractor muscles appear large in the drawings, being attached at one end to the base of the foot and at the other to the shell just anterior to the posterior adductor muscle. (Fig. 19 *pr*, pl. XLIX.) This structure in reality consists of two parts, the byssal apparatus and the muscle proper. These retractor muscles have become very much reduced. They no longer serve to retract the foot, but have taken on a new function, that of supporting the byssus.

VISCERAL MASS.

The main body of the visceral mass is approximately cone shaped, with the apex at the anterior end. It is slightly flattened dorso-ventrally and at the posterior end there is a slender horn which projects back below the pericardium between the posterior retractor muscles. Its hindermost extremity rests upon the adductor muscle. (Fig. 18, pl. XLIX, and fig. 9, *m*.) The visceral mass includes the digestive and reproductive organs. The liver, which surrounds the stomach, fills the anterior part. The reproductive organs fill the remainder of the space not occupied by the coils of the intestine. The sexes are separate and are easily distinguished by the color of the reproductive organ, which shows through the thin body wall. The testis is white, as shown in figure 16, plate XLVIII, while the ovary is orange red. The main duct, which carries the reproductive elements to the exterior, opens into the kidney very near the renal aperture. (Fig. 6, *g*.) Fertilization of the eggs takes place after they are extruded into the water.

FOOT AND BYSSUS.

The foot is cone shaped and is attached to the anterior end of the visceral mass. At its base a large opening, from which the byssus protrudes, is to be found. (Fig. 16, pl. XLVIII.) From this point a groove extends along the ventral surface of the foot to a point near its tip. (Fig. 15, *g*.) The byssal gland is situated in the floor of this groove and is continued back of the foot into the posterior retractor muscles. The foot can be protruded, and it is probably of service in attaching the byssus.

KIDNEY.

The kidneys are two in number, and each consists of a glandular and a nonglandular portion. They lie between the gills on the ventral side of the body, just anterior to the abductor muscle. They hang down into the central suprabranchial chamber as two dark colored bags and are very conspicuous organs, requiring no dissection to expose them. (Fig. 20, K, pl. L.) Each is in open communication with the pericardial chamber above and each opens below into the suprabranchial chamber by a large tube, which ends at the summit of a papilla. The glandular portion forms the prominent sac mentioned above and lies about midway between the two extremities of the kidney. For convenience of description the kidney may be divided into three portions: First, a

tube (*a*, fig. 6) which opens into the pericardium; second, a short tube (*b*) which opens to the exterior; third, a central pouch (*c*) into which the tubes *a* and *b* open at their inner ends. This central pouch is large and irregular in shape. One branch of it extends upward over the posterior retractor of the foot and ends beneath the pericardium. (Fig. 6, *e*.) This portion of the kidney is probably homologous with a kidney-like organ which Grobben (5) found in a number of lamellibranchs extending as a fold into the pericardium and connected below with a large sinus, which he believed to belong to the kidney. In *Atrina* it is plainly a branch of the main kidney.

The glandular portion (fig. 6, *h*) is located at the posterior and outer end of the main pouch. It is quite extensive and is colored dark brown on account of the reddish brown excretory material which is inclosed by its cells. All other parts of the kidney appear colorless and thin walled.

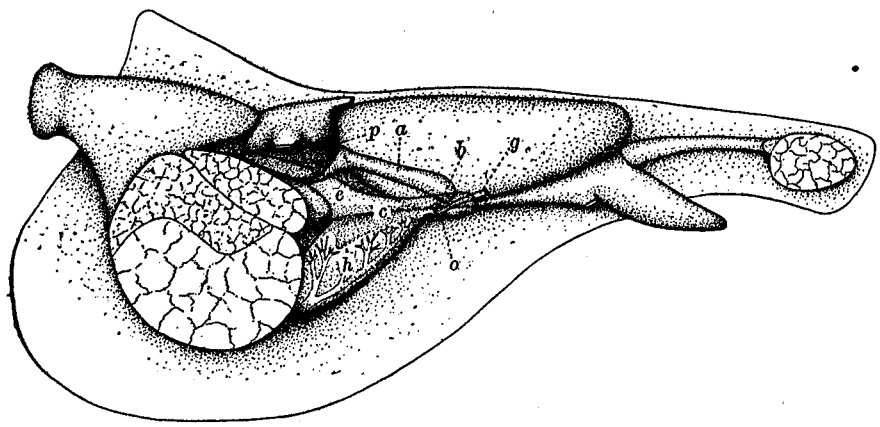

FIG. 6.—Drawing of the kidney in position, showing three well-marked parts, a tube (*a*) opening into the pericardium, a tube (*b*) opening to the exterior, and a large central pouch (*c*) into which tubes *a* and *b* open at their inner ends; *e* represents a prolongation of pouch *c* which extends upward beneath the pericardium; *g*, the genital duct; *k*, the glandular portion of the kidney; *p*, the pericardium.

It will be noticed that this kidney differs considerably from the usual type, which is typically a coiled tube. In the form under consideration it may once have been a true coiled pouch. Its transformation may have come about by the fusion of the two branches of the central loop to form the single large pouch.

While working with living specimens I frequently saw quantities of yellowish-brown material expelled from the kidneys. When examined under the miscroscope this material proved to consist of very numerous vacuolated cell-like bodies, which were filled with yellowish-brown or reddish-brown globules of excretory matter. Each excreted body had a tuft of extremely long cilia which were still active. (Fig. 7.) After collecting and fixing some of this excreted matter I stained it with iron-alum hæmatoxylin to see if there were nuclei present. None were found and I believe that none are thrown off. Paraffin sections of the glandular portions of the kidney show the epithelial cells to be greatly vacuolated and filled with this excretory matter. (Fig. 8.) The vacuole is located in the outer end of the cell and there is very little protoplasm

surrounding it. The nucleus is seen in the basal end of the cell and is surrounded by dense protoplasm. Certain cells show a constriction below the vacuole, as if they were in process of being divided. Other cells show this process farther advanced, and appear as if they were drawn out by some force which was stretching them into two. The nuclei in these cells are to be seen in the basal half, and it appears also that very little cytoplasm is thrown off with the vacuole. This method of excretion, although uncommon, is not especially wasteful, as would appear from the statements of investigators who have written upon this subject and maintained that the entire cells are excreted in the mollusks studied by them. Of course this may take place in some; but excretion in *Atrina* is not of that wasteful character.

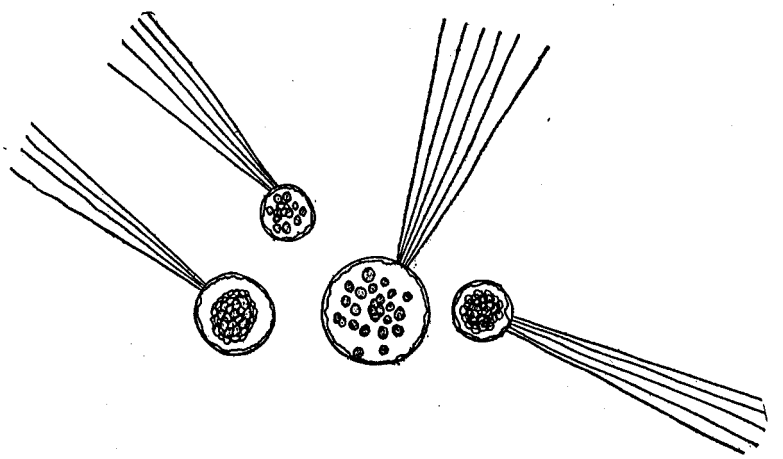

FIG. 7.—Bodies excreted from the kidney, formed by the pinching off of the vacuolated tips of the cells. Note the tuft of long cilia on each and the concretions of waste material within the vacuole.

DIGESTIVE TRACT.

The stomach is a large asymetrical pouch which adheres closely to the dorsal wall of the visceral mass. On the left side it is attached to the ventral wall by a strand of muscle tissue. The ducts of the liver open into it at two points, one on the right and one on the left. (Fig. 9, *d*.) A part of the epithelium lining the roof of the stomach is differentiated as a conspicuous gland which forms a prominent ridge within the cavity of the stomach. The anterior end of the crystalline style adheres closely to this gland.

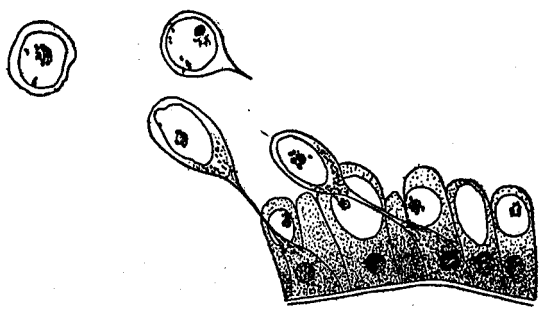

FIG. 8.—Section of the glandular portion of the kidney showing the formation and excretion of vacuoles by constriction.

The intestine originates at the posterior end of the stomach and passes to the extreme posterior end of the visceral mass, where it bends sharply to the right and passes anteriorly as far as the stomach. It then makes a large loop and again passes posteriorly, traverses the ventricle and mantle gland, to end behind the adductor muscle (Fig. 9.)

The part of the intestine nearest the stomach possesses a feebly developed typhlosole, while the remainder has it very strongly developed. A large crystalline style lies in

the part of the intestine which has the typhlosole feebly developed. This crystalline body is largest near the stomach and tapers gradually to a point and ends just beyond the first bend of the intestine, where the typhlosole becomes prominent. The latter structure is much swollen and gelatinous at this point, so that it almost obliterates the cavity of the intestine.

Several theories have been advanced to explain the nature of the crystalline style. Mytra (10) seems to have shown pretty conclusively that it contains an enzyme which will digest starch. He thinks it is a secretion from the liver. Pelseneer (11) has held for a long time that its function is that of protection. He thinks it forms a protective coat for the intestine and surrounds rough particles of sand and diatom shells which might otherwise injure the delicate tissues. I find a structureless coat or cuticle of

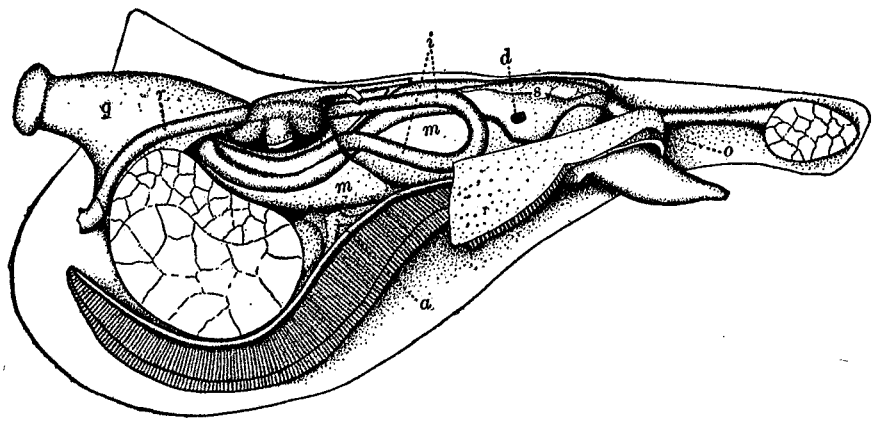

FIG. 9.—Drawing of the digestive system in position. *g*, Mantle gland; *m*, visceral mass; *o*, mouth; *s*, stomach; *d*, opening of liver ducts into stomach; *i*, intestine; *r*, rectum.

some kind lining a considerable part of the wall of the intestine. This may be formed from the crystalline style and may serve to protect the epithelial lining of the intestine.

NERVOUS SYSTEM.

The central nervous system consists of three pairs of ganglia which are connected by nerve tracts, or commissures, in the usual way. One member of each pair of ganglia is situated on the right side of the body and the other directly opposite it on the left. Each ganglion supplies nerves to tissues situated on its own side of the body only, and since those of the right and left are alike in number and distribution they will be described as coming off in pairs. The pedal ganglia are fused more or less to form a single mass, but the line of separation is plainly discernible. (Fig. 10, *pg.*) They are situated at the base of the foot and they give off three pairs of nerves posteriorly which are distributed to the byssal apparatus and retractor muscles of the foot. They also give rise to one pair of nerves from their lower anterior surfaces, which penetrate the foot.

The cerebral ganglia are situated wide apart, there being one on each side of the esophagus. They are connected by a nerve ring which passes over the esophagus. (Fig. 10 and 12, *cc*.) They give off a number of nerves, usually seven pairs, to the palps. A very large nerve leaves the anterior end of the ganglion and passes parallel to the cerebral connective for a short distance and then bends outward and enters the mantle. Just before it enters the mantle it gives off a branch, which continues forward for a short distance above the anterior retractor muscle of the foot. This branch then bends outward and ventrally, penetrates the tissue of the retractor muscle, from which it finally emerges and enters the anterior adductor. (Fig. 12.) The mantle nerve having entered the mantle divides into a number of branches, all of which unite with the circumpallial nerve, to be described later. Each cerebral ganglion communicates with the corresponding pedal ganglion by a short, thick connective. A complete nerve ring is thus formed around the esophagus. (Fig. 10.)

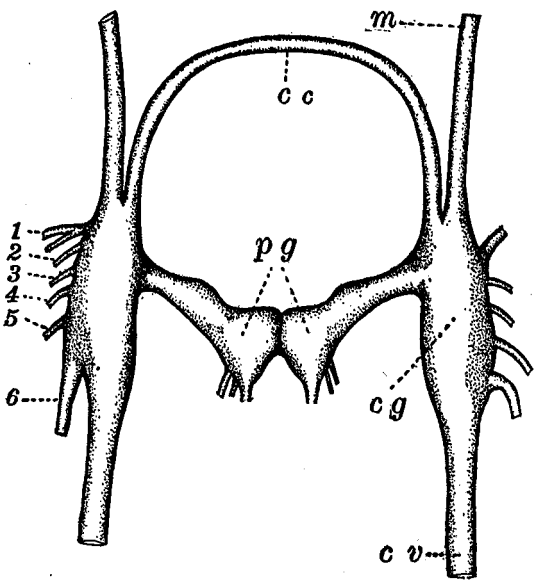

FIG. 10.—Drawing of the cerebral and pedal ganglia with their connectives. *cg*, Cerebral ganglion; *pg*, pedal ganglia; *cv*, cerebro visceral connective; *cc*, cerebral connective; *m*, nerve to mantle and anterior adductor; *1*, *2*, *3*, *4*, *5*, and *6*, nerves to the palps.

The visceral ganglia are situated on the ventral face of the adductor, just posterior to the kidney. They lie near together and are connected by a very thick commissure which contains many nerve cells. (Figs. 11 and 12, *vg*.) A large cerebro-visceral connective passes through the kidney and visceral mass between the cerebral and visceral ganglia. (Fig. 12, *c*.) The visceral ganglia give off four pairs of nerves to the posterior, which pass over the ventral surface of the adductor. (Fig. 19, *1*, *3*, *3*, and *4*.) Three of these finally bend outward and enter the mantle. Their course in the mantle may be seen in figure 12, *1*, *2*, and *3*. Most of the branches of these nerves unite with the circumpallial nerve, but a few from the most anterior of the three lose themselves in the tissue of the mantle. The fourth pair of nerves, described above as lying on the ventral surface of the adductor, does not reach the mantle, but passes near the rectum and enters the muscles of the mantle gland. Judging from their close connection with the muscles of this organ, one is led to believe that they are distributed to the muscles only. Another pair of nerves which arises from the visceral connectives (fig. 11, *5*) passes on the surface of the adductor in the opposite direction from those just described and enters the tissue of the mantle gland. These nerves are most likely distributed to the glandular

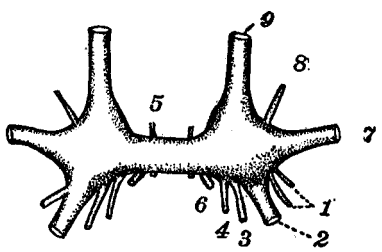

FIG. 11.—Drawing of the visceral ganglia. *1*, *2*, and *3*, nerves to the mantle; *4* and *5*, to mantle gland; *6*, to adductor; *7*, to gills; *8*, to kidneys; *9*, the cerebro visceral connective.

portion of this structure, since they do not seem to be closely associated with muscles. The other nerves which belong to the visceral ganglia are the following: A pair of large nerves which penetrate the adductor muscles (fig. 11, *6*), a large pair to the posterior portions of the gills (fig. 11, 7), and a pair of very small nerves (fig. 11, *8*), which are distributed to the kidneys. I have been unable to find the nerves to the anterior part of the gills. These nerves, however, arise from the visceral ganglia, as can be proven by experimental methods. If the gills are isolated from the cerebral and pedal ganglia by cutting all possible connectives, they will still contract when the posterior part of the mantle is stimulated. The anterior part of the gills will contract under these conditions, even after the large nerve to the posterior part of these organs has been cut. It is therefore evident that the nerve supply of the gills comes entirely from the visceral ganglia.

The circumpallial nerve lies near the edge of the mantle, to which it gives off numerous small nerves. (Fig. 12, *cp*.) It runs entirely around the mantle, passing across the mid line at either end, and thus forms a complete ring. Although it seems to contain

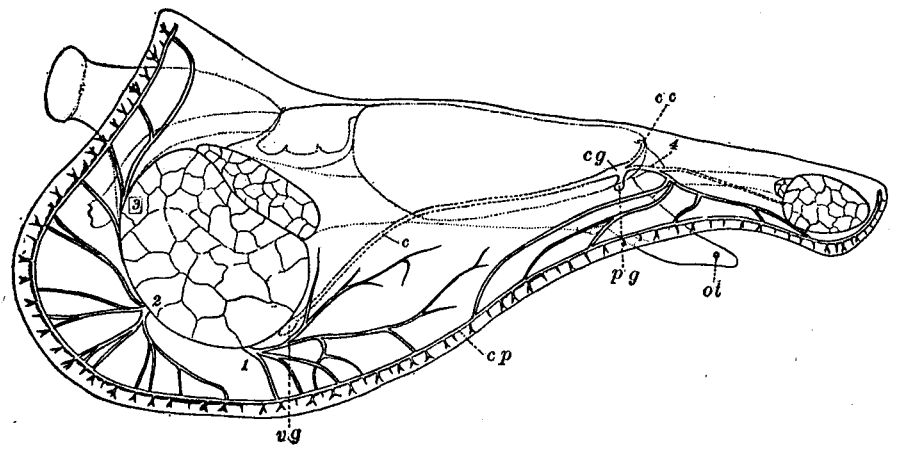

FIG. 12.—Drawing to show distribution of mantle nerves. *cg*, Cerebral ganglion; *pg*, pedal ganglion; *cc*, cerebral connective; *c*, cerebro visceral connective, *cp*, circumpallial connective; *1*, *2*, and *3*, mantle nerves from the visceral ganglion; *4*, mantle nerves from the cerebral ganglion; *ol*, otocyst.

many nuclei it has no motor nerve cells. If the nerves from the cerebral and visceral ganglia are cut the mantle is paralyzed. The neuclei which might be mistaken for nerve cells probably belong to the nerve sheath.

A number of experiments were performed to determine which parts of the body are supplied with nerves from each ganglion. The experimental and anatomical evidence agree and there seems to be little if any overlapping. Each ganglion seems to supply its own definite regions of the body. The visceral ganglion controls the posterior part of the mantle, posterior adductor muscle, gills, mantle gland, and kidneys. The cerebral ganglia control the anterior part of the mantle, the palps, anterior adductor, and anterior retractor muscles. The cerebral and pedal ganglia together control the foot, posterior retractor muscle, and byssus. The nerves to the viscera and heart were not discovered. A more complete account of the experimental study of the nervous system of this form is given in a paper published in the Johns Hopkins University circular for June, 1909 (4). The most interesting feature of this work was the discovery of reflexes. For example,

when the mantle is stimulated gently opposite the anterior end of the gills, the anterior part of the gills contract, while the posterior part of these organs remains quiet. A stronger stimulus causes the whole of the gills, as well as other parts, to contract.

SENSE ORGANS

OTOCYSTS.

The otocyst in *Atrina* is located very near the tip of the foot and has therefore a very unusual position. (Fig. 12, *ot.*) It varies greatly in size in different specimens and may be a degenerating organ. In some specimens it was found to be an extremely

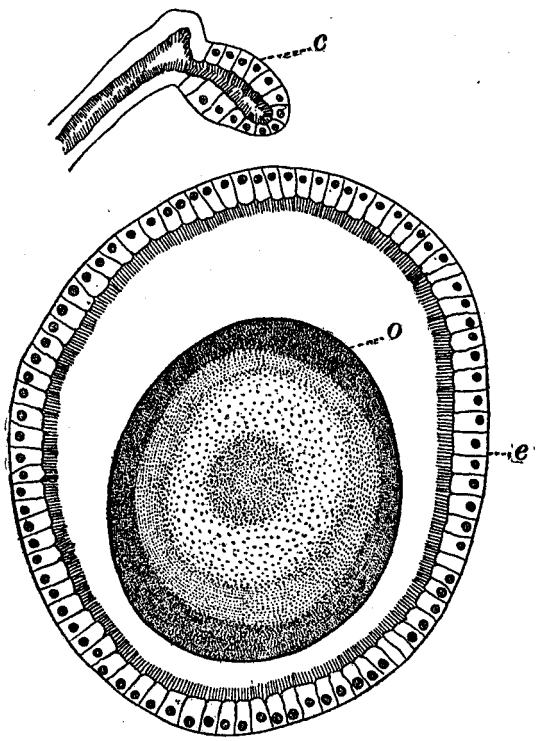

FIG. 13.—Drawing of a transverse section of one lobe of the otocyst, outlined with a camera lucida. *c*, Ciliated tube connecting the otocyst with the exterior; *e*, ciliated epithelium forming the wall of the otocyst; *o*, otolith showing concentric structure.

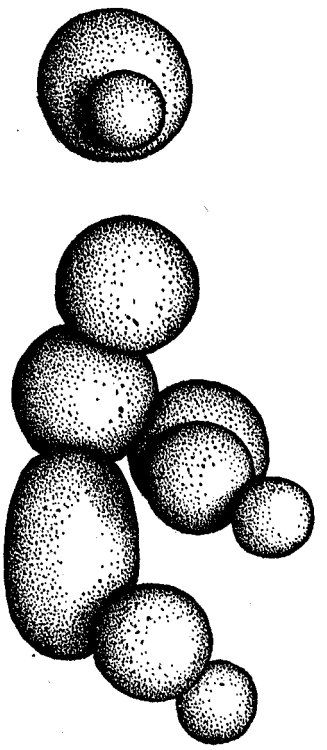

FIG. 14.—Reconstruction of the compound otocyst from a series of sections.

small sac lined by ciliated epithelium containing no otolith. In others it is a large lobed structure with an otolith in each lobe. The otoliths (fig. 13, *o*) show a concentric structure. Figure 14 represents a reconstruction of the otocyst from a series of sections, and shows that in this specimen there were two or three otocysts in place of one, the usual number. There are three ciliated canals leading in toward the otocysts from the outside and although they could not be traced into the otocysts they came so near that there is scarcely any doubt but that they are the tubes formed by the invagination of the ectoderm, which gave rise to the otocysts. (Figs. 13 and 15, *c.*) The evidence indicates therefore that there are three otocysts in this specimen formed by independent

invaginations of the ectoderm. Some of the numerous lobes seen in figure 14 were formed by division of the original otocysts. Some of the lobes are completely separate from the rest while the cavities of others communicate with those of their neighbors. If there is a nerve connected with the otocyst, it was not discovered.

OSPHRADIUM.

The osphradium consists of a small patch of sensory epithelium situated directly ventral to the visceral ganglion at the origin of the branchial nerve. (Fig. 20, *o*, pl. L.) It is large enough to be seen without magnification and appears to be colorless. When examined under the microscope, however, its cells are seen to contain a yellow pigment. Nerve fibers are distributed to the osphradium from a ganglionic mass which surrounds the base of the branchial nerve. This nervous tissue appears to be a part of the visceral ganglion, but Pelseneer insists that the osphradium receives its nerve supply from the cerebro-visceral commissure and hence from the cerebral ganglion. I have no preparations to show that this is the case. This sense organ is said to be used for testing the purity of the water, whatever that may mean.

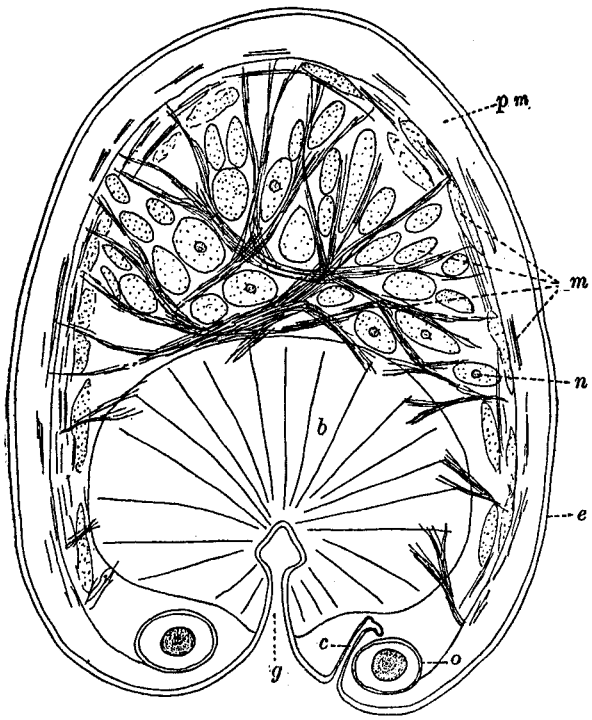

FIG. 15.—Drawing of transverse section of the foot showing the position of the otocyst. (Outlined with camera lucida.) *b*, Byssal gland; *g*, ventral groove in the foot; *m*, circular and transverse and longitudinal muscles; *n*, nerves; *o*, otocyst; *c*, ciliated tube which has given rise to the otocyst by invagination from the ectoderm; *p m*, undifferentiated mesoblast.

SUMMARY.

1. The arterial system of the two sides is not symmetrical, as may be readily seen by a comparison of figures 17 and 18, which represent the arteries of the right and left sides, respectively.

2. The venous system lacks the "sinus venosus" which is commonly present in lamellibranchs and which receives the blood from all parts of the body previous to entering the kidney. This sinus or a substitute for it is a necessary part of the mechanism described by Menegaux for extruding the foot and other organs whose movement is due to blood pressure.

3. The blood in traversing the kidney passes through a closed capillary system.

4. The blood which enters the gills must pass through a capillary system before emerging again.

5. There is no pallial line but the mantle is attached to the shell at a single point just ventral to the adductor muscle. As a consequence the mantle can be withdrawn a considerable distance from the edge of the shell. After being contracted the mantle again reaches the edge by creeping outward upon the shell.

6. The spines on the outer surface of the shell are formed by little tongues of the mantle which creep out into them during their growth period.

7. The mantle gland which Menegaux calls the "appendice" is probably a "swab" for keeping the mantle free from dirt.

8. The kidney excretes vacuoles containing quantities of concretions, but little protoplasm and no nuclei are thrown off.

9. Each ganglion supplies a definite region of the body and there is little overlapping. Reflex arcs were shown to exist.

10. The otocyst is located in the end of the foot far from the pedal ganglion and is a variable structure, sometimes consisting of as many as eight lobes and sometimes of only one. In one instance three separate ciliated tubes connecting them with the outside were discovered. This indicates that they have arisen from three separate invaginations of the ectoderm. This is the first instance of this sort found in lamellibranchs above the Protobranchia.

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EXPLANATION OF PLATES.

PLATE XLVIII.

Fig. 16. Drawing of a specimen natural size to show the relative position and appearance of the various organs. One shell valve, one mantle lobe, and the posterior half of the gills of one side have been removed. P A, posterior adductor; A, anterior adductor; C, posterior retractor of the foot; P, palps; G, gill; F, foot; B, byssus; M, mantle gland; R, rectum; K, the portion of the kidney which communicates with the pericardium; T, testis; D, ciliated canal of the mantle which carries débris from the mantle chamber.

PLATE XLIX.

Fig. 17. Drawing of the arteries of the right side of the body and of the left mantle lobe, the shell, right mantle lobe, gills, and kidneys having been removed. *h*, heart; *t*, tube which carries the blood from the gills to the auricle, here shown cut off just below the auricle; *v*, anterior aorta; *p*, posterior aorta; *m*, mantle artery; *g*, cerebral and pedal ganglia; *op*, and *ip*, arteries to the outer and inner palps, respectively.

Fig. 18. Drawing of the arteries of the left side of the body, the shell, left mantle, gills, posterior retractor muscles of the foot and kidneys having been removed; *m*, visceral mass; *a*, artery to the retractor muscles which have been removed. The distribution of the other arteries is easily made out in the drawing. Only the main trunk of the mantle arteries is shown here, but they are similar to those represented in figure 17.

Fig. 19. Drawing of the principal veins of the right side of the body, the shell, right mantle lobe, and gills having been removed. *pr*, posterior retractor muscle of the foot; *ar*, anterior retractor of the foot; *v*, the large venous trunk which enters the kidney and breaks up into capillariæ; 1, 2, and 3, veins from the foot and byssal apparatus, they receive blood from a large sinus which lies just at the base of the foot; *k*, the vein which gathers the blood from the kidney and carries it to the gills. It is here shown cut off at the point where it entered the gills.

PLATE L.

Fig. 20. Semidiagrammatic drawing of a specimen, ventral side up, to show the veins which enter the kidneys and those which emerge from them. The shell, part of the left mantle, and the gills of the left side have been removed. One kidney is cut open to show that the large vein upon entering the kidney breaks up into capillaries. F, foot; G, gill; G′, the upper border of the reflexed lamella of the gill; K, kidney; O, osphradium; 1, 2, and 3, mantle nerves from the visceral ganglion which lies upon the adductor muscle at the posterior end of the kidneys; 4, nerve to mantle gland; V, vein entering the kidney (the same as the vessel labeled V in fig. 19); *x*, the vessel which carries the blood from the kidney to the gills; *y*, the vessel which receives the blood from vessel *x* and distributes it to all parts of the gill.

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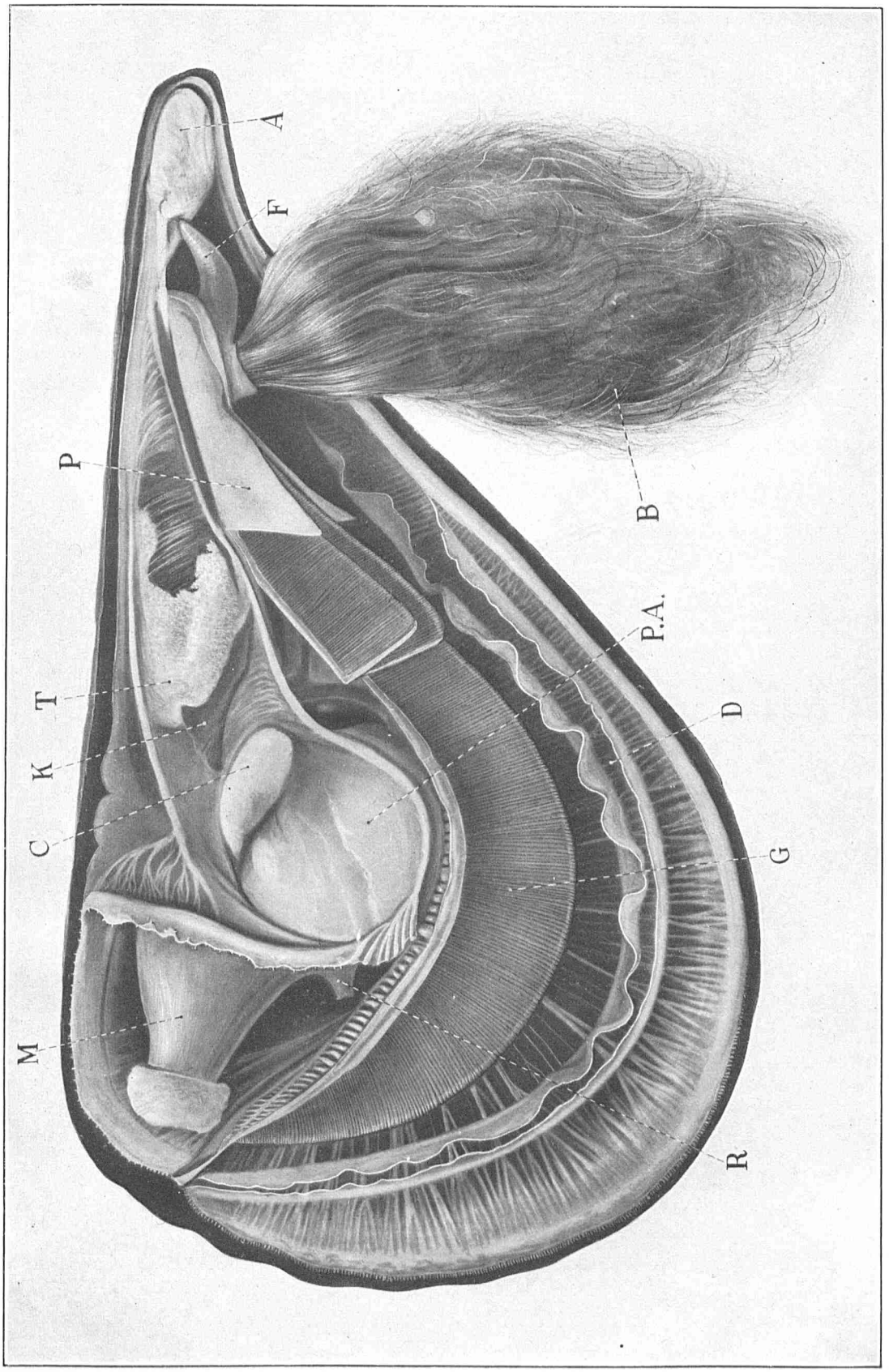

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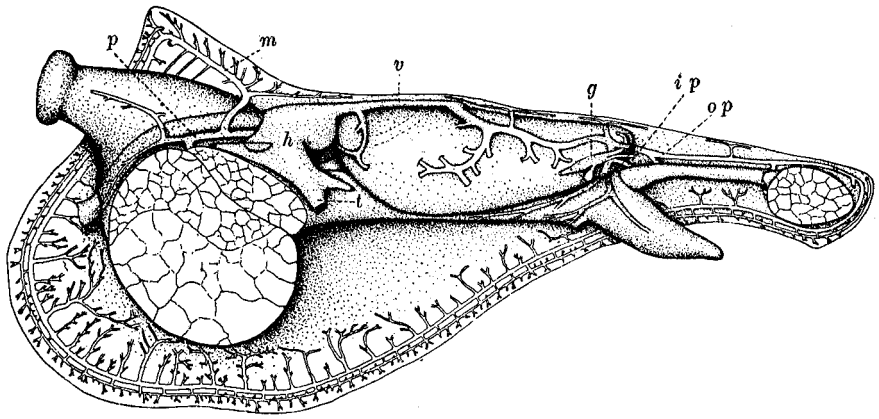

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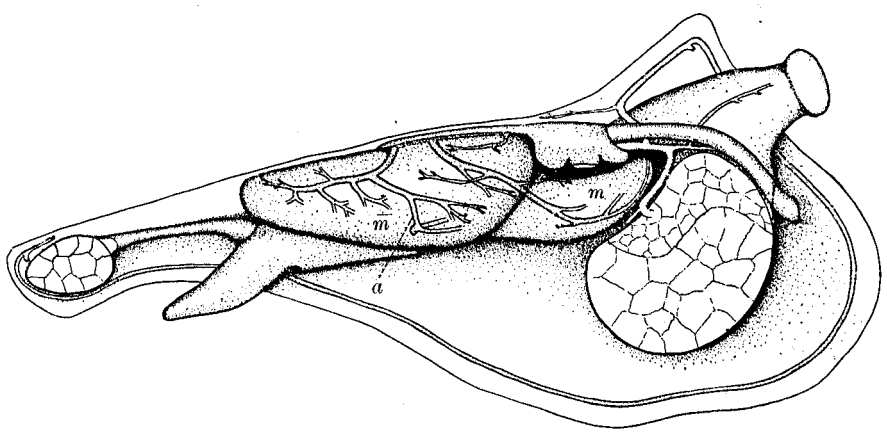

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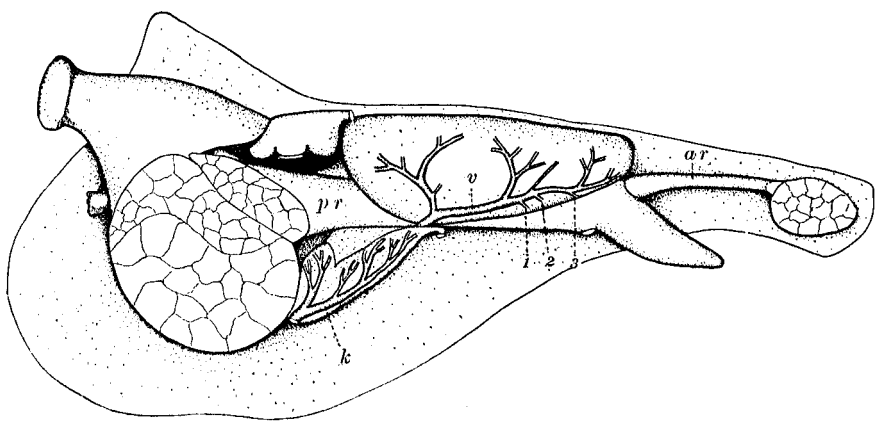

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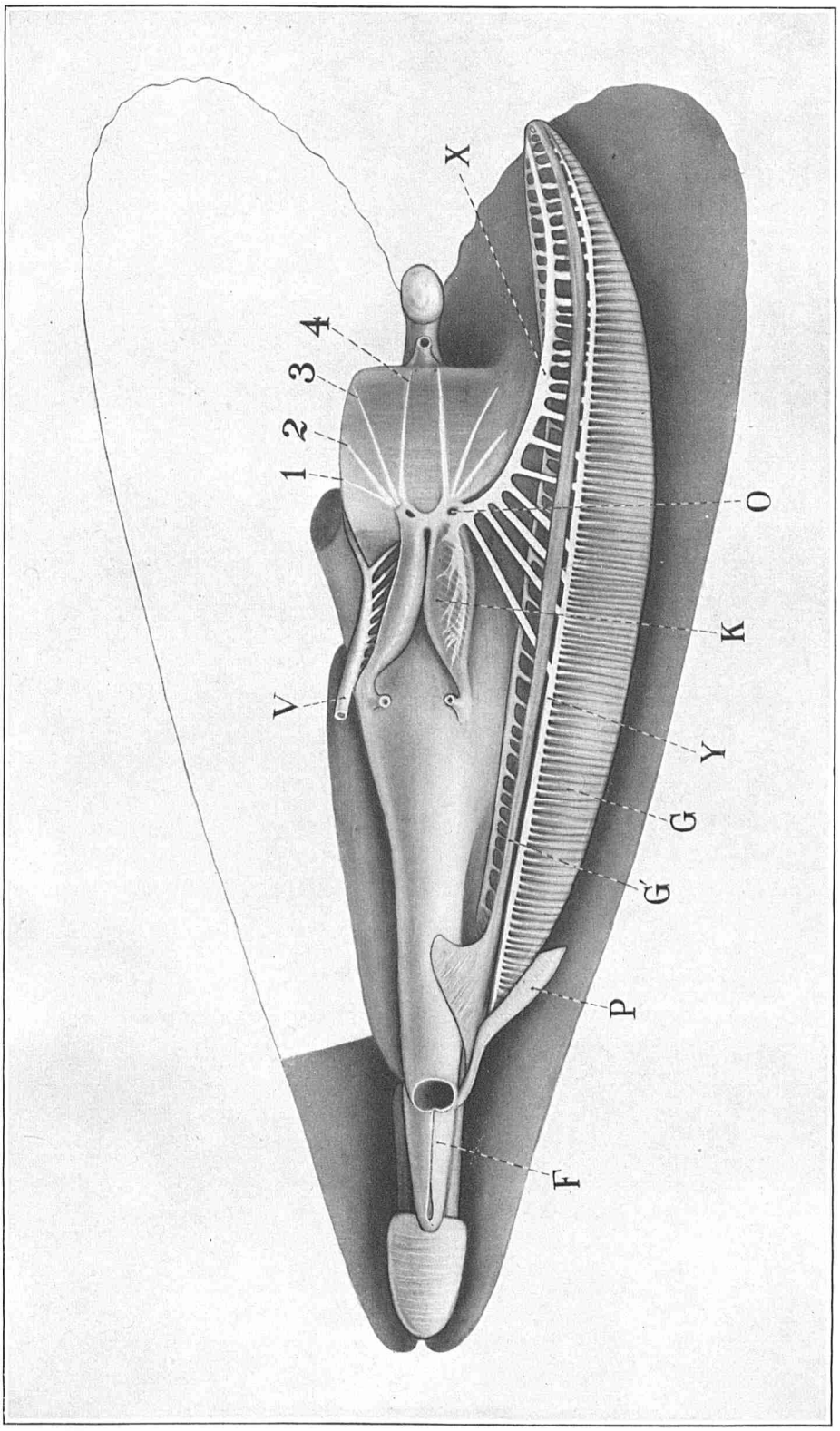

FIG. 20.

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