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BROWN UNIVERSITY

11

PROVIDENCE, RHODE ISLAND

CONTRIBUTIONS

FROM THE

BIOLOGICAL LABORATORY

(formerly Anatomical Laboratory)

VI



ISSUED OCTOBER, 1909

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PREFACE

The papers which are collected in this sixth volume of Contributions have been written by officers or students in the Department of Biology of Brown University, and have recently appeared in various scientific Journals. In the Table of Contents and on the title page of each paper will be found the place and time of publication. At the end of the volume is a complete list of the papers published in the preceding volumes of this series.

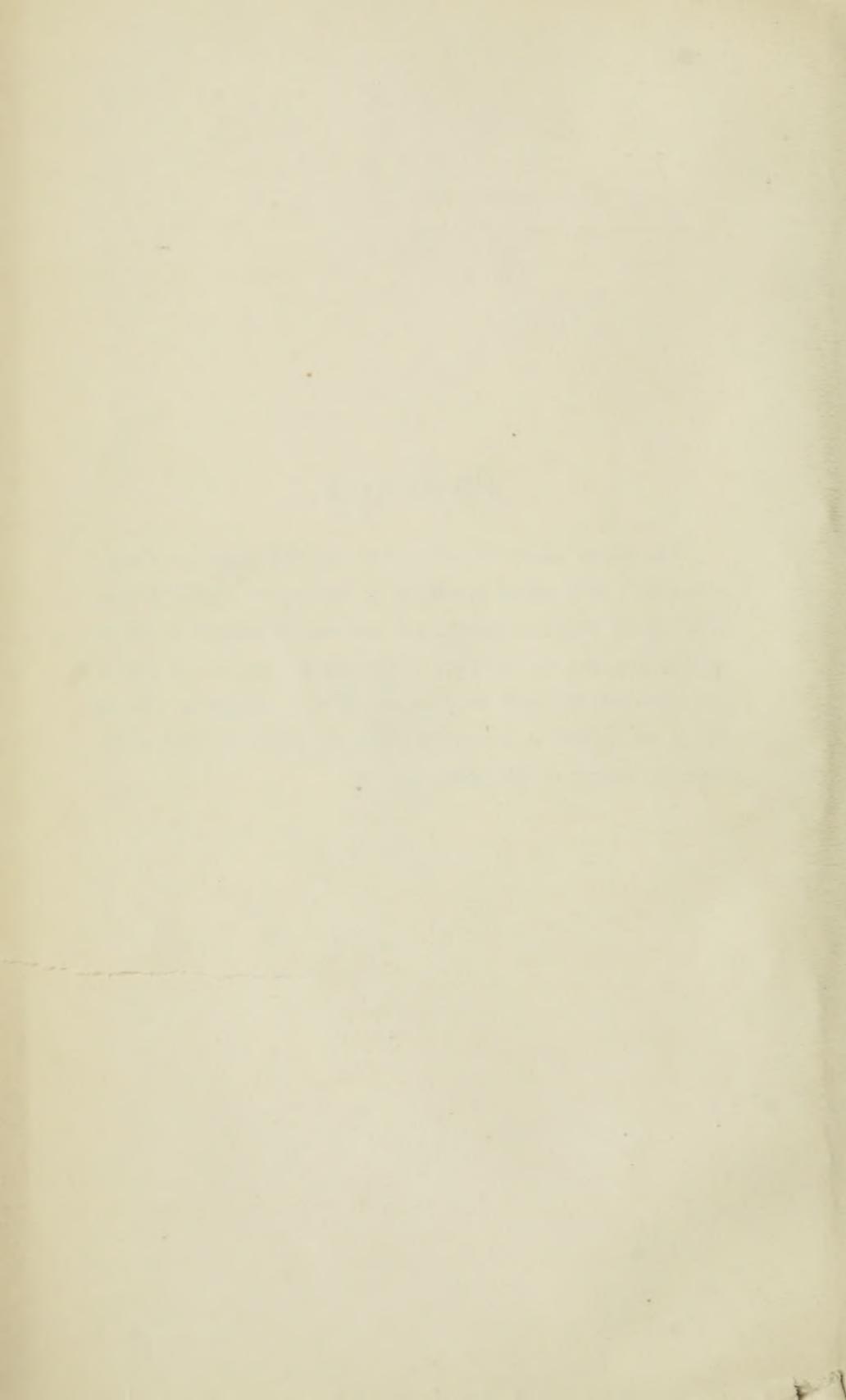


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LIST OF THE RHODE ISLAND COPEPODA, PHYL-
LOPODA, AND OCTRACODA, WITH NEW
SPECIES OF COPEPODA.

BY LEONARD W. WILLIAMS.

Thirty-seventh Annual Report of the Commissioners of Inland Fisheries
of Rhode Island. 1907. Special Paper No. 30.

LIST OF THE RHODE ISLAND
Copepoda, Phyllopoda, and Ostracoda,

WITH

NEW SPECIES OF COPEPODA.

DR. LEONARD W. WILLIAMS,

HARVARD MEDICAL SCHOOL.

1907.

SPECIAL PAPER No. 30.

REPRINTED FROM THE THIRTY-SEVENTH ANNUAL REPORT OF THE COMMISSIONERS
OF INLAND FISHERIES OF RHODE ISLAND.

A LIST OF THE RHODE ISLAND COPEPODA, PHYLLOPODA,
AND OSTRACODA WITH NEW SPECIES OF COPEPODA.

THREE PLATES.

LEONARD W. WILLIAMS.

The Entomostraca, the class to which these orders belong, is a group of crustacea which in vast numbers inhabits nearly all bodies of water, fresh or salt. The economic value of these minute forms at first glance seems slight, but their importance as a food supply, the effect of the numbers which live as parasites on fish, and the work they perform in destroying other still more minute forms, injurious to fish, make them a group by no means negligible by the practical fish culturist. Many small fish undoubtedly depend on copepods and phyllopods for food. The stomachs of young pickerel (*Esox reticulata*) which we examined were filled with the remains of phyllopods, while larval lobsters were proved conclusively to prefer copepods and phyllopods to other food. Many food fish subsist partially at least on entomostracas, and the appearance of "schools" of fish may depend directly or indirectly on the presence of these crustacea. The entomostraca, therefore, are one of the most important links in food supply between the lower plants and animals and the higher animals.

This list makes no pretence at completeness, but merely brings together all previously recorded species and those identified in the tows taken during a year and a half. Further work could easily enlarge the list, as the entomostracal fauna of the State is very rich and has received but little study. No especial attempt has been made to obtain fresh-water forms, but such as have been identified are included. The marine forms were largely secured by towing

during the winter in upper Narragansett Bay, and in summer in the Wickford region and in Charlestown Pond, a brackish inlet from the ocean.

A special examination was made of the common mollusks to find whether they were inhabited by copepods. The mussels and scallops yielded negative results, but the common clam (*Mya arenaria*) was found to be almost invariably the host of a new copepod which occurred also in the quahog (*Venus mercenaria*) and in the sea clam (*Maetra solidissima*). It had been hoped to secure a large number of the forms parasitic on fish, but diligent search throught the summer discovered only a few species, the fish in Narragansett Bay being apparently unusually free from parasitic copepods. Our thanks are here due to Mr. Henry C. Tracy for specimens of a number of parasitic forms.

The species starred in the list are recorded from Rhode Island for the first time.

COPEPODA.

Argulus laticauda Smith.

On tautog and eel. Wickford and Charlestown Pond.

Argulus megalops Smith.

On flounder. Matunuck.

**Argulus funduli* Kröyer.

On *Fundulus heteroclitus*. Wickford.

Caligus rapax Milne Edwards.

On the skate, dogfish, and many other fish. Cox Ledge.

(M. J. Rathbun: Fauna of New England, 5. List of the Crustacea. Boston Soc. Nat. Hist.)

**Lepeophtheirus edwardsi* Wilson.

On flounder. Wickford.

Dinematura latifolia Steenstrup & Lütken.

On *Lamna cornubica*. Cox Ledge. (Rathbun's List.)

**Lernæenicus radiatus* (Lesueur).

On menhaden. Wickford and off Montauk Point.

Clavella uncinata (O. F. Müller).

On cod and haddock. Cox Ledge. (Rathbun's List.)

Calanus finmarchicus (Gunnerus).

Narragansett Bay. January. This species, so well known as the food of the pollock whale, appeared in winter tows only.

Pseudocalanus elongatus (Boeck).

Narragansett Bay. January and February.

Centropages hamatus (Lilljeborg).

Narragansett Bay. Common throughout the year.

Pseudodiaptomus coronatus Williams.

Narragansett Bay and Charlestown Pond. Abundant throughout the year. Many pairs *in copula* were taken during the summer in Mill Cove, Wickford.

Our attention has been called to the similarity between this species and *P. pelagicus* Herrick from the Gulf of Mexico, and we admit the striking resemblance in general features. We suspect that Herrick's description and drawings, upon which we depended and which certainly cannot be harmonized with our specimens, may represent a species of which ours is a northern variety. A comparison of the type specimens would be necessary to settle this point. We may note in passing that the structure which Herrick describes as a spermatophore is, in our specimens, a reduced egg-sac containing two, occasionally three, eggs.

Temora longicornis (O. F. Müller).

Narragansett Bay. Abundant throughout the year.

Eurytemora americana Williams.

Narragansett Bay. Throughout the year.

Eurytemora hirunoides (Nordquist).

Narragansett Bay and Charlestown Pond.

Eurytemora herdmani Thompson & Scott.

Wickford. Abundant in summer.

Acartia tonsa Dana.

Narragansett Bay and Charlestown Pond. Summer.

Acartia clausii Giesbrecht.

Narragansett Bay. Throughout the year.

Tortanus setacaudatus Williams.

Narragansett Bay and Charlestown Pond. Though occurring in winter tows in the bay, this species was not found at all in summer tows in the Wickford region.

Oithona plumifera Baird.

Narragansett Bay. February.

Oithona similis Claus.

Wickford. Summer.

**Oithona nana* Giesbrecht

Wickford. This is the first record of the occurrence of this species in American waters.

**Cyclops serrulatus* Fischer.

Wickford and Fruit Hill ponds.

**Cyclops lucidulus* Koch.

Fruit Hill.

**Cyclops leuckarti* Claus.

Mill Pond, Wickford.

Longipedia coronata Claus.

Narragansett Bay and Charlestown Pond.

Ectinosoma normani T. & A. Scott.

Charlestown Pond. Summer.

Ectinosoma curtiorne Boeck.

Wickford and Charlestown Pond.

Microstella norvegica (Boeck).

Narragansett Bay.

Tachidius littoralis Poppe.

Upper Narragansett Bay.

Tachidius brevicornis (Müller).

Charlestown Pond. Summer.

Parategastes sphaericus (Claus).

Wickford and Charlestown Pond.

Diosaccus tenuicornis (Claus).

Wickford and Charlestown Pond.

Dactylopusia vulgaris (G. O. Sars).

Wickford and Charlestown Pond.

Thalestris serrulata Brady.

The record for this species rests on one specimen from Rocky Point.

Harpacticus uniremis Kröyer.

Upper Narragansett Bay.

Harpacticus chelifera (Müller).

Wickford and Charlestown Pond. Many of the specimens show points of resemblance to *H. gracilis*.

Idya furcata (Baird).

Narragansett Bay. Common.

**Ilyopsyllus natans* n. sp. Plate I.

Body heavy, short, and pear-shaped, except that its ventral edge is almost straight while its back is correspondingly elevated. Color, opaque reddish-brown with scattered brilliant red spots. Rostrum, strong, large, and jointed at base; its apex with two down-curved, ciliated, movable spines. Eye, large, red, T-shaped, with three lenses in front, one on each side, and one in the middle in base of rostrum. The 1st of the ten segments is very large, strongly convex above, and has nearly straight ventral and posterior edges. The following segments taper rapidly to the small abdomen. Thoracic segments of nearly equal width; ventro-lateral angles of first three free thoracic segments form triangular, acute processes, that of the 2nd and 3rd has also an accessory tooth. Preanal abdominal segments of equal width; anal segment very short with a blunt, median, dorsal projection. Posterior edge of the abdominal segments spinose on the belly and sides. Furca short, spinose, with a small, jointed dorsal seta, a minute inner bristle, and two terminal setæ; inner terminal seta as long as body, its proximal half broad and naked, its distal

half tapering abruptly and plumose exteriorly; outer seta one fourth as long as inner, plumose exteriorly.

Female:—First antenna short, less than half as long as the head segment, and six-jointed; 1st joint large, quadrate, with a row of coarse spines on the inner side of its upper surface; 2nd joint as broad as the first, very short, and prolonged in front into a rounded prominence fringed with blunt spines; 3rd joint smaller, bearing on its anterior distal angle a large esthetask, one third longer than the antenna, and supported by a 2-jointed accessory branch; 4th, 5th, and 6th joints small, about equal, and bearing a number of bristles. Second antenna longer and heavier than the first, three-jointed; 1st and 2nd joints large, a little longer than broad, the 2nd spined on the upper edge at the end; 3rd joint more slender, bearing six strong, curved spines of unequal length. Mandibles and maxillæ reduced and adapted for sucking. Mandible pointed at the end, bearing a two-jointed palp and forming with its mate a tube-like trough. First joint of palp small; 2nd joint elongated and bearing two bristles, one slender and long, the other shorter and plumose on both edges. First maxilla (?) about a third as long as the mandible, and similar in shape, but with two or three slender teeth at apex. The maxillæ appear to be partially enclosed in the mandibular tube. The 2nd maxilla was not found. The maxillipeds are partially united, having a common quadrate basal joint; each branch is further made up of two joints, the first long and slender, the second minute and bearing a rather long seta.

The basipodite of the 1st foot is formed of two broad, heavy joints, each spinose anteriorly, the second with two heavy curved spines at the distal angles; inner ramus 2-jointed, the 2nd joint somewhat longer than the first, with two terminal spines, the inner about a third longer than the outer and slightly plumose on the outer side; outer ramus 3-jointed, twice as long as inner, each joint spinose distally and with a strong curved spine at the external distal angle, last joint with two additional terminal spines. Second to 4th feet alike, both rami 3-jointed and with slender setæ sparingly and delicately plumose.

Fifth feet forming a symmetrical plate, each side of which is three-lobed, the external lobe bearing a short curved bristle.

Male.—First antenna 8-jointed; two basal joints like those of female antenna; 3rd joint shorter than in the female with similar accessory branch and esthetask; 4th joint of similar size and shape to the 3rd joint of the female antenna, but with an esthetask upon an unjointed projection; 5th joint smaller, broader than long; 6th joint longer than broad, concave in front; 7th and 8th joints small; 7th with a projecting knob in front, 8th with four moderately long bristles.

The 5 foot is similar to that of the female, but is more slender and lacks the bristles.

Length, 0.47 mm.

This species is very similar to *I. coriaceus* B. & R. (Brady & Robertson, Ann. and Mag. Nat. Hist., ser. 4, vol. xii, p. 132, pl. i), figs. 1-5. 1873; and Brady's Monograph of the British Copepoda, vol. ii, p. 148, pl. lxxxii, figs. 1-10. 1880), and to *I. holothuriæ* (Edwards) (C. L. Edwards, *Abacola holothuriæ*, Arch. f. Nat. p. 92, pl. 5, figs. 1-17. 1891), but differs markedly from them in its habit of swimming actively near the surface. It was taken in a number of surface tows in the channel of Mill Cove, Wickford. The rostrum and 1st antenna of the female are very similar to those of *I. holothuriæ*. The 1st foot of male and female and the mouth-parts are similar to those of *I. coriaceus*. This species has 5th feet entirely different from those figured by Edwards, and we do not find the organ between the fourth limbs of male figured by Brady.

**Lichomolgus fucicolus* Brady.

Wickford and Charlestown Pond.

**Lichomolgus adherens* n. sp. PLATE II.

Female.—Thorax ovate; cephalic segment forming more than half of thorax, three free thoracic segments nearly equally broad, outer angles rounded. Abdomen 6-jointed, $\frac{1}{18} \frac{2}{22} \frac{3}{15} \frac{4}{30} \frac{5}{18} \frac{6}{16} \frac{7}{20}$. First and 2nd (genital) segments broader than the others; pos-

terior edge of anal segment beset with spines. Furca with branches slightly divergent, each branch twice as long as broad and bearing two dorsal and four terminal setæ; dorsal setæ short, the outer slightly in advance of the inner; inner terminal seta one-half longer than furca, plumose; 2nd bristle as long as abdomen, jointed at base and plumose; 3rd bristle more than half as long as second and like it jointed at base and plumose; outer bristle shorter than furca, slender, naked. First antenna 7-jointed; length of joints $\frac{1}{18}$ $\frac{2}{22}$ $\frac{3}{15}$ $\frac{4}{20}$ $\frac{5}{18}$ $\frac{6}{16}$ $\frac{7}{30}$ shorter than the cephalic segment; 1st two joints with many flaccid bristles, other joint with fewer bristles. Second antenna 4-jointed; 1st as long as other three combined; 2nd joint about one-third as long as 1st, expanded at tip and bent backward so that the distal limb of the antenna is nearly parallel to the proximal limb; 3rd joint short with three or four strongly curved stiff bristles upon its distal lower angle; 4th joint with seven long curved unequal terminal bristles; the upper edges of the last two joints are fringed with short spines. Mandible strong with a hooked toothed and jointed terminal claw; palp(?) one-jointed with three strong, and as many slender, bristles. First maxilla(?) one-jointed with three irregular lancet-like bristles. Second maxilla two-jointed; proximal joint much swollen with two lancet-like plumose bristles on its inner edge; distal joint small, with one large heavy claw and two heavy bristles. Maxilliped two-jointed; proximal joint bearing a small lobe (inner ramus?) with two large bristles; distal joint long, broadly elliptical, with a single two-branched terminal claw, anterior branch bristle-like, posterior branch larger, broad, with four or more bristles on its posterior edge. First to 4th feet with both rami three-jointed. First foot with bristles and spines divergent; 4th foot scarcely differing from the third. Fifth foot two-jointed; distal joint elliptical, twice as long as broad, with two spines on the distal portion of the outer edge, one terminal spine and a short terminal bristle. Two egg sacs. Male not found. Length 1.2 mm.

Wickford, very abundant under small stones between tides.

**Lichomolgus major*, n. sp. Plate III.

Large, long female, (1.3 mm. male 1.9 mm. without caudal setæ), of transparent grayish or pinkish color. Body tapers regularly from the cephalic segment.

Female.—Three free thoracic segments of equal width and rounded at the sides. Abdomen 5-jointed, relative length of joints and furca $\frac{1}{8}$ $\frac{2}{12}$ $\frac{3}{7}$ $\frac{4}{7}$ $\frac{5}{11}$ $\frac{6}{13}$. Furca six times as long as broad, with six setæ; one on outer edge nearer the proximal than the distal end of furca, a minute dorsal bristle, and four terminal setæ, inner and outer minute, 2nd twice the length of furca, 3rd one-half the length of furca. The lower portion of posterior edges of the abdominal joints and the lower surface of the furca fringed with heavy short spines. First antenna 6-jointed, a little more than one-half the length of head segment, beset with short bristles, relative length of joints $\frac{1}{16}$ $\frac{2}{34}$ $\frac{3}{20}$ $\frac{4}{8}$ $\frac{5}{12}$ $\frac{6}{17}$. Second antenna 4-jointed, 1st joint long and directed forward and inward, 2nd and 3rd short, 4th slightly longer and armed below with heavy triangular spines, with two heavy terminal claws and three heavy terminal setæ. Labrum ending in an acute, backwardly directed spine. Mandible with an apparently movable terminal claw which has at base a hemispherical pad beset with recurved bristles. First maxilla with a single shoe-shaped joint from whose tip arises one long and two short bristles; lower surface with a similar trio of bristles. Second maxilla 2-jointed basal joint swollen, terminal joint heavy, straight, spine-like, with one bristle midway upon its posterior edge. Maxilliped absent (?).

First to 4th swimming feet with both rami 3-jointed. Many of the bristles and spines of the legs are irregularly swollen or constricted. The sternite between each pair of legs forms a ridge which is shaped like half of a dumb-bell and has several heavy, flat, spines on each rounded projection. The spines of all legs are entire. Distal joint of basipodite of 1st leg with a broad spine upon its internal angle. The edges of both rami and of the basipodite as well as the distal edge of the 2nd joint of the basipodite are fringed with heavy, triangular, acute spines. Fourth foot does not differ from the others. Fifth foot 2-jointed, 1st joint short with a single bristle upon a slight

stalk, distal joint three times as long as broad, with a conical end and with two heavy serrate outer spines, a long serrate terminal spine, and a short stalked bristle on its upper surface near the distal end. The outer angle of the basal, and the outer side and end of the distal joint are covered with short, heavy, unjointed spines.

Male.—Thorax like that of female. Abdomen 6-jointed, relative length, $\frac{1}{23}$ $\frac{2}{50}$ $\frac{3}{50}$ $\frac{4}{33}$ $\frac{5}{36}$ $\frac{6}{48}$ $\frac{6}{5}$. Second joint swollen, bearing on each side a fringe of spines and a single bristle. Abdomen otherwise as in female. Antenna and mouth parts as in the female except that a large 3-jointed maxilliped is present, 1st and 2nd joints of maxilliped of equal length; 2nd swollen and with a number of acute tubercles upon its inner side near the base and two rows of tubercles near the distal end of the joint, with a short bristle at the proximal end of each row of tubercles; distal joint sickle-shaped and serrate, enlarged at base and bearing there a small bristle. Feet as in female.

Wickford and Matunuck, in the common clam (*Mya arenaria*) the quahog (*Venus mercenaria*) and in the sea clam (*Macra solidissima*). Almost every clam and quahog which we opened contained one or more of these copepods in the mantle cavity. A very characteristic metanauplius which is very abundant in the Bay during the spring and summer, resembles this species, and though all efforts to rear the metanauplius were unsuccessful, we suspect that it is the young of this species.

PHYLLOPODA.

**Ceriodaphnia reticulata* Jurine.

Mill Pond, Wickford.

**Sida crystallina* (Müller)

Mill Pond, Wickford.

**Pseudosida tridentata* Herrick.

Mill Pond, Wickford.

**Scapholeberis mucronata* (O. F. Müller).

Wickford. Common throughout the eastern United States.

**Podon polyphemoides* Leuckart.

Abundant in the tows taken in the middle of Narragansett Bay together with the following species. Summer.

**Evadne normanni* Lovén.

Abundant in tows from Wickford to Newport. Summer. We have been able to find no previous American record for this or the preceding species.

**Camptocerus macrurus* (O. F. Müller).

Mill Pond, Wickford.

**Polyphemus pediculus* (Linné).

Mill Pond, Wickford.

Limnetis gouldii Baird.

Near Providence. (A. S. Packard, Twelfth ann. rept. U. S. geol. & geogr. sur. for 1878 (1883), pt. 1.)

Eubbranchipus vernalis (Verrill).

Pawtucket, Newport. (Packard.)

OSTRACODA.

**Sarsiella zostericola* Cushman.

Wickford. In tow taken at night. This species has been previously reported from the Wood's Hole region only.

**Loxoconcha impressa* (Baird).

Wickford. On eel grass and in dredgings.

Plate I. ILIOPSYLLUS NATANS. n. sp.

- ♀ Female, x 20.
R Rostrum, eye, and basal joints of first antenna of female, x 360.
F Furca, x 44.
A¹♂ First antenna of male, x 360.
A¹♀ First antenna of female, x 360.
P⁵♀ Fifth pair of swimming feet of female, x 360.
P⁵♂ Fifth pair of swimming feet of male, x 360.
MP Maxillipeds, x 360.
MX Maxilla (first or second?), x 360.
M Mandible, x 360.
P¹♂ First swimming foot of male, x 360.
P¹♀ First swimming foot of female, x 360.
A² Second antenna, x 360.

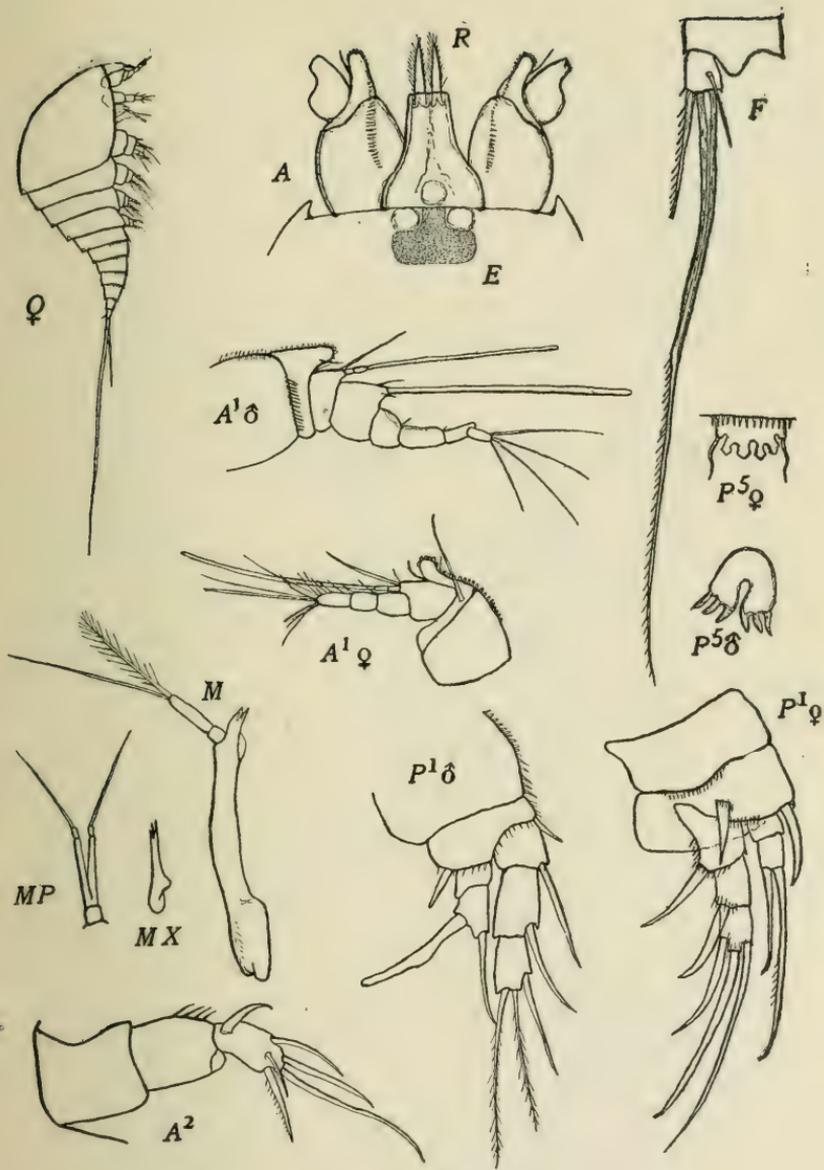


PLATE I.

Tliopsyllus Natans n. sp.

Plate II. LICHOMOLGUS ADHERENS. n. sp.

- ♀ Female, x 57.
N Nauplius, x 370.
A¹ First antenna, x 260.
A² Second antenna, x 260.
M Mandible, x 260.
MX¹ First maxilla, x 260.
MX² Second maxilla, x 260.
MP¹ Maxilliped, x 260.
P⁴ Fourth foot, x 260.
P⁵ Fifth foot, x 260.

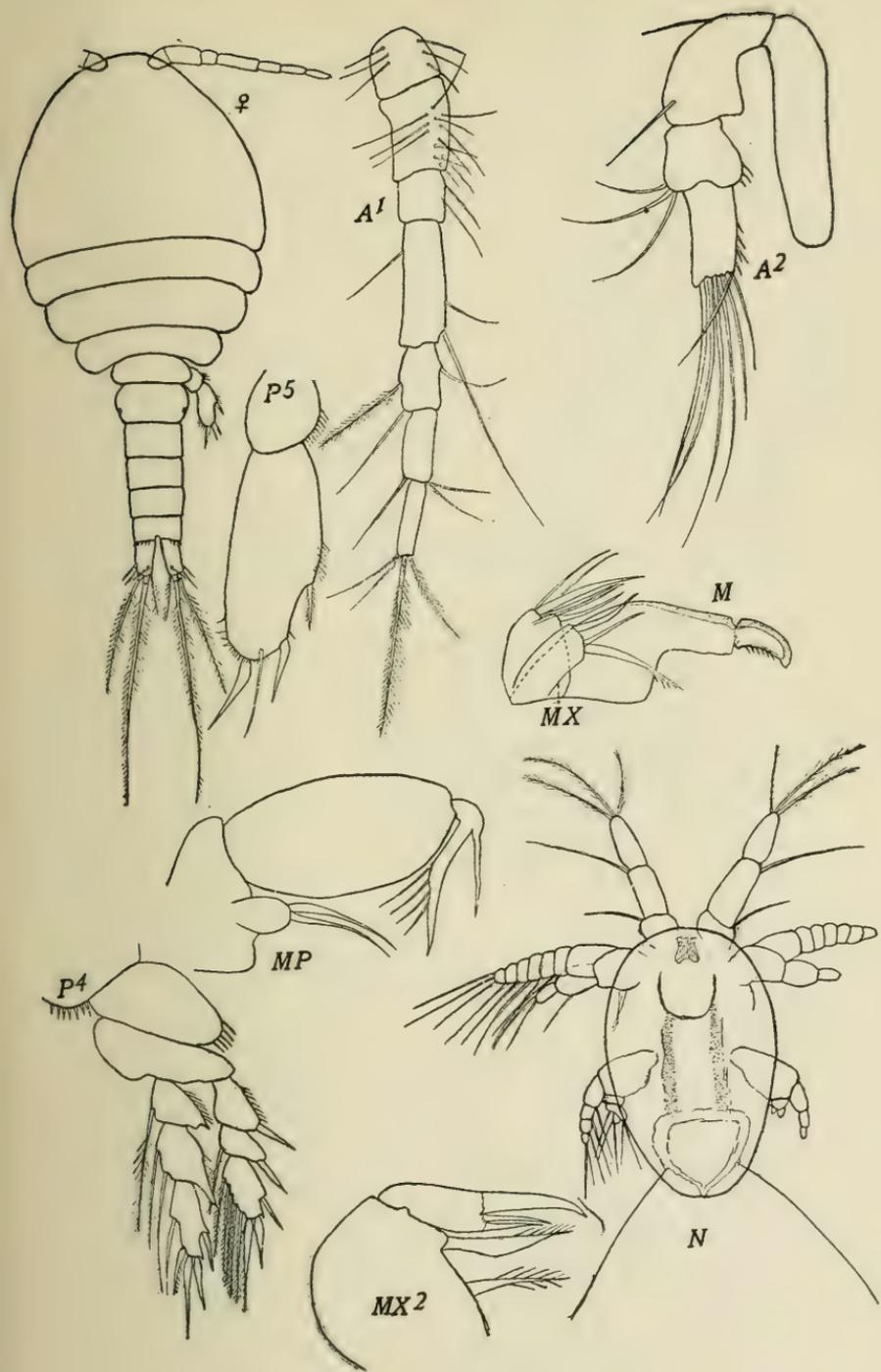


PLATE II.

Tichomoligus adherens n. sp.

Plate III. LICHOMOLGUS MAJOR. n. sp.

- ♀ Female, x 44.
A¹ First antenna, x 260.
A² Second antenna, x 260.
M Mandible, x 260.
MX¹ First maxilla, x 260.
MX² Second maxilla, x 260.
MP Maxilliped, x 260.
P⁵ Fifth foot, x 260.

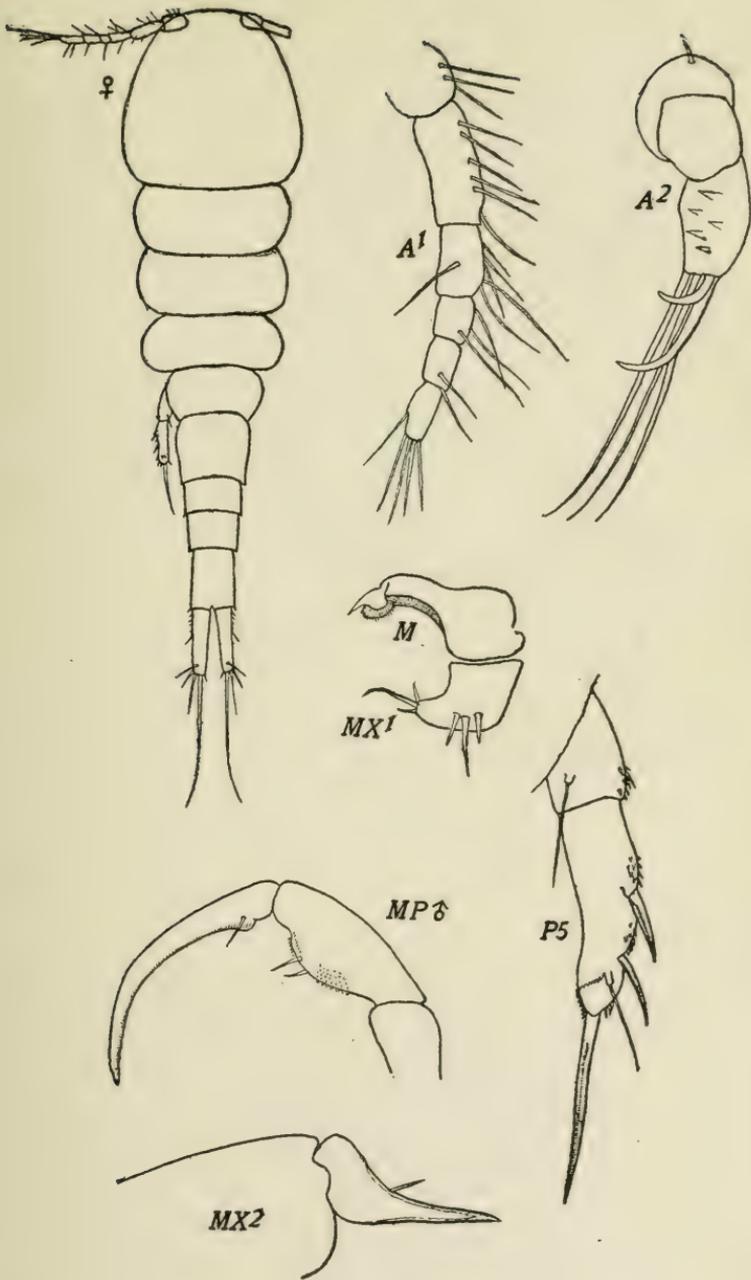


PLATE III.
Tichomolgus major n. sp.

REGENERATED AND ABNORMAL APPENDAGES
IN THE LOBSTER.

BY VICTOR E. EMMEL.

Thirty-seventh Annual Report of the Commissioners of Inland Fisheries
of Rhode Island. 1907. Special Paper No. 31.

REGENERATED AND ABNORMAL
APPENDAGES IN THE LOBSTER.

PLATES I TO X.

VICTOR E. EMMEL,
BROWN UNIVERSITY.

1907

SPECIAL PAPER No. 31.

REPRINTED FROM THE THIRTY-SEVENTH ANNUAL REPORT OF THE COMMISSIONERS
OF INLAND FISHERIES OF RHODE ISLAND.

REGENERATED AND ABNORMAL APPENDAGES IN THE LOBSTER.

BY VICTOR E. EMMEL,

BROWN UNIVERSITY, PROVIDENCE, R. I.

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REGENERATED AND ABNORMAL APPENDAGES IN THE LOBSTER.

I.

INTRODUCTION.

Probably most fishermen can recall some instance of a lobster with abnormal claws; specimens with claws marked by peculiar spurs and split tips, or again others which may have the two great chelæ just alike, and very rarely even a lobster with two or more extra claws and limbs. These curious abnormalities have long attracted the attention of museum and curio collectors, and recently they have acquired a considerable degree of interest as phases of the general problem of developmental mechanics.

A number of early writers have described deformities in various crustaceans, but Faxon, in 1881, was one of the first to carefully review the subject and give a detailed description of deformities, especially of those found in the lobster. Bateson, in his masterly work on "Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species," brought together all the authentic cases of abnormal structures known at his time, not only in crustaceans, but in the whole animal kingdom, classified them, and endeavored to determine the laws to which such variations might conform. Herrick ('95), in his study of the "American Lobster," devotes a chapter to "Variations in Structure," which adds materially to Bateson's data. More recently, contributions have been made by Andrews ('04), who describes "An Aberrant Limb in the Crayfish;" Zeleny ('05 a) records the "Regeneration of a Double Chelæ in the Fiddler Crab;" and Prizibram ('05) has made an exhaustive study of the symmetry and asymmetry of limbs in his monograph on "Die Heterochelie bei Decapoden Crustacun."

The importance of a careful study of abnormal structures is well emphasized by Bateson: "To collect and codify the facts of variation is, I submit, the first duty of the naturalist. This work should be undertaken if only to rid our science of that excessive burden of contradictory assumptions by which it is now oppressed. Whatever be our views of descent, variation is the common basis of them all. As the first step towards the systematic study of variation, we need a compact catalogue of the known facts, a list which shall contain, as far as possible, all cases of variation observed" (p. vi). The following data may be valuable as contributing something to such a list, and further—since some of these variations are authentic regeneration products—they may serve in determining one source of origin for such structures.

Much of the material about to be described was obtained by experiments made at the experiment station of the Rhode Island Commission of Inland Fisheries, and from the commission's collection at the State House, in charge of Secretary Morton. Mr. Cartland kindly aided me in securing drawings from his collection at Pemaquid Beach, Maine. And through the courtesy of the United States Fish Commission, we were able to obtain possession of a most rare specimen of triple chelæ. The use of the epidiascope at the anatomical laboratory of Brown University has also greatly facilitated the production of accurate drawings.*

II.

ABNORMAL APPENDAGES.

A. *Explanation of Terms.*

The following terms will be used in the sense indicated below:

Chelæ: The pair of appendages which carry the "great forceps" or claws.

Chelipeds: The appendages, including both the chelæ and the thoracic limbs, or walking legs.

* A method, it may be added, which is not only equally as accurate as the camera lucida, but makes it possible to draw objects of such a large size as would be practically impossible by means of the latter instrument.

The various segments of the cheliped, as shown, for example, in Fig. 6, will be designated as follows:

Dactyl (D): The first segment, *i. e.*, counting in a disto-proximal direction.

Propodite (Pr): The second segment.

Index (I): The distal part of the propodite which opposes the dactyl and forms one jaw of the claw.

Carpopodite (C): The third segment.

Meropodite (M): The fourth segment.

Ischiopodite (Is): The fifth segment.

Basipodite (Bs): The sixth or basal segment (not shown in Fig. 6).

All these segments are united by flexible joints, with the exception of the last two segments, the basipodite and ischiopodite. The latter two segments are fused together into one immovable piece, but there is still a distinct groove marking the two segments. It is always at this groove that separation occurs when the limb is thrown off by autotomy.

B. *Abnormal Chelipeds found in the Lobster.*

We will first describe the abnormal structures which we have obtained from museum collections or have found on lobsters taken from the traps; leaving for a later section those abnormalities which were experimentally obtained as regeneration products.

1. *Extra Processes arising from the Normal Dactyl.*

Specimen No. 1. Fig. 1. (Left Chela).

The propodite or index (I) part of this claw appears to be normal in every respect, except that there are two scars (a, a') along its smooth outer border; these scars may possibly have been connected with the origin of the abnormalities in the remaining part of the claw. The dentition of the index clearly shows that it belongs to the "crusher" type of chelæ. The dactyl (D) is strongly curved and twisted upward from its normal plane. Consequently when the

claw is closed the dactyl is not in normal opposition, but crosses over the upper face of the index. It is also dentated with the crusher type of teeth.

From the smooth or morphologically dorsal border of the dactyl arises two extra spurs or processes (D'R', D'L') which practically lie in the longitudinal dorso-ventral plane of the claw. One of the borders of each of these two abnormal processes is toothed, and the spatial relations are such that the toothed margins are turned toward each other, while the opposite smooth borders are turned away from each other. The character of the dentition is such that traces of "periodic sequence" may be seen, *i. e.*, teeth are arrayed in groups (p) characterized by larger prominent teeth, with smaller teeth intercolated between them. (See Scheme of Stahr, '98.) Along these dentate margins are tufts of tactile hairs (h). With respect to dentition and the presence of tactile hairs, therefore, these two processes seem to resemble a "nipper" more than a "crusher" type of claw. The general form of the remaining part of the dactyl, together with the fact that it is dentated with the crushing teeth characteristic of the opposing index, clearly shows that D is the original or normal dactyl, and D'R', D'L', the extra or abnormal parts. I have indicated these two processes as D'R' and D'L' because, as will be shown in a later discussion, according to Bateson's principles, these two abnormal parts are to be interpreted as a complementary pair of extra right and left dactyls.

This specimen, together with No. 4, is preserved in Mr. Cartland's collection of curios at Pemaquid Beach, Maine.

Specimen No. 2. Fig. 2 (Left Chela).

The propodite or index (I) of this chela is of the normal "nipper" type. Apparently the only scar upon it is an indentation on its lower surface, (indicated by the dotted line (a) in the figure). The dactyl (D) is bent dorsally upward at an angle of about 45 degrees from its normal position: otherwise it deviates but slightly in position and moves in the normal plant of motion. The teeth are of

the nipper type. The tip of the dactyl is broken, but it may be readily seen that its original length must have been practically of the size necessary for normal opposition with the index; this, together with its general form, marks this part of the claw as the original or normal dactyl.

The extra process $D'(R'+L')$ arises from the toothed border of the dactyl. It deviates slightly posteriorly or outward from the normal plane of motion for the dactyl. The two borders facing the dentate margins of the dactyl and index are both set with pointed "nipper" teeth. When the jaw is closed, however, the dentate margin of the extra process does not meet the index in a normal manner. Each toothed border of this claw is also fringed with tufts of tactile hairs.

This and specimen No. 4 are in the commission's collection of marine life. No. 2 came from Narragansett Bay off Beaver Tail, and was brought to Secretary Morton on September 5, 1906, by deputy, Mr. T. Luth.

2. *Abnormal Processes arising from the Normal Propodite.*

a. *Two Extra Dactyls and Double Extra Indexes.*

Specimen No. 3. Fig. 3 (Left Chela).

This curious specimen has been so sadly defaced and deformed that one would hardly recognize it as the cheliped of a lobster. As may be seen in the figure, the normal dactyl (D) and index (I) have been nipped off close to the joint, as the result, no doubt, of some submarine combat. The exposed ends of the stumps are covered with a dark-brown blood clot. While there are not enough characters left to determine conclusively the structure of the original parts, still, from the general slender form of the stumps and the tufts of tactile hairs (h) at the base of the dactyl, it seems evident that the original claws were of the "nipper" type of chelæ. That these two stumps represent the normal index and dactyl is inferred, not only because they are larger than the other similar structures on this

chela, but also because their morphological surfaces are structurally continuous throughout the limb. In regard to position, the index and dactyl are thrown horizontally outward at an angle of about 45 degrees from its normal relations to the chelæ.

At the inner or morphologically dorsal side of the second segment (d) there is a broad expansion of the propodite, so that this segment appears practically double, and is almost twice its ordinary size. Upon the periphery of this extra propodite structure are set two extra segments (D'R' and D'L'). They are practically equal in size, and each of these segments forms a true joint with the propodite. The tip of one of these extra parts (D'L') has been broken off, and a small area (a) is also gone from its toothed border. The general form and relation of these two extra segments clearly show that they are both dactyls; the character of the dentition, together with scattered tufts of tactile hair, also brings these two dactyls under the "nipper" type of claws.

Between these two extra dactyls there projects from the propodite a small spur I' (R+L). A closer examination of this process showed that it was slightly bifurcated at its tip; and what is still more significant, that down two of its opposite sides there is a more or less regular row of rudimentary teeth. These two rows of teeth lie in a common plane with the two dactyls; consequently, the relations are such that the toothed borders of the flexed dactyls play upon the rudimentary teeth of this process, in a manner very similar to that of a normal dactyl and index. The evidence, then, seems to justify the conclusion that this extra structure is morphologically really a double index. And, therefore, that this double index, together with the two dactyls, represents two extra claws.

In this abnormal chela, then, we have three claws. The extra pair is at about right angles with the normal claw, and the three claws also lie practically in a common plane. The significance of the fact that D and D'R', D'R' and D'L', are respectively minor images of each other will be taken up later under the head of "Discussion."

The remaining proximal segments of this chela appear practically normal, except that they are rather thick and stubby:—The third segment or carpopodite (c), especially, is unusually broad and massive. The carpopodite is also marked by a transverse groove or indentation on its dorsal surface (not shown in the drawing), which appears as if the limb had been pinched or sharply flexed upon itself at some time when the chela was in a more plastic condition.

b. *Two Extra Indices and Double Extra Dactyl.*

Specimen No. 4. Fig. 4 (Right Chela).

In this chela it is evident that the parts I and D are the normal segments of the claw. The dactyl (D) is in normal condition, except that a small part of the tip has been broken off. The propodite is also apparently normal in all parts, except the region in which the abnormal structures about to be described have arisen. The toothed borders of the index and dactyl present the dentition and tactile hairs characteristic of a true "nipper" claw.

Upon the outer border of the index is a large and prominent abnormal process, IL and IR. This abnormality takes its origin from a region rather intermediate between the morphologically posterior and ventral surfaces, but arising more directly posteriorly than ventrally. It is about half the length of the normal propodite, and at its greatest width it is much broader than the normal index. Beginning at the distal extremity of the process, and at right angles to the plane of the drawing, is a deep fissure (f), which extends some distance posteriorly and separates the tip of the process into two distinct parts. Along each side of this fissure and parallel with it is a slight ridge dentated with a row of pointed teeth. These two dentated ridges continue in a parallel direction beyond the fissure and extend almost to the proximal end of the process. On the outer side of each row of teeth are tufts of tactile hairs. It has already been implied that the fissure which separates the distal tips does not extend far down between these two dentate ridges;

at about the third of the distance it disappears and is succeeded by a slightly convex surface which continues proximally throughout the remaining region between the dentate margins. At about the middle of this convex surface arises a large sharply-pointed spur or tooth. Finally, it is most important to note that at the extreme proximal region of the abnormal process is a short stump D' (R+L) which projects upward from the surface, and is located at the terminous of the two rows of teeth. The form of this stump is such that its posterior surface is convex, while the anterior surface facing the rows of teeth is flattened. The top of the stump clearly shows that it is the remnant of a larger segment which has been broken off.

The facts just described lead us to the conclusion that this abnormal process is morphologically a double index; the fissure and dentate margins indicate the outlines of these extra indices, and the large spur between them is a double "lock-tooth" corresponding to the "lock-tooth" (t) on the normal index. This double "lock-tooth," together with the pointed teeth and tactile hairs on each index, places these indices under the category of "nipper claws." Moreover, the stump at the base of these indices suggests a still further morphological interpretation. For while this stump is too small to furnish positive evidence as to the character of the original structure, still its form and position strongly indicate that it is the remnant of a former double dactyl. If this inference is correct, it follows that the abnormal process of this chela is morphologically equivalent to two extra "nipper claws."

3. *Two Extra Chelæ arising from the Meropodite.*

Specimen No. 5. Fig. 5 (Right Chela).

All of the preceding abnormal chelæ were studied as dried specimens. But the next chela to be described was discovered on a live lobster taken off cape Newagen, Maine. We left chela of this lobster was a normal nipper, but on the right chela, instead of one, there were *three* distinct claws. The animal was transferred to the

United States Lobster Hatchery at Booth-bay Harbor, Maine, where, through the kindness of Prof. F. P. Gorham and Superintendent Captain Hahn, I was given an opportunity to study the living specimen. Through the courtesy of Dr. H. M. Smith, deputy commissioner of the United States Bureau of Fisheries, the lobster was later transferred to the experiment station of the Rhode Island Commission of Inland Fisheries, at Wickford, R. I.

In our description of this extraordinary chela we will begin with proximal segment or ischiopodite (Is). This abnormally large and distorted segment does not readily lend itself to discription; in a general way, however, it may be compared to triangular prism. One of the edges of this prism will then be ventral (v), and the prismatic surface opposite this edge will correspond to the dorso-lateral face of the segment. This dorso-lateral surface of the segment is also marked by a triangular-shaped scar or indentation (a), which may possibly have been casually connected with the origin of the more distal abnormalities.

Proceeding to the meropodite, we find that the sides corresponding to our imaginary prism for the ischiopodite are no longer parallel, but diverge very rapidly. The meropodite broadens out distally and finally terminates in two forks or branches (m, m'). The groove between these forks is at a slight angle to the dorso-ventral plane of the normal limb.

The question now arises which of these two forks is to be regarded as the representative of the normal chela. This can be determined by tracing the continuity of morphological surfaces in a disto-proximal direction. An examination of the surface structure shows that fork m is morphologically continuous from the distal extremity, through the ischiopodite to the basal segment or basipodite, where it forms apparently the entire joint with the later segment. On the other hand, the remainder of this compound meropodite meets the part just described more or less of an acute angle, giving one the impression of being grafted upon it. The right fork (m) is, there-

fore, to be regarded as the representative of the normal meropodite, while the left branch (m') is the extra or abnormal structure.

The remaining distal segments (C, D, I) of the normal chela present the usual characters, and with the claw (D I) opening in horizontal plane. The tips of the claw are bent slightly downward; a condition which may have been caused by a cramped position of these parts while hardening after the moult. At first sight it is not so clear whether this claw is a "nipper" or "crusher;" in its general form it is rather elongated and slender, like a nipper; but on the other hand, there is an almost entire absence of tactile hairs, and the dentition is characterized by the presence of "crusher" teeth. This claw is, therefore, of the crusher type, although in some respects it may be regarded as transitional between a nipper and crusher.*

Going back now to the abnormal part of the meropodite (m'), it is clearly evident that the next distal segment or carpopodite $C'(R+L)$, is morphologically double. It is very massive and more than twice the size of the corresponding normal segment (c); a longitudinal groove (g) divides it into two equal sections; the outer surface of each of these sections is set with a group of spines, and distally each half forms a true joint with the corresponding propodites, $P'R$ and $P'L$. Each half of this segment, with its joint and spines, is, therefore, homologous with the normal carpopodite. This double character of the abnormal carpopodite can also be traced back into the meropodite.

The morphological characters of the two extra claws ($R'+L'$) may be indicated in a word, as these claws are almost exact mirror images of each other. In general form the dactyls and indices of each claw are almost identical; the dentition consists of large tubercle-like teeth, with double teeth set near the angle of the jaw on each index; tactile hairs are almost entirely absent. Further details are not necessary, for it is evident at a glance that these two claws are both of the "crusher" type of chelæ.

In size these two extra claws are somewhat larger than the third

* A phenomena not uncommon in the lobster, especially in case of regenerated chelæ. See Emmel '06.

or normal claw. They do not lie in exactly parallel planes, but are inclined at a slight angle to each other and in such a way that the dactyls are nearer and the indices farther apart. Again, the common plane of motion for these two claws is at right angles to that of the normal chela. These spatial relations of the claws, together with the fact that the double extra carpopodite also lies at right angles to the corresponding normal segment, are points of considerable theoretical interest and will be discussed again later. Another point of interest is the color relations of the extreme left claw (R'). This claw in its development has become so completely reversed in its position that its *normally lower face now lies uppermost, and vice versa*. The development of the pigment layers has also been true to this reversal, so that the lower face of the claw as it now lies is much darker than its upper face.

In brief, then, *in this splendid specimen we have three chelæ in place of the normal single one. The three chelæ are morphologically distinct, even down to the last proximal segment. Consequently we have here a case of an almost complete "triplication" of this appendage.*

The lobster on which this triple chelæ was found was a male and measured about ten inches in length. After autotomously removing the abnormal chela, the lobster was transported to the experiment station at Wickford, R. I., and placed in a floating car. It was hoped that we might be able to keep the lobster alive through the winter in order to see what the next regeneration would produce. But, unfortunately, the animal died on September 13, 1906, so this interesting question remains unanswered. The cause of death is unknown, for another lobster of about equal size was brought by the writer from the Boothbay Hatchery to Wickford at the same time with the above specimen, and kept in the same floating car.*

*This lobster was a most rare bright blue colored specimen. I removed the right cheliped to see what would be the color of the next regenerated limb. By the middle of September the lobster had moulted and regenerated the chela, but it displayed the same bright blue coloration. A further note in regard to this blue lobster may be in place here. It is true that when adult lobsters are exposed to direct sunlight for a time, they frequently fade in color and assume a bluish tinge. But the present specimen, which was taken by Captain Over in Prospect Harbor, Maine, was evidently a case of a "true blue-lobster," whose color was not due to the action of sunlight, but rather to the fact that the carapace was naturally lacking in certain red pigments usually found in the shell.

This second is at the present date (January 30, 1907) still in a healthy condition.

4. *Similar Claws on both Sides of the Body.*

Specimen No. 6. Figs. 6-9.

Besides the deformities consisting of various divisions and repetitions of a given limb, there is another category of abnormalities occasionally met with, which consists of similar chelæ developed on both sides of the body.

During the summer of 1905, among the lobsters caught in the traps near the experiment station, I found an adult specimen with two similar claws. The lobster was a male and measured $8\frac{1}{2}$ inches in length.

Figures 6 and 7 represent the original chelæ of this lobster. The right limb (Fig. 7) is slightly larger than the left, but otherwise they are very similar in character. Both claws are rather elongated and slender in form. The joints between the dactyl and index is placed well down toward the proximal region of the propodite. Tactile hairs are in a dense fringe along the dentate margins of each jaw. The narrow pointed teeth in each jaw are included in linear series, except a stout displaced tooth about midway in dentition of each index, which forms the "lock" to the claw. These two claws, therefore, are not only similar in practically every respect, but they are also of the "nipper" type of chelæ.

The following experimental data were also obtained: Soon after the lobster was taken from the traps, an operation was performed in which both chelipeds were autotomously removed on July 14, 1905. Soon after the amputation of these limbs another pair of chelæ began to regenerate from the remaining stumps or basipodites. The following observations were made:

	Date.	Length of Lobster.	Type of Chelæ	Length of Regenerating Chelæ.	
				Right.	Left.
Mutilation.	July 14	217 mm.	Both "Nippers"	160 mm.*	150 mm.*
Observation.	" 28	pap.	pap.
"	Aug. 20	13 mm.	14 mm.
"	" 30	18 mm.	18 mm.
"	Sept. 2	21 mm.	21 mm.
"	" 9	25 mm.	25 mm.
Moulted.	Oct. 5	227 mm.	Both "Nippers"	130 mm.	128 mm.

* Original normal chelæ.

From this data it may be seen that the lobster moulted on October 5, eighty-six days after the amputation. The chelæ, which had regenerated by this time, are shown in figures 8 and 9. Here again both appendages are not only very similiar in form, but the arrangement of the pointed cutting teeth and the presence of tactile hairs clearly show that this pair of regenerated limbs are also of the "nipper" type of chelæ.

III.

REGENERATED ABNORMAL CHELIPEDS.

It will be observed that all of the abnormal appendages so far described were found either in museum collections or on lobsters taken from the traps, and consequently we have no positive data as to their origin. The next specimens about to be described were obtained during a series of experiments on regeneration made at the Experiment Station.

1. *The Regeneration of a Triple Claw on a Walking Leg.*

Specimen No. 7. Figs. 10-18.

The lobster on which this abnormal regeneration occurred was a female and measured 8 3-16 inches in length. The animal had been recently taken from the traps and placed in a floating car. It was in normal condition, and its chelæ showed the usual asymmetry, with

a "crusher" on the left and a "nipper" on the right. On July 26, 1905, both chelipeds, together with the second and third right walking legs, were autotomously removed. Soon after the limbs began to regenerate a curious *extra bud* was observed on the regenerating second right walking leg. The data obtained for this abnormal leg is given in the following table:

	Date.	Length of Lobster.	Length of Regenerating Leg.	Remarks.
Mutilation.....	July 26	215 mm.	Original leg was normal and measured 196 mm.
Observations...	Aug. 18	3 mm.
"	" 29	9 mm.	Attention was attracted for the first time to a double bud.* See Fig. 10.
"	Sept. 9	19 mm.
"	" 10	21 mm.	Extra bud became injured.* See Fig. 13.
Moulted.....	" 28	227 mm.	62 mm.

Fortunately, attention was attracted rather early to the extra bud growing out from the regenerating leg. It became possible, therefore, to learn something of the history of this abnormal limb, and also secure several drawings at different stages of its growth. We will describe, first, the development; and, second, the morphological characters of this regenerated leg.

a. Development.

The development of this regenerating leg, by days, was as follows:

Thirty-fifth day. Fig. 10.—It was on the thirty-fourth day after mutilation that the abnormal regeneration was observed. In the drawing made on the following day (Fig. 11) it will be seen that in addition to the usual regenerating structure there is an extra process

*This was, no doubt, caused by the limb accidentally rubbing against some obstacle as the lobster moved about in the car. The injury consisted in brushing the extra bud abruptly upward (Fig. 13) from the original position in which it was growing.

branching off from the third segment or carpopodite (c). This abnormal bud takes its origin from the ventral surface of the carpopodite, but instead of growing upward in a normal direction it makes an abrupt bend and hangs down. At this stage of the regeneration the outlines for all the normal segments except the basal one are all clearly defined, and the groove (g) for the jaws of the claw is well developed. The extra bud at this time also showed two definite segments, 1 and 2, which apparently corresponded, respectively, to the dactyl and propodite of the normal limb.

Forty-third day. Figs. 11 and 12.—At this stage the basal segment or ischiopodite (IS) is now also becoming differentiated. Observing the abnormal bud more closely, a distinct longitudinal cleavage was found in the tip of the propodite segment (2), which divided this segment into two equal parts, I'R' and I'L'. In the extra dactyl there was only a slight indication of a similar bifurcation (g). In size, the propodite of the abnormal bud was somewhat smaller than the corresponding normal segment, the two segments measuring, respectively, $6\frac{1}{2}$ mm. and $7\frac{1}{3}$ mm. The general color of the regenerating limb is now beginning to show a darker hue. In the preceding stage it was characterized by a bright red or pinkish color, but at the present stage dark blue pigments are developing at the joints for the various segments.

Forty-eighth day. Figs. 13 and 14.—On the forty-seventh day of regeneration an accident occurred in which the abnormal bud was mechanically displaced and thrown abruptly upward, so that it assumed a position practically parallel with the distal extremity of the normal limb. This displacement was probably the result of striking against some obstacle as the lobster moved about in the car. A wound or rupture (w) was at the same time produced at the union of the extra bud with the normal limb, which was so severe that I feared the abnormal bud would eventually become completely separated from the limb and lost. But fortunately the wound healed and the abnormal structures survived through the next moult.

On the sixty-fifth day the lobster moulted and the regenerated limb now assumed the proportions shown in figure 15.

b. Morphological Characteristics. Figs. 15-18.

Beginning with the distal extremity of the normal leg, it may be readily seen that the dactyl (D) and propodite (PR) are normal in form, have the usual distribution of hairs and serrated teeth upon the jaws formed by the dactyl and index, and the claw itself opens upward in the normal dorso-ventral plane. The third segment or carpopodite (c) is relatively very broad, and massive, with its distal region split into two unequal forks. The larger of these two forks represents the normal segment, while the smaller abnormal one (c') shunts off from the lower surface (slightly posterior of ventral) of the carpopodite at an angle of about 45 degrees. The last two proximal segments are abnormally thick and massive. One noticeable feature in the meropodite (m) is a variation in the form of the V-shaped groove on the distal ventral surface, into which the third segment plays when in motion. Normally, this groove is single, but in the present specimen there are two grooves, as shown in figure 16, g, g'. One of these grooves (g') is considerably larger than the other, but it is difficult to determine from the external form which one represents the normal structure. The last proximal segment (IS), aside from its relatively great size, shows two unusual markings: the one is a triangular-like scar (s), which may possibly be the result of a previous injury, although I observed nothing of the sort before the moult occurred; the other marking is a slight groove (g'') at right angles to the scar just described. This slight groove on the ischropodite, together with the double groove on the meropodite (Fig. 16, g, g'), indicate that these segments may be morphologically doubled by the proximal extension of the abnormal process on the carpopodite (c).

Turning our attention now to the abnormal branch of the carpopodite, it may be observed that it tapers rapidly distally, to relatively

small dimensions. The irregular form at this region (Fig. 17, a) is partially the effect of the injury received during its development. Just distal to this irregular region is a rudimentary joint? (j). It is indeed rather badly deformed, but it still presents the characteristics of a joint between the carpopodite and the next distal segment. I watched the live lobster to see whether it had any ability to move this abnormal claw. Occasionally there was a display of activity in which the abnormal structure would be carried past the posterior face of the normal propodite, so that its plane of motion would be at an angle of approximately 45 degrees to the corresponding plane of motion for the normal propodite. But it was very rarely that this abnormal process was seen to function in this manner, and, indeed, this might be expected in view of the severe injuries which the musculature at its base sustained during development.

Farther distally, *i. e.*, beyond the joint just described, this abnormal structure enlarges again and finally terminates distally in three large prongs, Figure 17, I'R', I'L', and D'(R+L). Upon closer examination it becomes evident that IR and IL represent two extra indices. They diverge from each other at an angle of about 45 degrees. The dorsal border of each index is dentated with a row of serrated teeth (Fig. 18, T); the tips are capped with the usual horny points; neither prong has any indication of a joint, and their morphological continuity with the propodite is most clearly evinced by a row of hair on the ventral surface of each index (Fig. 17, h, h'): These two rows of hair begin at the distal extremity of each index, continue proximally along the ventral surfaces in two distinct linear series, and extend down almost the entire length of the abnormal propodite.

The third prong D'(R+L) is even more interesting; for while at first glance it may appear single, it is evidently morphologically a double dactyl. It takes its origin from the dorsal surface of the propodite, near the angle at the base of the two indices; and projects upwards at right angles to this pair of indices. Near the base is a constriction (Fig. 18, j) which may be interpreted as a rudimentary joint, although I was unable to observe that it was func-

tional as such. The two lateral surfaces of this compound structure are each dentated by a row of serrated teeth (T, T). These two rows of teeth begin near the rudimentary joint and traverse the opposite lateral surfaces in a distal direction; distally they converge but do not quite meet over the flattened and slightly furrowed tip of the extremity. The tactile hairs are grouped more or less about these dentated margins. The evidence that this abnormal structure represents the double dactyl seems even more conclusive when it is perceived that if we were to split the whole structure in a dorso-ventral plane, each half, with its row of teeth, would form a dactyl for the opposing index.

According to the above interpretation, the abnormal structure on this walking leg is morphologically a double claw, composed of two extra dactyls and a compound index. That this abnormality may extend farther into the proximal segments of the normal limb has already been indicated in the preceding description of certain structural features in the meropodite and ischiopodite. In this walking leg, therefore, we have a clear case of a "triple-claw" which has arisen through a process of regeneration.

2. *Other Experiments and Observations on Abnormalities in Regenerating Limbs.*

Aside from the fact that the triple claw just described has arisen through regenerative processes, I can add nothing further in regard to the factors casually related to its origin. As a preliminary, however, to a further experimental study of this subject, it seems desirable to record here the following observations:

a. An Extra Bud on Regenerating Leg.

The first case is that of a regenerating fourth left leg. On July 27, 1903, in one of my experiments, an 8-inch male lobster was mutilated by cutting off the first pair of swimmerets. At this time the fourth left leg of this lobster was gone, but it soon began to regener-

ate. By the time this regenerating leg had attained a length of 9 mm. (August 28), my attention was attracted to an unusual bud-like process on the regenerating limb. Figure 19, drawn three days later (August 31), shows the location of this abnormal protuberance (b) on the basal segment or ischiopodite. The general appearance of this protuberance suggested that it might be the beginning of another extra limb, similar to specimen No. 7; but this did not prove to be the case, for instead of growing larger, this abnormal bud began to decrease in size, and by September 9 it had almost entirely degenerated and disappeared.

The lobster in which this abnormal phenomenon appeared was an 8-inch male specimen which was being used in an experiment on the regeneration of the abdominal appendages. After the extra bud just described had degenerated, I cut off the regenerating leg just above the basal segment, to see if the degenerating bud might be made to grow again; but no result was obtained, because the entire stump was finally dropped.

b. A Double Regenerating Papilla.

In another lobster two regenerating papillæ (pp. 1, pp 2) were discovered, as shown in figure 20. These two papillæ were in the stump of the second right leg from which the limb had been autotomously removed on July 26. When these two protuberances were first observed (August 18) they were about $2\frac{1}{2}$ mm. in height; the inner one (pp 1) being slightly the larger. At first it was anticipated that these papillæ might develop into two limbs, but this did not occur. The growth of the outer bud became retarded and it increased but little more in size (see Fig. 21), while on the other hand, the inner bud grew at the usual rate and finally differentiated into a normal thoracic leg.

In both the above cases it seems at least a plausible suggestion that some of the regenerating cells may have been temporarily shunted off in an abnormal direction from the direct course of

development, but were later re-absorbed by the predominating normal regenerative processes.

c. Various Methods of Mutilation and Results.

The observations just recorded suggested the possibility of getting similar results by artificial mutilation. In one experiment the tips of regenerating buds were touched with a redhot forceps. I thought it might be possible to destroy certain cells of the regenerating structure and thus produce an abnormality in these parts. Although six or more buds at different stages of development were operated upon, no positive results were attained. The wound would nearly always heal over and the regenerative processes proceed again in a normal manner.

A different method of mutilation was then tried by cutting the regenerating buds at various regions. In about six cases the tips of the buds were slit with a sharp instrument; six more specimens were injured by nipping out small pieces from the fundamentals of various segments; and again, in other instances, the buds were cut off at different levels. These mutilations were made upon buds at all stages of development, ranging from minute papillæ up to stages, in which the segments were clearly evident, but in no instance was an abnormal structure obtained. In all cases the result was either that the whole regenerating bud would be finally dropped at its base, or else the wound would heal and the regeneration continue. An illustration of the latter result is shown in Figure 22. This regenerating bud had been cut near the tip with a pair of fine scissors. The wound healed rapidly, and the direction of growth among the regenerating cells was such that the scar (s) was finally pushed to one side. After the moult only a slight trace of the wound was evident.

In a third experiment, mutilations were made by cutting normal limbs at various levels. In all these mutilations of this character, the limbs were either autotomously dropped after the operation, or else regeneration began at the region of injury. This experiment was

made primarily for the purpose of comparing the power of regeneration at different levels of the appendages, but one of the results was so unusual that it may be fittingly described here. In one of the lobsters the normal second left leg, the propodite had been cut off at a level just above the second distal joint. The structure which regenerated at this cut was the very small claw shown in Figure 23. This rather remarkable structure was very rudimentary and no evidence of its being functional was observed.

With the exception of this last case the artificial mutilations thus far attempted, therefore, have not given any very promising results, but still this is no ground for discontinuing such experiments. They only show that we have not yet discovered just where we may insert an obstacle between the cogwheels, if the figure is permitted, which will cause the growing machine to duplicate its products.

3. *The Regeneration of Two Crusher Claws.*

As far as I am aware the following two specimens are the only authentic cases on record in which a lobster has developed a crushing chela on each side of the body through the process of regeneration. Accordingly, a somewhat detailed description of these specimens will be given.

a. Data.

Specimen No. 8. Figs. 24-31.

This lobster is the same animal which regenerated the triple claw on the walking leg described on page 113. It will be recalled that it had been recently taken from the trap, was a female, and measured 8 3-16 inches in length. On July 26, 1905, both chelæ and the second and third right walking legs were autotomously removed by pinching the tip of the limb with a forceps. On September 28, sixty-four days after the amputation, the lobster moulted and then measured 8½ inches. It had, meantime, regenerated both chelæ, and the second and third right thoracic legs.

The original chelæ of this lobster were of the normal asymmetrical type. The left claw (Fig. 24) was a completely developed "crusher," characterized by the wide massive claws with an almost entire absence of tactile hairs, and by the presence of broad tubercle-like teeth. The right chela (Fig. 25) was of a characteristic "nipping" type, with a relatively slender claw, pointed cutting teeth, and a fringe of tactile hairs along the jaws. The right and left chelæ measured, respectively, 146 and 140 mm. in length.

Soon after the amputation of these limbs another pair of chelæ began to regenerate from the remaining stump or basipodite. On July 18, twenty-three days after the amputation, the regenerating buds measured 5 mm. in length. By the time the segments of the future limbs were well outlined, attention was drawn to the very similar appearance of the two regenerating structures. Usually, as the lobster approaches the culmination of the moulting period, the regenerating chelæ become so clearly differentiated that a distinction between the "crusher" and "nipper" can often be readily detected. In the present case, however, no characteristic differences could be observed between the right and left regenerating buds, and, moreover, the general morphological appearance of each was such that it led to the prediction that both were developing into the crushing type of claws. The correctness of this prediction was shown at the next moult.

After the lobster had moulted, the regenerated chelæ resumed their normal shape and both measured 63 mm. in length. Each cheliped was very similar to the other in form, and displayed the morphological characters of a true "crusher." All the other appendages were in a normal condition except the regenerated second right leg, which had developed the triple claw previously described.

Specimen No. 9. Figs. 32-35.

This specimen was an 8-inch male lobster. On August 4, 1906, both chelæ and the second left leg were autotomously removed. As in the preceding case, the original chelæ were of the normal

asymmetrical type, only in this specimen the right chela (Fig. 33) was the crusher, and the left, the nipper (Fig. 32). They both measured 162 mm. in length.

Soon after the amputation another pair of chelæ began to regenerate. By the time the segments of the future limbs were well outlined, the two regenerating chelæ in this case again looked very much alike. And the fact that their external characteristics also resembled those of a crusher, led me to anticipate that both limbs would develop chelæ of the "crusher" type. By the middle of October, 1906, the lobster had moulted and regenerated both chilipeds and the second left leg. When the chelæ had hardened and assumed their normal shape, they were practically equal in size and each measured 111 mm. in length. Both chelipeds were remarkably similar in structure and each displayed the characters of a true "crusher" claw. The second left leg had also regenerated, but it, as well as all the other appendages, were in a normal condition.

After these lobsters had moulted, the limbs were again removed and an attempt made to keep the lobsters through the winter in order to see what type of chelæ would be reproduced by the next regeneration. Unfortunately, the unnatural conditions under which it was necessary to keep lobsters during the winter resulted in the death of lobster No. 8 on January 6, 1906. But so far we have been more successful with the other specimen, and lobster No. 9 is at the present date (February 1, 1907) still in a healthy condition at the experiment station. It may yet be possible, therefore, to obtain an answer for the question as to what will be the character of the next regenerated chelæ.

b. Morphological Comparison of the Normal and Regenerated Chelæ.

Specimen No. 8. Figs. 24-31.

The morphological comparison of the normal and regenerated chelæ of the lobster may be best presented by making, first, a detailed analysis of some of the characters not clearly shown in the photo-

graphs. For this purpose drawings (Figs. 28-31) have been made of the index or propodite part of each claw to show the characteristic dentition and distribution of tactile hairs.

The original right "nipper" index (Fig. 30) is of a characteristic normal type. Tactile hairs (h) are distributed in a dense fringe on each side of the dentated margin and along the distal outer border of the jaw. The teeth are narrow and pointed. These cutting teeth are arranged in a linear series, and in a periodic sequence with a formula of 1:4:3:4:2:4:3:4 for a perfect period (P).* All the teeth of the propodite are included in the single linear series, except a stout displaced tooth (t) about midway in the dentate margin, which forms the "lock" to the claw (Herrick, '05). Another characteristic feature in the arrangement of the teeth is that at the posterior part of the jaw the single series of teeth are shunted off toward the upper face of the propodite in the direction of the upper or outer side of (γ) the joint (j) formed by the union of the two segments of the claw.

The original left claw (Fig. 29) is a typical normal "crusher." The index or propodite part of the claw, in marked contrast to the morphological characters just described for the "nipper," is characterized by the almost entire absence of tactile hairs, only a few isolated tufts (h') remaining near the angle of the jaw. The "stout displaced tooth" of the nipper is absent. Instead of the pointed cutting teeth, the jaw is dentated with broad "crushing" tubercles (t) formed by the fusion of periodic teeth (according to Herrick, '05). A normal feature in the dentition is the double row of tubercle teeth (t^2) at the posterior part of the index. An equally typical feature is that these two rows of teeth do not shunt off toward one side of the joint, as in the "nipper," but are arranged along either side of the median line of the jaw.

In this lobster the propodite of the *regenerated left claw* (Fig. 28) closely resembled the original "crusher." No tactile hairs are apparent, except a few tufts (h) near the angle of the jaw. The

*According to the scheme of Stahr ('98) and Herrick ('05).

teeth (t) are broad and tubercle-like in form; periodic sequence in arrangement is not evident, and at the posterior part of the jaw the characteristic "double-crushing" teeth have re-appeared.

The *regenerated right claw*, on the other hand, is plainly unlike the original "nipper." If we examine the propodite part of the claw (Fig. 31), it is seen that only a few tufts of tactile hairs (h) have regenerated in place of the prominent fringe on the former claw. The teeth are not like the pointed "cutters," but are of the broad tubercle form; and finally, the wide departure of the regenerated structure from the original "nipping" type, and its identity as a "crusher" is completely established by the presence of the characteristic *double toothed arrangement of the tubercles* (t'^2) at the posterior part of the jaw.

Specimen No. 9. Figs. 32-35.

The description just given for the preceding specimen applies with equal truth to the morphological characters of the chelæ for the second lobster. Only in the later case the positions of the nipper and crusher are just reversed; so that the original crusher claw (Fig. 33) is on the right, and the original nipper (Fig. 32) on the left, side of the body.

The regenerated right claw (Fig. 35) closely resembled the original crusher, while the regenerated left claw (Fig. 34), on the other hand, is plainly unlike the original nipper. In both claws no tactile hairs are apparent on either dactyls or indices, except a few tufts near the angle of the jaws; the teeth are broad and tubercle-like in form; periodic sequence in dentition is not evident; and finally, as in the preceding case, the identity of these two regenerated claws as crushers is completely established by the presence of double-crushing teeth at the posterior dentate margin of each index.

The detailed morphological analysis of the original and regenerated chelæ of both lobsters is more completely compared in the following tabulated data:

(A)=Lobster No. 8. (B)=Lobster No. 9.

	Normal:	Normal:	Regenerated:	Regenerated:
	(A.) Original left claw. Fig. 24. (B.) Original right claw. Fig. 33.	(A.) Original right claw. Fig. 25. (B.) Original left claw. Fig. 32.	(A.) Left claw. Fig. 26. (B.) Right claw. Fig. 35.	(A.) Right claw. Fig. 27. (B.) Left claw. Fig. 34.
General form.	Relatively short and stubby; distinctly bent.	Relatively long and slender; nearly straight.	Relatively short and stubby; distinctly bent.	Relatively short and stubby; distinctly bent.
Dentition.	Broad tubercle-like "crushing" teeth; occasional indications of periodic sequence.	Pointed "cutting" teeth; arranged in periodic sequence with formula 1:4:3:4:2:4:3:4.*	Broad tubercle-like "crushing" teeth; occasional indications of periodic sequence.	Broad tubercle-like "crushing" teeth; occasional indications of periodic sequence.
Tactile hairs.	No tactile hairs, except a few tufts near angle of jaw.	Dense fringe on either side of dentate margin.	No tactile hairs, except a few tufts near angle of jaw.	No tactile hairs, except a few tufts near angle of jaw.
General form.	Broad and massive.	Comparatively slender and tapering toward apex.	Comparatively broad and massive.	Comparatively broad and massive.
Dentition.	Broad tubercle-like "crushing" teeth. Double posteriorly near angle of jaw.	Pointed "cutting" teeth, arranged in a single linear series, with a stout distal placed tooth near the middle of the dentate margin.	Broad tubercle-like "crushing" teeth. Double posteriorly near angle of jaw.	Broad tubercle-like "crushing" teeth. Double posteriorly near angle of jaw.
Tactile hairs.	No tactile hairs, except a few tufts near angle of jaw.	Dense fringe on either side of dentate margin, and along the outer distal border of the under face.	No tactile hairs, except a few tufts near angle of jaw.	No tactile hairs, except a few tufts near angle of jaw.

Dactyl.

Propodite.

Ratio of length of daetylopodite to greatest width of propodite.	(A) $\frac{43 \text{ mm.}}{40 \text{ mm.}} = 1.1$ (B) $\frac{46 \text{ mm.}}{43 \text{ mm.}} = 1.0$ **	(A) $\frac{52 \text{ mm.}}{34 \text{ mm.}} = 1.6$ (B) $\frac{55 \text{ mm.}}{35 \text{ mm.}} = 1.3$	(A) $\frac{31 \text{ mm.}^*}{25 \text{ mm.}} = 1.2$ (B) $\frac{32 \text{ mm.}}{26 \text{ mm.}} = 1.2$	(A) $\frac{29 \text{ mm.}}{25 \text{ mm.}} = 1.2$ (B) $\frac{32 \text{ mm.}}{27 \text{ mm.}} = 1.2$
Ratio of length of daetylopodite to the distance on the propodite from angle of jaw to the 2d joint.	(A) $\frac{43 \text{ mm.}}{38 \text{ mm.}} = 1.1$ (B) $\frac{46 \text{ mm.}}{44 \text{ mm.}} = 1.0$	(A) $\frac{52 \text{ mm.}}{38 \text{ mm.}} = 1.4$ (B) $\frac{55 \text{ mm.}}{42 \text{ mm.}} = 1.3$	(A) $\frac{31 \text{ mm.}}{26 \text{ mm.}} = 1.2$ (B) $\frac{32 \text{ mm.}}{26 \text{ mm.}} = 1.1$	(A) $\frac{29 \text{ mm.}}{26 \text{ mm.}} = 1.1$ (B) $\frac{32 \text{ mm.}}{30 \text{ mm.}} = 1.1$
Dominant characters in each claw	"Crusher."	"Nipper."	"Crusher."	"Crusher."

*Compare schema of Stahr ('98) and Herrick ('05).

†Third spine slightly below the direct line of the others.

‡Posterior spine is double, and the third is below the direct line of the others.

§Posterior spine double; second one is below direct line.

||In specimen B, the tactile hairs have been greatly worn off.

**In specimen B, the measurement for the daetyl was taken from the tip of the index because the tip of the daetyl was gone.

C. Resumé.

a. The normally asymmetrical chelæ of two adult lobsters were autotomously removed. The right claw of lobster No. 8 was a "nipper," and the left a "crusher;" in lobster No. 9, left was the nipper, and the right a crusher.

b. After amputation the chelæ of both lobsters regenerated, but the regenerative processes did not reproduce the original asymmetrical types of chelæ. The regenerated left claw of No. 8 and the regenerated right claw of No. 9 were both true "crushers" like the original claws; but the regenerated right claw of No. 8 and the left of No. 9 had the general characters, not of the original "nipper," but of a typical "crusher."

c. A close analysis of the structural features of the latter two regenerated claws demonstrated that, in *all* their morphological characters, they respectively, corresponded point for point, with both the normal and the regenerated crushers of the opposite sides, in respect to the general form, size, and proportions, in the shape and arrangement of the teeth, and even in the number and distribution of the tufts of tactile hairs.

The regenerated claws of these two lobsters are, therefore, symmetrical in form, and in both specimens they are of the "crushing" type of chelæ.

IV.

DISCUSSION.

1. *Frequency of Occurrence of these Various Types of Abnormalities.*

Specimens Nos. 1 and 2. (Figs. 1 and 2.)

Cases of extra processes arising from the dactyl are the most common of crustacean deformities. For the lobster, Faxon describes at least three cases similar to specimen No. 1, with two extra processes upon the smooth border of the dactyl, (Faxon, Plate I, Figs. 1, 2, and 8). He further states that "there are several speci-

mens similar to this in the collection of the Peabody Academy of Science, Salem, and two or three in the collection of the Boston Society of Natural History" (p. 258). Herrick (Fig. 191) describes another similar instance, and Bateson, in figure 186, No. 1, shows an abnormality almost exactly parallel to our specimen No. 1.

There does not, however, seem to be a record of an extra process on the *toothed* border of the dactyl as in specimen No. 2. The nearest approach to it is that of Faxon (Plate I, Fig. 9), which has a double-toothed process on the toothed border of the index, instead of upon the dactyl.

Specimen No. 3. (Fig. 3.)

There seems to be no authentic record of a lobster claw similar to this one. Faxon does, indeed, cite the case of two chelæ on one of the legs of a lobster (Plate II, Fig. 2), which Bateson was inclined to regard as a case of a chela with an extra pair of dactyls and indices. Faxon states: "This leg is provided with two chelæ. One of them has the ordinary form and structure, but is bent at a strong angle with the long axis of the leg. The second claw appears to have budded off from an amputated surface of the propodite. It consists of two fingers, which have the form of the normal dactylus and index but neither is articulated with the other at the base" (p. 261). Bateson (p. 530) interpreted Faxon's extra "dactylus and index" as a "complementary pair of extra dactyls," and he thought it was possible to bring this abnormal claw into the category of "two extra dactyls and a double extra index" by interpreting a certain protuberance shown in Faxon's figure, as a double extra index. But it seems that Bateson was here lead into an error, as the result of inaccurate drawing; for Andrews ('05), referring to this same specimen, states that he has been informed by Faxon that "the artist unfortunately represented a protuberance which does not exist" (p. 82). Consequently, this case of Faxon's must be excluded from "the category of claws with two extra dactyls and a double extra index."

It should be added, however, that while the present abnormal claw is apparently the first case of this kind recorded for the lobster, a few cases of somewhat similar deformities have been found among other crustacea (see Bateson, 528-530).

Specimen No. 4. (Fig. 4.)

It will be recalled that this specimen was described as a normal claw with two extra indices and an extra double dactyl arising from the normal index. This form of abnormality is very rare. Bateson describes a number of cases among crabs and lobsters in which two extra indices alone arise from the normal index, but there seems to be no record of two extra indices plus a double extra dactyl.

Specimen No. 5. (Fig. 5.)

This is a most remarkable case of the "triplication" of chelæ. Apparently the only recorded specimen which approaches it is the right chela of a lobster described by Faxon (Plate II, Fig. 6). In Faxon's specimen the meropodite divides distally into two parts, each bearing an articulated appendage. One of these two branches is a normal chela, but the morphological character of the abnormal branch remains a question. The carpopodite of this latter structure is not normal in form, "but is slenderer, subcylindrical, and much more spiny." It "bears at its distal extremity an abortive propodus in the shape of a small stump-like segment, bifurcated at the end and armed with a blunt spinous tubercle on its inner margin" (p. 263). Interpretations of this abnormal and rudimentary structure differ; Bateson is inclined to consider it as "morphologically a double structure" (p. 536), and, consequently, that the whole limb may be a triple chela. But Faxon does not regard this extra structure as double, and thinks that in this specimen we have an approach to a duplication, rather than a triplication, of chelæ.

At any rate, in our present specimen there can be no question as to its triple character, at least as far down as the meropodite if not

farther. And this case is evidently the nearest approach to a true triplication of the chela yet discovered in the lobster.

Specimen No. 6. (Figs. 6-9.)

Normally in the adult lobster the "great claws" are almost invariably asymmetrical with reference to each other—the claw on one side being a "crusher" and the other a "nipper." The crusher claw seems to occur about as frequently on one side of the body as the other,* but it is only very rarely that we find an adult lobster with both chelæ alike. In examining over 2,400 lobsters Herrick ('96) found only 3 which had similar claws on each side of the body (p. 143); and in a personal examination of over 600 specimens as they came from the traps at the experiment station, I found only one lobster with both claws alike. This specimen, therefore, makes the fourth lobster out of 3,000 which has been found with both claws alike. It is important, moreover, to note here that these four cases were *all of the "nipper" type of chelæ.*

Specimen No. 7. (Figs. 10-18.)

This case of a triple claw is especially unusual because it occurs upon a walking leg. The fact that such abnormalities are very seldom found on a walking leg has been pointed out by Andrews ('04) in his statement that: "Of the thirty cases of abnormal appendages quoted by Bateson, two are of the antennæ, four are of non-chelate legs, and all the rest of chelæ except one, which is a chelate walking leg and of the eleven additional cases given by Herrick, only two are of the walking legs" (p. 81).

Incomparing the present specimen with other described cases in

*It is an interesting question whether this right and left "handedness" of the lobster is inherited and congenital, or whether it may be determined during development and by other factors. I hope later to give the results of some experiments now almost completed, in which I have tried to throw the crusher to either side of the body by making appropriate mutilations during the larval stages; *i. e.*, at a stage before the claws have differentiated into crusher or nipper. For a further discussion of this subject see an article in *Science* (Emmel, '07), in which it is shown that the results so far attained in these experiments establish a strong presumption that the right or left handed asymmetry of the lobster may be determined by other than hereditary factors.

crustacea, I was unable to find that either Bateson, Faxon, or Herrick record an instance of a double extra claw arising from the third segment or carpopodite. The only case at all similar to it is that of a crayfish, *Astacus fluviatilis*; this most "unique" specimen differed, however, from the present case, in that, instead of *two* there were three extra chelæ which arose from the carpopodite. (See Bateson, No. 827.)

Specimens Nos. 8 and 9. (Fig. 24-35.)

The fact that in the four specimens out of over 3,000 lobsters which were found with similar chelæ (see specimen No. 4) the claws were all of the nipper type emphasizes the point that it is extremely rare to meet with a lobster with two "crusher" claws. Indeed it has been a matter of considerable doubt whether or not a lobster is ever found with a crushing claw on each of the two "great chelæ;" for in the adult lobster the "great" claws are almost invariably asymmetrical with reference to each other—the claw on one side being "nipper" and the other a "crusher." On the other hand, in the young lobster (*i. e.*, in the fourth, fifth, and sixth stages) the two claws are alike and similar to the nipping type; and the fact that in the rare instances in which symmetrical claws have been found in adult lobsters both were always of the "nipping" or embryonic type has created a strong presumption that a "crushing" claw would not be developed on each chela of this crustacean.

Until a year ago the only case recorded of two crusher chelæ on the lobster was in a footnote to Herrick's ('96) description of variations in the form of lobster chelæ: "I have heard of a single case reported by a fisherman, where similiar crushing claws were developed on both sides of the body" (p. 143). To Prziham, writing in 1901, this seemed such an incredible phenomenon that, in view of the theoretical reasons indicated in the preceding paragraph, he concluded that: "Der eine Fall von einer Hautung beiderseitigen" crushing-claw, von dem Herrick nur vom Hörensagen durch Fischer

Kenntni's erheilt, wird wohl in der Reich der Fischermythen zu verweisen sein" (p. 333).*

Apparently it was not until the year 1906 that any authentic account was given of a lobster with two crushing chelæ. During this year two such lobsters were recorded; one of these was specimen No. 8 of the present article, which was obtained in 1905 (see Emmel, '06); the other was reported for a European lobster by Dr. W. T. Colman, in the Proceedings of the Zoölogical Society of London for 1906. On page 633 of that journal is "exhibited the photograph of a lobster (*Homarus grammarus*, Linn.) with symmetrically developed chelæ [*i. e.*, two crushers], recently presented to the Natural History Museum by the Directors of Harrod's Stores, Ltd." (p. 634). Finally, lobster No. 9 of this report adds a third specimen to the list. We have now on record, therefore, at least three authentic cases of lobsters with similar crushing claws.

2. *The Theoretical Significance of these Abnormal Structures.*

A. *Limbs with Paired Extra Processes.*

1. *Bateson's Principles for Secondary Symmetry.*

Bateson, in his masterly work on variation, has been able to formulate certain relations or principles to which a great majority of variations seem to conform. These relations are all the more striking because they enable one even to predict with a considerable degree of accuracy what certain characteristics of a given abnormality will be! A brief statement of certain of these principles which refer especially to crustacea seems necessary here before discussing the theoretical aspect of the present cases.

There are at least three possible categories for crustacean limbs

*I must hasten to add here, however, that this opinion of Przibram's in regard to the mythological character of Herrick's lobster does not represent his later conclusion. In a previous article I (Emmel, '06) unfortunately overlooked Przibram's latest conclusion on this matter in his recent work on "Die Heterochelie bei decapoden Crustaceen," 1905. And, in a recent letter, he has kindly called my attention to the fact that in this monograph he has withdrawn his earlier opinion as to the mythological character of said lobster. I therefore gladly take this first opportunity to correct my previous oversight.

with abnormal extra processes. The first of these categories would include all those cases in which two limbs or parts of limbs are identical copies of the normal appendage for which they stand, and consequently belong to the same side of the body, or, in Bateson's terminology, are in "succession." The second category would include all cases in which two limbs or parts of limbs are mirror images of each other; *i. e.*, they represent a complementary pair of right and left appendages.

In regard to the first category, no authentic case is known which conforms to it. In every case so far recorded "no right arm is ever succeeded on the same side of the body by another arm properly formed as right and no crustacean has two right legs in succession, where one should be" (Bateson, 529). Bateson records nine cases of crustacean limbs apparently double in the sense of the second category; and Zeleny ('05) has carefully described the "regeneration of a double chela in the fiddler crab." But Bateson hesitates to admit the existence of such double structures, and that there should be such a thing as a double limb (in the sense of this second category) "has always," he remarks, "seemed to me most strange;" he thinks it possible rather that one of the members of such a pair may generally be regarded as itself really double. Bateson, therefore, was able to exclude nearly all cases of so-called double limbs from these two categories, and established the important point that the great majority of abnormal crustacean limbs—including most cases of apparent double appendages—can be brought under a *third* category of variations; a category, namely, in which the extra limb or extra parts of a limb are themselves morphologically double.

In the course of the following discussion it will become evident that all of the cases of extra processes described in this paper may be brought under this third category.

A closer study of this class of abnormal structures brings us to a discussion of certain characteristic principles. It has been discovered that there is a remarkable degree of regularity in the morphological and spatial relations, not only between the two members of

the extra pair of limbs, but also between this pair and the normal appendage. Bateson has formulated these relations under certain principles of secondary symmetry, which he expressed in the following two rules:

I. "The long axis of the normal appendage and of the two extra appendages are in one plane; of the two extra appendages one is, therefore, nearer to the axis of the normal appendage, and the other is remoter from it."

II. "The nearer of the two extra appendages is in structure and position formed as the image of the normal appendage in a plane mirror placed between the normal appendage and the nearer one, at right angles to the plane of the three axes; and the remoter appendage is the image of the nearer in a plane mirror similarly placed between the two extra appendages."

"Transverse sections of the three appendages taken at homologous points are thus images of each other in parallel mirrors" (p. 479).

In the lobster, therefore, according to these rules, in any case of two extra legs or claws, these two *extra* parts will be a complementary pair, one member of which will belong to the right and the other to the left side of the body. Furthermore, the member of the pair which is nearest the normal limb will always be the one corresponding to the other side of the body.

Let us now see how the specimens with extra processes described in the present paper will conform to these principles. With regard to the universal character of these rules, Bateson observes that "It would not be true to assert that these rules are followed with mathematical precision, but in the main they hold good" (p. 482). And it is remarkable to what extent these rules hold for the present specimens; for it will be seen that the characteristic relations which might have been predicted on the basis of Bateson's principles are actually found in almost every case.

For our present purpose these specimens arrange themselves conveniently under two groups:

- a. Extra process repeating but one segment, *i. e.*, the distal segment or dactyl.
- b. Extra processes repeating more than one segment.

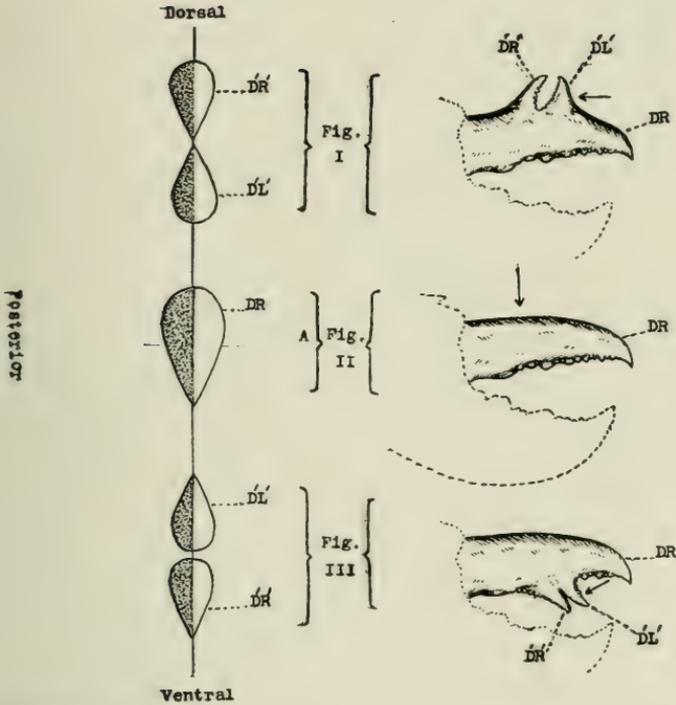
2. *Extra Processes Repeating but One Segment, i. e., the Distal Segment or Dactyl.*

Specimens Nos. 1 and 2.

Bateson's rules for secondary symmetry will apply to extra processes arising from any morphological surface of the normal limb; *i. e.*, arising from the morphologically ventral, dorsal, anterior, and posterior surfaces, or from an intermediate position. Accordingly, given the morphological surface origin of the extra processes, we can state theoretically what the spatial relations will be. Now for specimens Nos. 1 and 2, the abnormal structures in the former arises from the smooth or morphologically *dorsal* surface of the dactyl, and in the latter the origin is from the toothed or *ventral* border of the same segment. The following diagram has been drawn to show what the relations for these two positions should theoretically be for the right dactyl of a lobster claw.

In the figure at the left of this diagram, Fig. I represents a cross section of a dactyl taken through the dorso-ventral plane. Figs. II and III each represent cross sections for a pair of extra processes arising, respectively, from the dorsal and ventral surfaces of a normal dactyl; the section in each case is in the dorso-ventral plane and through points homologous to those of the normal section in Fig. I. In each of these sections the pointed portion represents the toothed or ventral border, and opposite oval portion represent the dorsal or smooth border of the dactyl; the light and shaded areas, respectively, indicate the anterior and posterior sides of the segment. It will be observed that these sections have been placed in the relations demanded by Bateson's rules; for in each pair of extra parts (Figs. II and III) "the nearer of the two extra appendages" (D'L') is the mirror image of the normal appendage (DR), and "the remoter

Diagram A.



DR.—Normal right dactyl.

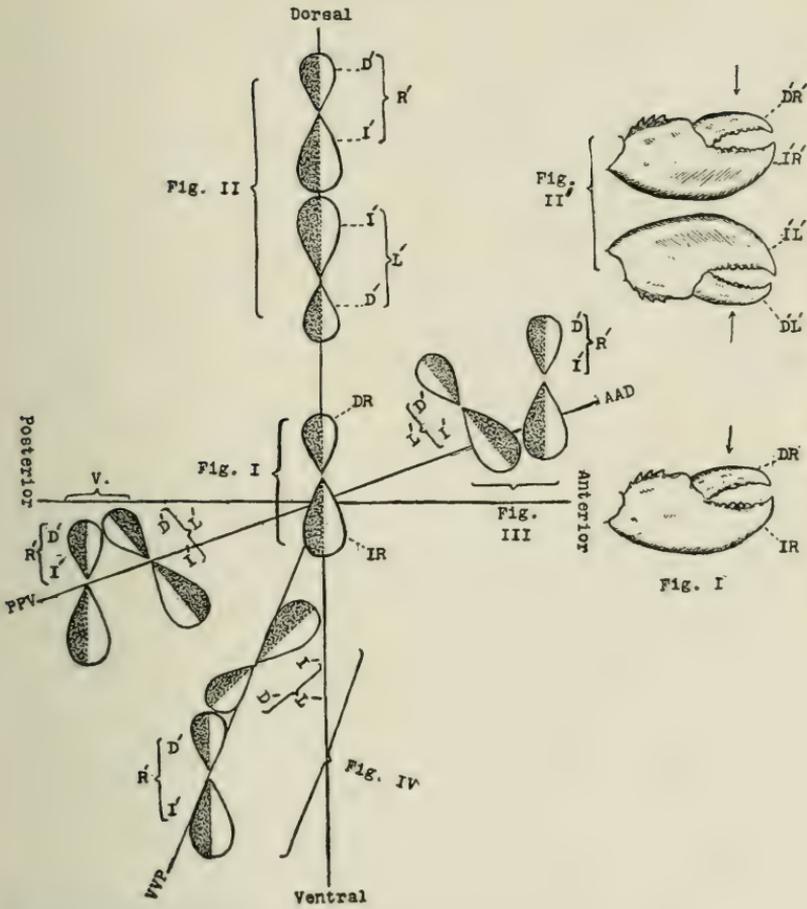
D'R'.—Extra right dactyl.

D'L'.—Extra left dactyl.

A.—Anterior.

The arrow (→) indicates the plane of section shown in the corresponding figure at the left in the diagram.

Diagram B.



DR.—Normal right dactyl.

IR.—Normal left index.

D'R' and D'L', respectively, represent the extra right and left dactyls.

I'R' and I'L', respectively, represent the extra right and left indices.

The arrow (→) indicates the plane of section shown in the corresponding figure at the left in the diagram.

appendage" (D'R') is the mirror "image of the nearer" one (D'L').

The claws sketched at the right of the diagram may make clearer the significance of these relations. The arrow in each figure indicates the plane of section shown in the corresponding figures at the left.

One of the important points in this diagram is that a definite morphological relation distinguishes the dorsal (Fig. II) and ventral positions (Fig. III) from each other. Namely, that when a pair of extra processes arise on the dorsal or smooth border of the dactyl, they turn their *toothed* or ventral borders toward each other (Fig. II); but on the other hand, when the abnormal processes occur on the ventral or toothed surface of the dactyl, they turn their *smooth* borders toward each other (Fig. III).

We may now compare our actual specimens with the theoretical relations just described. In specimen No. 1 the abnormal pair of process arise from the dorsal surface, and consequently their relations should correspond to those given for the dorsal position in the diagram. A glance at the specimen quickly shows that such is actually the case; the toothed borders oppose each other; the two extra processes are mirror images of each other, and the one nearer the normal dactyl is also the mirror image of this segment; and, finally, it is readily seen that the process nearer the normal segment may be interpreted as an extra left dactyl (D'L') and the other process as an extra right dactyl (D'R'), and consequently that these two abnormal structures evidently morphologically represent an extra and complementary pair of dactyls. In specimen No. 2 the abnormal part arises on the toothed border of the dactyl, and the relations should correspond to those shown for the ventral position in Fig. II of the diagram. In this case the abnormal part is not spatially separated into two distinct processes, nor is there even a slight bifurcation at the tip to indicate that it is a double structure. On the other hand, however, this abnormal process is itself symmetrical in form, and, accepting Bateson's interpretation that "whenever an extra part is itself symmetrical it always may be a double structure," we may

regard this process as consisting of two fused extra dactyls. Interpreted in this way, it will be seen that we might split this abnormal part in such a way that we would have two extra processes which could be shown to conform to all the criteria in regard to mirror images, relation of the toothed borders, etc., as in the preceding case.

Specimens 1 and 2 may, therefore, be regarded as conforming with Bateson's principles for secondary symmetry. And, indeed, the above somewhat elaborate demonstration of this fact would hardly be necessary were it not that it finds its justification as an introduction to the following more complicated cases.

3. *Extra Processes Repeating more than One Segment.*

This group includes specimens Nos. 3, 4, 5, and 7. The extra segments for each of these four segments arise from the following morphological surfaces of the appendage; No. 3, from the dorsal surface; No. 4, somewhat ventral to the posterior surface; No. 5 slightly dorsal from the direct anterior face: and, finally, in specimen No. 7, the abnormal structure arises slightly posterior from the ventral surface. The comparison of the actual spatial relations among the elements of these abnormal limbs, with the relations theoretically demanded by Bateson's principles, will be facilitated by the following diagram. (Diagram B.)

The figures I-V in this diagram represent cross sections of the normal and extra claws taken through homologous points on the dactyls and indices. In each case the smaller section represents the dactyl, and the larger one, the index. As in the preceding diagram, the pointed portion of each cross section indicates the toothed margins of each jaw, and the light and dark areas, respectively, indicate the anterior and posterior surfaces. Fig. I shows a section through the normal dactyl and index of the right chela; the sections in figures II-V represent the extra pair of claws for the specimens about to be described, and show the theoretical relations of these claws corresponding to the surface origin given for each specimen.

Figures I' and II' at the right, represent, respectively, a normal claw and a pair of extra claws for the purpose of illustrating the significance of the relations shown in Figs. I and II. The extra pair of claws (Fig. II') arise from the dorsal surface of the appendage, and the arrow in each case indicates the plane of section shown in the corresponding diagrams. By means of this illustration the relations indicated by the cross sections in the remaining figures may be readily perceived.

Specimen No. 3. (Dorsal origin of abnormal structure. See Diagram, Fig. II.)

A glance at the drawing for this specimen is sufficient to show that the two extra dactyls and the double extra index conform almost exactly with the theoretical relations for the dorsal position; the three pairs of claws lie in the same plane; the extra dactyls and double index are minor images of each other, and the extra dactyl nearer the normal dactyl is also a minor image of the latter. While comparing this specimen with the diagram it will be kept in mind, of course, that the present specimen is a *left* chela.

Specimen No. 4. (See diagram, Fig. V, position PPV.)

In this specimen the abnormal parts arise from a position slightly ventral of the posterior surface. Here again the actual relations between the normal and abnormal claws correspond to the theoretical schema. The morphologically anterior surfaces are in opposition; but they are inclined at such an angle that the toothed margins are turned toward each other, while the ventral or smooth borders of each claw are thrown apart. It may also be observed that here, again, the extra index nearer the normal index is a mirror image of the latter and belongs to the right or opposite side of the body.

Specimen No. 5. (Origin slightly dorsal of the anterior surface. See diagram, Fig. III, position AAD.)

This specimen presents certain peculiar exceptions to Bateson's

principles, but we will first observe the points in which there is agreement. The pair of extra chelæ are mirror images of each other, and the chela nearest the normal claw is also the mirror image of the latter and belongs to the opposite side of the body, *i. e.*, it is a left chela.

So far the relations seem to conform to the principles of secondary symmetry, but a closer examination reveals a wide variation. The extra pair of chela arise somewhat dorsally of the morphologically anterior surface, and this places in it the position AAD of our diagram. Theoretically, therefore, the extra claws should have their posterior faces opposing each other (the dark sides in the diagrammatic sections); the claws should be inclined at such an angle to each other that the indices should be brought toward each other and the dactyls thrown apart; and, furthermore, the anterior faces of the normal claw and of the member of the extra pair lying nearest it, should also be in opposition (see diagram). But upon examining the actual specimen, we find these relation to be just the reverse from the theoretical requirements; for instead of the posterior it is the *anterior* faces of the extra pair which are opposed; in place of the indices, it is the *dactyls* which are thrown toward each other; and, finally, it is the *posterior*, and not the anterior faces of the normal claw and the nearer abnormal chela, which are in opposition.

At first I was at a loss as to how to account for this apparent contradiction. But finally the idea suggested itself that this whole difficulty could be explained by taking into account the process of "torsion" which takes place during the development of the "great chelæ" of the lobster. It is a well-known fact that, both in the ontogeny (Herrick, '05) and in the regeneration (Emmel '06) of the chelipeds, "The terminal segments gradually rotate over and inward," so that a torsion of about 90 degrees is produced and the claw now opens inward on the naturally characteristic horizontal plane" (Emmel, '06, p. 613). This means, therefore, that in our present specimen the upper surface of the normal claw as shown in the drawing should be its morphologically posterior surface, and such is actually the case. But now, curiously enough, it seems that each

member of the pair of extra claws have in turn also *rotated another 90 degrees* during this development; and each of the extra claws has thus come to assume a position practically at right angles to the normal chela. In a word, we have the remarkable conditions here that, while the normal has rotated in the usual manner through an angle of 90 degrees, each of the extra chelæ, or the other hand, has gone through a torsion of 180 degrees.

Now if we were to turn these three chela backwards again to the position they originally held at the beginning of developmental torsion, it is surprising how closely their relations will then in every respect conform to our principles for secondary symmetry; for, if in the case of the two extra chela, both claws are rotated 180 degrees on their long axis, the claw nearer the normal chela being turned contra-clockwise and the other claw clock-wise, it will be seen that their *anterior* faces will then be opposed, and the *indices* in place of the dactyls will be thrown toward each other. Finally, if in a similar manner we rotate the normal chela clock-wise 90 degrees, it is evident that instead of the posterior, the morphologically *anterior* faces of the normal and the nearer extra claws will now be in opposition. By thus taking into account the developmental history of the lobster cheliped, it seems clear, therefore, that the morphological relations between the members of this triple chela do not fundamentally contradict, but rather furnish a remarkable confirmation of the principles of secondary symmetry as formulated by Bateson.

This factor of "torsion" does not seem to have been considered in previous discussions of crustacean deformities, but it may possibly serve to clear up other exceptional cases. A case in point is the right cheliped of a lobster described by Faxon (Plate II, Fig. 6) and Bateson (No. 826). With reference to this specimen Faxon states that, "curiously, the supernumerary carpus is set upon the meros in a position almost the reverse of that of the normal carpus. . . . It is as if the normal carpus were rotated upon the meros nearly 180 degrees to the left. . . . This distortion seems to me very singular, and I think nothing like it has been observed among

insects" (p. 263). Bateson placed this specimen under his list of "exceptional cases" and offers no explanation for the unusual conditions pointed out by Faxon. It seems clear, however, that the relations which Faxon regarded as very singular in this case may be adequately accounted for as the result of the torsion of the normal and abnormal chelæ during their development.*

Specimen No. 7. (See diagram, Fig. IV, position VVP.)

In this specimen the extra parts appear to arise slightly posterior to the ventral surface of the leg. It will be seen in the diagram for this position that the two extra claws should be inclined to each other at an obtuse angle of at least 150 degrees. But in specimen No. 7 there is a great variation from this; for instead of 150 degrees, the two extra claws are inclined to each other at an angle of not more than 45 degrees,—a relation which corresponds to a more posterior point of origin (see diagram, Fig. V, position PPV). Furthermore, the relation between the minor images also correspond to a point of surface origin farther posterior than is apparently actually the case. While this specimen, therefore, seems to furnish a variation from the above principles, it should, however, be taken into consideration that a severe injury was sustained by these extra claws during their regeneration and that, consequently, this variation in relations may be largely due to an interrupted development in which the two claws were inhibited from diverging in their angular relations as widely as they might otherwise have done.

On the whole, then, we may conclude the discussion of these six cases of abnormal appendages with the observation that with a few minor exceptions these six specimens conform to a remarkable degree with what might have been theoretically predicted, and that they

*Since writing the above paragraph I have re-examined Bateson's work and find that he has suggested explaining certain irregularities among vertebrate limbs in something of a similar manner. He observes that in the case of double limbs among vertebrates, "there is generally a relation of images between the extra pair," but "a definite geometrical relation between them and the normal limb is seen more rarely." And he suggests "that this may be in part at least attributed to the normal twisting of the vertebrate limb, especially of the hind limb, from its original position" (p. 556).

consequently furnish an additional confirmation of the principles of secondary symmetry as formulated by Bateson.

B. Symmetrical Chelæ.

Specimens Nos. 6, 8, and 9.

It seems difficult at present to bring the regeneration of two "crusher" claws in the lobster under any definite principles of regulation or developmental mechanics.

The phenomenon of two similar "nipper" chelæ, indeed, does not seem so remarkable, especially when we take into account the larval development. The adult lobster normally has two distinct types of claws; the more primitive toothed or "nipping" claw, and the larger and phylogenetically younger (according to Stahr, '98, and Przibram, '01) "crushing" claw. But in the larval stages, on the contrary, both are similar and of the nipper type. At about the sixth stage (Hadley, '05) one of these claws begins to differentiate into a "crusher." During ensuing moults this claw passes through transitional stages and is finally completely transformed into a crusher claw. It seems very plausible, therefore, that the presence of two similar "nipping" chelæ in an adult lobster, as in specimen No. 6, may be accounted for as due to a retarded differentiation during normal development.

Furthermore, the writer has found in several experiments that when the crushing claw has been autotomously removed, the regenerated "crusher" is not always distinguishable as such, but may rather present characteristics intermediate or transitional between the more primitive nipping and the more highly developed crushing type (Emmel, '06). If the crusher claw is phylogenetically the younger type, this might, perhaps, be expected, for then this variation in the regenerating structure may be regarded as a reversion to the phylogenetically older or nipping type of claw. We may thus, in another way, again account for a lobster with two "similar nipping" chela.

But the regeneration of two *crusher* claws can not be brought into either of these two categories; for, of course, they can not be explained as due to a "retarded differentiation," nor does it appear that they may be regarded as a "reversion to a phylogenetically later type." It is apparently impossible to interpret such a regeneration as a case of "compensatory regulation" in Zeleny's ('05) sense, for the regenerated chelæ are almost identically similar both in size and form. Nor is it clear that they can be brought under the category of "revisal" phenomena, if by this term we imply a reversed order of asymmetry. At present, therefore, this phenomenon must rather be described merely as the *substitution* by regeneration of a "crushing" claw in place of an original "nipping" claw.

I have no suggestion to offer in explanation of these two cases of the regeneration of similar crusher chelæ. Evidently the regenerative cells in the stump remaining after autotomy may have the potentiality of either a "crushing" or "nipping" claw. But what factors determined that a claw of the crusher type be produced is another question. Wilson's ('03) suggestion for *Alpheus*, "that the initial factor (Auslösung) that sets in motion the complex process of differentiation of which either side is capable is primarily only a difference in the amount of material on the two sides" (p. 210), can hardly apply here, for the chelæ were both removed autotomously and at the same time, consequently there seems no reason to believe that the "amount of material" was unequal on the two sides. As far as the present data goes, the regeneration of similar "crushing" claws still remains unexplained.

3. *Regarding the Origin of Abnormal Appendages.*

a. *Discussion of Theories with Special Reference to the Regeneration Theory.*

Three possible theories have been proposed for the origin of abnormal chelæ among crustacea:

1. That they are congenital or inherited.

2. That they are caused by injuries sustained after moulting.
3. That they are regenerative products.

But there is considerable divergence of opinion regarding the relative importance of these different theories.

Faxon, in discussing his case of "duplicate" chela in *Homarus*, which resembles somewhat specimen No. 5, of our list, remarks that "whether this monstrosity be congenital, or the result of injuries received later in life, I can not tell" (p. 263); although later, when referring to this same case he adds, that "it is very probable that we are dealing with a monstrosity which is not the result of injury" (p. 267). Again, in regard to another case, a double index and two dactyls (Plate I, Fig. 13), he thinks that "one can easily believe that this is a congenital monstrosity" (p. 260). A fair interpretation of Faxon's conclusions seems to be that he is inclined to consider all cases of duplicate or triple chelæ as congenital in their origin, while he considers that simpler deformities, as, for example, specimens 1 and 2 of our list, "are more naturally explained as malformations arising from injuries received after moulting" (p. 260).

Bateson evidently gives least importance to the second and third theories, for, in regard to this question, he says: "A good many authors from the time of Rösel von Rosenhof onward, have said that these cases are a result of injury, or of regeneration after injury. For this belief I know no ground. It should be remembered as an additional difficulty in the way of this belief, that when the limb of a crab or lobster is injured it is usually thrown off bodily, while the extra parts most often spring from the periphery of the chela" (p. 526).

Andrews, in discussing his case of "an aberrant limb in a crayfish," states that "The appearance of the limb suggests a new growth following some injury in which the material for claw making was partly severed and displaced." As to when this injury may have occurred, he merely suggests that it "might happen, we can suppose, not only in the egg and in the young, but in the adult, especially at the periods of shedding when the interior of the claw is soft and the blood

peculiar;" or, again, that probably "such a monstrosity as this might arise in regeneration following an injury to the propodite" (p. 83).

Herriek, ('95) on the one hand, is inclined to favor the regeneration theory for these deformities. Although he points out that "repetition of parts, however, occurs in many insects and vertebrates where no such regeneration of lost appendages is known," he finally concludes that "while it would appear that the various deformities which have been described can not be explained as the result of injuries and the attempted regeneration of injured parts, . . . yet I can not escape the conviction that the problem is in some way directly concerned with that of regeneration" (p. 148).

But in regard to lobsters with similar chelæ, Herriek evidently favors the congenital theory; for in his discussion of symmetrical chelæ, he states "That there seems to be about as much variation as regards the details here mentioned in normal symmetrical claws as in the abnormal symmetrical ones, and it is probable that in either case the conditions met with are to some extent congenital" (p. 144). Quite recently Dr. Calman's ('06) case of a lobster with two crusher claws has been interpreted as further discrediting the regeneration theory for symmetrical chelæ, as may be seen in the following statement: "It has been supposed that this might be due to regeneration after injury, since it is known that in *Brachyura*, on the removal of the crushing claw, a cutting claw is regenerated. Przibram,* however, failed to obtain such "heteromorphic" regeneration in the lobster, and the present specimen throws still further doubt on the regeneration theory, since it possesses well-developed and quite typical crushing chelæ on both sides of the body" (p. 634).

In this brief review of theories for abnormal chelæ, it appears that the majority of the above investigators have emphasized the origin of such abnormalities through congenital sources, and injuries after moulting; while others have discussed the possibility of their being regeneration products. But it is important to note that in no case

*'02, p. 12, and '05, p. 191.

have any of these writers furnished positive experimental evidence for their conclusions. I have been unable to find in their descriptions any proof that double limbs or symmetrical crusher chela have ever arisen in a congenital manner. While the theory of injuries after moulting seems very plausible, proof still remains to be produced. Apparently the first case of double claws of which the origin and history is positively known is the specimen recently described by Zeleny ('05); who, in one of his experiments, obtained the regeneration of a double chela in the fiddler crab. It is evident, then, that before we can hope to clear up this question, we need more accurate data on the formation of these abnormal structures.

Specimens Nos. 7, 8, 9, may be something of a contribution toward this required data. Attention has been called to the fact that *all these cases are regeneration products*. In these specimens we have at least two authentic cases of the regeneration of similar crushing chelæ, and one case of the regeneration of a triple claw of the type which both Faxon and Bateson were strongly inclined to be only congenital in origin. These three cases, together with Zeleny's, serve, therefore, *to establish the process of regeneration as a factor in the origin of abnormalities in crustacean limbs*.

b. Further Considerations Favoring the Regeneration Theory.

1. *That the Abnormal Crustacean Limbs Found so far have been only on Adult Animals.*

If double or triple claws are congenital in their origin, we might expect to occasionally meet such abnormalities in very young lobsters. The lobster hatchery at the experiment station of the Rhode Island Commission of Inland Fisheries furnishes an excellent opportunity for such observations. But among the hundreds of thousands of lobsters reared yearly from the egg, no case of chela repetition has yet been reported; and I have also personally examined with care something over 2,000 fourth and fifth-stage lobsters without observing a single case of duplication of parts in the chelipeds.

I have also casually examined many thousands of young "fry" as they were being individually counted and taken from the hatching pools during the hatching season, but I did not find a lobster with double limbs.

2. *That the Great Majority of these Deformities are also Found only on the More Distal Segments of the Limbs.*

In some sixty-five cases of abnormal chelæ recorded by Bateson, all but *three* of these deformed parts are found on the two distal segments of the appendage. It will be recalled that Bateson considered one difficulty in the regeneration theory to consist in the fact "that when the limb of a crab or lobster is injured it is usually thrown off bodily;" although it should be observed that he hastened to add that "since, according to Heinekin, such mutilated parts are sometimes retained, this must not be insisted upon" (p. 526). Now it is quite true that when the limb is injured the whole appendage may be autotomously thrown off, but this requires an important qualification; for whether the limb is always thrown off or not depends upon the character and location of injury. In some experiments on regeneration ('05) I had occasion to mutilate the limbs of lobsters at different levels of the appendages. In the course of these mutilations I found that if the cheliped or leg was crushed by a pair of tweezers the whole limb was almost invariably autotomously dropped, practically regardless of the region of injury. But by the exercise of considerable care it was discovered that if the tip of the limb was cut off with a quick, sharp stroke, the remainder of the appendage was usually retained. On the contrary, however, if the cut was made near the base of the appendages, say in the region of the ischiopodite and meropodite, the remaining stumps were usually dropped. Furthermore, I have since found that the same conditions also hold true for regenerating buds; if the buds are injured near the tip the remaining structure is much less likely to be dropped than if the injuries are made in the proximal regions. In view of the fact, therefore, that in proximal

wounds the whole limb is usually autotomised, while in distal injuries the limbs are quite frequently retained and the lost parts restored by regeneration,—it follows that if abnormal structures do arise as the result of the injury of normal and regenerating buds, it would be most natural to expect that such abnormal structures would be most frequently found on the distal segments. In our examination of Faxon's and Bateson's lists, we have found that this is exactly the case.

Taking into account, then, these relations between the nature of the injury, autotomy, and regeneration, it appears, therefore, that the fact that the great majority of crustacean deformities occur on the distal segments of the limb readily lends itself to the interpretation that they are the result of regenerative processes.

3. *The Regeneration of Extra Legs Following an Artificial Splitting of Nerves.*

3. A third point of importance is the effect of injuries which involve a division of the nerve. Miss Reed ('04) in her study of regeneration mentions certain results which she obtained in the hermit crab by splitting the stump of the leg lengthwise after autotomy had taken place. "In several cases after splitting the stump, two extra legs appeared in a short while. Sections through this region show that the nerve is split, one branch going to each leg. It is probable that a new leg was developed at each end of the split nerve, since in all other cases where only one leg regenerated the nerve shows no sign of any injury. In this case it is probable that the nerve was not cut" (p. 315). Unfortunately, Miss Reed has not described these regenerated extra legs, but this result is certainly very suggestive; it not only furnishes further evidence for the origin of extra structures through regenerative processes, but also indicates an important method for future experiments. In view of these results one is also tempted to ask whether the rare case of triple legs recorded by Bateson for the European lobster (No. 808) may not

have arisen through an accidental fracture of the nerve stump and a consequent triple regeneration.

In the conclusion of this study of abnormal structures, therefore, we may say that sufficient evidence has now been adduced to prove that both abnormal symmetrical and duplicated appendages among crustacea do arise through the process of regeneration. And the experimental results so far attained indicate that we may yet be able to control the formation of these abnormalities by proper mutilation, and thus open up for experimental study an important field of organic variation.

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REFERENCE LETTERS FOR PLATES I—IX.

- a, a'. Injured regions.
- BS. Sixth limb segment or basipodite.
- C. Third segment or carpopodite.
- C'(R+L). Double extra carpopodite.
- D. First segment or dactyl.
- D'L. Extra left dactyl.
- D'R. Extra right dactyl.
- D'(R+L). Abnormal processes interpreted as being morphologically double extra dactyls.
- g. Groove.
- h. Tactile hairs.
- I. Jaw part of second segment or index.
- IS. Fifth segment or ischiopodite.
- I'R'. Extra right index.
- I'L'. Extra left index.
- I'(R+L). Abnormal process interpreted as being morphologically double extra indices.
- j. Joint.
- L'. Extra left chela.
- M. Fourth segment or meropodite.
- M'. Extra meropodite.
- P. Group of teeth in periodic sequence.
- pp. Papilla.
- Pr. Second segment or propodite.
- P'R'. Extra right propodite.
- P'L'. Extra left propodite.
- R'. Extra right chela.
- S. Scar.
- t. Teeth.
- t". Characteristic double teeth on crusher claw.
- v. Ventral surface.
1. 2. The two parts of the extra bud shown in Figs. 10-14.

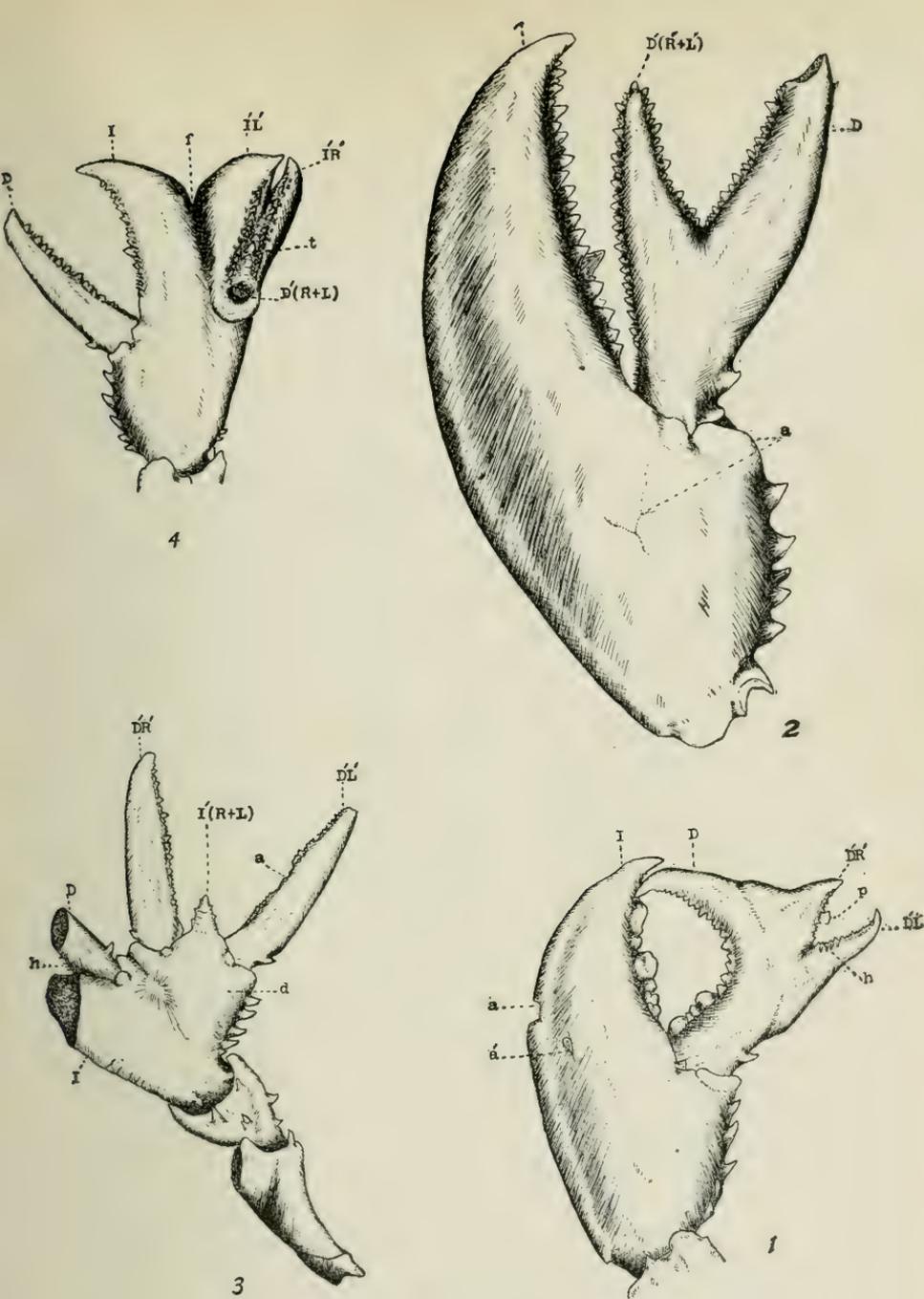


PLATE I.

Fig. 1 (Page 103).—Crusher claw of left chela with two extra processes (D'R', D'L') on the outer or smooth border of the normal dactyl. ($\frac{1}{2}$ x natural size.)

Fig. 2 (Page 104).—Nipper claw of left chela with an extra process D'(R'+L') on the inner or toothed border of dactyl. ($\frac{2}{3}$ x.)

Fig. 3 (Page 105).—Left chela with two extra dactyls (D'R', D'L'), and an extra double index, I'(R+L). ($\frac{2}{3}$ x.)

Fig. 4 (Page 107).—Nipper claw on right chela with two extra indices (I'L', I'R') and the stump of a double extra dactyl (?), D'(R+L). ($\frac{1}{2}$ x.)

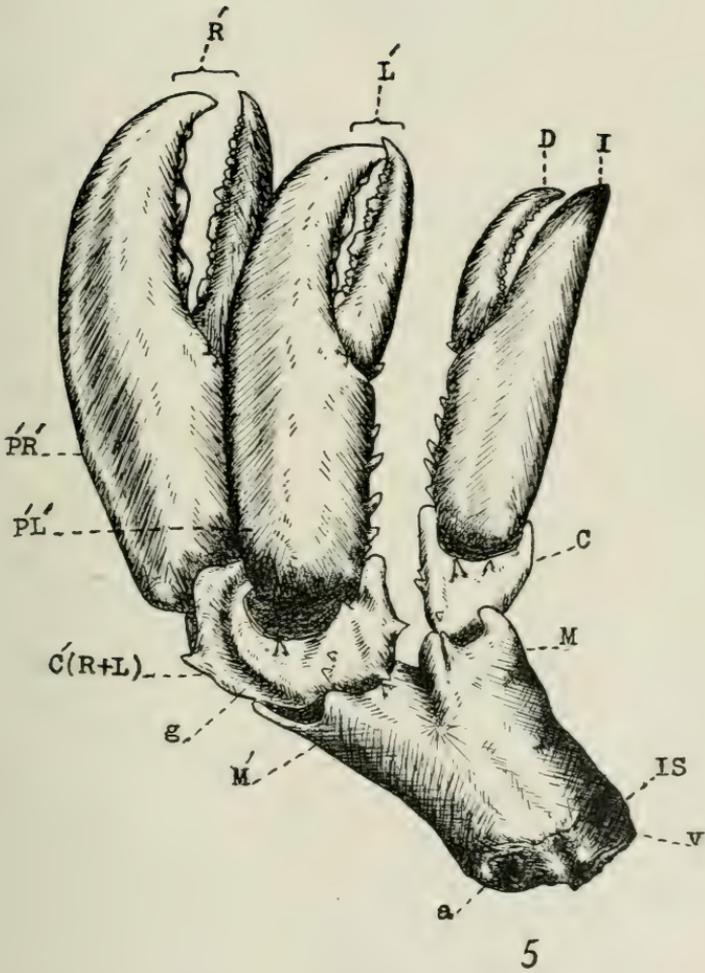


PLATE II.

Fig. 5 (Page 108).—Abnormal right chela consisting of the approximately normal claw (D; I) plus the two extra claws R' and L'. This appears to be one of the most perfect cases of triple claws so far recorded for the lobster. (Natural size.)

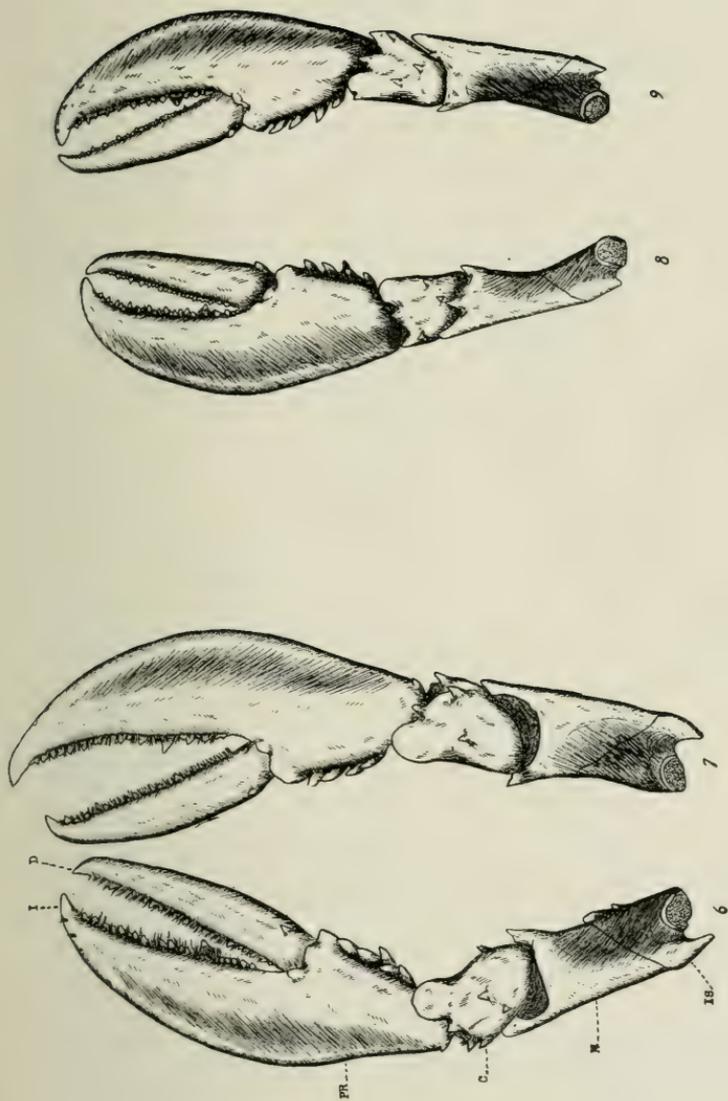


PLATE III.

Figs. 6 and 7 (Page 112).—Abnormally symmetrical chelae of the nipper type. Figures 6 and 7 respectively, represent the left and right limbs. ($\frac{1}{2}$ x.)

Figs. 8 and 9.—Chelae which regenerated after the amputation of the original symmetrical limbs shown in Figures 6 and 7. The regenerative processes have reproduced the previous abnormal symmetry. ($\frac{1}{2}$ x.)

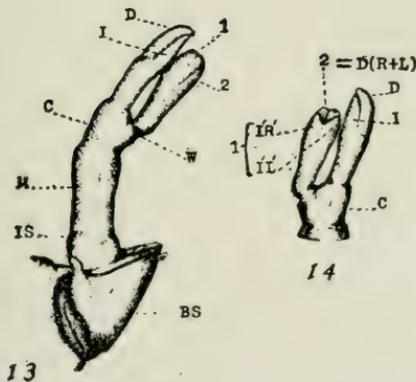
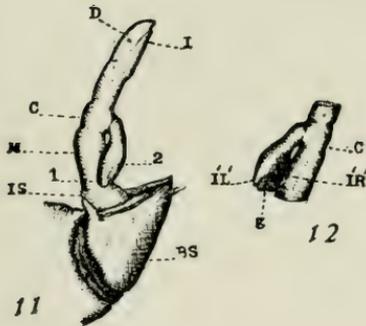
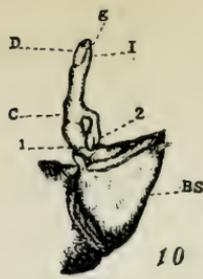


PLATE IV.

Figs. 10-15 (Page 113).—Successive stages in the regeneration of a double extra claw on a second right walking leg. ($1\frac{1}{2} \times$.)

Fig. 10.—Thirty-fifth day after the amputation of the original leg, showing the development of an extra bud (1, 2). (Posterior view.)

Fig. 11.—Forty-third day of regeneration. (Posterior view.)

Fig. 12.—Anterior view of the extra bud.

Fig. 13.—Forty-eighth day. Extra bud had been accidentally injured and pushed upward. (Posterior view.)

Fig. 14.—Anterior view of the extra bud.

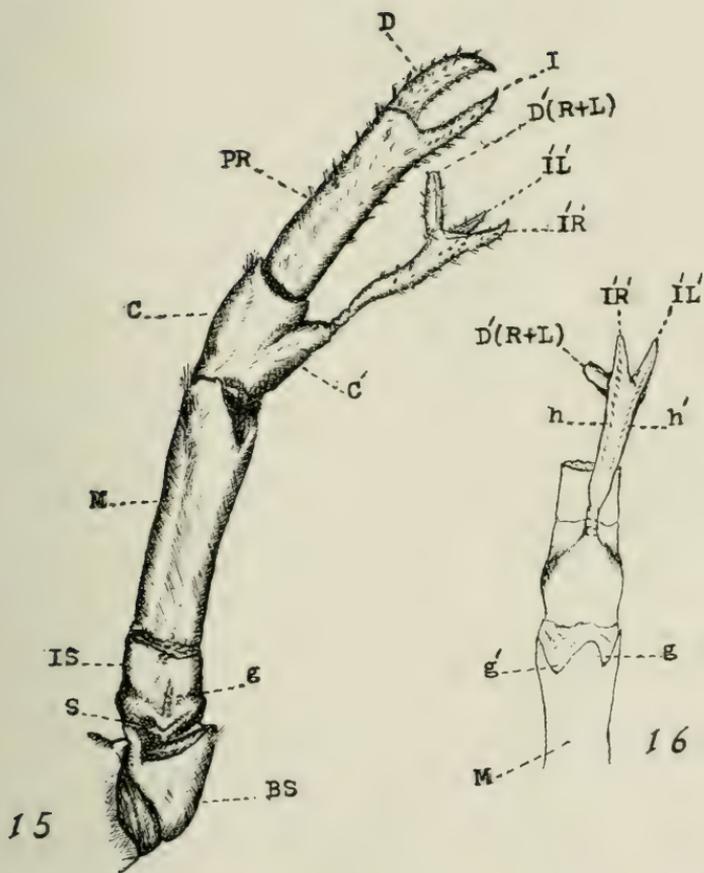


PLATE V.

Fig. 15 (Page 116).—Regenerated right walking leg with a pair of extra claws D'(R+L), IL', and IR'. Drawn just after the moult. See earlier stages shown in Figures 10–14. (Posterior view. $1\frac{1}{2}$ x.)

Fig. 16.—Sketch of ventral view of the extra claws to show the two indices, IR' and IL'. ($1\frac{1}{2}$ x.)

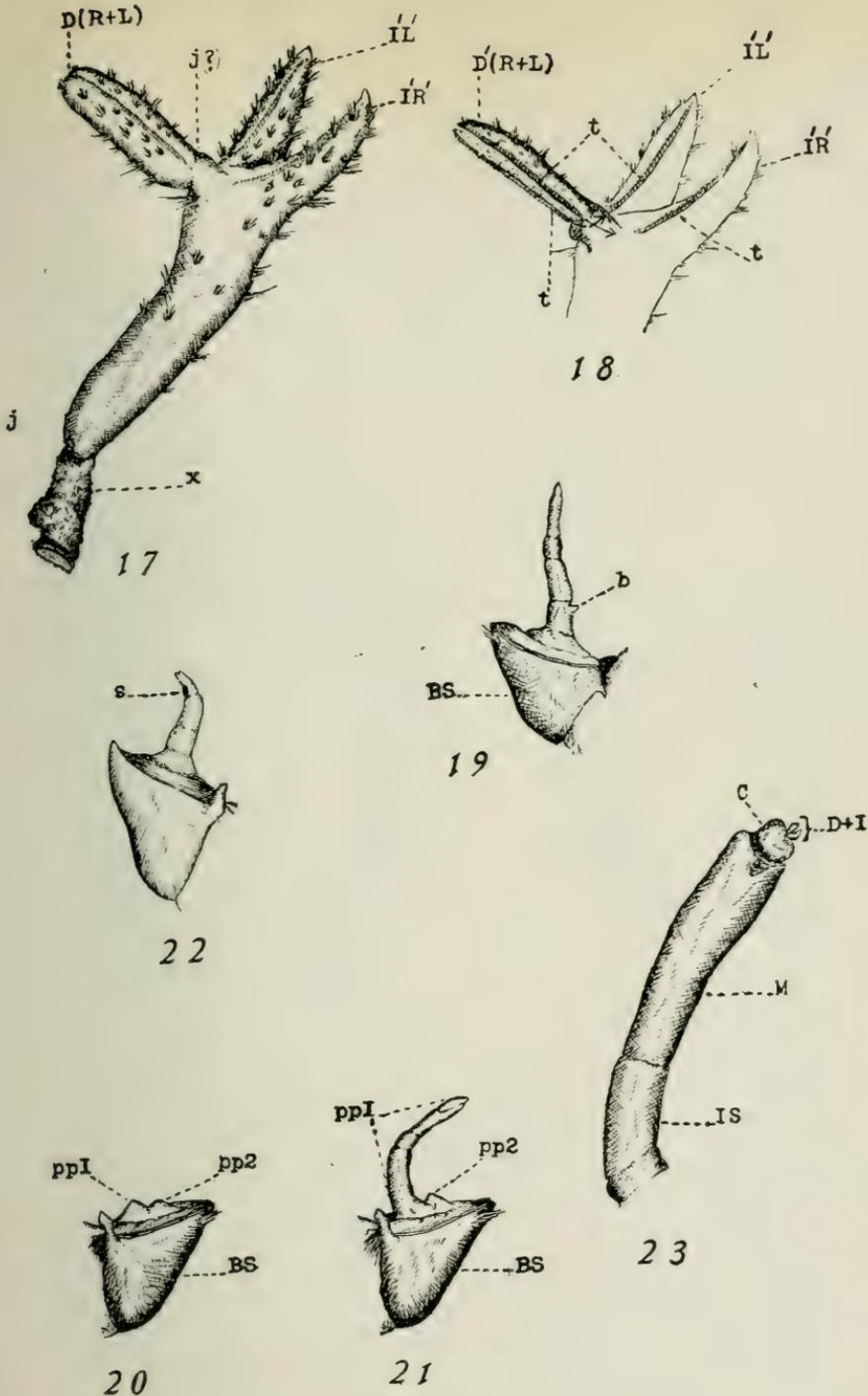


PLATE VI.

Figs. 17 and 18 (Page 116). Drawings to indicate the structure and relations in the extra claws shown in Figure 15. (Posterior view. 4 x.)

Fig. 19 (Page 118).—Regenerating fourth left leg with an abnormal bud (b). (4 x.)

Figs. 20, 21 (Page 119).—Two regenerating papillae, (pp. 1 pp 2) on a second right leg. (Posterior view. 2 x.)

Fig. 22 (Page 120).—Regenerating bud of a walking leg. The tip had been cut off at the region indicated by the scar (s), but had grown out again. (2 x.)

Fig. 23 (Page 121).—An unusual rudimentary claw (D+I) which regenerated on the tip of a leg which had been cut off just above the second distal joint. (1½ x.)



PLATE VII

Figs. 24-27 (Page 121).—Figs. 24 and 25 are photographs of the original normal chelæ of an 8-inch female lobster, showing the usual asymmetry of claws with a nipper on the right (Fig. 25) and a crusher on the left (Fig. 24). (About $\frac{1}{2}$ natural size.)

Figs. 26 and 27.—Photographs of the left and right chelæ, respectively, which regenerated after the amputation of the original limbs. In this case two crushers, in place of the former nipper and crusher, have regenerated. (About $\frac{1}{2}$ natural size.)

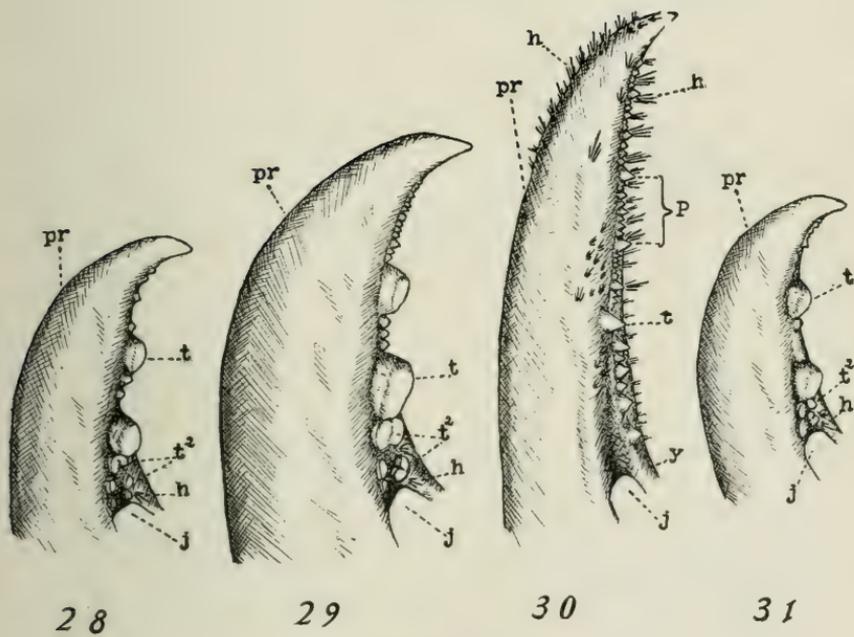


PLATE VIII.

Figs. 28-31 (Page 121).—4-3 natural size. Figs. 29 and 30 show the index or propodite part of the original claws represented in Plate VII, Figs. 24 and 25. Fig. 29, index of normal left crusher. (Drawn from the upper face.) Fig. 30, index of normal right nipper. (Drawn from the lower face.)

Figs. 28 and 31 represent the index of the regenerated claws shown in Plate VII, Figs. 26 and 27. Fig. 28, index of regenerated left crusher. (Drawn from upper face.) Fig. 31 index of regenerated right claw. (Drawn from lower face.)

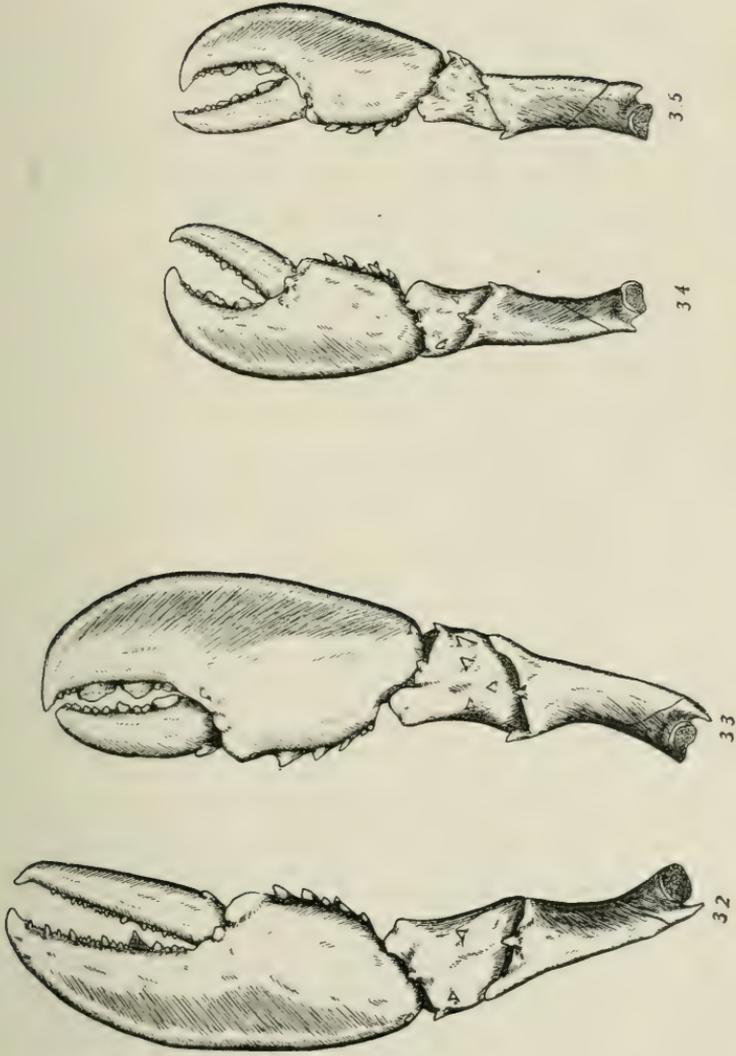


PLATE IX.

Figs. 32-35 (Page 125).—(3 x.) Figs. 32 and 33 show the original normal chelae of an 8-inch male lobster; the left is a crusher (Fig. 32) and the right a nipper (Fig. 33). Figs. 34 and 35.—The left and right chelae, respectively, which regenerated after the amputation of the original limbs. The regenerative processes have produced two crushers in place of the normal nipper and crusher.

THE STOMACH OF THE LOBSTER AND THE
FOOD OF LARVAL LOBSTERS.

BY LEONARD W. WILLIAMS.

Thirty-seventh Annual Report of the Commissioners of Inland Fisheries
of Rhode Island. 1907. Special Paper No. 32.

THE STOMACH OF THE LOBSTER AND THE FOOD OF LARVAL LOBSTERS.

DR. LEONARD W. WILLIAMS,
HARVARD MEDICAL SCHOOL.

1907

SPECIAL PAPER No. 32

REPRINTED FROM THE THIRTY-SEVENTH ANNUAL REPORT OF THE COMMISSIONERS
OF INLAND FISHERIES OF RHODE ISLAND.

THE STOMACH OF THE LOBSTER AND THE FOOD OF LARVAL LOBSTERS.

LEONARD W. WILLIAMS, PH. D.

The external anatomy of the bizarre and attractive larval lobsters has been studied, described, and figured with great care, but the internal anatomy of these forms has received scant attention, and for this reason we hope that the work recorded here will be of interest.

The Commission of Inland Fisheries of Rhode Island is studying the various problems, anatomical, biological, and physiological, concerning the natural history of the lobster in connection with its experimental and economic work of hatching and rearing lobsters at the Wickford station. As a part of this work, we were asked to investigate the food of the larval lobsters in the hatching and rearing bags of the station. While examining the alimentary canal of many lobsters we discovered the metamorphosis of the stomach which we here figure and describe. This work naturally demanded an understanding of the adult stomach, and, not finding satisfactory descriptions of the structure and functions of the adult stomach, we were compelled to extend our work to include the anatomy of the stomach of lobsters of all ages.

We are indebted to the Commissioners of Inland Fisheries, especially to Dr. A. D. Mead, for the opportunity to do this work, and to Mr. V. E. Emmel and to Mr. P. B. Hadley for the use of serial sections of young lobsters prepared by them.

THE STOMACH OF THE ADULT LOBSTER.

The Mouth.

The mouth of the lobster lies on the lower surface of the head between the mandibles which, when closed, hide the mouth opening. Just in front of the mandibles there is a large median fleshy lobe, the labrum, or upper lip, which forms the anterior margin of the mouth opening. When the mouth is closed, the hinder surface of the labrum projects backward as a median vertical ridge which is prolonged upward through the œsophagus and which makes the mouth V-shaped. The sides of the mouth are formed by a pair of rounded ridges which become higher and converge posteriorly where each ridge expands into a flat boot-shaped plate which is fringed with bristles. These two lobes form the metastoma, or lower lip, which projects downward in the narrow cleft between the mandibles and the first maxillæ. The dilation of the mouth is affected by the pulling forward of the posterior ridge of the labrum so that the opening becomes approximately circular.

The Œsophagus.

The œsophagus is a short vertical canal which passes upward from the mouth between the circumœsophageal connectives and enters the lower side of the stomach. The empty œsophagus is externally cylindrical, except that it is somewhat flattened laterally. The ridge which is a vertical prolongation of the labrum projects backward into the lumen of the œsophagus and makes it trough-shaped (V-shaped) in cross section.

This ridge is everted forward during dilation of the œsophagus, and so serves to increase largely the size of the œsophagus.

The Stomach.

The stomach, in all stages, is divided by an oblique constriction into a capacious anterior storage chamber, the cardiac portion of

the stomach or cardiac sac, and a small posterior straining and sorting chamber, the pyloric portion of the stomach or pyloric sac. Corresponding to the external constriction, internally there is a grinding apparatus which, in the adult form of the stomach, consists of a median tooth and a pair of lateral teeth.

The wall of the stomach is formed of four layers of tissue:

1. An outer layer of connective tissue. This sheet stretches over the irregularities of the stomach and gives the whole exterior a somewhat rounded form. In places this outer layer of the stomach is covered by the vascular epithelium (Plate VI, Fig. 9).

2. A layer of loose connective tissue. This tissue fills up the irregular cavities between the inner and outer contours of the stomach wall and contains the blood vessels and intrinsic muscles of the stomach.

3. The gastric epithelium. This varies in thickness and, correspondingly, in the shape of the cells according to the thickness of the chitinous stomach lining.

4. The chitinous lining of the stomach. This is generally covered with setæ of various kinds and in places it is thickened. A deposition of lime in these thickened areas converts them into "the ossicles" which form the skeleton of the gastric mill.

The Gastric Ossicles and Muscles.

In the American lobster the gastric ossicles are essentially like those of the European lobster (*Homarus vulgaris*) and the crayfish (*Astacus fluviatilis*), which have been adequately described by Milne Edwards, Oesterlen, Huxley, and T. J. Parker, hence we will omit an extended description of them. We will give generally two names for each ossicle, the shorter names used by Huxley and Parker, and the longer but more descriptive names of Albert. Beginning at the anterior end of the dorsal surface:

1. The cardiac ossicle or anterior dorsal cardiac plate. This covers nearly the whole of the dorsal surface of the cardiac sac. In

our specimens it is divided by a transverse joint into two plates. The anterior plate is calcified only at the postero-ventral angles. The anterior gastric muscles (Plate I, Fig. 1), a pair of heavy flattened muscles, arise from the procephalic processes (which are reniform plates attached to the septa between the eyes and the rostrum) and are inserted upon the anterior end of the anterior portion of the dorsal cardiac plate.

2. The urocardiac ossicle or posterior dorsal cardiac plate. This is narrower than the cardiac ossicle and inclines downward and backward so as to form part of the posterior wall of the cardiac sac.

3. The prepyloric ossicle or median tooth. This forms the antero-dorsal wall of the pyloric sac.

4. The pyloric ossicle or anterior dorsal pyloric plate. This plate is covered by the insertion of the posterior gastric muscles which arise from the carapace just in front of the cervical groove and from the internal ridge corresponding to the groove.

On the upper part of the side of the stomach there are:

5. The pterocardiac ossicle or anterior dorso-lateral plate.

6. The zygo-cardiac ossicle or middle dorso-lateral cardiac plate or lateral tooth. This is an irregular parallelogramic vertical plate whose upper anterior angle is bent outward and downward to articulate with the lower end of the pterocardiac ossicle and whose upper posterior angle is turned inward nearly to the pyloric ossicle. The inner surface of the lower edge of this plate is heavy and irregular and forms the grinding surface of the lateral tooth.

7. The anterior dorso-lateral pyloric plate. This is a triangular plate interposed between the lateral tooth and the pyloric plate. The postero-lateral gastric muscle arises from an area of the carapace bounded behind by the cervical groove, below by the branchio-cardiac groove, and above by the posterior gastric muscle and, passing inward, forward, and downward, is inserted upon the anterior dorso-lateral pyloric plate. The division between the posterior and postero-lateral gastric muscles and between the pyloric and anterior dorso-lateral pyloric plates seems to be lacking in other forms or to

have been overlooked by everyone except Albert and is, in our opinion, of great importance (see page 158). The cardio-pyloric muscle, a small band, extends from the upper end of the anterior dorso-lateral pyloric plate and the adjacent upper edge of the lateral tooth forward above the outer end of the cardiac ossicle to the upper part of the anterior edge of the ptero-cardiac ossicle.

The plates, teeth, and muscles described above form the essential parts of the gastric mill, which consists of two portions, the median and the lateral, which are so closely connected that their actions are absolutely coördinated.

The median portion of the gastric mill includes the four median plates mentioned above and the anterior and posterior gastric muscles. The two horizontal plates, the cardiac and pyloric, are connected by the urocardiac plate and the median tooth, the former being attached to the latter at the junction of its lower and middle thirds. The contraction of the anterior and posterior gastric muscles draws apart the cardiac and pyloric plates and as these plates separate the urocardiac ossicle pulls the lower end of the median tooth forward, the former acting as the power applied to the latter as a lever of the third order at a point about two-thirds of the length of the lever from the fulcrum, *i. e.*, the articulation of the median tooth with the pyloric plate. Thus the median tooth is drawn forward with great force.

The lateral portion of the gastric mill consists of:

The pterocardiac bar which is hinged on the outer end of the cardiac plate so as to make a right angle with that plate and so that its lower end moves from the position of rest inward and backward in a vertical plane inclined forward at an angle of 75 or 80 degrees with the sagittal axis; the lateral tooth whose anterior upper angle is attached to the pterocardiac bar and so moves inward and backward with that point and whose posterior upper angle is fixed to the outer anterior angle of the pyloric plate; and the anterior dorso-lateral pyloric plate which receives the insertion of the postero-lateral gastric muscle and which is attached to the posterior edge of the lateral tooth. The

posterior intermediate cardiac bar is attached to the lower side of the lateral tooth at a point about one-third of its length from the anterior end.

The separation of the cardiac and pyloric plates necessitates a downward, inward, and upward swing of the anterior upper angle of the lateral tooth which carries the anterior end of the grinding surface of that tooth toward the median line. At the same time the contraction of the postero-lateral gastric muscles pulls the posterior end of the lateral tooth outward and upward, and the tooth, rotating on the line between its articulations with the upper end of the anterior dorso-lateral pyloric plate and with the posterior intermediate cardiac plate, drives its anterior cusps inward with considerable force. When the gastric muscles relax the elasticity of the structures, coupled with the pull of the cardio-pyloric muscles, draws the median tooth backward and the lateral teeth outward.

Returning to the enumeration of the ossicles of the stomach we find on its sides the following:

8. The gastrolithic bar. This is a sigmoid bar whose upturned posterior end articulates with the pterocardiac ossicle, the anterior end of the lateral tooth, and the bar to be described next. Its anterior end follows for a short distance the upper edge of the gastrolithic plate, which is a triangularly ovate epithelial plate that during the latter part of the period between molts secretes a thick plate of lime, the gastrolith (see page 172).

9. The accessory lateral cardiac ossicle or upper intermediate cardiac bar extends with a gentle curve backward and then downward from between the preceding bar and the pterocardiac bar to:

10. The infero-lateral tooth, which is an irregular plate with three acute cusps upon its anterior edge.

11. The lower intermediate cardiac bar. This extends backward from the preceding tooth to:

12. The upper ventro-lateral cardiac bar, which passes forward along the ventral side of the cardiac sac to the œsophagus where it bears upon its upper side:

13. The antero-lateral cardiac bar. This bar extends obliquely upward and forward almost to the antero-ventral angle of the gastrolith.

The posterior lateral dilator muscle arises from the postero-lateral angle of the mandibular sternum, extends upward, inward, and backward to its insertion upon the antero-lateral cardiac bar.

14. Immediately below the upper ventro-lateral cardiac bar lies the lower ventro-lateral cardiac bar, which has much the same shape as that bar but extends farther backward. The posterior ends of these two bars are hinged upon one another so that they open and shut like a pair of pincers.

15. The ventral cardiac plate. This is a small oval median plate lying between the posterior ends of the lower ventro-lateral cardiac bars.

16. The posterior intermediate cardiac bar passes obliquely upward and forward from the posterior end of the lower ventro-lateral cardiac bar to the lateral tooth.

The lower lateral cardiac constrictor muscle extends upward and forward from the entire upper edge of the lower ventro-lateral cardiac bar to a slight thickening of the stomach wall which lies midway between the gastrolith and the lower ventro-lateral cardiac bar. The contraction of this muscle draws together the two edges of a fold of the stomach wall and thus causes the fold to project farther into the lumen of stomach.

The ventral cardiac constrictor extends between the right and left lower ventro-lateral cardiac bars.

The cardiac sac is irregularly ovate. Its greatest width lies between the pterocardiac ossicles and its smaller end opens into the pyloric sac. Its dorsal surface follows the curvature of the adjacent carapace and its anterior surface is uniformly convex when distended. The somewhat flattened sides of the sac converge below so that its ventral surface is reduced to a narrow band between the ventro-lateral cardiac bars and a larger area in front of the oesophagus.

As the stomach becomes empty its anterior wall is drawn inward in the form of a pair of large upper folds and a pair of smaller lower folds. At the same time the portions of the side wall of the sac above and below the gastrolith push, respectively, inward and downward, and upward and inward over the inner surface of the gastrolith.

The dorsal dilator muscle arises from the dorsal surface of the carapace, and, as it passes downward and backward, its fibres diverge and are inserted upon the upper part of the anterior wall of the stomach.

The anterior dilator muscle is a moderately strong round muscle, which arises from the outer surface of the socket of the eye, passes backward and slightly downward to the outer surface of the lower fold of the anterior wall of the stomach. The anterior lateral dilator muscle arises with the posterior lateral dilator from the mandibular sternum and is inserted upon the lower part of the anterior wall of the stomach.

The upper lateral cardiac constrictor muscle is a fan-shaped muscle which extends from its broad origin on the upper edge of the lateral tooth to the posterior end of the lower ventro-lateral cardiac bar. The middle lateral cardiac constrictor muscle arises from the upper end of the upper intermediate cardiac bar, and, extending downward and backward, is inserted in front of the preceding muscle.

Removing the muscles and the loose tissue of the second layer of the stomach wall, we expose the following invaginations of the two inner layers of the stomach wall which correspond to internal projections. A deep broad dorsal pit which extends downward between the median tooth and the urocardiac bar to the cavity of the tooth. On each side of the median tooth there is an oval elevation, the posterior dorsal pad, which projects inward into the space between the median and lateral teeth and the outer wall of the stomach, and which is densely covered with downwardly directed bristles. Just in front of this pad is a small cusp which forms the postero-lateral angle of the urocardiac plate. This cusp is connected with its mate by a strong transverse ridge on the upper side of the plate. These cusps form a kind of flange on each side of the median tooth which

prevents it from going too far down between the lateral teeth. A little in front and outside of this cusp there is another elevation, the anterior dorsal pad, which is covered with downwardly directed bristles. A deep longitudinal groove extends backward from the lower side of the gastrolith into the lateral tooth. Just below the anterior end of the lateral tooth a deep tubular invagination, whose walls form the upper lateral pad, extends upward in front of the tooth. Behind the infero-lateral tooth, below the lateral tooth, and below and behind the preceding pit, is a larger, but shallower, pit, the middle lateral pad.

The œsophageal opening is guarded by a median and a pair of lateral valves. The median valve is formed by a triangular broadening of the upper end of the vertical ridge of the œsophagus. The lateral walls of the œsophagus are prolonged upward into a ridge-like valve which nearly encircles the œsophageal opening and which is higher on each side than behind the opening. The three valves are covered with a thick pile of long slender bristles which point towards the stomach.

The anterior constrictor muscle arises from the middle of the mandibular sternum and, passing backward and slightly upward, is inserted upon the upper edge of the median œsophageal valve. Its contraction pulls down the anterior wall of the stomach and causes it to fold inward.

The anterior wall of the stomach is covered with a similar coat of bristles which are inclined in various directions in such a manner that when the anterior folds are pushed inward the bristles point toward the gastric mill. The upper wall of the stomach is smooth, as also is the inner face of the gastrolith.

Upon the inside of the stomach we find the anterior two thirds of the upper part of the side occupied by the smooth surface of the gastrolith and the posterior one-third by the upper and middle lateral pads. The lower part of the side is formed by a large lateral plate which is bounded below by the upper ventro-lateral cardiac bar, above by the lower intermediate cardiac bar, the infero-lateral tooth,

and the gastrolith, and in front by the anterior lateral bar. The lower edge of this plate forms a large fold, the lower lateral pad, which overlaps the ventral surface of the stomach so as to enclose on each side a deep groove which extends the whole length of the ventro-lateral cardiac bar, *i. e.*, from the œsophagus to the pyloric sac.

The ventral surface of the sac is raised into a low narrow median ridge which ends abruptly above the ventral cardiac plate in a rounded point. Near the middle of this ridge, there begins on each side a ridge which quickly becomes higher posteriorly and, meeting its mate, the two spread out in a broad deeply channeled elevation, the cardio-pyloric valve, which has, in addition to its bilobed channeled anterior portion, a median posterior lobe. Its anterior surface is covered with a close pile of short, strong, upwardly and backwardly directed bristles, and the posterior lobe is armed with long upwardly directed bristles. The posterior portion of the lower edge of the lower lateral pad and the posterior edge of the middle lateral pad overlap the edges of the cardio-pyloric valve.

Each of the two grooves between the ventral and lateral walls of the cardiac sac is divided by a row of long, large, close-set, backwardly inclined bristles into two canals; an upper and outer, the upper cardiac canal, and a lower and inner, the lower cardiac canal. The bristles of the ventral ridge and of the lower lateral pad interlock so as to enclose both of these canals and the bristles separating them interlock with the bristles of the lower lateral pad, so that material can enter the upper cardiac canal only by passing through the lower canal and between the bristles which separate the canals. The outer and upper wall of the upper canal is smooth, while the lower and inner wall of the lower canal is closely beset with very short, heavy, upwardly-pointed bristles. The lower cardiac canal opens posteriorly into the groove upon the anterior surface of the cardio-pyloric valve, while the upper cardiac canal passes beside the valve and opens into the lower canal of the pyloric sac.

The Pyloric Sac.

The pyloric sac is irregularly ovate and is considerably flattened laterally. Its cavity is a narrow vertical slit which is partially divided by ridges and pads into an upper and lower chamber and an upper, a middle, and two lower canals.

The opening from the pyloric sac into the intestine is guarded by four valves: The dorsal pyloric valve or "funnel"* is a pen-point shaped plate which reaches far into the intestine and partly separates the intestinal cæcum from the remainder of the intestinal cavity. The right and left lateral pyloric valves are triangular plates fringed with bristles and attached to the sides of the gastro-intestinal opening. They enclose a narrow passage which leads upward into the concavity of the dorsal valve. The ventral pyloric valve is a broad triangular horizontal plate which is separated from each lateral valve by a deep sinus and whose upper surface is covered with bristles. The wall of the intestine is attached to the bases of the dorsal and lateral valves, to the edge of the sinus between the lateral and ventral valves, and to the edges of the ventral valve. The intestinal cæcum is a broad pear-shaped evagination of the intestinal wall. It extends upward and forward over the posterior part of the dorsal wall of the stomach. The tubular duct of each half of the liver or digestive gland, an immense compound tubular gland, opens into the intestine between the ventral and the corresponding lateral pyloric valve. Jordan has shown that the finely comminuted food from the lower canal of the pyloric sac passes into the liver and is there digested and absorbed.

The dorsal surface of the pyloric sac is directed upward and backward, and is divided into two convexities and one concavity. The anterior convexity is formed by the pyloric and the anterior dorso-lateral pyloric plates, and it forms the roof of the upper pyloric

*That the funnel is not an essential structure is shown by the fact that a perfectly well, actively feeding lobster examined by us had lost the funnel. It probably acts as a valve to prevent the return of material to the stomach as is shown by the fact that it is sometimes found drawn down across the mouth of the middle canal.

chamber which extends forward to the median tooth and downward to the level of the lateral tooth, where two longitudinally oval pads, the upper and lower pyloric pads, projecting from each side and covered with forwardly directed bristles, separate the upper pyloric chamber from the lower. The posterior convexity of the dorsal wall of the pyloric sac is formed by the middle dorsal pyloric plate (17), whose upper end and lateral edges are more heavily calcified than the remainder of the plate.

The superior dilator arises from the carapace in front of the cervical groove and, passing downward and forward, is inserted upon the middle dorsal pyloric plate.

18. The posterior dorsal pyloric plate is a small, scarcely calcified, dorsally concave, oval plate which supports the dorsal pyloric valve and which is covered with numerous backwardly directed bristles. The concavity of the dorsal wall is formed by this plate and is filled by the intestinal cæcum.

An inwardly projecting ridge which is supported by the corresponding edge of the middle dorsal pyloric plate, and which is covered anteriorly with long thick-set bristles directed forward and upward, separates the lower pyloric chamber from the upper canal. This canal extends the whole length of the middle dorsal pyloric plate and divides posteriorly, passing around the posterior dorsal pyloric plate in a pair of lateral canals which are formed by the wall of the pyloric sac adjacent to that plate and which open upward into the intestinal cæcum.

19. The upper intermediate pyloric bar passes forward horizontally from the upper end of the middle dorsal pyloric plate across the side of the pyloric sac. It supports the upper edge of the outwardly convex wall of the lower pyloric chamber.

20. The posterior intermediate plate is irregularly triangular and is concave inwardly. Its broad base supports the lateral pyloric valve. Its antero-dorsal edge supports the ridge that forms the lower side of the middle chamber. This ridge is heavily beset with bristles which seem to radiate upward, inward, and downward from

the center of the ridge: those which are directed inward are curved downward at the tip as though bent down by the force of the food current. The wall of the lower chamber bears a few slender forwardly directed bristles. At the level of the posterior dorsal pyloric plate the ridges which form the upper and lower boundaries of the lower chamber meet and close completely the posterior end of that chamber. The right and left posterior intermediate pyloric plates enclose the middle canal, which is narrow in front and broadens posteriorly.

Each lower pyloric canal is divided into an anterior portion lying between the middle and lower intermediate pyloric plates and a posterior portion enclosed between the posterior part of the middle intermediate and the ventral pyloric plates. The posterior parts of the lower pyloric canals form the most essential structure of the pyloric sac, and they are contained in the lateral pouches.

21. The middle intermediate pyloric plate extends in a sigmoid curve from the posterior end of the lower ventro-lateral cardiac bar upward, backward, downward, and then backward and upward again. The plate is broad in the middle and narrower at each end. It is almost bisected by a curved cleft which reaches from its lower edge nearly to its upper edge and divides the portions connected respectively with the anterior and posterior portions of the lower canal.

22. The lower intermediate pyloric plate is roughly quadrilateral and is concave ventrally. It is connected with the lower ventro-lateral cardiac bar and, forming the floor of the pyloric sac behind and on the outer side of the cardio-pyloric valve, it supports the posterior side of that valve.

23. The ventral pyloric plate is formed by two pointed half-spiral portions which extend from the tips of the lateral pouches forward, inward, and upward, and unite in the median line, forming there a prow-like septum which projects upward between the posterior portions of the two lower canals. This septum supports the median portion of the ventral pyloric valve and is continued backward as a

horizontal oval plate which lies between the lower edges of the lateral pyloric valve and separates the posterior ends of the middle and lower canals. The concave upper surface of each half of the ventral pyloric plate is covered by high parallel ridges which arise at the anterior edge of the plate and pass backward to a point two-thirds of the width of the plate from its anterior edge, where each ridge ends in a heavy band of chitin which diverges upward to the upper wall of the lower canal. Each ridge and band bears upon its distal or mesial side a row of close-set bristles which overlap the next ridge and band. These bristles cut off from the posterior part of the lower canal a number of parallel canals which open into a large transverse canal, the ventral part of the posterior portion of the pyloric canal.

The bands, ridges, and bristles form a fine-meshed sieve over which the food stream passes. The fluids and the fine-grained portion of the food pass from the dorsal part of the canal through the sieve into the ventral part of the canal, and through it, as Jordan has shown, into the liver whose duct opens into the posterior end of the ventral part of the lower canal. The particles which can not pass through the filter are carried inward and upward into the middle pyloric canal.

24. The posterior lateral intermediate plate is an irregular calcification which lies between the middle and posterior intermediate pyloric plates and the lateral pyloric valve. It faces the corresponding side of the septum of the pyloric plate.

The Muscles of the Pyloric Sac.

The upper constrictor muscle arises from the posterior part of the lower edge of the pyloric ossicle and, passing downward, and slightly forward, is inserted upon the anterior end of the middle intermediate pyloric plate.

The lower pyloric constrictor muscle arises from the middle dorsal pyloric plate and, its fibers converging, is inserted upon the middle intermediate pyloric plate behind the preceding.

The lateral pyloric constrictor muscle is a short, broad muscle which extends from the concave anterior surface of the middle inter-

mediate pyloric plate to the corresponding edge of the lower intermediate pyloric plate.

The inferior pyloric dilator muscle has a double origin and a double insertion. One head arises from the cephalic apodeme near the œsophagus; the other head arises from the lower ventro-lateral cardiac bar. These bands, passing backward, unite, and then the muscle divides: One branch is inserted on the anterior surface of the lower intermediate pyloric bar; the other, uniting with the corresponding muscle from the other side, is inserted upon the median portion of the ventral pyloric plate.

Before attempting to explain the action of this extremely complicated stomach it is well to summarize briefly the facts described in detail above.

The bristles of the cardiac sac are all directed toward the gastric mill with the apparent exception that those of the lower part of the side walls are directed downward and backward.

All the bristles of the pyloric sac except those of the lower and middle canals are also directed *toward* the gastric mill.

The alternate contraction and expansion of the anterior, posterior, and postero-lateral gastric muscles (assisted feebly by the cardio-pyloric muscle and the elasticity of the stomach wall) cause the median tooth to move back and forth across the surfaces of the lateral teeth and also cause the lateral teeth to move inward.

The contraction of the lower lateral constrictor pushes the lower lateral pad inward and backward.

The cardio-pyloric valve is practically hinged upon the posterior ends of the ventro-lateral cardiac bars, and we believe that it is driven forward and upward by the contraction of the upper and middle lateral cardiac constrictors.

Again, we must remember that the upper cardiac canal leads along the base of the cardiac sac to the beginning of the lower pyloric canal. This canal passes along the base of the pyloric sac to the lateral pouches, where the coarser particles of the food are separated from the remainder.

Finally, we maintain that particles between plates which move back and forth on one another, and which are covered with bristles all inclined in one direction, will invariably be carried in the direction of the inclination of the bristles. If this be so, the *modus operandi* of the stomach is as follows: (Plate III, Fig. 3) Food entering the stomach is retained by the œsophageal valve and is carried backward and upward between the lateral plates, the lower and middle lateral pads, and the cardio-pyloric valve to the gastric mill: Here it is partly comminuted and the greater part of it is carried forward by the median tooth; some of it, however, is carried into the pyloric chambers, and the fluids with minute particles of food filter backward and forward from the chambers into the upper and middle canals. The food entering the middle canal is carried backward between the lateral valves to the gut. That entering the upper canal is carried through it into the intestinal cœcum. The larger particles of food are retained by the marginal bristles of the middle pyloric chamber, and the upward sweep of the bristles upon the posterior lobe of the cardio-pyloric valve carries them again to the mill. The larger portion of the food and that containing large pieces is retained in the cardiac sac, and the fluids with small particles of food percolate downward into the ventral part of the sac and are drawn by the inward and outward movements of the upper and lower ventro-lateral cardiac bars into one of the lower cardiac canals. From this canal the finest particles pass into the upper cardiac canal and through it into the mouth of the lower pyloric canal. The food passes through this canal into the lateral pouch where it is subjected to a final sifting, the most minute parts and the fluids pass down through the sieve into the liver, while the less minute particles are carried upward into the middle pyloric canal and through it into the gut.

Thus four streams of food material enter the intestine:

1. Two streams from the right and left branches of the dorsal pyloric canal. These pass outward around the posterior dorsal pyloric plate and the base of the dorsal valve into the capacious intestinal cœcum.

2. A stream from the middle pyloric canal. This contains the rejected material from the lateral pouch and is probably formed almost wholly by that material. Bristles from five to fifteen mm. long are the only large objects which we have found in the pyloric sac. These pass through the lower chamber and the middle canal. It is possible, however, that the relaxation of the constrictor muscles may allow relatively large objects to pass through the sac.

3. A stream from the lower canal. This contains the greater part of the material brought into the pyloric sac by the upper cardiac canal. In addition, it doubtless contains a portion of the fluids which enter the pyloric sac through the upper and lower chamber and which gravitate into the canal. The coarser particles are removed from the lower canal by the sieve of the lateral pouch and are carried into the middle canal. This lower stream of food enters the lobes of the liver and is there, in part at least, digested and absorbed.

The view of the function of the stomach which is here presented is in radical disagreement with the common explanation which, without accounting for the final disposition of particles caught by the bristles of the pyloric sac, regards the sac merely as a filter. It is in slight disagreement with the admirable work of Jordan who failed to discover the cardiac canals and so was led to believe that the food stream entered the lateral pouches from the middle canal.

The Stomach of Larval Lobsters.

The stomach of lobsters of the fourth stage is like that of the adult. The less strongly calcified plates of the adult, for example, the anterior lateral, the upper intermediate, and lower intermediate cardiac bars, and the anterior dorso-lateral cardiac plate, are not recognizable in the stomachs of the earlier stages which have the adult form. The stomachs of lobsters of the first, second, and third stages (the larval stages) have the same general form and musculature (extrinsic and intrinsic) as the adult stomach. These stages are unlike the adult in the following important points:

1. The gastrolith is not present.
2. Calcifications of the stomach wall are entirely lacking and the gastric "ossicles" are formed entirely by thickenings of chitin.
3. The dorsal cardiac plate is covered internally with sparsely arranged pairs of slender bristles and extends laterally over a large part of the areas on the sides of the stomach occupied in the adult by the gastroliths.
4. The gastric mill differs more or less fundamentally from that of the adult.

The upper and lower cardiac canals, the cardio-pyloric valve, the lower pyloric canal, and the pyloric valves, which are the most essential structures of the stomach, retain through all stages the same form and relationship.

The Stomach of the Third-Stage Lobster. (Plate VII, Fig. 11.)

The stomach of the third-stage lobster is the first of the series in which the gastric mill appears. The median tooth is comparatively small and ends in a round median knob and a pair of lateral cusps which remind one of the bilobed form of the median tooth of *Astacus*. The anterior dorsal and posterior dorsal pads are united in a single large lateral pad covered with backwardly directed bristles. The lateral tooth appears with its accessory cusp and with the general form of the adult tooth. The infero-lateral tooth is also present and has one large and one small cusp. The middle and lower cardiac pads have the same form as in the adult.

The ventral surface of the cardiac sac of the stomach of this, and also of the first, second, and fourth-stage lobsters, unlike that of the adult, is covered with small brushes of bristles. The simplest of these (Plate V, Fig. 5 A) consists of two parallel bristles, and the more complete brushes have three, four, or more bristles which are inserted upon a slightly crescentic ridge. The bristles which separate the upper and lower cardiac canals in the stomach of this and of the first and second stages are round and are not plumose. The cardio-

pyloric valve is relatively higher, it lacks the posterior lobe, and it is armed with long heavy bristles.

The Stomach of the Second-Stage Lobster. (Plate IX, Fig. 15.)

The stomach of the second-stage lobster (and of the first) lacks the median, lateral, and infero-lateral teeth. In the place of the first, there is a high grooved projection from the dorsal wall of the stomach. This is very much like the cardio-pyloric valve, and we will call it the dorsal cardio-pyloric valve. Its sharp edge bears a row of long heavy serrate spines which point downward and forward. The cardio-pyloric valve is high and is similarly armed.

Between the cardio-pyloric and the dorsal cardio-pyloric valves, on each side of the stomach, there is a long (partly double) row of bristles like those of the cardio-pyloric valve, but directed inward and backward. The postero-lateral gastric muscle is inserted upon the plate of chitin which supports this row of spines.

The pyloric sac seems to be divided into a broad upper, and a lower canal. All the bristles of the sac are directed backward.

The Stomach of the First-Stage Lobster. (Plate X, Fig. 16.)

The stomach of the first-stage lobster is like that of the second-stage lobster, except that it is more nearly tubular and that it has thinner walls and fewer bristles.

In conclusion, we wish to call attention to the following facts:

1. That while the gastric mill of the adult is a grinding and crushing organ, that of the first and second-stage lobsters is a tearing and shredding organ.

2. That the lower pyloric canal, the lateral pouch, and the two cardiac canals remain throughout the whole metamorphosis essentially unchanged, and that their persistence is suggestive of their importance.

THE GASTROLITH.

(Plate V, Fig. 5, and Plate VI, Figs. 7 and 8.)

The gastrolith is an irregular triangularly-ovate plate of lime, formed of numerous angular prisms that extend from the epithelium of the stomach wall to a plate of chitin which lines the stomach and which is secreted early in the period between two molts by the epithelium which later produces the gastrolith. Each prism appears first as a disc in the center of an irregular shallow pit in the secretory epithelium and gradually is pushed inward until it becomes a slender irregular prism whose inner and outer ends are rounded. These prisms increase in size until they fit snugly together and their rounded ends give the surfaces of the gastrolith a knobbed appearance. The gastrolith becomes quite thick before the molt (one-quarter of an inch in a lobster 11 inches long [Herrick], .5 mm. in a fourth-stage lobster). After the molt the gastrolith falls into the lumen of the stomach, is broken up, and dissolved in a few hours.

Two rival theories of the function of the gastrolith are widely known, and we will present a third theory which is a modification of the older of the two theories in accordance with some newly discovered facts. The older theory regards the gastroliths as a mass of mineral matter reserved when the old shell is cast for the hardening of the new shell. The objection offered to this theory is that the gastroliths are entirely too small to be effective for this purpose. Herrick suggests that the gastroliths are formed by the deposition of the lime absorbed from the shell in preparation for the molt and that they have no further important function than to remove a temporary excess of lime from the blood.

Thanks to the courtesy of the Commission of Inland Fisheries, we had at our disposal last summer a large number of larval lobsters of known age.

We found that the gastroliths do not appear in the first three stages, nor would we expect mineral matter in the wall of the stomach

when absent from the skeleton generally as is the case in these larval lobsters. We found that the older fourth-stage lobsters, and also fifth-stage and older lobsters, have gastroliths. This observation is suggestive because it shows that the gastroliths appear in conjunction with the limy skeleton, since the fourth is the first stage in which the lobster has a calcareous skeleton. So far as we know, the gastroliths have not been found before in lobsters smaller than $7\frac{1}{2}$ inches.

We determined to discover, if possible, the time of appearance, the rate of growth, and the rapidity of solution of the gastroliths in fourth and early fifth-stage lobsters. At the beginning of our observations for this purpose we had about 500 fourth-stage lobsters which molted from the third stage on the night of August 7 and 8.

Mr. Emmel, who obtained these lobsters for experiments on regeneration, and to whom we are indebted for the opportunity to perform this collateral experiment, isolated a number of these in bottles and fed them daily as controls. After removing a number of others for mutilation, the remaining lobsters were kept in a large receptacle and fed daily. The controls began to molt on the eighth day, but the molting of the reserve supply was delayed until the eleventh or twelfth day.

We examined the stomachs of several lobsters each day, and found that the gastroliths appeared on the fourth day—that is, the gastroliths begin to be formed in the middle, or at the beginning of the middle third, of the eight to twelve day period.

At the periphery of the ovately-triangular area, which is finally covered to a considerable thickness by the gastrolith, the calcification begins with the formation of irregular discs which are thick at the edge and thinner toward the center of the gastrolith where at first each disc is undefined, but later has a definite edge which, for a long time, is markedly thinner than the outer edge. The calcification proceeds by the thickening of the peripheral discs, by the addition of central discs, and by the gradual expansion of all the

discs until they unite and so form the gastrolith. Each disc become one of the prisms of the gastrolith.

On the fifth and on subsequent days, the gastrolith was perceptibly thicker and more complete up to the eighth day, after which we did not observe any increase in size, although the growth probably continued.

After the molt we found that the gastroliths are dissolved within a few hours and that they may either remain *in situ* or fall into the lumen of the stomach and be broken up during the process of dissolution.

There proceeds *pari passu* with the dissolution of the gastroliths a hardening of the gastric teeth, of the mandibles, and then of the chelipeds and abdominal tergites.

As soon as the gastroliths are dissolved 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.

These observations do not in the least contradict those of other workers, but merely extend into a new field. They suggest the following conclusions, which are somewhat contradictory to Herriek's theory of the function of the gastrolith.

It seems improbable that the preparation for the molt, by a softening of the shell and by a corresponding deposition in the gastrolith of the excess of lime from the blood, begins at or before the middle of the period between the molts.

The hardening of the gastric teeth and mandibles before any other skeletal structures, the hardening of the chelipeds, and the subsequent eating of the shell contribute to make us believe that the gastroliths are a supply of lime reserved for the hardening of these structures so that the relatively vast supply of mineral matter in the cast and in other shells may be made available quickly for the hardening of the new shell.

THE FOOD OF LARVAL AND YOUNG LOBSTERS.

The lobsters used for the work recorded here were taken from the large hatching bags of the Wickford Station in July and August of last year. The eggs were hatching rapidly at the time, and for this reason the lobsters in each bag were nearly of the same age. The lobsters were taken from the bags for examination at different times and on different days, so as to avoid as far as possible accidental factors.

It is the rule of the station to put a generous supply of finely chopped clams into each bag every three hours, and hence we may infer that food other than particles of clam was taken, at least in the majority of cases, in preference to the clam.

Each lot of lobsters is started in a clean bag, but organisms drawn into the bag through the bottom window seem unable or unwilling to escape, probably because the rotatory current is much stronger than the radial, outgoing, current, and soon a mass of plants and animals is crowded into the bag. The algæ and sessile diatoms attach themselves to strings of clam cuticle which is not usually eaten by the lobster, or to other fibrous matter, and sooner or later the colonies become attached to the bag and, with the tubes of annelids and amphipods, form a dense moss-like coating upon the bag. The following forms were found in the bags or upon their walls:

Acartia tonsa, very abundant.

Centropages hamatus, very abundant.

Amphipods, very abundant.

Harpacticus chelifer.

Diosaccus tenuicornis.

Balanus eburneus, very abundant at times.

Loxomacha impressa.

Decapod larvæ (crabs, shrimps ?).

Many larval and young gastropods and bivalves.

Caprella geometrica, abundant.

Larval *Polydora ciliatum* and other larval worms.

Many nauplii.

Striatella.

Melosira.

Grammatophora.

Schizonema,

Non-colonial diatoms.

Young algæ, red and brown.

The stomach and intestine were dissected from each lobster, teased on a slide, and examined.

The stomachs and intestine of all lobsters except those of very young first-stage lobsters contained a number of diatoms which do not seem to be taken as food, but merely because it is impossible to avoid these omnipresent organisms. The lobsters examined were taken at random, except that very dark colored lobsters (shedders) were avoided because, as Mr. Emmel has shown, these do not eat at all for some time before the molt.

One hundred lobsters, twenty-five from each of the first four stages, were examined, and the results are presented in the appended table. In presenting this table we must mention the fact that, while particles of clam and small animals lacking hard parts may readily have failed to be recognized, the characteristic scales, tracheæ, wings, and compound eyes of insects are readily and positively recognized: moreover, the fifth limbs, spermatophores, and the antennæ of copepods are so characteristic that three species were positively identified, *i. e.*, *Acartia tonsa*, *Centropages hamatus*, and *Harpacticus chelifer*.

TABLE SHOWING THE CONTENTS OF THE STOMACH OF ONE HUNDRED LARVAL AND FOURTH-STAGE LOBSTERS.

STAGE.	1st.	2d.	3d.	4th.	TOTAL.
Empty.....	17	3	1	7	28
With copepods.....	2	19	13	3	37%
Per cent. with copepods.....	8	76	52	12	37
Lobsters.....	0	1 ?	1 ?	1	3
Diatoms.....	Few.	All.	All.	Nearly all.
Clam.....	0	1 ?	0	7	8
Insects.....					4
Chitin.....			2*	
Unrecognizable matter.....	1	2	5	3	11

*One decapod larva; 1 amphipod ?.

The number of copepods found in the stomachs of the second and third-stage lobsters is very surprising, and, although it must be taken in connection with the fact that copepods swarm in the bags, it seems to indicate that these larvæ prefer live copepods to dead clams.

The absence of parts of larval lobsters is quite astonishing, in view of the well-known omnivorousness and cannibalism of lobsters, and we believe that this indicates that a lobster in the presence of abundant food will not attack his kind. In this connection one record is particularly interesting: a number of fourth-stage lobsters which had not been fed for several hours were examined and the stomachs were empty or contained masses of the cuticle of the clam which is regularly rejected by the lobster. Moreover, some of these hungry lobsters left in a finger bowl did not attack one another, *i. e.*, lobsters hungry enough to eat what they ordinarily refuse will not attack one another (unless, perhaps, one or more of the number is newly molted).

The insects eaten are found floating on the water, sometimes alive, for we saw a full grown cricket fall into a tub containing fourth-stage

lobsters, and, despite its struggles, it was soon dragged under, dismembered, and eaten by a swarm of lobsters.

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EXPLANATION OF PLATES.

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|-------|---------|-----|---|--------|
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| “ | II, “ | 2. | Median section of the stomach. | x 4. |
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| “ | “ “ | 9. | Section through the gastrolithic plate of a fourth-stage lobster just before the molt. | x 260. |
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| “ | VII, “ | 11. | Floor of the stomach of the third-stage lobster. | x 57. |
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| “ | “ “ | 14. | Stomach of a third-stage lobster. | x 20. |
| | | A. | Lateral tooth. | x 57. |
| | | B. | Median tooth. | x 57. |

Plate IX, Fig. 15. Stomach of a second-stage lobster.

“ X, “ 16. Stomach of a first-stage lobster.

1. Cardiac ossicle or anterior dorsal cardiac plate.
- 1'. Posterior part of above plate.
2. Urocardiac ossicle or posterior dorsal cardiac plate.
3. The prepyloric ossicle or median tooth.
4. Pyloric ossicle or anterior dorsal pyloric plate.
5. Pterocardiac ossicle or anterior dorso-lateral cardiac plate.
6. Zygo-cardiac ossicle or lateral tooth.
- 6'. Lateral bristle plate of larval stomach.
7. Anterior dorso-lateral pyloric plate.
8. Gastrolithic bar.
9. Accessory lateral cardiac ossicle or upper intermediate cardiac bar.
10. Infero-lateral tooth.
11. Lower intermediate cardiac bar.
12. Upper ventro-lateral cardiac bar.
13. Antero-lateral cardiac bar.
14. Lower ventro-lateral cardiac bar.
15. Ventral cardiac plate.
16. Posterior intermediate cardiac bar.
17. The middle dorsal pyloric plate.
18. The posterior dorsal pyloric plate.
19. The upper intermediate pyloric plate.
20. The posterior intermediate pyloric plate.
21. The middle intermediate pyloric plate.
22. The lower intermediate pyloric plate.
23. The ventral pyloric plate.
24. The posterior lateral intermediate pyloric plate.
- A' The lower lateral dilator.
- A.D. Lower anterior dilator.
- A.D.' Anterior dilator.
- A.P. Posterior dorsal pad.
- C. Lateral pyloric pouch.
- C.M. Intestinal cæcum.
- C.C. Partition of bristles between the upper and lower cardiac canals.
- C.P. Cardio-pyloric valve.
- C.P.' The dorsal cardio-pyloric valve.
- D. Dorsal pyloric valve.
- D.C. The upper pyloric canal.
- D.P. Posterior dorsal pad.

- E. Oesophagus.
E'. The median valve of the oesophagus.
G. Gastrolith.
G'. The gastrolithic epithelium.
H. The hepatic duct.
I. The intestine.
L. Lateral pyloric valve.
L.C. Lower pyloric chamber.
L.D. Lateral dilator.
L.G. Postero-lateral gastric muscle.
L.P. Lower cardiac pad.
L.P'. Lower pyloric pad.
L.T. Lateral tooth.
M. Upper cardiac canal.
M.C. Middle pyloric canal.
M.P. Middle cardiac pad.
N. Lower cardiac canal.
P.G. Posterior gastric muscle.
Q. Posterior opening of the upper cardiac canal.
R. Upper cardiac constrictor.
S. Middle cardiac constrictor.
S.D. Superior dilator.
T. Lower cardiac constrictor.
U.P. Upper lateral cardiac pad.
U.P'. Upper pyloric pad.
V. Ventral pyloric valve.
V'. Septum between middle pyloric and lower pyloric canals.
V.C. Lower pyloric canal.
V.C'. Ventral portion of the lower pyloric canal.
V.D. Ventral dilator.
V.E. Vascular epithelium.
W. Connective tissue wall of stomach.
X. Upper pyloric constrictor.
Y. Lower pyloric constrictor.
Z. Lateral pyloric constrictor.

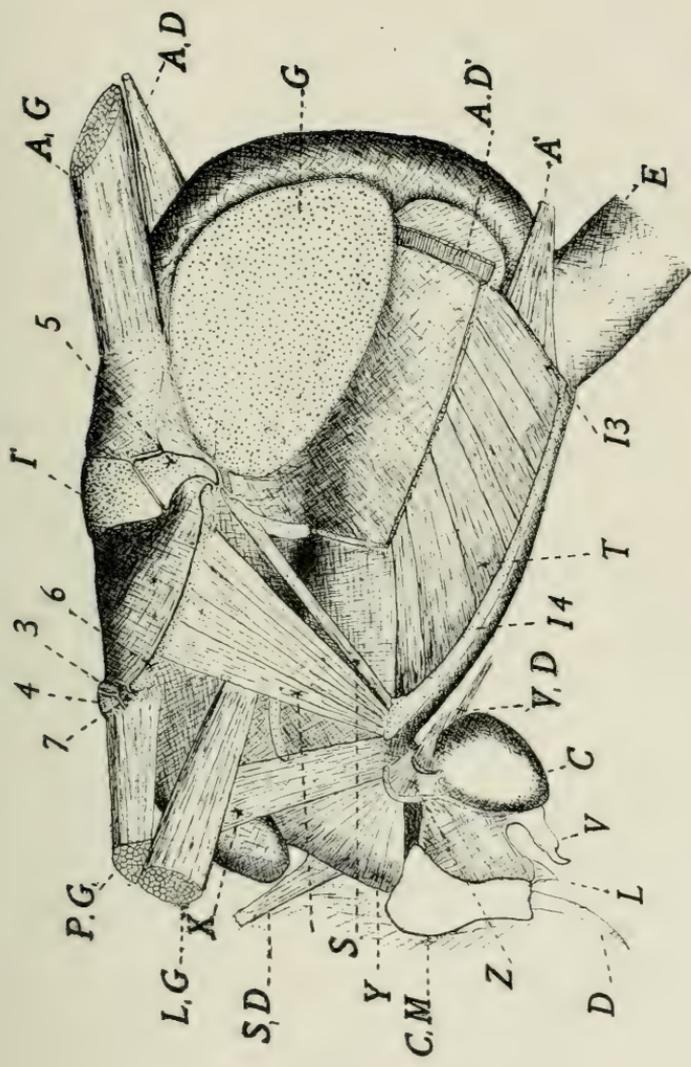


PLATE I.

Fig. 1.—Stomach of an adult lobster. x 4.

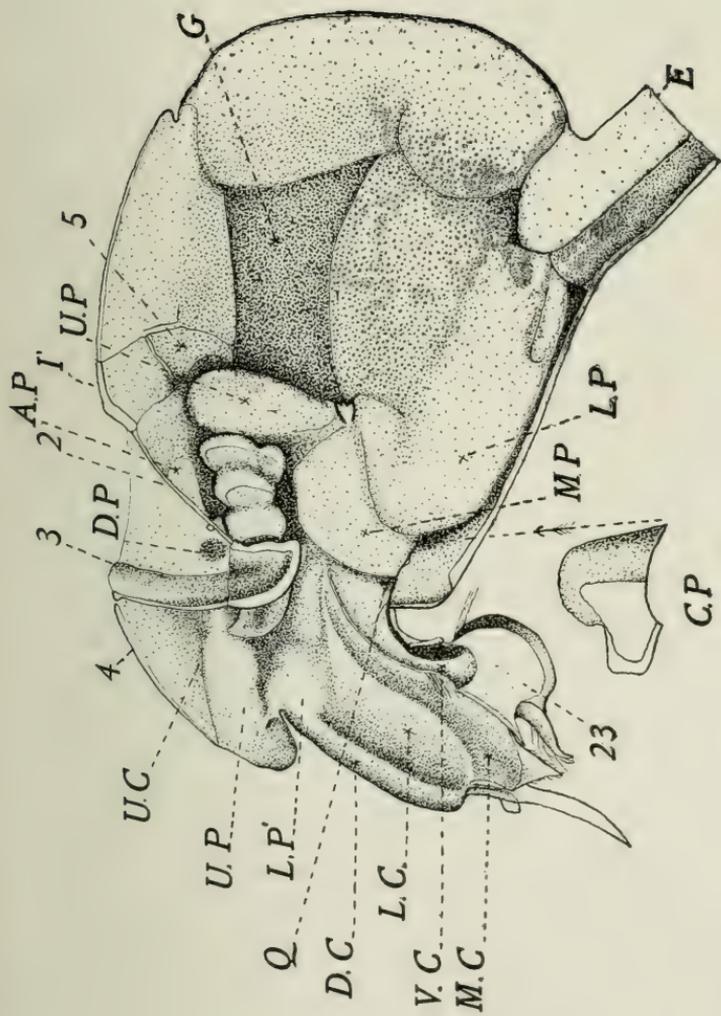


PLATE II.

Fig. 2.—Interior of the stomach of the adult. x 4.

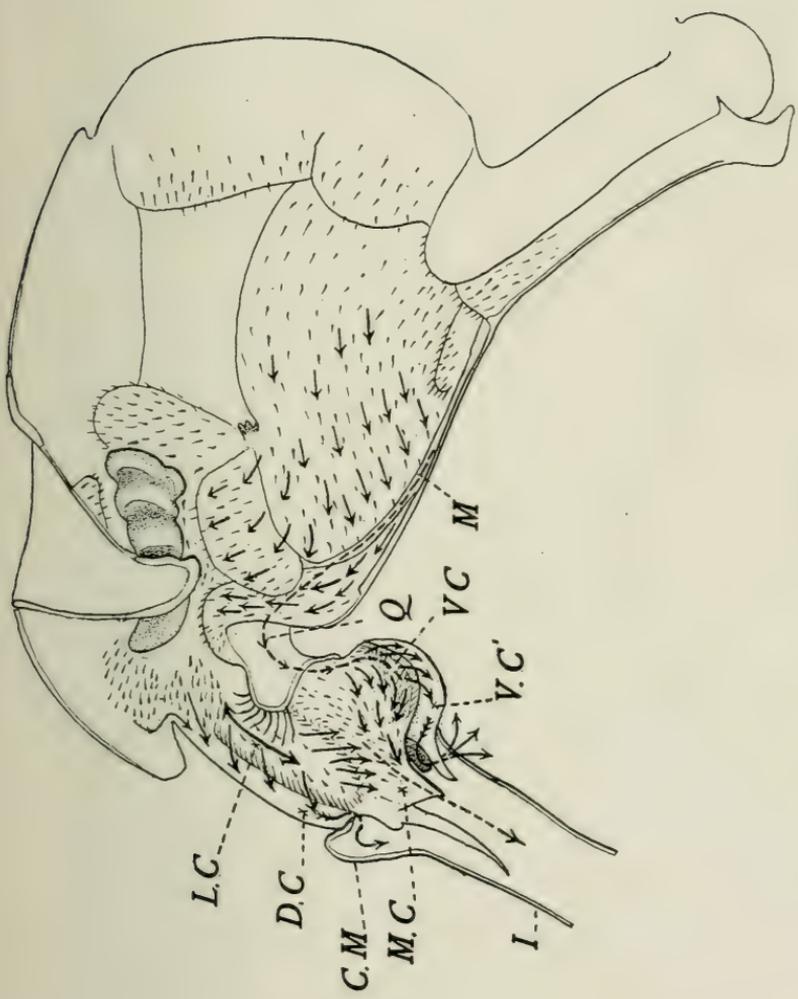


PLATE III.

Fig. 3.—Diagram showing the course of food in the stomach of the lobster.

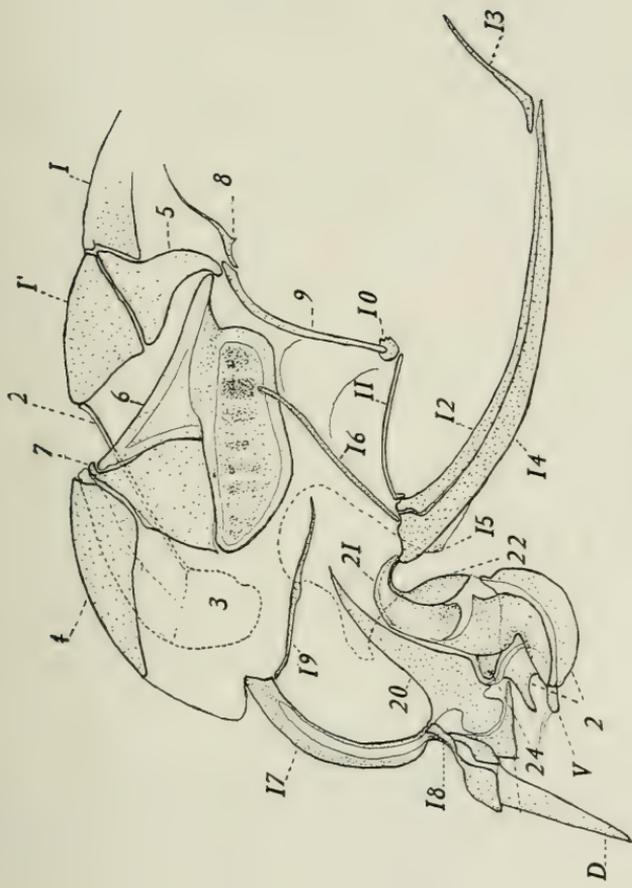


PLATE IV.

Fig. 4.—Diagram showing the osseles of the stomach of the lobster. x 4.

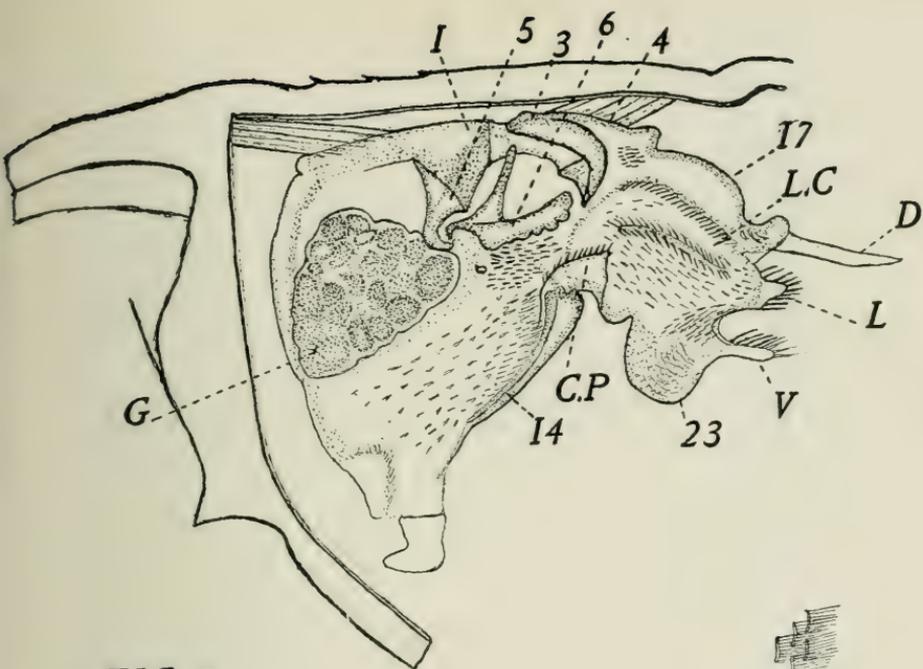


FIG. 5

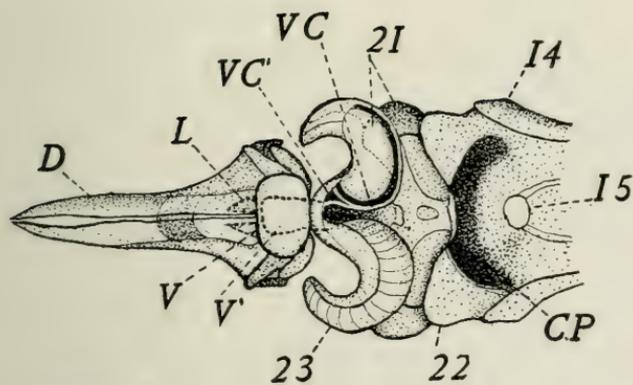


FIG. 6

PLATE V.

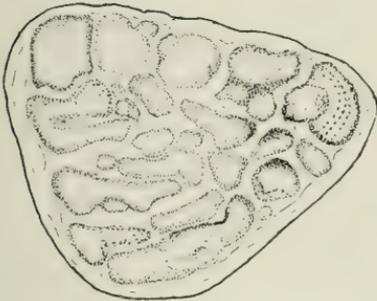
Fig. 5.—Stomach of a fourth-stage lobster. x 11.

Fig. 6.—Ventral surface of the cardiac portion of an adult lobster. x 6.

FIG. 7



FIG. 8



G

FIG. 9

G'

W

VE

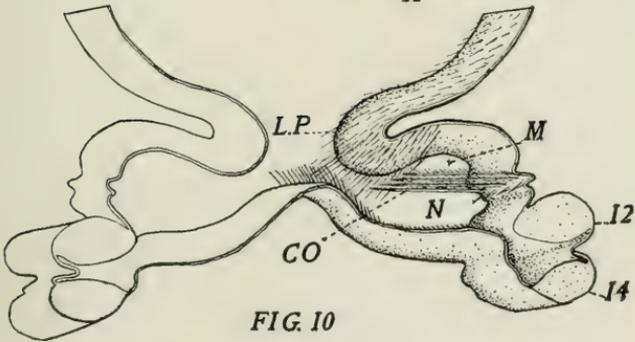
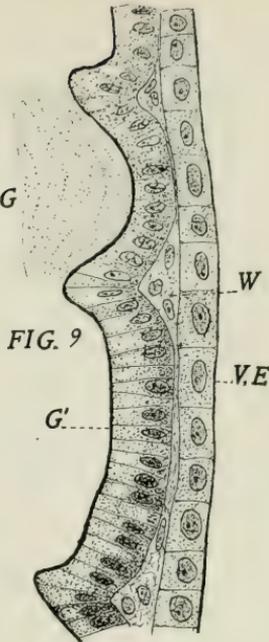


FIG. 10

PLATE VI.

- Fig. 7.*—Gastrolith of a fourth-stage lobster, five days after the molt. x 20.
- Fig. 8.*—Gastrolith of a fourth-stage lobster eight days after the molt.
- Fig. 9.*—Section through the gastrolithic plate of a fourth-stage lobster killed a short time before the molt to the fifth stage. x 260.
- Fig. 10.*—Section through the base of the cardiac portion of the stomach of an adult lobster, a short distance in front of the cardio-pyloric valve. x 6.

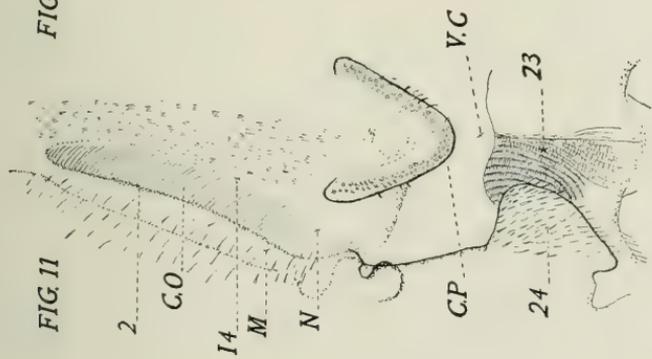


FIG. 11

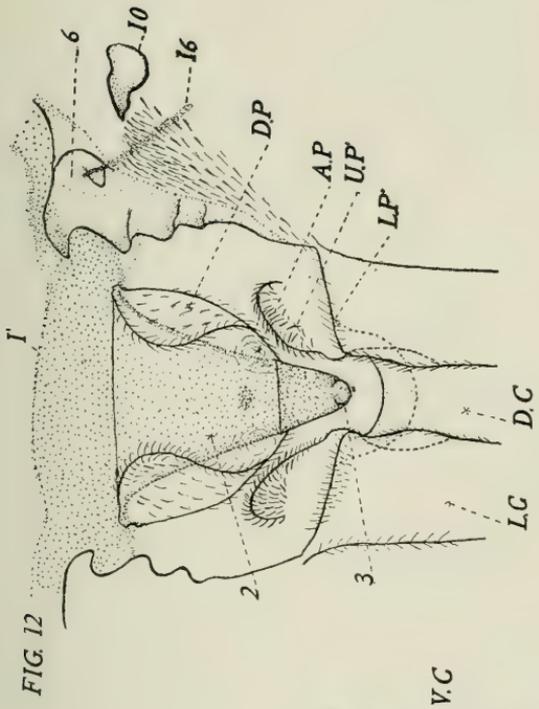


FIG. 12

PLATE VII.

Fig. 11.—Lower wall of the stomach of a third-stage lobster. x 57.

Fig. 12.—Upper wall of the stomach of a fourth-stage lobster. x 27

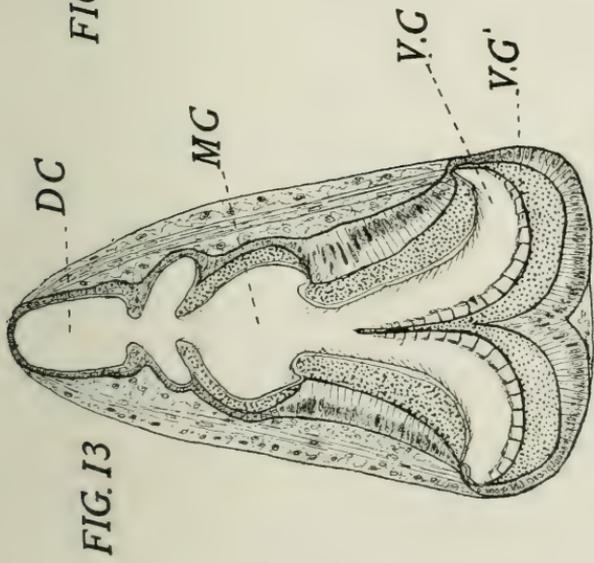


FIG. 13

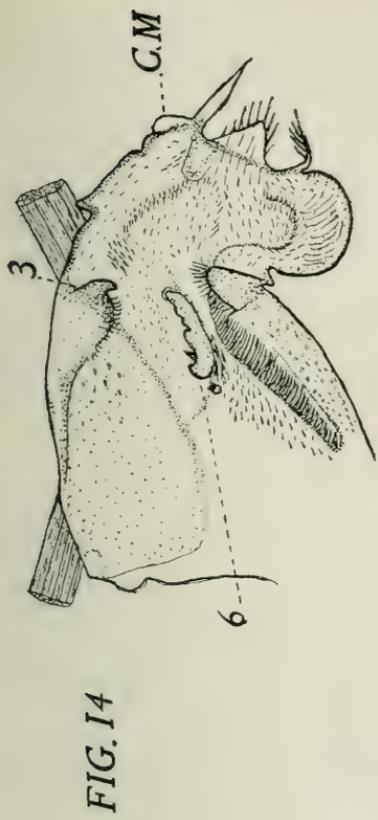


FIG. 14

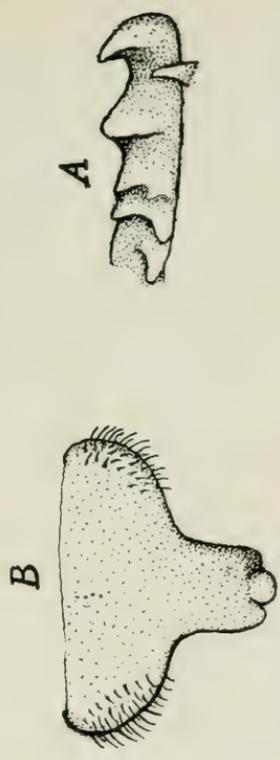


PLATE VIII.

Fig. 13.—Transverse section through the pyloric portion of a fourth-stage lobster, a short time before the molt to the fifth stage. x 27.
 Fig. 14.—Stomach of a third-stage lobster. x 40. A. Median tooth. x 115. B. Lateral tooth. x 115.

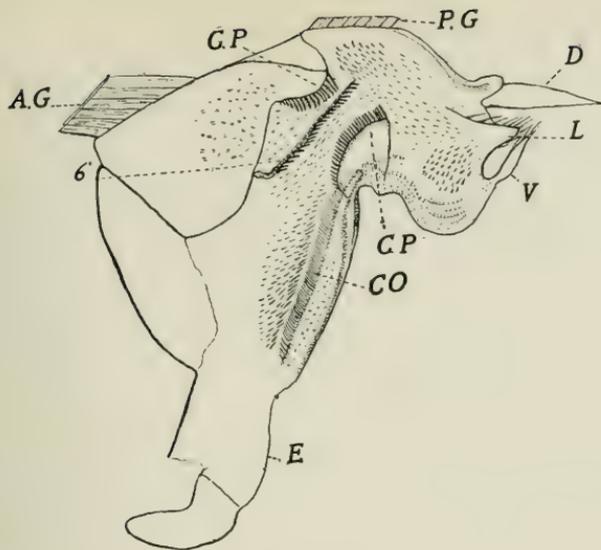


PLATE IX.

Fig. 15.—Stomach of a second-stage lobster. x 44.

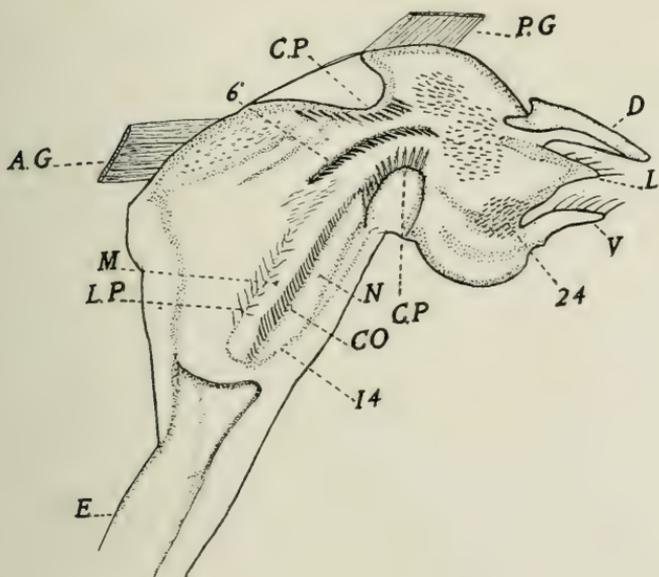


PLATE X.

Fig. 16.—Stomach of a first-stage lobster. x 57.

THE FISHES OF RHODE ISLAND.

V.—THE FLAT-FISHES.

BY HENRY C. TRACY.

Thirty-eighth Annual Report of the Commissioners of Inland Fisheries of Rhode Island. 1907. Special Paper No. 36.

THE FISHES OF RHODE ISLAND.

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PLATES I TO IX.

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BROWN UNIVERSITY.

1907.

SPECIAL PAPER No. 36.

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COMMISSIONERS OF THE INLAND FISHERIES OF RHODE ISLAND.

THE FISHES OF RHODE ISLAND.*

V. THE FLAT-FISHES.

BY HENRY C. TRACY, A. M.,

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The flat-fishes and flounders comprise a group which is in many respects one of the most interesting among the fishes. Their abundance in all seas and their excellent food qualities has long made them of very great value to man. Another factor which contributes greatly to their value to man is their availability; many species of the family find their most natural abode in shallow waters near the shore, where they are easily accessible to all fishermen, even to those who work with the most primitive methods; in most localities, also, one or more species of flat-fishes are present in considerable abundance during every season of the year, and so afford a constant supply of valuable fish. Thus the value of the flat-fishes to man compares very favorably with that of those fishes whose vast wandering schools sometimes furnish immense quantities of fish but which are very irregular in their visitations and subject to great variations in abundance.

The flat-fishes also possess a peculiar interest, since they furnish a striking illustration of the modification of an animal to a certain specialized mode of life. They show how unique may be the direction

* Previous papers in this series are as follows:

- I. A List of the Fishes of Rhode Island, 36th Report, 1905, page 38.
- II The Common Fishes of the Herring Family, 36th Report, 1905, page 100.
- III. The Fishes of the Mackerel Family, 37th Report, 1906, page 33.
- IV. A List of Rare Fishes Taken in Rhode Island in the Year 1906, 37th Report, 1906, page 65.

which changes in form and structure of animals may take in order that they may become adapted to the conditions of their environment. The flat-fishes are exclusively bottom fishes; they are somewhat sluggish in habit, feed mostly on bottom invertebrates, and seldom leave the bottom except for relatively short excursions in the pursuit of food or when disturbed. To a fish of this sluggish mode of life, such an inconspicuousness in appearance as will cause it to be overlooked by its enemies and prevent it from frightening its prey will largely increase its chances of survival. In the case of such bottom fishes as the flat-fishes, and the skates and rays, this advantage is secured partly by a protective coloration, perhaps, and partly by an extreme flattening out of the body of the fish. The skates and rays are flattened in a vertical direction, but the flat-fishes are strongly compressed from side to side; therefore we find in the flat-fishes the unique condition that when in the natural position, whether swimming horizontally through the water or resting on the bottom, their upper and lower surfaces correspond in reality to the sides of other fishes. By this sidewise flattening, the dorsal fin, which runs along the middle line of the back, and the anal fin, which runs along the mid-ventral line, are prominently brought out to the "edges" of the fish and by this relative change in position become capable of being used more directly in forward propulsion than is the case with the unpaired fins of most fishes. Thus it would appear that the problem of producing a powerful means of propulsion in a fish which has to meet the requirements of the structural change demanded by an existence confined almost exclusively to the bottom, has been solved by nature in two different ways, viz.: in the case of the skates and rays, by bringing about a great extension of the pectoral fins as a result of a very considerable vertical compression (this is accompanied by an almost complete disappearance of the unpaired fins); and in the flat-fishes, by a mechanical adjustment resulting from an extreme lateral flattening, which gives a great mechanical advantage to the unpaired fins. The whole of the flat posterior portion of the body, as well as the broad, strong tail-fin, is used also

in forward propulsion. The greater efficiency of the swimming apparatus which results from the lateral compression may be a partial explanation of the greater speed in swimming and the greater precision of movement which the flat-fishes show as compared with the slow, clumsy, lumbering movements of the skates and rays.

This sidewise flattening of the fish and the fact that the fish in its natural horizontal position must have one of its sides constantly turned away from the light involve considerable modifications in its structure. The unpaired fins increase in extent and area to the degree corresponding to their increased importance in propulsion; the dorsal fin extends forward onto the head nearly down to the snout; the body cavity becomes so shortened that the anus is shifted much further forward, and thus the anal fin is brought to extend along all except a comparatively small fraction of the ventral edge of the fish. The area of these fins is also increased by a lengthening of the fin-rays. The paired fins, in most species, since from their position they are of comparatively little use to the fish, have become reduced or wanting. The tail-fin in many species has become increased in area and strengthened by a hypural bone. Changes in pigmentation also occur; the pigmented area in most species is entirely confined to the upper or light-exposed side, while the whole under side becomes colorless like the ventral side of other fishes. The color of the upper side is capable of considerable variation from light to dark according to the prevailing shade of the background.

The mouth parts in some of the species have undergone changes. In the fishes of the Turbot and Halibut tribes the jaws remain unaffected by the change in position of the fish; in these, the mouth is large, symmetrical, toothed around the whole border, and does not partake of the twist of the remainder of the head. In the Flounder tribe (*Pleuronectinæ*), that part of the mouth which belongs to the eyed side has become somewhat contracted and twisted, but on the under side the jaws remain straight and normally toothed. In the case of the soles, the mouth has become very asymmetrical

and much distorted toward the blind side, and the teeth are very small or obsolete.

The most remarkable of the structural changes which accompany the sidewise modification of the body of the flat-fishes are the changes which result in bringing the eye which normally belongs to the side turned toward the bottom over onto the side that is exposed to the light. Both eyes, therefore, come to lie on the upper side of the head; the fish thus loses its bilateral symmetry, and the head acquires its peculiar twisted appearance. These changes are not confined to the eye merely, but involve a considerable torsion of the bones of the head, and an asymmetry of the nerves connected with the displaced parts. These aspects of the asymmetry will be very briefly referred to later, but for details, reference must be made to special papers which deal with the osteology of the flat-fishes.

The degree of asymmetry in the different species is an adaptation correlated with their habits. Those fishes like the halibut, sand-dab, and summer flounder, which are the more free-swimming, and which feed to a considerable extent on other fishes, are the more symmetrical; the displaced eye is nearer the line of the profile, and the mouth parts of the two sides are scarcely different. In the forms like the winter flounder, which live more upon the bottom and in the shallow water and which subsist largely on the bottom invertebrates, and eat other fishes very little, the asymmetry of the eyes has gone further, while the mouth has become twisted toward the under side, and those portions of the jaws which are on the upper side remain relatively undeveloped. It is in the soles that the asymmetry of both eyes and mouth has gone to its greatest extreme. These fishes live on the bottom almost entirely, and probably obtain most of their food by grubbing in the mud. The mouth in this species has become very much twisted. From these facts it may be inferred that the asymmetry of the mouth is independent and secondary to that of the eyes. The asymmetry of the eyes is the result of the need of having both eyes on the side toward the light, while the asymmetry of the mouth is a

secondary adaptation to different external conditions and to different methods of securing food.

The process by which the asymmetry of the eyes is reached in the course of the development of the individual is an interesting one.

Young flat-fishes, when first hatched out from the egg, are symmetrical, and swim upright. A little later, while the bones of the head are still in a cartilaginous condition, the fish turns over on one side, and in the course of a few days the eye of the under side has moved clear around so as to take up its position on the upper side. The details of this transformation have been a subject of a lively controversy for the last half century. Steenstrup (1863) first studied the migration of the eye; he described it as sinking in through the tissues of the head and coming out on the other side. Malm (1868) maintained, on the contrary, that in the species observed by him the eye which belonged to what was to become the under side of the fish, moved over the profile of the head to take its position on the upper side. After some years of controversy it was found by Alexander Agassiz, and others, that both these early investigators were right, and that each had described the process as it actually seemed to take place in the species with which he was working. It has, however, now been established that the process does not essentially differ in either case; according to this view, the asymmetry of the head is not primarily due to the mere migration of the eye from the under side of the head, but is the result of a twisting of the whole ocular region of the head and involves an extensive torsion of the bones of the orbital and preorbital region. The process has been described as follows: "the whole of the cranium in the region of the orbit rotates on its longitudinal axis until the two eyes instead of occupying a horizontal plane have assumed a vertical one"* and one eye is dorsal to the other. At least this seems to be true for species in which the development has been completely worked out. If, at the time of metamorphosis, the dorsal fin does not extend down over the frontal region of the head,

* Cole and Johnstone, *Pleuronectes*, L. M. B. C. Memoirs, 1901, 9.

the torsion of the cranium carries the eye over the line of the profile; in other species the dorsal fin has already extended down to the snout before metamorphosis has taken place, and in this case the eye has to pass under the tissues supporting the forward extension of the dorsal fin and thus seems to pass from side to side through the head.

The attempts to explain how these unique modifications in the flat-fishes were brought about, probably originated with Lamarck nearly one hundred years ago. As he was the first to conceive and apply systematically a thoroughgoing theory of descent, no one before him had ever recognized that there was any such problem as the origin of the flat-fishes. In accordance with his theory of "use and disuse," he considered that the shifting of the position of the flat-fishes was due to the fact that they acquired the habit of living in shallow water, and then were forced to swim on their sides in order to follow their prey near the shore; the eye on the lower side, as the result of the constant straining upward toward the light, finally, in the course of many generations, migrated over to the other side. A very similar explanation has been recently offered by Cunningham (1897). "The action of the eye-muscles would probably have some effect [in twisting the orbital region], and the weight of the fish, resting on the ground, would force the lower eye-ball toward the upper side, and so distort the face. In all probability both these influences have contributed to the result." *He also suggests an explanation of the forward extension of the median fins on the same basis; the constant action of the numerous small muscles attached to the fin-rays in the young fish would tend to differentiate an increasing number of rays from the embryonic tissue "while the direction of the muscular strains, the constant endeavor by muscular contraction to draw forward the anterior ends of the fins, would determine the direction of their extension. Thus the mode in which the fins were used would produce in the course of generations the structure and relations which they now possess." There are various

* Cunningham, *Science Progress*, 6, 1897, 502-3.

objections to these hypotheses. Cole and Johnstone,* in an exhaustive paper on the anatomy and osteology of the Plaice (*Pleuronectes*), have shown that the mechanical relations existing between the eye muscles and the bones of the frontal and prefrontal region are such that the contraction of the eye-muscles could not have caused the facial asymmetry. The suggestion that the weight of the body of the fish when turned over on its side aided in pushing the eye over onto the other side, apparently can not be invoked to explain the appearance of asymmetry in the development of the individual, at least, since there seems to be no particular tendency on the part of the larval fishes to turn over on its side until after the eye has begun its migration. This is true of some species at any rate, for Williams† states that the specimens which he captured and kept in the laboratory during the metamorphosis showed in resting no preference for either side until the eye was near the mid-line. If it seems unlikely that larval fishes could have been modified in this way, it seems even more improbable that the hypothetical symmetrical ancestor in the adult form when the bones and other structures had become fixed should have become modified in any such way. Objections of a more general nature against the above explanations are the objections which can be alleged against any theory involving the assumption of the inheritance of acquired characters, but such detailed criticisms of this theory of course have no place in this paper.

The question of the origin of the modifications of the flat-fishes inevitably involves the general theories of evolution. Here it will be possible, to consider only very briefly, the bearing of these theories upon this problem. The development of the flat-fish, as briefly outlined above, shows that the asymmetry does not express itself outwardly until some days after the fish is out of the egg, yet there is evidence which seems to substantially sanction the inference that for its origin in ontogeny, the asymmetry goes back to the germ. That there is some real difference between the organization of the

* Op. cit.

†Reference to the work cited will be found in the foot-note to page 79.

eggs of the right-handed species and those of the left-handed species is shown by the fact that the eggs of most of the right-sided species have no oil-globule, while the eggs of most of the left-sided species have a single oil-globule. This applies to the Flounder family only, and is not true of the Soles (*Solida*). It is difficult to imagine that the presence of the oil-globule has any reference to the external conditions, since the eggs of all the species of flat-fishes (except those of the Winter Flounders *Pseudopleuronectes*) are pelagic and, therefore, apparently at least, subject to similar conditions. This apparent relation between right and left-sidedness and the presence of the oil-globule may, of course be a mere coincidence, yet the facts are so striking that it does not seem to be doing violence to reasonable inference if we believe that such a coincidence is a significant one and based on a real difference in germinal structure. If this is true, then the asymmetry of the fish must be inherent in the germ.

There is another line of evidence, of much greater force, which seems to point unquestionably to the germ as the source of these modifications. The relation of the optic nerves in the chiasma in fishes has been studied by Prof. G. H. Parker. In the bony fishes the optic nerves cross each other in the chiasma without any intermingling of fibers. In the ordinary bony fishes it is apparently a matter of chance whether the right or left nerve is above the other in the chiasma. In 1,000 specimens of ten common species, 486 had the left nerve uppermost and 514 the right nerve. In individual species, similar figures hold true; for example in the haddock, 48 had the left nerve uppermost, and 52 the right nerve. In the flounders, however, a different law holds true and the arrangement of the nerves in the chiasma is not a matter of indifference. Of flounders with eyes on the left side, 131 individuals, representing nine species, all have the right nerve uppermost. Two hundred and thirty dextral flounders, representing sixteen species, had the left nerve uppermost. This is not true of the soles, however; in them the arrangement of the chiasma is apparently a matter of chance as in other bony fishes and has no relation with the asymmetry of the

fish. But in the case of flounders, it seems to be always true that the optic nerve growing out to form the eye that is later to migrate over to the other side always passes above the other in the optic chiasma. The only exception to this is in the case of reversed flounders in which the relation of the nerves in the chiasma conforms to that of the species and does not deviate with the exceptional reversal. The case seems to be analogous to that of some of the snails in which it is possible to trace the asymmetry back to the eight-celled stage of the embryo, except that here, at the present time at least, it is not possible to demonstrate the asymmetry at nearly so early a stage.

It is the necessary implication of the Lamarekian hypothesis that the adaptative modifications acquired through "use and disuse" must appear in, and, originally at least, have their source in, that stage in the development of the individual which is affected by the change of environment; the "use and disuse" of an organ or part would not be called into play in any other stages, and so could not directly produce modifications in them. Thus, in the case of flat-fishes, the change to a bottom existence takes place after the free-swimming stage has been assumed. Their modifications must be adaptations to conditions of life first encountered in that stage and can not be referred back for their origin to any earlier stage or to the germ. Of course we must allow that the potentiality of producing the modifications of the late stages must be present in the earlier stages and in the germ, though there is no apparent reason for assuming that the modifications themselves are projected back to any earlier stage than that at which they are called out by the reaction to the environment. No germinal modifications arising in the egg itself is demanded in this case, for it encounters no new conditions because the eggs of all flat-fishes (with one exception) are pelagic and, therefore, subject to conditions which, as far as we can see, are not different from those of many other fishes. Lamarekian theories, then, as applied to the flat-fishes, must be considered to imply that the modifications found in the adult have been superposed

upon the original symmetrical constitution of the fish at some time in the larval stage as a result of conditions acting on that stage. If we look to the germ, then, we should find in it no evidences of asymmetry, if the Lamarekian theory be the true hypothesis. But, on the contrary, evidence adduced above has shown that there is an asymmetry in the egg which could not have been produced by external forces and which appears at so early a stage that it could not have been produced by the direct effect of "use and disuse." The argument of the Lamarekians, in order to escape from this difficulty would be, of course, that the modifications of the larval and adult stages, which had become fixed by the cumulative effect of repeated actions, became reflected back into earlier and earlier stages until finally the germinal organization itself had become definitely and permanently affected. Of course there is no evidence at present known which will enable anyone to deny positively that such might be the case or that it might thus be capable of explaining the facts in question, but it would certainly seem that the theory would have to be stretched beyond its limits if we are required to believe that if a flat-fish turns over on its right side until the tendency became fixed, the effect of this process on the germinal structure would be to produce an oil-globule in the egg, while if the fish turns over on its left side through a sufficient number of generations, the effect is such as to produce no oil-globule in the egg. It is scarcely less difficult to admit that the asymmetry having become fixed in the larva and adult stages as a result of voluntary attempts at adaptation through a series of generations might become reflected back into such a very early period in the germ as to affect the direction of the growth of the eye-stalk which, at any time, is only indirectly affected by "use and disuse" and only at a very much later stage. But even if we admit this as a possibility, it seems difficult to reconcile this hypothesis with the condition found in the soles, in which the asymmetry has gone considerably further, but has not been able to bring about any constant relation of the optic nerves in the chiasma.

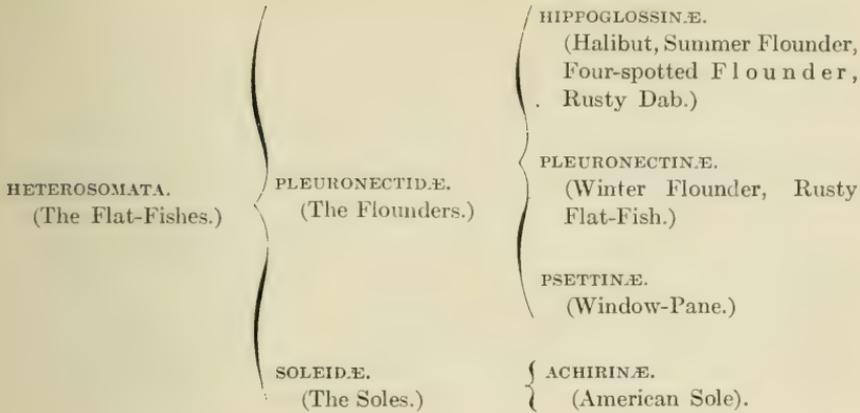
Thus the Lamarekian explanations of the asymmetry of the flat-fishes seem to be difficult to accept, since the necessary mechanical requirements are not met by the bone and muscle arrangements of the head, and because it is difficult to consider the "use and disuse" theory as accounting satisfactorily for the evidences of asymmetry in the germinal organization. The more fundamental difficulties which are inherent in any Lamarekian hypothesis would, if it were possible to consider them here, give still greater force to these objections. It is sufficient to say that the lack of evidence in support of alleged cases of inheritance of acquired characters gives such force to the *a priori* objections to that theory that, on general grounds alone, we would be justified in rejecting Lamarekian explanations of the origin of the modifications of the flat-fishes.

A much more satisfactory hypothesis to account for the structural modifications of the flat-fishes is that furnished by the theory of natural selection. This theory as applied to the flat-fishes can be accepted at the present time with much better grace than was possible before the theory of mutation had been suggested. The flat-fishes present a problem which is an excellent example of a class of cases which have long been a *bête noir* to the theory of natural selection. It has not been easy, previously, to understand how slight tendencies of symmetrical fishes to assume other than the upright position could confer upon their possessors such advantages in the struggle for existence that natural selection could have been an effective factor in causing their survival. But according to the mutation theory we may assume that a considerable degree of the characteristic modification of flat-fishes was produced all at once as a result of some alteration in the structure of the germ cell; this is consistent with the facts of the case, since evidence adduced above indicates that we are to look for the source of the origin of these characters in the germ cell. These changes or mutations might be great enough to make the new form differ from the old so far that it was enabled to secure a somewhat greater advantage in the struggle for existence by becoming more closely adapted to a bottom existence

than the old forms and thus to appropriate for itself a hitherto unclaimed field for its home. Thus natural selection could act and allow the new forms to become permanent. These early modifications having been established, further changes then may be assumed to have arisen by continued mutation and become fixed by natural selection and ultimately to have produced the great variety of existing species and their adaptation to the varying conditions of bottom existence.

According to this theory, the ultimate source of the modifications of the flat-fishes is to be looked for in the germ cell and in the unknown factors which caused essential changes in the germinal structure of the egg of the symmetrical ancestor of the flat-fishes. Just what this change was, to what cause it was originally referable, how the structure of the germ-cell of the asymmetrical fishes differs from that of the symmetrical fishes, such questions must be left until the theory of evolution by mutation has so far advanced that it can show how mutations result from the conditions which influence germinal structure.

From the systematic point of view, the flat-fishes are grouped together as a suborder called the *Heterosomata*; they are further divided into two families, the Flounder family (*Pleuronectidæ*) and the Sole family (*Solidæ*). The so-called American Sole is the only common representative of the Sole family in American North Atlantic waters; all the other common flat-fishes belong to the Flounder family. The species belonging to the Flounder family may be grouped into three sub-groups or tribes, the Halibut tribe (*Hippoglossinæ*), the Flounder tribe (*Pleuronectinæ*), and the Turbot tribe (*Psettinaæ*). Their classification may be put into synoptic form as follows:



The ancestry and kinship of the flat-fishes are wholly uncertain. They have usually been placed with the cod-fishes, and it has been assumed that both these groups have descended from some common or nearly related form; it is, however, with much reason that Dr. Boulenger has recently called attention to the close relationship of the flat-fishes to the Zeoidea (the John Dories, or Zeus-like fishes), and he suggested that both these types may have descended from a common stock.

There are some interesting facts regarding the geographical distribution of the various species of the flat-fishes. The fishes of the Flounder tribe (*Pleuronectinæ*) and almost all of the Halibut tribe (*Hippoglossinæ*) are arctic and antarctic in their distribution; the species belonging to the Turbot tribe (*Psettinæ*) are nearly all confined to warm water. Since all the fishes of the Turbot tribe, and those of the Halibut tribe which are found in warm water are left-sided species, while the cold-water halibuts and all of the Flounder tribe are right-sided species, it follows that nearly all the warm-water flounders are left-sided species and the cold-water flounders are right-sided. This peculiar relation may be a coincidence merely, but it is certainly very remarkable that we should find the Summer Flounder and the Four-Spotted Flounder and a few other species of that group to be left-sided and in warm water, while the majority of the fishes of that tribe are right-sided and inhabit cold

water, and that this should agree exactly with the conditions in the Turbot tribe, on the one hand, and the Flounder tribe on the other. There are some of the Californian flat-fishes which, as we might perhaps expect, may perhaps be considered to form transition groups: some species of those waters are right-sided and some are left-sided, and in some species it seems to be true that the fishes are indifferently right or left, or at least reversed individuals are common. These interesting facts suggest to us that natural selection may favor sinistral fishes in the tropics and dextral fishes in cold water. It is difficult to imagine this, though right- and left-handedness may be dependent on conditions in the environment of which we know nothing.

Another remarkable condition is the relation which seems to exist between the number of vertebræ possessed by the various species and their geographical distribution. It is true of other groups of fishes that in some cases their northern representatives have an increased number of vertebræ, but this relation is shown in a striking way in the Flounder family. The following are the averages of the numbers of vertebræ found in the species of the three tribes of the Flounder family:

Flounder Tribe (*Pleuronectinæ*).

Average number of vertebræ in 13 species, 42.

All these species live in northern waters.

Halibut Tribe (*Hippoglossinæ*).

Average number of vertebræ in 15 species, 41.

Of these 15 species, 4 are cold water and 9 occur along the Californian and Middle Atlantic and Gulf Coasts.

Turbot Tribe (*Psettinæ*).

Average number of vertebræ in 20 species, 34.6.

These are tropical or sub-tropical species.

The causes of this remarkable relation are not fully understood. It has been suggested that the reduction in the number of vertebræ of the warm-water species is a result of the higher specialization demanded of those fishes living in the tropics where the struggle for

existence is more strenuous, because of the greater abundance of life in those waters.

In Rhode Island waters are found eight species of flat-fishes which represent the chief groups of the suborder *Heterosomata*. The technical description of the tribes, genera, and species follows:*

A. PLEURONECTIDÆ. The Flounder Family.

Preopercula margin distinct, and not hidden by scales; eyes large and well separated; mouth large or moderate; teeth present.

I. HIPPOGLOSSINÆ. The Halibut Tribe.

Large mouthed flounders with ventral fins symmetrical; jaws and teeth nearly equal on both sides. Pectoral and ventral fins well developed, the ventral fins similar in position and in form of base, the ventral fin of the eyed-side and not being attached along the ridge of the abdomen.

HIPPOGLOSSUS. Halibut.

Eyes and color on the right side. Form oblong, not strongly compressed. Mouth wide, oblique; teeth in the upper jaw in two series, those below in one; anterior teeth in upper jaw and lateral teeth in lower, strong; no teeth on vomer or palatines; lower pharyngeal teeth in two rows. Dorsal fin beginning above the eye, its middle rays elevated, the posteral rays of dorsal and anal bifid; cordal fin lunate; ventral fins both lateral. Scales very small, cycloid; lateral line arched in front. Gill rakers few, short, compressed, wide set, vertebræ 16+34. Largest of the flounders.

1. *Hippoglossus hippoglossus*. *The Halibut*.

Body elongate, not strongly compressed, deep mesially; head broad; eyes large, separated by a very broad flattish area; the lower eye slightly advanced; mouth large, maxillary reaching middle of orbit. Depth of body one-third its total length; head moderately

*The technical description of these fishes has been taken from "The Fishes of North America," by Jordan and Evermann.

long, its length contained $3\frac{3}{4}$ times in total length. D. 105; A. 78; P. 19; V. 6; scales 150+. Color, nearly uniform dark brown; blind side white.

HIPPOGLOSSIDES.

Eyes and color on the right side. Body oblong, moderately compressed; mouth rather large, with one row of sharp teeth on each jaw; no teeth on vomer or palatines; gill rakers rather long and slender; scales etenoid; lateral line straight; dorsal fin low in front, beginning over or before the eye; ventrals both lateral; caudal double truncate, produced behind.

2. *Hippoglossoides platessoides.* *The Rough Dab.*

Body ovate; mouth moderate, oblique; maxillary narrow, reaching to below pupil, $2\frac{2}{3}$ in length of head; teeth rather small, conical, larger anterior in one row in each jaw, those in the lower largest. Eyes rather large; the lower jaw included, but with a projecting knob at the chin; snout thick, scaly. Interorbital space narrow, with a raised obtuse ridge entirely covered with rough scales in about six series; mandible with a series of scales; gill rakers rather short and robust, not toothed, about ten below angle, the longest less than one-third length of eye; fins with small, rough scales; a strong preanal spine; pectoral not quite one-half length of head. Head contained $3\frac{3}{4}$ times in length of body; depth, $2\frac{1}{2}$ times in body. D. 88; A. 70; scales 90 (pores). Color reddish brown, nearly plain.

PARALICHTHYS.

Eyes and color on left side. Body oblong; mouth large, oblique; each jaw with a single row of usually slender and sharp teeth, which are more or less enlarged anteriorly; no teeth on vomer or palatine. Gill rakers slender. Scales small, weakly etenoid or ciliated; lateral lines simple, arched anteriorly. Dorsal fin beginning before the eye, its anterior rays not produced; both ventrals lateral;

caudal fin double truncate, or double concave, its middle rays produced; no anal spine.

3. *Paralichthys dentatus.* *The Summer Flounder.*

Head contained $3\frac{1}{2}$ to 4 in body; depth 2 2-5; caudal $1\frac{1}{4}$. D. 86-91; A. 65-71; lateral line 108 (tubes). Body ovate; maxillary reaching past posterior margin of eye; mouth large, oblique, the gape curved. Canines large, conical, wide set; gill rakers comparatively long and slender, longest two-thirds eye, $5 + 15$ to $6 + 18$ in number; interorbital area a rather flattish ridge, in the adult about equal to vertical diameter of eye, narrower in the young, forming a bony ridge; scales cycloid, each with numerous small accessory scales; vertebræ $11 + 30$. Color in life, light olive brown; adults were very numerous, small white spots on body and vertical fins; sometimes a series of larger white spots along basis of dorsal and anal fins; about 14 ocellated dark spots on side, these sometimes little conspicuous, but always present; a series of four or five along base of dorsal, and three or four along base of anal, those of the two series opposite, and forming pairs; two pairs of smaller less distinct spots midway between these basal series and the lateral line anteriorly, with a small one on lateral line in the center between them; a large distinct spot on lateral line behind middle of straight portion; fins without the round dark blotches.

4. *Paralichthys oblongus.* *Four-spotted Flounder.*

Head contained four times its body; depth $2\frac{1}{4}$ of body. D. 72; A. 60; Scales 93. Body comparatively elongate, strongly compressed. Eyes large, nearly four in head, separated by a prominent, narrow, sharp ridge. Upper jaw with very numerous small, close-set teeth laterally, and four or five canines in front; the lateral teeth abruptly smaller than the anterior; each side of lower jaw with seven to ten teeth. Chin prominent. Maxillary narrow, reaching past middle of pupil, $2\frac{1}{4}$ in length of head. Gape curved; gill rakers short and toothed behind, $2 + 8$. Scales weakly ctenoid or cycloid.

Dorsal low, beginning over front of eye, some of the anterior rays exerted, but not elongate the longest rays behind middle of fin, not quite one-half head; anal spine obsolete. Grayish, thickly mottled with darker and somewhat translucent; four large, horizontally oblong, black ocelli, each surrounded by a pinkish area, one just behind middle of the body below the dorsal, one opposite this above anal, two similar smaller spots below last rays of dorsal and above last of anal.

II. PLEURONECTINÆ. The Flounder Tribe.

Mouth small, unsymmetrical, the jaws on the eyed-side with nearly straight outline, the bones on the blind strongly curved; dentition chiefly developed on the blind side; eyes large; pectoral fins well developed; vertical fins well separated; ventral fins nearly or quite symmetrical, that of the eyed-side not prolonged along the ridge of the abdomen; anal spine usually strong. Body dextral.

LIMANDA.

Teeth chiefly uniserial; lateral line with a distinct arch in front, and without accessory dorsal branch; scales imbricated, rough etenoid; vertebræ about 40. Differs from *Pseudopleuronectes* by the arch in the lateral line.

5. *Limanda ferruginea*. *Rusty Dab*.

Head 4 in length, depth 2 1-5. D. 85; A. 62; Scales 100. Body ovate-elliptical, strongly compressed; teeth small, conical, close-set, in a single series on each side in each jaw, about 11 + 30 in the lower jaw; snout projecting, forming a strong angle above upper eye, with descending profile; gill rakers of moderate length, very weak, not toothed; eyes moderate; the lower slightly in advance of upper, separated by a high very narrow ridge, which is scaled posteriorly, and is continued backward as an inconspicuous but rough ridge to the beginning of the lateral line; scales imbricate, nearly uniform, those

on the right side rough ctenoid, those on the left side nearly or quite smooth; scales on body rougher than cheeks; caudal peduncle short, higher than long; dorsal inserted over eye, its middle rays highest; pectoral less than two-fifths head; caudal rounded; anal spine present; lateral line simple, with a rather low arch in front; a concealed spine behind ventrals; ventral of colored side partly lateral, the other wholly so; anal spine strong. Brownish olive, with numerous, irregular, reddish spots; fins similarly marked; left side with caudal fin, caudal peduncle, and margins of dorsal and anal fins lemon yellow.

PSEUDOPLEURONECTES.

Body oblong; the scales firm, strongly ctenoid on eyed side in both sexes; fin rays scaly; mouth small; teeth uniserial, incisor-like, close set, all more or less blunt; the lower pharyngeals very narrow, each with two rows of separate, conical teeth. This genus is distinguished from *Limanda*, which it closely resembles, by the want of arch in the lateral line.

6. *Pseudopleuronectes americanus*. *The Winter Flounder*.

Head four times in length; depth $2\frac{1}{4}$. D. 65; A. 48; Scales 83. Body elliptical; an angle above eye. Head covered above with imbricated, strongly ctenoid scales, similar to those on the body; blind side of head nearly naked; interorbital space rather broad, strongly convex, its width one-half eye, entirely scales; teeth compressed incisor-like, widened toward tips, close set, forming a continuous cutting edge; some of teeth often emarginate, sometimes movable; right side of each jaw toothless. Highest dorsal raised less than length of pectorals, and more than one-half length of head; anal spines present. Dark rusty brown, spotted or nearly plain; young are olive brown, more or less spotted and blotched with reddish.

III. PSETTINÆ.

Large mouthed flounders, with the ventral fins unsymmetrical. Mouth symmetrical; gape wide; lower pharyngeals narrow, with

rows of small sharp teeth; teeth on jaws, acute; eyes not minute; pectorals and ventrals well developed; ventral fins dissimilar in form and position, that of the left side inserted on the ridge of the abdomen, its base extended along this ridge, its rays more or less wide apart; vertebræ in moderate or small number, 31 to 45. Body sinistral. Species chiefly tropical or subtropical.

LOPHOPSETTA.

Eyes and color on the left side. Body broadly ovate, strongly compressed, pellucid; mouth large, oblique, the maxillary reaching to beyond eye; teeth subequal, in narrow bands, or in single series; a small patch of teeth on the vomer. Scales small, cycloid, imbricate, the skin without bony tubercles. Lateral line strongly arched in front, without accessory branch. Dorsal fin beginning on the snout, its anterior rays exerted; anal fin not preceded by a spine; ventral of left side free from anal inserted nearly on the ridge of the abdomen, its base broad, the rays well separated; pectoral and ventral fins moderate. Nearly related to the European genus *Bothus*, and to the European Turbot, *Psetta*.

7. *Lophopsetta maculata*. *The Window Pane or the Sand Dab*.

Head $3\frac{1}{2}$ in length; depth 1 3-5. D. 65; A. 52; Scales 85. Body broadly rhomboid, strongly compressed, translucent in life; mouth large, the maxillary reaching nearly to posterior margin of eye, maxillary of eyed side with a bony tubercle on its anterior end; jaws subequal, the lower with a sharp knob at symphysis; teeth in each jaw in one series laterally, in a very narrow band in front; interorbital space rather broad, slightly concave, its posterior third or fourth with scales; gill rakers short and slender, about 8 + 25; maxillary, mandibles, snout, and the greater part of interorbital naked; scales on head and body cycloid, loosely imbricated, those on the blind side a little smaller. Anterior rays of dorsal produced, their ends branched and free, the first on tip of snout, the rays at the beginning

of posterior third of fin the highest; origin of anal directly under angle of preopercle; base of ventrals long, that of the eyed side extending along ridge of body from notch in isthmus to front of anal, base of ventral on blind side shorter; pectoral reaching past curve on eyed side, its mate much smaller; cordal rather long. Color light olive brown, almost translucent, everywhere marbled with paler, and with many small, irregular, sharply defined black spots; dorsal, anal, and caudal with larger, round, blended spots of dark brown; pectoral with brown, interrupted cross lines.

B. SOLEIDAE.

Body oblong or elongate, usually scaly; mouth very small, much twisted toward the eyed side; the teeth in villiform bands, very small or obsolete; eyes small, close together, with or without a bony ridge between them; edge of preopercle adnate, concealed by the skin and scales; the gill openings narrow, the gill membranes adnate to the shoulder girdle above; pectoral fins small or wanting; ventral fins small, one or both sometimes wanting. Vertebræ usually in increased numbers. Similar to the *Pleuronectidæ* in structure, but much degraded, the fins and teeth having lost many of their distinctive qualities. They are naturally divisible into three sub-families, each quite distinct from the others, and possibly independently descended or degraded from normal *Pleuronectidæ*.

ACHIRUS.

Eyes and color on the right side. Body oblong, bluntly rounded anteriorly. Head small; eyes small, close together, the upper eye in advance of the lower, the two separated by a bony ridge; mouth small, somewhat turned toward the colored side; nasal flaps present, the nostril of the blind side fringed; lip of the colored side fringed; teeth very small, on blind side only; the gill openings rather narrow, but confluent below, not reduced to a slit; the branchiostegal region scaled. Head closely scaled everywhere; scales on the blind side

anteriorly with their pectinations more or less produced forming cirri; scales with both sides extremely rough, extending on the fins. Lateral lines straight, simple; edge of preopercle covered by the scales. Dorsal beginning on the snout, low in front and thickly scaled, its rays divided; anal fin similar without spine; caudal fin convex; caudal peduncle very short and deep; pectoral fin of left side wanting, that of right side small or obsolete; ventral rays three or four, the ventral fin of the colored side long, connected with anal by membrane.

8. *Achirus fasciatus.* *The American Sole.*

Head 4 in body; depth 1 4-5. D. 50-55; A. 37-46; Scales 66-75. Body broad, irregularly elliptical; mouth moderate, reaching just past front of lower eye; right lower lip fringed; eyes very small, the upper one in advance of the lower; nostril ending in a wide tube, nearer lower eye than tip of snout; interorbital space with scales, more than one-half eye; head and body scaled with strongly ctenoid scales, none of them with hair-like appendages; lateral line nearly straight; gill opening short, about twice as long as maxillary. Origin of dorsal on tip of snout; last few rays of dorsal and anal rapidly decreasing, giving the fins a truncate appearance posteriorly; pectorals wholly wanting; caudal rounded. Color dusky olive, more or less mottled, and with about eight dark, vertical stripes, these varying very much in width and in number; blind side often with round, dark spots, specially northern specimens usually immaculate in southern ones. Vertebrae 8 + 20.

The following artificial key, based on the most obvious external characters, may be useful in distinguishing these species:

A.—RIGHT-SIDED SPECIES.

I. MOUTH LARGE, SYMMETRICAL.

1. **The Halibut.**

Lateral line with an arch in front; size very large; scales smooth.

2. The Rough Dab.

Lateral line straight; scales rough;
length 20 inches or less.

II. MOUTH NOT LARGE, UNSYMMETRICAL, AND AT END OF SNOUT.**3. The Rusty Flat-Fish.**

Lateral line with arch in front.

4. The Winter Flounder.

Lateral line straight.

III. MOUTH VERY SMALL, VERY UNSYMMETRICAL, THE SNOUT PROJECTING BEYOND THE MOUTH.**5. The American Sole.**

Dusky olive in color, mottled, with several dark vertical stripes; the under side usually has a large number of round, dark spots.

B.—LEFT-SIDED SPECIES.**I. VENTRAL FINS NOT ON THE RIDGE OF THE ABDOMEN; BODY OBLONG; COLOR DARK.****6. The Summer Flounder.**

Color olive brown, profusely mottled with white, dark and ocellated spots.

7. The Four-Spotted Flounder.

Color grayish, mottled with darker spots; four large, oblong, black, ocellated spots on posterior half of body.

II. VENTRAL FIN OF LEFT SIDE PLACED NEARLY ON THE RIDGE OF ABDOMEN; BODY OVATE AND EXTREMELY THIN.

S. The Window Pane or Sand Dab.

Light olive brown in color, translucent, marbled with paler and with many small dark spots.

The remainder of this paper is intended to present, as fully as space will allow, the most important facts which have been ascertained regarding the life history and life conditions of those individual species of flat-fishes which are present in Rhode Island waters. Pictures of these species are shown in Plates I to IX.*

THE HALIBUT.

(*Hippoglossus hippoglossus*.)

PLATE I.

I. *Distribution and Habitat.* The natural habitat of the halibut is in the cold water of the northern seas; it is widely distributed along both shores of the North Atlantic and the North Pacific, and it ranges well up into the Arctic regions. The water in which it is most frequently found is never of a higher temperature than 45° F., and often but little above 32° F. The northern limit of its range has never been determined; it occurs along the whole west coast of Greenland, is abundant at Iceland and Spitzbergen, and has been observed on both sides of the North Cape. In the Pacific, halibut are most abundant in the Gulf of Alaska, and they have been taken as far north as Behring Straits. There is no reason for doubting that the southern shores of the Arctic Ocean along both continents

* Plates I to VI and Plate VIII and IX are reproduced from Goode's "Natural History of Aquatic Animals," 1884; Plate VII is reproduced from "American Food and Game Fishes," 1902, by Jordan and Evermann.

are inhabited by this species. Its usual southward range on the European coast is to the English Channel, but stray specimens have sometimes been taken in deep water off the coast of France. On the American coast of the Atlantic, its natural southerly limit is Cape Cod, but occasional individuals wander southward to Sandy Hook. It is said that halibut were formerly quite abundant about Vineyard Sound and Block Island, but for many years they have been very rare south of Cape Cod. There is no record of a capture of a halibut south of Sandy Hook, where several large ones have been captured in winter. On the Pacific coast, they range southward to the Farallones off San Francisco. The geographical range of the halibut coincides closely with that of the cod, though the latter is somewhat less confined to cold, since it ranges 4° or 5° F. further south; the cod, also, in winter is very abundant off the southern shore of New England where the halibut is very rare, while the halibut also strays further out into deeper and colder water than the cod.

In Rhode Island waters only a few instances of the capture of halibut have been recorded in the last quarter of a century. In February, 1876, a few were taken about eight miles from the southeast point of Block Island; on May 1, 1876, off Watch Hill, an eighty-pound halibut was taken, the first in that vicinity for many years; during that same month many halibut were taken about ten miles southeast of Montauk Point; one or two in the last sixty years have been taken off the outer shore of Fisher's Island; on April 16, 1900, a one-hundred-pound halibut was brought to Newport which had been captured with others off Block Island by a cod fisherman.

The normal habitat of the halibut is upon the offshore banks and the edges of the continental slope; it is found in all depths ranging from shoal water near shore out to a depth of three hundred fathoms or more. It seems to be most abundant at considerable depths, from fifty to one hundred fifty fathoms.

In the course of the last century the center of the abundance of this species seems to have shifted many times. A hundred years

ago halibut were exceedingly abundant in Massachusetts bay.* From 1830 to 1850 they were very abundant on George's Banks; since 1850 they have partially disappeared from this region, and the fishermen have been constantly following them to other banks and out into deeper and deeper water. Since 1874 the fisheries have been carried on almost exclusively in the gulleys between the off-shore banks and on the outer edges of the banks in water one hundred to three hundred fifty fathoms in depth.

II. *Migrations.* Very little is definitely known regarding the migrations of the halibut. Throughout the year they are present on the edges of all the banks from George's to the Grand Bank in deep water from a hundred to two hundred and fifty fathoms. Whatever annual migrations they undertake are probably not extensive, but, as far as can be ascertained, are limited to relatively small movements between deep and shallow water according to the seasonal changes of the temperature. The only consideration pointing definitely to such a movement is the fact that during winter and early spring halibut are sometimes found to be more numerous in shallow water. They are also found further south during the colder months of the year, as is shown by the fact that the months from February to May include the only authentically recorded cases of halibut in water south of Cape Cod. This seasonal movement, however, can be only very slight in extent, and apparently does not take place with any regularity.

In the preceding section, mention was made of the fact that there is a larger, more extensive, movement, in which the halibut are moving constantly into deeper and deeper water. The only explanation suggested for this is that the halibut live in large schools, and as soon as they have exhausted the food supply in any particular locality, they move on to fresh feeding grounds. None of their migrations have any apparent connection with their reproductive activity.

III. *Reproduction.* Comparatively little is known with regard

* Goode, Na. Hist. of Aquatic Animals, 1884.

to the spawning habits of the halibut. The testimony of observers seems to indicate a spawning season in American waters lasting through the summer and into the autumn. On the European coast, according to Cunningham, the halibut spawns from April to August, and the period may extend somewhat in both directions.*

Ripe eggs of the halibut have been seen only rarely, while the fertilized eggs of this species are entirely unknown. McIntosh† describes some fresh and apparently ripe eggs which were taken in May, 1892. Their diameter ranged from 3.07 mm. to 3.81 mm. (3-20 inch). The yolk was colorless and translucent; there was no oil globule. The capsule egg was very thin and collapsable. Another sample of ripe eggs was secured the same year; these averaged from 3.4 mm. to 3.7 mm. in diameter. On the 5th of May, 1893, half a gallon of ripe eggs was obtained from a fish from Bergen Bank; the diameter of these averaged from 3.08 mm. to 3.8 mm. These eggs were apparently buoyant when alive; they are thus perhaps the largest pelagic eggs known. As yet there is no record that any scientist has ever examined ripe eggs of halibut from American waters.

The earliest known stage of the halibut is that described by Dr. Peterson of the Danish Zoölogical Station. It was procured in Christiansand; it measured 32 mm. (1 3-8 inch). This was still in the free-swimming condition, as was indicated by the position of the left eye, which had only just commenced to move forward and upward; it had 104 rays in the dorsal fin, 88 in its anal, 22 in its caudal; the mouth was large and the gill cover had a row of spines.‡

Young halibut about 12 inches long, 3 3-4 inches across at the widest part, have occasionally been found in the water of shallow bays, like that of St. Andrews; this seems to indicate that after passing their earliest stages in deep water, they seek shallow water for a certain portion, at least, of their adolescent period, and then

* Marketable Marine Fishes, 1896, 243.

† British Marine Food-Fishes, 1897, 315.

‡ British Marine Food Fishes, 1897, 318. This specimen was first mentioned by Collet in his "Norges Fiske" (Plate XII, Fig 10).

pass back again to the deep water in their adult condition. In color, the young forms mentioned above are dull olive marbled with darker blotches, and also with reddish spots and touches on the body and fins. In America none of the young stages have been recorded.

Nothing is known of the rate of growth of the halibut. The smallest known specimen from our coast was about five inches long; this was dredged by Prof. Verrill in the Strait of Canso.

IV. *Food.* The halibut is, like the cod, a voracious and omnivorous feeder. The most important portion of their diet probably consists of crustaceans like crabs, lobsters, etc., and molluscs, such as clams, muscles, snails, etc. They also feed largely upon fishes, particularly flat-fish and flounders. Young cod, haddock, and cusk, are also very commonly eaten by them. Young halibut feed upon shrimp and young flat-fishes.

V. *Size.* The halibut is among the largest of the bony fishes; it is surpassed in size only by the swordfish, the horse mackerel and tarpon. The male is said to be seldom over fifty pounds in weight, while the average sized female is probably between 100 and 150 pounds. A number of exceptionally large individuals are authentically recorded. In July, 1879, two individuals were taken near Race Point, one of which weighed 359 pounds, the other 401 pounds. Goode states that he has record of ten or twelve taken on the New England coast between 1870 and 1880, each of which weighed between 300 and 400 pounds. Nilsson, the Swedish ichthyologist, mentions a halibut taken on that coast which weighed 720 pounds.

THE ROUGH DAB.

(*Hippoglossoides platessoides.*)

PLATE II.

I. *Distribution and Habitat.* In its range and distribution this species is much like the halibut. It is found on both coasts of the Atlantic, and from the arctic regions ranges south to Long Island

and the coast of England. It is common in forty fathoms of water off the coast of Iceland. Its habitat is, however, more limited than that of the halibut, since it occurs only in rather deep water; it is rarely taken from water less than twenty fathoms, but on the other hand it does not descend to such great depths, since it is not known to be present beyond eighty fathoms. It is a rather common food fish in northern waters, particularly in England and Scandinavia, though it is never very abundant anywhere. In summer it is found only in deep water, but in winter it approaches nearer the coast. It is not abundant enough in Rhode Island waters to make it of any importance in this locality as a food fish. It has doubtless been taken in winter many times without being discriminated by the fishermen from other species; it is not unusual in deep water off southern Massachusetts and Rhode Island. It is not common at Woods Hole, though it has been taken in winter in shallow water.*

II. *Reproduction.* For practically all our knowledge regarding the habits of this fish we are indebted to European observers. The following account of its eggs and spawning habits is on the authority of McIntosh and Masterman,† and of course refers to observations on the European variety (*limandoides*). In British waters specimens of this species with ripe eggs are found from February to May, and are most numerous in March. On the Scandinavian coast the spawning season is apparently during February and March.

The eggs of this species had been known since 1884, but were not definitely identified until 1895. The egg is buoyant and translucent, and when first extruded from the oviduct measures about 1.2 mm. (1-20 inch). After being in sea water for about twelve hours, a considerable amount of water is taken up inside the outer capsule so that the diameter of the egg increases and becomes about 1.8 mm. (1-14 inch). The eggs hatch in about fourteen days.

III. *Food.* In the tenth Report of the Scottish Board of Fisheries are given the results of examination of the contents of 569 stomachs

* Proc. U. S. Mus., 1880, 471.

† Smith, Fishes of Woods Hole, Bull. U. S. Fish Com., 1897, 108.

of this species taken from the Firth of the Fourth. The different kinds of marine animals found occurred in the following percentages: crustacea in 44 per cent. (shrimp of various kinds, hermit crabs, swimming crabs); echinoderms in 22 per cent. (sandstars, brittle stars, common starfish); fishes in 14 per cent. (gobies, whittings, young dabs); marine worms in 9 per cent.; molluses in 6 per cent.*

IV. *Size.* In American waters this fish exceptionally reaches a length of 20 to 24 inches; its weight ranges from 2 to 5 pounds. Dr. Fulton found that off the east coast of Scotland the smallest ripe male was 5 inches long, while the average length of mature males was 6.5. The smallest ripe female was 5 inches long, the largest 16.5 inches, with an average length of 8.8 inches.

THE SUMMER FLOUNDER.

(*Paralichthys dentatus.*)

PLATE III.

I. *Distribution and Habitat.* This fish is confined to the American coast of the Atlantic, and is more particularly a warm-water fish than most of the common species of the family. It ranges from Cape Cod to Florida, though it is rare south of Charleston. The center of its abundance seems to be in the waters about Rhode Island, Connecticut, and Long Island, where it is taken in very large numbers during the summer.

The fish of this species begin to appear in inshore waters in May and are taken in water from 2 to 20 fathoms in depth until October. They then move out into deeper water for the winter. Unlike the winter flounder, which has a preference for grassy and muddy bottoms, the fishes of this species are apparently more abundant where the bottom is sandy. They are somewhat gregarious in their habits, but like most of the species of this family, they do not possess this tendency in any marked degree. Their movements are probably

* Cunningham, op. cit., 244

adjusted in accordance with seasonal changes of temperature and also with the variations in the abundance of food in particular localities.

II. *Reproduction.* Practically nothing is known of the breeding habits of this species. It has never been found with mature eggs, nor is there any record that anyone has ever seen any of the younger stages. Goode states that the smallest specimens certainly known were eight or nine inches in length. The above considerations seem to indicate the probability that the summer flounder spawns in deep water away from the shores in the winter, and that the young do not enter shallow water until they have reached an advanced stage of development.

III. *Food.* Their food is like that of most of the flat-fishes; it consists of small fishes, crustaceans, molluses, sand-dollars and squid. Specimens taken from trap usually have such fishes as butter-fish and scup in their stomachs, though these they have probably eaten from necessity on account of the artificial conditions under which they are confined.

IV. *Size.* The average length is from 16 to 30 inches, and the average weight about $2\frac{1}{2}$ pounds. Exceptionally it reaches a length of 3 feet and a weight of 15 pounds.

THE FOUR SPOTTED FLOUNDER.

(*Paralichthys oblongus.*)

PLATE IV.

I. *Distribution and Habitat.* The limits of the geographical range of this species have never been very accurately determined. Its distribution is apparently very limited, since it is not recorded south of New York and has been taken only very rarely north of Cape Cod. In 1877 a single specimen was captured at the mouth of Salem harbor by the United States Fish Commission. It is said to be most abundant on the coast of New York and the neighboring

islands. In Rhode Island it is taken somewhat frequently in outside waters, but is only rarely found in Narragansett Bay. May, June, and early July are the only months in the year when it approaches near enough to the shore to be taken in the fish-traps. At Woods Hole, it is stated by Dr. Smith that this species is most abundant in June, particularly about the time of the scup run. Its normal habitat is in somewhat deeper water than that of the preceding species; according to Goode, it is the most abundant in 10 to 20 fathoms of water. Several specimens of this species were taken in 100 fathoms of water off the Rhode Island coast by the *Fish Hawk* in September, 1880.

II. *Reproduction.* The testimony of numerous observers agrees that this species spawns in May. The eggs have been experimentally hatched by the United States Fish Commission at Woods Hole. The eggs are buoyant, 1-26 of an inch in diameter, and they hatch in eight days when the mean water temperature is 51° to 56° F.* The young of this species have very rarely been observed, but in the autumn of 1885 and 1886 large numbers 2 or 3 inches were seined at Woods Hole.

III. *Food.* The food of this fish is much like that of most of the other members of the Flat-Fish family. All bottom animals contribute largely to its diet. The stomach of most specimens examined contained the remains of annelids, molluscs, the smaller crustacea, and small fishes.

IV. *Size.* It seldom attains a length of over 14 inches, and usually weighs about a pound.

THE RUSTY FLAT-FISH.

(*Limanda ferruginea.*)

PLATE V.

I. *Habitat and Distribution.* This species inhabits the American coast of the Atlantic from Labrador to New York. DeKay reported

* Smith, Fishes of Woods Hole, Bull. U. S. Fish Com., 1897, 108.

this flat-fish to be very rare and occurring only in deep water. It is very common in Vineyard Sound and is observed in water 10 to 12 fathoms deep, where it is present throughout the year. Numbers are often caught, incidentally, while fishing on the bottom for other species. In Great Harbor, Woods Hole, a few are taken in fyke nets in winter. *Specimens have been taken on the Pecten ground, off Watch Hill, Rhode Island.

II. *Reproduction.* Little is definitely known with regard to the reproduction of this fish. Stephen R. Williams, while collecting young flat-fishes at Woods Hole in June, 1898 and 1899, in the course of his investigations on the development of the winter flounder, found two apparently different larval forms of flat-fishes. These were of different sizes; the smaller at the end of the period of the metamorphosis measured 8 to 9 mm.; the larger at the metamorphosis measured 13 to 14 mm., and were more bulky and had somewhat more pigment. These larger, more pigmented, specimens were considered by Williams as possibly the young of the rusty flat-fish (*L. ferruginea*).†

III. *Food.* Examination of the stomach contents of this fish have shown crustacea, molluscs, annelids, and small fishes.

IV. *Size.* The average size is stated to be about 14 inches in length. The specimen described by DeKay was 18 inches long and 8.5 inches broad.

THE WINTER FLOUNDER.

(*Pseudopleuronectes americanus*.)

PLATE VI.

I. *Habitat and Distribution.* This species has an extensive range along the American coast of the Atlantic; it is abundant from Labrador to Chesapeake Bay. It has a preference for muddy and

* Smith, loc. cit.

† Changes Accompanying the Migration of the Eye in *Pseudopleuronectes Americanus*. Stephen R. Williams, Bul. Mus. Comp. Zool., Vol. XL, No. 1, 1902, 4.

grassy bottoms. It apparently undergoes no extensive migrations, since it is a permanent resident and is captured through the year. It is much more abundant, however, from October to May than in the summer, when only scattering specimens are taken in the traps. This shows a slight tendency for these fishes to move out from the warm inshore areas during the summer months into the deeper colder waters.

II. *Reproduction.* The spawning season of the winter flounder is from February to April. The eggs are 1-30 inch in diameter; they are very glutinous when first extruded from the body and stick together in large masses and adhere to whatever objects they touch. The eggs are demersal, that is, they sink to the bottom; in this respect they are an exception to the eggs of all the other species of this family. The artificial hatching of the eggs has been carried on very extensively at Woods Hole by the United States Fish Commission. The eggs hatch in 17 or 18 days when the average water temperature is 37° or 38° F. The average number of eggs to a fish is 500,000. On March 6, 1899, 1,462,000 eggs or 30 fluid ounces were taken from a fish that weighed 3½ pounds after spawning. The spawning fish are very abundant and are captured in fyke nets on hard clay bottom in water 6 to 15 feet deep.*

III. *Food.* The winter flounder feeds mostly on the small invertebrates of muddy bottoms. As the mouth of this species is smaller than that of most of the flat-fishes, its diet is more limited and other fishes form a less important portion of its food. It feeds largely on crabs, small shells, shrimp, squids, and annelids.

IV. *Size.* Its usual length is from 12 to 15 inches. The average weight of specimens taken in shallow water is something over a pound, while fishes taken further out in deeper water are larger and average about two pounds.

Young specimens are very frequent in inshore waters, and are often taken in the seine on sandy shores. At the Experiment Station of

* Smith, loc. cit.

the Rhode Island Fish Commission at Wickford young specimens of this species are often found in the hatching boxes during the latter part of May. Williams,* at Woods Hole, succeeded in getting quantities of young in larval stages at and about the time of metamorphosis. These were present all through the month of June, though by the 20th of the month all of this species had metamorphosed. He obtained these specimens by towing with a coarse scrim tow-net near the wall of the "outer basin" of the United States Fish Commission wharf during the rising tide. "They are most abundant on clear days when the wind is on shore and the tide comes in from the east. On very calm or rough days they are not plentiful. My most successful skimmings were made early in June, and twice I obtained as many as one hundred young fish during the inward flow of the current (three to four hours)." Williams states that the young reach a length of 75 mm. (3 inches) by the end of August, when they were about seven months old. This statement apparently refers to specimens kept under artificial conditions.

V. *Color Variations.* This species is remarkably subject to apparently abnormal color variations. Doctor Mitchell described two color varieties of the winter flounder. "One of these had a yellow margin on the lower side, surrounding the white of that side. This border was three-quarters of an inch wide and in striking contrast with the pearl of the contiguous parts within it and the brown of the adjacent fins. The other variety, obtained April 9th, 1815, has a whiteness of the upper side and nearly as clear as that of the nether surface over rather more than half its extent. The anterior part is blanched in this manner."† The dorsal, anal, and ventral fins were lighter than is usually the case, and their rays were tintured with yellow.

DeKay mentions a specimen obtained in April which he describes as "not only reversed but doubled." "Its color on both sides was uniform bronze with a white patch on its right side near the chin,

* Williams, loc. cit.

* Quoted from Dr. T. H. Bean, *Fishes of N. Y.* Bull. N. Y. State Mus., 60, 1903, 729.

almost entirely denuded of scales; it had a singular protuberance over the eye, noticed by Dr. Mitchell in his *melanogaster*.*

A dark-bellied variety appeared in Greenwich Bay, R. I., in 1897. They had first appeared some years before that, but in that year attained their maximum abundance, which was estimated to amount to 33 per cent. of the whole number of flat-fish. The numbers of this colored variety gradually declined so that in 1900 they were estimated at 4 per cent., and they have since almost entirely disappeared.†

SAND-DAB.

(*Lophopsetta maculata*.)

PLATE VII.

I. *Habitat and Distribution.* This species ranges from Casco Bay to South Carolina. It is abundant everywhere in shallow water, particularly on sandy bottoms. It is present in Rhode Island waters throughout the year. This fish reaches a length of ten or twelve inches, and is very abundant and its flesh of good flavor, yet it is of no commercial importance because, on account of its extreme thinness, the amount of its flesh is so small that it is of little use as food. It is in fact so thin that it is quite translucent, which fact is the source of one of its common names "The Window Pane."

II. *Reproduction.* The sand-dab spawns in the early part of June. The eggs are buoyant, non-adhesive, 1-24 of an inch in diameter, and hatch in eight days when the average temperature is 51° to 56° F. According to Dr. Smith, there is a large run of these fishes at Woods Hole in June during the spawning period.

III. *Food.* The food of this species seems to consist chiefly of small fish, and the smaller bottom invertebrates like small crabs and annelids.

* Quoted from DeKay, N. Y. Fauna, Fishes, 1842, 296, Pl. 49, Fig. 158.

† Bull. U. S. Fish Comm., 19, 1899, 305.

Report of R. I. Fish Comm., 31, 1900, 19.

IV. *Size.* The average length of the adult sand-dab is about 11 inches; they probably seldom attain the weight of a pound. Young specimens are rather common in shallow water with a sandy bottom. Williams,* 1898 and 1899, found many larval specimens at Woods Hole closely associated with the young of the winter flounder. Some of these specimens he kept for some time in artificial enclosures and observed their growth. They grew very rapidly, much more so than the flounders. One which measured 10 mm. (2-5) inch in length and 5 mm. (1-5 inch) in depth during eleven days grew to 22 mm. (9-10 inch) in length and 12 mm. ($\frac{1}{2}$ inch) in depth. Specimens 2 and 3 inches long are often taken in the seine along sandy beaches after the middle of July.

THE AMERICAN SOLE.

(*Achirus fasciatus.*)

PLATE VIII, AND IX.

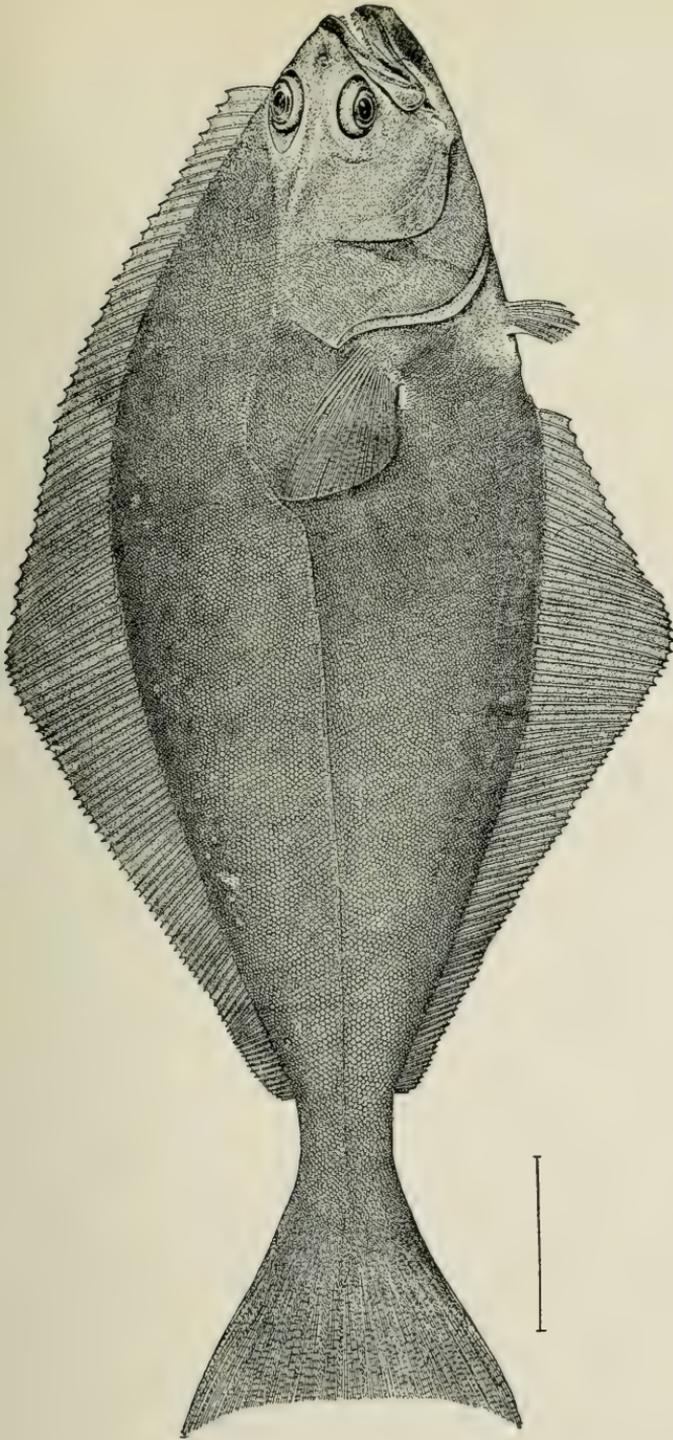
I. *Habitat and Distribution.* This species is the only common representative of the Sole family on the American side of the Atlantic. It is found along the Atlantic and Gulf coasts from Cape Ann to Brazos, San Diego. It is common in shallow water at the mouths of rivers with sandy bottoms, and often ascends rivers for considerable distances above tide water. They are somewhat rare in Narragansett Bay, but a few are taken in the traps each year. It seems to be more commonly present during summer and early fall; Dr. Smith states that at Woods Hole it is present the year round. Nothing is known of its breeding habits. On account of its small size it is of no commercial importance, though its flesh is said to be of good flavor.

The sole of European fame is not found in American waters. Two or three attempts have been made by United States Fish Commission to introduce it from English waters, but apparently without success.

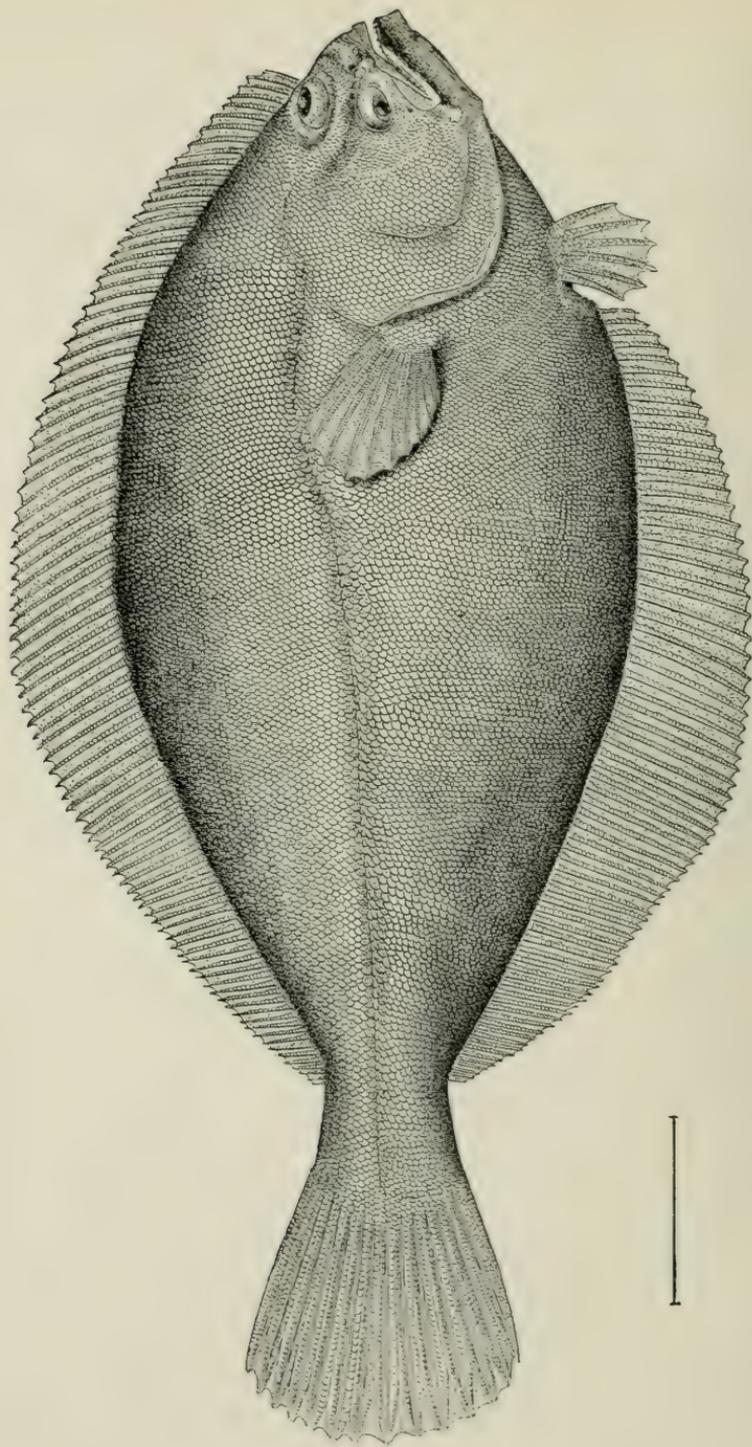
* Williams, loc. cit.

II. *Food.* Few observations have been made of the character of the food of this species. It seems to be a vegetarian, to a great extent at least, if not exclusively, since Dr. Linton, in 1899, examined eight specimens and found in their stomachs only vegetable debris, which appeared to consist mostly of *Fucus* and eel-grass.

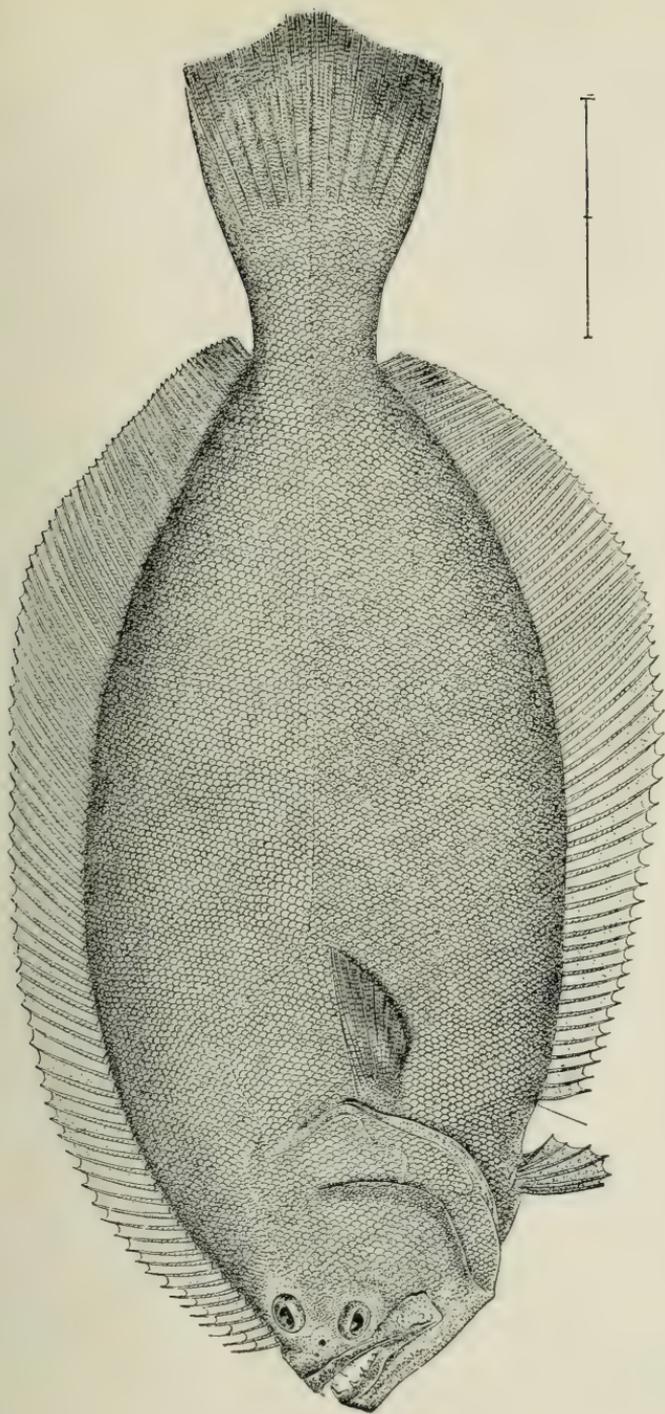
III. *Size.* This is the smallest of American flat-fishes. It seldom exceeds five or six inches in length.



THE HALIBUT.
(*Hippoglossus hippoglossus*).
PLATE I.

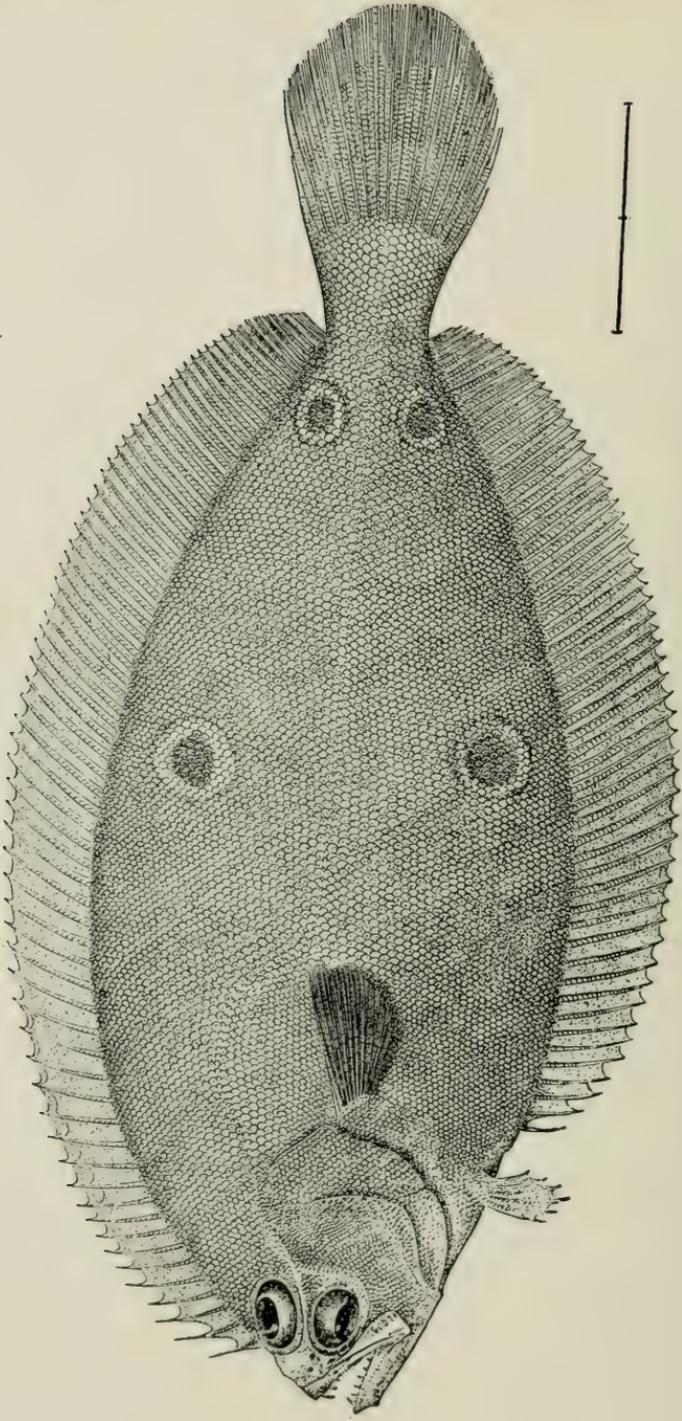


THE ROUGH DAB.
(*Hippoglossoides platessoides*).
PLATE II.

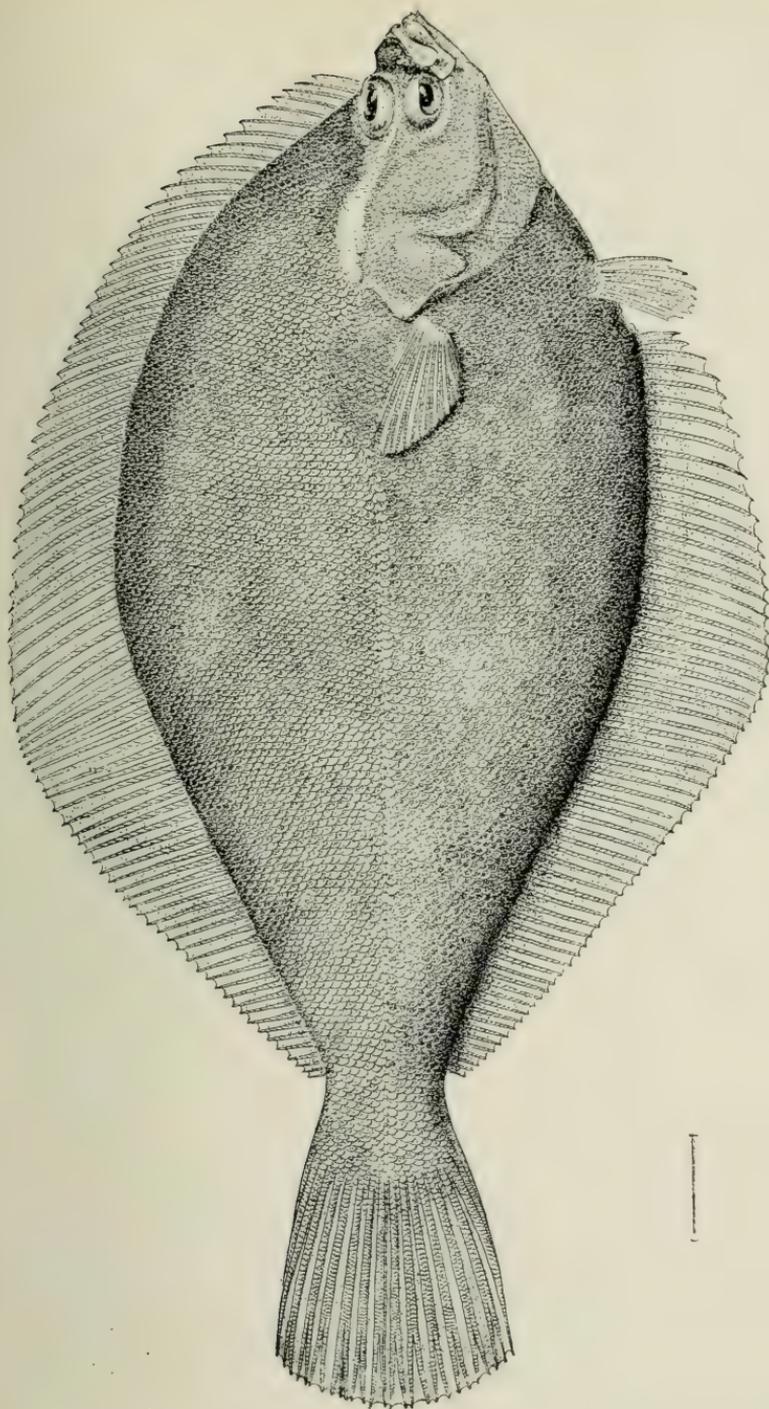


THE SUMMER FLOUNDER.
(*Paralichthys dentatus*).

PLATE III.

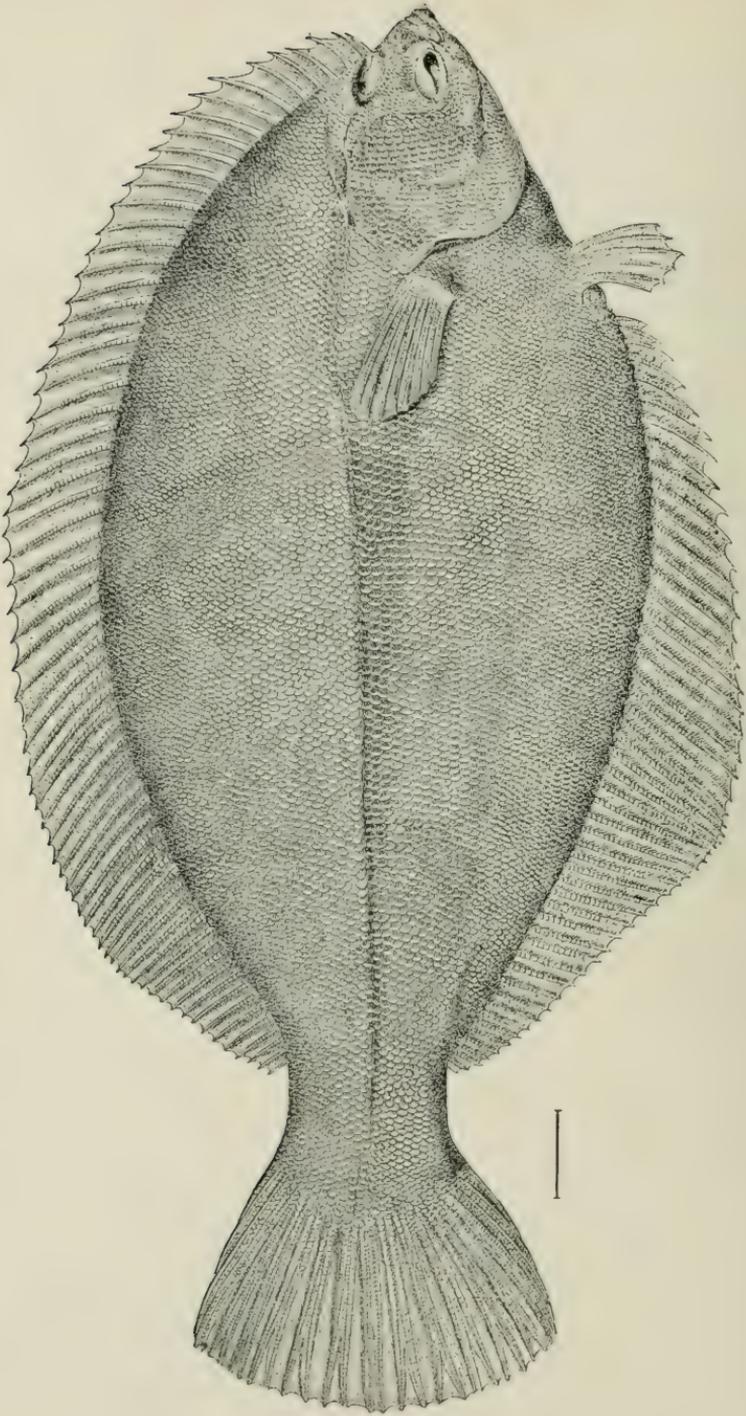


THE FOUR SPOTTED FLOUNDER.
(*Paralichthys oblongus*).
PLATE IV.

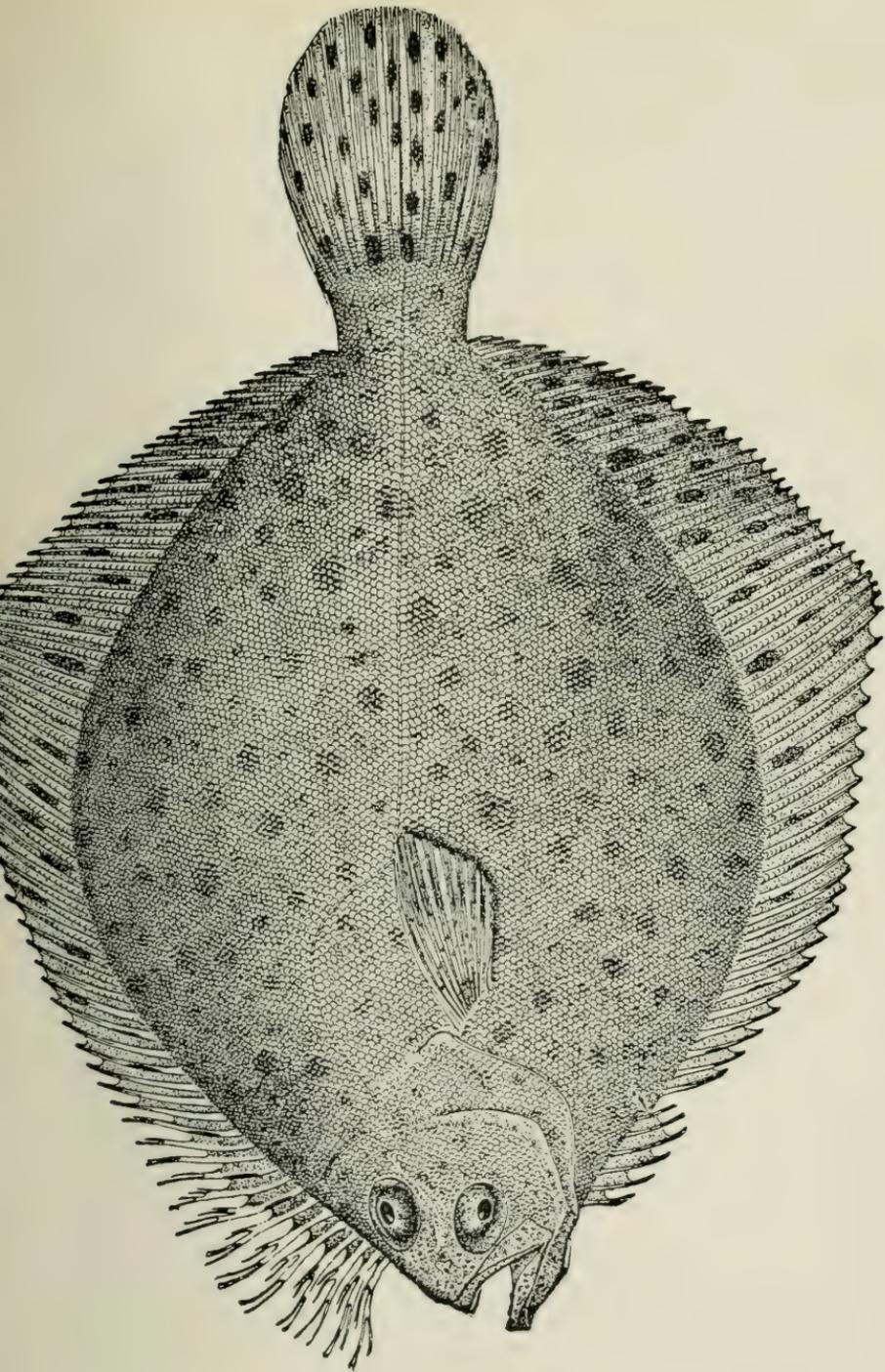


THE RUSTY FLAT-FISH.
(*Limanda ferruginea*).

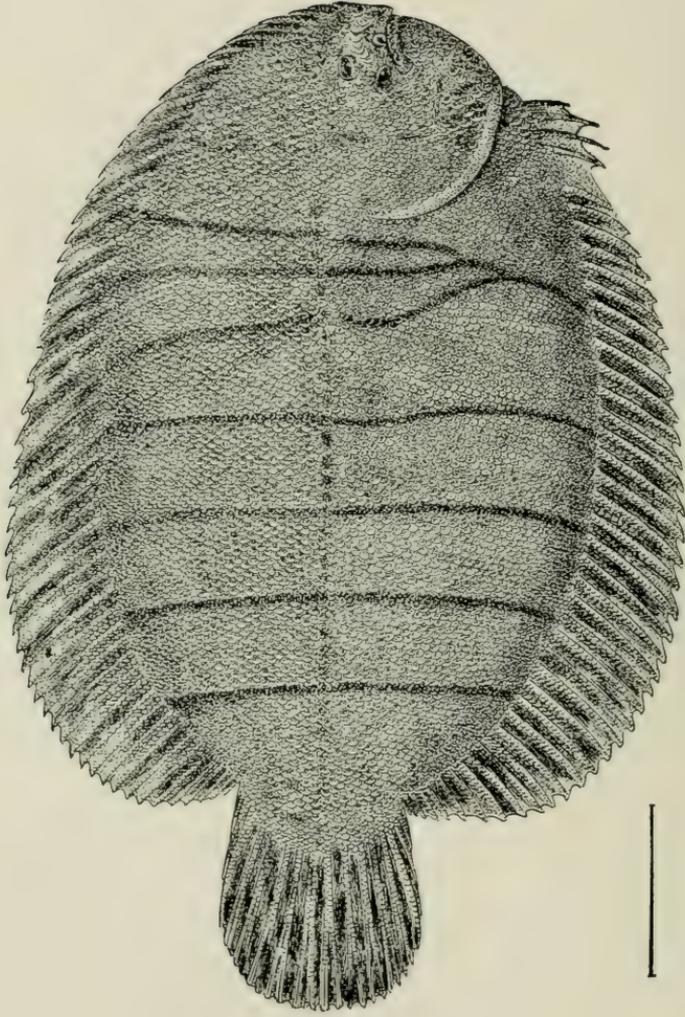
PLATE V.



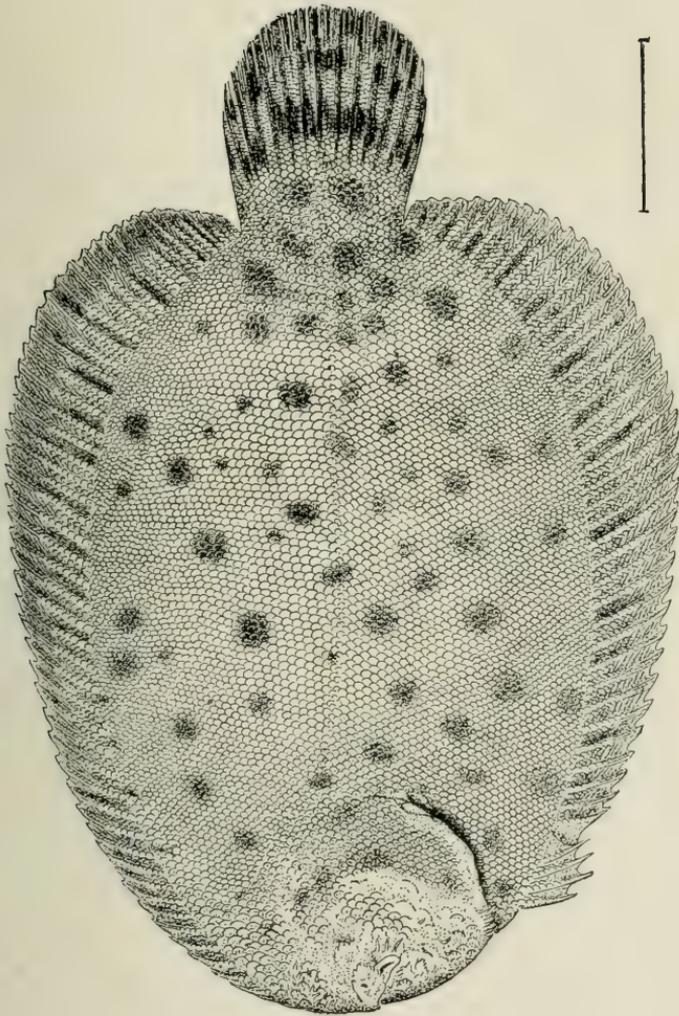
THE WINTER FLOUNDER.
(*Pseudopleuronectes americanus*.)
PLATE VI.



THE SAND DAR.
(*Lophopsetta maculata*).
PLATE VII.



THE AMERICAN SOLE.
(*Achirus fasciatus*.)
Upper side.
PLATE VIII.



THE AMERICAN SOLE.
(*Achirus fasciatus*)
Under Side.
PLATE IX.

THE FISHES OF RHODE ISLAND.
VI.—A DESCRIPTION OF TWO YOUNG SPECIMENS
OF SQUETEAGUE (*CYNOSCION REGALIS*), WITH
NOTES ON THE RATE OF THEIR
GROWTH.

BY HENRY C. TRACY.

Thirty-eighth Annual Report of the Commissioners of Inland Fisheries of Rhode Island. 1907. Special Paper No. 37.

THE FISHES OF RHODE ISLAND.

VI.—A DESCRIPTION OF TWO YOUNG
SPECIMENS OF SQUETEAGUE (CY-
NOSCION REGALIS), WITH NOTES
ON THE RATE OF THEIR GROWTH.

PLATES X AND XI.

HENRY C. TRACY, A. M.,
BROWN UNIVERSITY.

1907.

SPECIAL PAPER No. 37.

REPRINTED FROM THE THIRTY-EIGHTH ANNUAL REPORT OF THE
COMMISSIONERS OF THE INLAND FISHERIES OF RHODE ISLAND.

THE FISHES OF RHODE ISLAND.

VI. A DESCRIPTION OF TWO YOUNG SPECIMENS OF SQUETEAGUE (*CYNOSCION REGALIS*) WITH NOTES ON THE RATE OF THEIR GROWTH.

(WITH TWO FIGURES.)

BY HENRY C. TRACY, A. M.,

BROWN UNIVERSITY.

The identification of the eggs and of the larval and adolescent stages of any species of fish is a necessary preliminary to the investigation of its life history. Without the means of determining the species to which eggs and young belong, it is of course impossible to obtain evidence regarding the times and places of spawning, the habits of the young, the conditions which influence their lives, their migrations, etc. Any addition, therefore, to our at present somewhat meager knowledge of the younger stages of the marine fishes is of value. This present paper is intended to present a few notes regarding the rate of growth of young squeteague (*Cynoscion regalis*) and to describe two specimens smaller than any of that species yet described.

The only systematic attempt that has been made to investigate the life history of the squeteague was that of Eigenmann (1901), which was undertaken at the request of the United States Fish Commission. He was able to ascertain many important facts regarding the young of this species, though the very earliest stages were not obtained by him. The smallest specimen that he secured

was taken at the head of Narragansett Bay and was 25 mm. (1 inch) in length as measured to the base of the caudal fin. The smallest specimen which he figured in his report* was 32 mm. (1.3 inches).

The two specimens referred to in this paper were taken in Mill Cove, Wickford harbor, at the Experiment Station of the Rhode Island Commission of Inland Fisheries; they were found in the canvas bags which are used in the rearing of the young lobster fry. One of these young squeteague measures 12.5 mm. ($\frac{1}{2}$ inch) in length to the base of the caudal fin; the greatest depth of the body was 3.75 mm. (.15 inch), which is 30 per cent. of the length; the eye was about 1.2 mm. The other specimen was 6.5 mm. (.25 inch) in length, and 2 mm. (.08 inch) in depth, which was a little over 30 per cent. of the length; the eye was .7mm. in diameter. These measurements were made after the specimens had been killed (one according to Worcester's formula, the other in Zenker's fluid) and preserved in 80 per cent. alcohol, so that a very slight shrinkage may have taken place. Along with these there were also taken about a dozen others which ranged in size between the two mentioned above, and which were apparently of the same species. Several of these were kept in small cars until as late as October, during which time they become large enough to make certain the identification of these fishes as young squeteague.

The rearing bags used by the Rhode Island Fish Commission are made of heavy canvas and are 10 feet square and 4 feet deep. Circulation of water in them is maintained by a constantly revolving paddle which draws the water in at the bottom of the bag through a window of wire screen and drives it out through similar windows placed at two opposite sides.† These screens are made of copper wire-netting of 20 meshes to the inch. These young squeteague, then, could only have gotten into the bag by being drawn up through the bottom screen when they were still small enough to pass through

* Bull. U. S. Fish Commission, XXI, 1901, 45.

† For further details regarding the rearing plant and the construction of the canvas bags, see Report of the R. I. Fish Commission, 36, 1905, 120.

the meshes. This could only have been when they were less than perhaps slightly over 1 mm. in their greatest diameter, which probably corresponds to a length of perhaps about 3.5 mm. or 4 mm. It is therefore possible to get an approximate idea of the rate of growth of squeteague of this age.

These specimens were taken from the same bag on July 28; this bag was put into the water on July 11; the largest specimen, therefore, could not have been in the bag more than 17 days, and in that time or less it must have grown to 12.5 mm. from about 4 mm. or less. The conditions of life existing in these bags in which the lobster fry are so successfully reared apparently do not differ materially from those in the water outside, except that an abundant food supply is always present; nevertheless the conditions in these bags must be somewhat artificial, and how much these affect the rate of growth of the young squeteague is, at the present time, impossible to decide.

The finding of such small fry of the squeteague under such circumstances would ordinarily justify us in drawing further conclusions regarding the time and place of the spawning of this species. But unfortunately it is not possible to do so with certainty in this case. The writer of these notes, on July 3, at 9 A. M. fertilized artificially several thousand eggs of squeteague which were secured from fish traps out in Narragansett Bay. These hatched out about 1 A. M., July 5, and were released at the Experiment Station in the water of Mill Cove at 4 P. M. of the same day. It is thus impossible to know whether the specimens found on July 28 came of the lot released on July 5, or whether they came from eggs of squeteague which spawned naturally in the cove. It is evident, however, that the water of the cove is very favorable to the eggs, since they hatch with such facility there; the water there seems, also, to be well adapted for the younger stages of the fish, since they were present in the cove until after the middle of August at least, and those specimens which were kept in captivity thrived until killed by the cold weather in October. There is, therefore, in the present observations, nothing which does not tend

to support the generally accepted opinion that the squeteague spawns in inlets, sheltered coves, at the mouths of rivers, and in similar places.

The spawning time of the squeteague is usually considered to be about June 1; this opinion is based on the fact that some of the squeteague which come in at that time have ripe roes. This season (1907), however, owing to an exceptionally late spring, all marine life was much retarded in its seasonal development, and no squeteague with ripe roes were seen by the writer until after June 20, while they seemed to appear in the greatest numbers about the first of July. Therefore, if the specimens taken at the Experiment Station came from eggs which were spawned naturally in the cove, they could hardly be much over 40 days old and were probably less than 30 days old, since the chances are that they would have been hatched from eggs spawned at the time when spawning squeteague were present in the greatest numbers, which, in Narragansett Bay, seems, this year, to have been during the first week of July. The spawning in the coves would probably have taken place after, rather than before, the mature fishes appeared in the water of the bay outside. It will not be far from the truth, then, if the age of these young squeteague found in the cove be placed at between 20 and 30 days, and perhaps nearer the former time than the latter.

Two other specimens were later taken from the rearing bags, on the following dates: Specimen 25 mm. in length, found on August 8, in a bag which had been in the water for 12 days; specimen 29 mm. in length, taken on August 13, in a bag which had been in the water for 15 days. This latter specimen indicates an increase in length from about 4 mm., or less, up to 29 mm. during a period of not more than 15 days, and of course it may have been a somewhat less time.

The following are the sizes of squeteague taken by Eigenmann, and the dates and places of their capture:

Specimen 32mm. long, taken at Indian Point, July 5, 1900.

Specimen 41mm. long, taken at Indian Point, on the same date.

Specimen 70mm. long, taken at Indian Point, on the same date.

Specimen 95mm. long, taken at Wareham, August 9, 1900.

Specimen 120mm. long, taken at Wareham, August 22, 1900.

Specimen 200mm. long, taken at Vineyard Sound, September 7, 1900.

Several young squeteague from 80 to 100 mm. long were taken by the United States Fish Commission in Hadley harbor, near Woods Hole, on September 9, 1893. In all these cases, the spawning season was probably from two to five weeks earlier than in 1907.

Drawings of the two specimens taken on July 28 are shown in Plates X and XI. These are in outline and aim to show only such external characters as the form of the fins, mouth parts, gill covers, pigmentation, etc., which will make possible the future identification of young squeteague of these sizes.

In form and proportions these two specimens differ considerably from the adult and from the stages described by Eigenmann. The head and the eye are very large relatively, as is usually the case with the very young of fishes. The contour of the tail also differs, but the details of its development must be left until fresh specimens are available.

The specimen 6.5 mm. long is shown in Plate X, where it is magnified to twenty times the natural size. The greatest body depth is along a line drawn vertically a little behind the posterior margin of the eye. The embryonic fin-fold has not disappeared, though the spines of the unpaired fins are all well differentiated. The head is rounded in profile and the conical snout of the later stages is not yet developed. Teeth are present on the lower jaw. The bones of the gill-cover are only partially developed, so that at least five branchiostegals are visible from the side of the fish.

The pigmentation of the young squeteague is characteristic. This has been adequately described for the later stages by Eigenmann, but there are noticeable differences in these early stages. Reference to the plate shows the most important features of the arrangement of the color spots. Along the lateral line is a row of about eight rather large chromatophores aggregated into two groups, one of which is in that area of the skin between the anal fin and the posterior

end of the dorsal fin, and the other is below the anterior end of the soft dorsal. Each group has a few smaller chromatophores above and below it. The group under the posterior end of the dorsal fin was probably the first to appear. In this specimen, as shown in the plate, there was an enormous chromatophore in the skin just above the anal fin; this was apparently connected by processes with the color cells of the lateral line group just above it, and is probably the origin of the network of chromatophores which are found in a similar position in the later stages. These groups of pigment cells, when the young fish is looked at with the naked eye, have the effect of producing the appearance of two grayish or dusky bands on the sides, the anterior one of which is just beginning to appear and is much less pronounced than the posterior one. Other large expanded pigment spots are found in other places. The most conspicuous of these are scattered around the head region, particularly on the under side; a small clump is also found on the back near the beginning of the dorsal fin; two or three chromatophores are found along near the ventral edge of the caudal peduncle, while only one or two have yet appeared at the base of the caudal fin. The tissues of the fish are so transparent that the dense pigmentation of the posterior part of the body cavity is visible from the outside.

Plate XI shows the drawing of the specimen 12.5 mm. in length. It is here enlarged to ten times the natural size. The greatest body depth lies along a line drawn not far forward of the posterior margin of the gill-cover. Thus it is evident that the line of greatest body depth has shifted backward appreciably from the position which it occupied in the previous stage. The fins are fully differentiated and the embryonic fin-fold has completely disappeared. The snout has become somewhat pointed, though not so much so as in the later stages. The mouth has become more oblique; the maxillary and premaxillary have grown broader; the teeth of the lower jaw are large, strong, incurved, particularly along the sides; the teeth of the upper jaw are numerous but very minute; the opercular bones have grown downward and backward so that the branchiostegals are

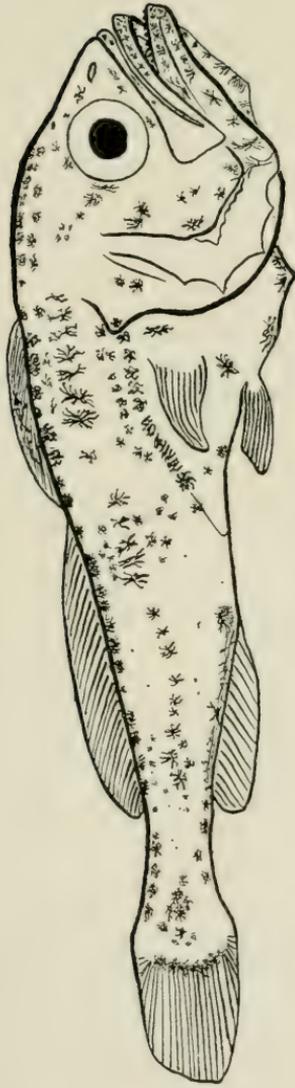
carried down ventrally in such a way as to be scarcely visible from the side.

In the pigmentation this stage differs considerable from the one just described. Chromatophores are present in greater numbers on every part of the fish. Those on the lateral line have increased in numbers so as to extend along nearly its whole length, and two new groups have been added, one just under the spinous dorsal, the other just in front of the base of the caudal fin. Thus to the naked eye the fish of this stage looks darker than one of the preceding, and the dusky bands on the side have increased to four. A row of branched, anastomosing chromatophores runs vertically along the base of the caudal fin-rays. A similar row of network-like chromatophores lies all along the base of the anal fin. Two or three rows of very compact chromatophores run along the back parallel to the insertion of the dorsal fin; three or four short lines of color cells run longitudinally on the top of the head. Two or three branched, somewhat tenuous pigment cells lie in the fin-membrance of the spinous dorsal. Scattered chromatophores occur along the gill-covers, on the upper and lower jaws, and on various other parts of the body.



YOUNG SQUETEAGUE.
(*Cynoscion regalis*).
6.5 mm. long. x20.

PLATE X.



YOUNG SQUETEAGUE.
(*Cynoscion regalis*).
12.5 mm. x10.

PLATE XI.

THE GROWTH AND TOXIN PRODUCTION OF
BACILLUS DIPHThERIAE UPON PROTEID-
FREE MEDIA.

BY PHILIP B. HADLEY.

The Journal of Infectious Diseases, Supplement No. 3, May, 1907, p. 95.

THE GROWTH AND TOXIN PRODUCTION OF *BACILLUS DIPHThERIAE* UPON PROTEID-FREE MEDIA.

PHILIP B. HADLEY.

(From the Bacteriological Laboratory of Brown University.)

OF all the problems which fall within the bounds of bacteriology today, one of the most important is that which concerns the production of toxins by certain pathogenic micro-organisms. The toxin of diphtheria has, no doubt, so far as its chemical nature and conditions of formation are concerned, received the greatest amount of study from investigators. It presents, moreover, a problem in the biochemistry of bacteria, than which, to the present time, no other has yielded more satisfactory results, considered both in their relation to pure science and to their practical application in the treatment and prevention of disease. And yet there are many points in regard to the ultimate nature of these toxic products, their relation to and interaction with the antitoxins, which, to say the least, are very far from being well understood. Furthermore, it is probable that these elements of the problem must remain a matter of speculation only, until a more adequate knowledge shall have been gained regarding the chemical nature of these toxic products, and the conditions which are either favorable or necessary to their formation.

Although, in the qualitative analysis of the toxic substance produced by *B. diphtheriae*, the investigator can recognize certain organic or inorganic bodies, he is still in the dark with reference to the ultimate proteid body, whose exact constitution he wishes to determine. It is difficult to determine whether the albumoses are the toxic products, or whether the true toxin may not, in some way, be associated with them. Some investigators assume that the toxin itself may be an enzyme which has a proteolytic action and produces the virulent, but secondary, toxic products in the body of the animal. Whatever answer may be given to these diverse and often contradictory views, the fact remains that the diphtheria organism, growing upon a proteid-free medium, can synthesize a toxic substance of a proteid nature; and that the toxin is probably not (as previously claimed by Brieger

and Fraenkel) a toxalbumen resulting from the splitting up of proteid bodies within the medium.

Among the first to determine that the toxin of *B. diphtheriae* could be formed in a proteid-free medium was Uschinsky.¹ Since his discovery, however, reports have appeared, from time to time, stating that success has not been met with in growing the diphtheria organism upon proteid-free media. In reply to some of these criticisms, Uschinsky says:²

Ich gebe zu dass auch ich viele Misserfolge gehabt habe. Jetzt aber besitze ich eine Kultur, welche auf meine Flüssigkeit vorzüglich wächst, und weit mehr Toxin produziert, als es bei mir früher der Fall war. Selbst 1½ c.cm. einer 4-6 Wochen alten filtrierten Kultur tödten sicher ein mittleres Meerschweinchen in 40-36 Stunden mit allen für Diphtherietoxin charakteristischen Erscheinungen.

Regarding the frequency of the growth upon his medium, Uschinsky continues:

Die Ursachen meiner und anderer Misserfolge scheinen mir darin zu bestehen, dass wirklich nicht eine jede Diphtheriekultur zum Wachsen auf eiweissfreier Nährlösung geeignet ist. Junge, frisch vom Menschen genommene Kulturen sind schwer auf dieser Lösung zu kultivieren; wogegen ältere, an saprophytische Lebensweise gewöhnte Kulturen leicht wachsen.

In the experiments about to be recorded, the writer has repeated Uschinsky's experiment, and has tried certain modifications of his medium together with some entirely new combinations. In all cases it was taken for granted that toxin-formations could not occur without at least a fair appearance of growth. With this fact in mind, the first aim of the writer was to obtain the best possible growth upon proteid-free media. Although in the first set of preliminary experiments the reaction of the media was adjusted to +0.45, as recommended by Hitchens,³ in the later work (including all the combinations of media herewith presented), the reaction was made slightly alkaline, as determined by litmus.

USCHINSKY'S MEDIUM.

The first proteid-free medium to be tried was that recommended by Uschinsky. This was made up as follows:

¹ Uschinsky, *Centralbl. f. Bakt.*, 1893, 14, p. 316.

² Uschinsky, *Centralbl. f. Bakt.*, 1897, 21, p. 146.

³ Hitchens, *Jour. Med. Res.*, 1905, 13, p. 523.

Water	1,000	parts
Glycerin	30-40	"
Sodium chloride	6	"
Di-Potassium phosphate	2.5	"
Ammonium lactate	6.5	"
Magnesium sulphate	0.3	"
Calcium chloride	0.1	"
Asparagin	3.2	"

Upon this medium the writer attempted to grow pure cultures of the granular, the barred, and the solid-staining¹ varieties of *B. diphtheriae*, obtained fresh from the nose and throat of patients suffering from diphtheria in the Providence hospitals. Out of 70 pure cultures tried, only two gave a growth upon Uschinsky's proteid-free medium, after an incubation of five days or more. In these two instances, furthermore, the growth was very slight and limited to the solid-staining varieties of the organism.

It is also perhaps noteworthy that in these cases, where several tubes of proteid-free media were inoculated from the *same* blood-serum culture, usually *only one or two tubes* would manifest a growth, thus seeming to indicate that even out of a pure culture of *B. diphtheriae*, there might be only a relatively small number of individual organisms which would immediately take up growth upon Uschinsky's medium; and furthermore, that these, either by chance or by peculiar fitness, proved to be the solid-staining types of the organism.

NEW COMBINATIONS.

After this trial of Uschinsky's medium, the writer made use of several other combinations of proteid-free media, all of which contained asparagin for the nitrogen basis and varied somewhat, both qualitatively and quantitatively, in respect to the salt constituents. Although an immediate growth of fresh cultures of *B. diphtheriae* upon these media did not usually occur, still on some of them the growth was more frequent and slightly more profuse than upon Uschinsky's medium. Among the many new combinations tried, especially the following may be mentioned:

Asparagin	1.50	parts
Glycerin	2.50	"
Sodium chloride	0.10	"
Di-Potassium phosphate	0.10	"
Potassium nitrate	0.03	"
Ammonium lactate	0.08	"
Distilled water to make	100.00	"

¹ Wesbrook's classification, *Trans. Assoc. Amer. Physicians*, 1900.

Upon this medium very few cultures of *B. diphtheriae* grew; in fact only two out of 20 grew at all, and these two were types of D² and E² (Wesbrook's classification).

In the following medium the percentage of glycerin and sodium chloride was increased, and calcium chloride and ammonium phosphate were added:

Asparagin	1.00 parts
Glycerin	4.00 "
Sodium chloride	0.60 "
Di-Potassium phosphate	0.03 "
Ammonium phosphate	1.75 "
Calcium chloride	0.01 "
Distilled water to make	100.00 "

In this medium six cultures grew slightly, but none very well. Of these six, three were D².

In the next medium ammonium lactate was omitted:

Asparagin	1.00 parts
Glycerin	4.00 "
Sodium chloride	0.60 "
Di-Potassium phosphate	0.30 "
Potassium nitrate	0.03 "
Calcium chloride	0.01 "
Ammonium phosphate	1.00 "
Distilled water to make	100.00 "

In this medium 14 cultures grew; one well, the others very slightly. Of the 14, eight were D², three were granular forms, and three barred. The one that grew most luxuriantly was a D².

Asparagin	1.00 parts
Glycerin	4.00 "
Di-Potassium phosphate	0.30 "
Magnesium sulphate	0.03 "
Potassium nitrate	0.03 "
Calcium chloride	0.01 "
Ammonium lactate	0.05 "
Ammonium phosphate	1.00 "
Distilled water to make	100.00 "

In the above medium, which, as will be noted, contains no sodium chloride, 27 cultures grew. Of these 27, seven grew fairly well, and 19 slightly. Of these 27, moreover, 12 were D², 6 were granular, and 9 were barred. The 2 which gave the most luxuriant growth were D².

The fifth lot of media had the following constitution:

Asparagin	1.00 parts
Glycerin	4.00 "
Sodium chloride	0.10 "
Di-Potassium phosphate	0.30 "
Magnesium sulphate	0.03 "
Ammonium lactate	0.50 "
Ammonium phosphate	1.00 "
Phosphate of iron	0.02 "
Distilled water to make	100.00 "

On the medium above mentioned, 18 cultures grew, most of them very slightly. Of these, 8 were D² or E,² 7 were granular, 2 were barred and 1 was a mixed culture. Owing to an accident, however, the results of growth in this series of tubes were incomplete.

In all of the above combinations of proteid-free media tried, the only source of nitrogen was either the ammonium salts or the asparagin. Generally speaking, the results in the growth or the toxin production of *B. diphtheriae* upon these media were not pronounced. In fact the growth was not sufficient to warrant the use of these media as a basis for the deeper problem of determining what definite constituents of the media favored or prevented the formation of the toxic products. But few inoculations of these first attempts at growth were made. The principal reasons for this were, that in the majority of cases the growth was too slight to even hint that there could be even the slightest toxin formation; in the second place, before the growth had progressed a suitable length of time, the rapid evaporation of the water from the tubes in the incubator so concentrated the medium that it either prevented further growth of the cultures, or produced an uncertainty as to the exact proportion of the ingredients in the solutions. It was always noticeable, however, that the forms which grew most persistently, in spite of the changes in the density of the medium, were the solid-staining varieties. Of these last, several inoculations were made, but in only one instance did the result indicate a very high degree of toxin production.

On the theory that one reason for the slight growth in the different varieties of media to which allusion has been made, might be the difficulty in assimilating the nitrogen from the ammonium compounds or from the asparagin, it was decided to make use of some other simple nitrogen-containing compounds, as glyocol or urea.

In general, the results obtained from the employment of glycol were far more encouraging than any results obtained through the use of asparagin. Urea, however, as also determined by Sullivan¹ in his work on the biochemistry of color-production by bacteria, was of little value, either in aiding the luxuriance of growth or for increasing the formation of toxin.

The first medium in which glycol furnished the nitrogen basis was made up as follows:

Glycerin	3.40 parts
Sodium chloride	0.60 "
Calcium chloride	0.08 "
Magnesium sulphate	0.32 "
Di-Potassium phosphate	0.23 "
Ammonium lactate	0.75 "
Glycol	0.10 "
Distilled water to make	100.00 "

Owing to the fact that several of the first few cultures with which this medium was inoculated grew without delay, a large number of cultures was not tried. The first two cultures which grew well had been on blood serum for a period of three weeks and were transferred to the proteid-free medium from a broth culture. Of these two, one was a culture of CC¹, the other of CC². Of a 16-day-old culture of CC² in the medium specified above, 5 c.cm. were inoculated into a guinea-pig weighing 533 grams. The pig died in 36 to 38 hours with the characteristic signs of diphtherial poisoning. The organism was recovered at the autopsy in the form of a D² culture.

In still another case, a culture of CC², having been grown for a period of 17 days in media of the same composition as the foregoing, killed a pig in 31 hours with typical diphtherial poisoning. In this case also, the organism was recovered in the form of a culture of C²D². These results appear to indicate that glycol, even in so small an amount as 0.1 per cent, is able to render possible, provided the other constituents of the medium are favorable, a good growth and a powerful toxin production of *B. diphtheriae* upon proteid-free media, even if the period of growth is no longer than 16 days. We recall that Uschinsky states that the period of growth of his cultures was from four to six weeks.

¹ Sullivan, *Jour. Med. Res.*, 1905, 14, p. 109.

TABLE 1.—Continued.

	5			6			7			8		
Am. Lactate.....	0.5			0.75			3.2			3.25		
Am. Phosphate.....	1.0											
Asparagin.....	1.0											
Cal. chloride.....							0.05			0.04		
Ferric phosphate.....	0.02			0.08								
Glycerin.....	4.0			3.4			15.0			17.0		
Glyocol.....				0.1						0.5		
Magnesium sulphate.....	0.03			0.32			0.15			0.16		
Potas. nitrate.....												
Di-Potas. phosphate.....	0.3			0.23			1.25			1.25		
Sodium chloride.....	0.1			0.6			3.0			3.0		
Urea.....							1.6			2.5		

	CD	C'D'	C²D²									
Growth.....	S	S	S	L	L	L		S	L	S	S	L
Toxin production.....				H	H					M	M	

EXPLANATION.—In every case except Nos. 7 and 8 water was added to make 100 parts; in these to make 500 parts. S=slight, G=good, L=luxuriant growth; H=Inoculation resulted in death in less than forty-eight hours; M=Inoculation resulted in death in more than forty-eight hours.

It may be stated here that the three last-mentioned combinations of proteid-free medium were also tried, made up with agar in solid form. Although many other forms of bacteria developed luxuriantly upon these media, the growth of *B. diphtheriae* was slight. It was, however, in several instances sufficiently rapid to enable the writer to make a diagnosis of the diphtheria organisms after a period of 12 hours' growth.

STUDY OF ADAPTATION.

One other point of incidental interest was to determine the possibility of adapting to a proteid-free medium cultures of *B. diphtheriae* which, when fresh from the throat of man, would not grow at all on the proteid-free combinations. It is a well-known fact that many plants may, through a long and gradual process of adaptation, be fitted to live and grow in a new and materially different environment. In the present case the adaptation process was carried on as follows: To one part of broth were added portions of the proteid-free medium, in the following parts: 1, 2, 4, 6, 8, 10, 14, 18, 25, 30, 40, 50, 60, 80, 100, 140, 180, 210, 240, until finally the proteid-free medium was reached in its purity. In this system of adaptation, the tubes were inoculated successively, each from the tube preceding. A period of from 24 to 36 hours was allowed for the growth in each of the first tubes of the series, while for the tubes in the last of the series a longer period of time was found to be necessary.

By this process of adaptation five cultures of *B. diphtheriae*, of which two were of the D² type and the other three the CC¹ type, were brought successfully to the eighteenth series of adaptation tubes, in which the medium contained one part of broth to 210 parts of proteid-free medium. In every instance the solid-staining forms grew the most luxuriantly. In every instance, moreover, except in one culture of D², a strong toxin was developed, and the degree of toxicity appeared to be directly proportional to the age of the culture. After the cultures had once taken a hold, so to speak, any increment in the proteid-free basis appeared to make little difference in the strength of the toxin produced in the tubes beyond the fourth series (i. e., broth 1 part, proteid-free medium 6 parts). The records of the inoculations of the barred and the granular forms during the process of adaptation may be tabulated as follows:

TABLE 2.

Series	Age of Culture	Composition	Killed in
1.....	3 weeks	Broth 1 pt.; Prot.-free 6 pts.	25 hours
2.....	2 weeks	Broth 1 pt.; Prot.-free 80 pts.	32 hours
3.....	3 weeks	Broth 1 pt.; Prot.-free 210 pts.	28 hours

These results seemed sufficiently definite to warrant the statement that certain forms of the diphtheria organism which will not grow normally upon a proteid-free medium can, by slow degrees, be fitted to such a life, and may be made to produce under such new life conditions a very strong toxin. There still remains a problem of interest to be solved in determining whether the adaptation results from a modification of the existing forms, or whether a selection of those varieties which are most suited to the new environment takes place. Regarding this question there are no data to be brought forward at this time.

PERIOD NECESSARY TO OBTAIN MAXIMUM TOXICITY.

There is a general unity in the opinion that the maximum toxicity for *B. diphtheriae* growing in broth is reached in from 40 to 50 hours after the inoculation. Uschinsky, on the other hand, ascertained that a period of from four to six weeks was required for the formation of a powerful toxin in his proteid-free media. In the tests which the

writer made in this regard, it was quite apparent that the food materials in a proteid-free medium were much more slowly assimilated than in the case of a broth culture. In the majority of cases at least a day was necessary before the growth was at all noticeable; and the growth was seldom heavy before three to five days had elapsed. A number of instances appeared to indicate that the degree of toxicity, at least within certain limits, was directly proportional to the time that the culture had been in incubation.

RELATION OF THE DEGREE OF TOXICITY TO THE FORM OF THE ORGANISM AND TO THE LUXURIANCE OF GROWTH.

There can be but little doubt that the granular forms, so called, of *B. diphtheriae* are, as a rule, the most virulent. The solid-staining varieties, on the other hand, appear to be non-pathogenic in the greater number of cases. And yet the results of the writer's observations permit of little doubt that a single morphological variety of the diphtheria organism is decidedly modifiable; and that not only may the granular types of the organism be resolved into the solid-staining forms, but that the opposite may also be true. Furthermore, it is clear that the solid-staining types may, either with a maintenance of their original form, or with a change of that form within the body of the animal, prove highly pathogenic for guinea-pigs. The observations in this regard, were only incidental to the main problem in hand; but, in view of the prevalent difference of opinion upon this question, they may perhaps be appropriately mentioned at this time. On the first trial, eleven inoculations of pure cultures of D² were given to guinea-pigs before one culture proved to be pathogenic. The twelfth, a D² type, killed in 39 hours, with all the usual signs of diphtherial poisoning. When the organism was again recovered, it was found to be of the barred variety. On several other occasions also, when granular forms were inoculated, barred and solid-staining forms were recovered. In three successive cases where two cultures of CC¹ and one culture of C¹ C², grown for 17 days upon proteid-free media, were inoculated into guinea-pigs, they killed in from 37 to 59 hours, with all the characteristic symptoms. Without an exception, when the organism was recovered from the bodies, the D² form was alone present. One of these recovered cultures of D², after 48 hours of incubation in broth, was inoculated into a guinea-pig and resulted in

death in 37 hours. The organism was recovered in the form of a D².

These facts appear to indicate beyond a doubt that important changes may be brought about in the form and toxin production of individual bacilli in a single culture of the organism; and that these different forms are determined in a great measure by the nature of the environment. Whether this distinct modification occurs as a result of a morphological change in all the individuals during a few successive generations, or whether by a less rapid process of selection and elimination of those morphological varieties, or different strains of the same morphological variety, which are not readily adaptable, this we are not yet able to determine. It is not altogether improbable, however, that there may be in the life of the diphtheria organism what may be roughly called a series of adaptive forms, each one of which may be best suited to a circumscribed condition of environment, there to produce, as the case may be, color, toxin, or even definite changes in form.

TOXICITY AND LUXURIANCE OF GROWTH.

As to the relation between the degree of toxicity and the luxuriance of growth, the experience of the writer would not warrant the drawing of any far-reaching conclusions. It is true, however, that the solid-staining types, whether they be true *B. diphtheriae*, pathogenic pseudo-diphtheria bacilli, or non-pathogenic pseudo-diphtheria bacilli grow more rapidly upon proteid-free media than do the granular types. Not only do the D² forms grow more rapidly, but the nature of their growth is far more luxuriant and of quite a different nature from that of the granular varieties. The typical growth for the granular type, on either broth or proteid-free media, is at the surface, where it forms a more or less delicate film. Upon shaking the tube, this film falls to the bottom as a fine precipitate or sediment. The medium from the surface to the bottom of the tube is, in the growth of the granular forms, nearly as clear as the contents of a sterile tube. It is the nature of the solid-staining types, on the other hand, instead of forming the surface growth and maintaining a clear mid-liquid, to produce in the medium a uniform cloudiness. This may, in time, settle to the bottom of the tube, but the medium never wholly loses its turbidity. This condition of growth was observable in all the

series of cultures in proteid-free media as well as in the latter part of the series of adaptation tubes which have been mentioned above. In summation it may be said that, although a high degree of toxicity may often accompany a luxuriant growth, luxuriance of growth can never be used as a criterion of the degree of toxicity.

It may be of interest to mention one other point regarding the so-called involution-forms of *B. diphtheriae*. These, known by Wesbrook's classification as the "A" varieties, are generally conceded to represent forms which have become attenuated, both in virulence and in luxuriance of growth. This is indicated by the fact that when a culture of *B. diphtheriae* is grown upon a medium unfavorable to its growth, many of these forms develop, and they are often common in the throats of those who are recovering from an attack of diphtheria. In the writer's experience, these forms often developed, at the very last, in tubes of proteid-free media wherein the granular, and less frequently the solid-staining types, had found growth most difficult. These same involution-forms, in at least three cases, in our experiments, produced such a rapid and luxuriant growth in broth, that we were deceived by their macroscopic appearance into believing that these particular tubes were contaminated with some one of the large, pellicle-forming spore-bearers. By the examination of one tube, however, it was found that there was naught in the tube but a pure culture of the "A" varieties of *B. diphtheriae*, and that these composed, not only the heavy pellicle, which, in 24 hours, had become so dense that it restrained the liquid portion when the tube was inverted, but also the rapidly growing individuals beneath the pellicle. These individuals were the largest that have ever come under our observation, many of them measuring nearly ten micra in length, and under $\frac{1}{8}$ -inch oil-immersion, rendering camera lucida drawings easily possible. It may also be noted that two of these cultures, referred to above, came originally from monstrous colonies growing upon blood-serum, one of which was 10 mm. in diameter. These were the only colonies of this nature ever seen by the writer.

SUMMARY.

1. *B. diphtheriae* will grow readily and luxuriantly in proteid-free media, and will produce therein as strong a toxin as in ordinary broth, though much more slowly.

2. Of the three nitrogen bases tried (asparagin, urea, and glycol), urea seemed to be of slight value, while glycol furnished the best growth and the strongest toxin. Asparagin appeared to give better results than urea, though it was not as satisfactory as was glycol. There is no added value to be gained by using any two, or even three, of these compounds together.

3. Upon the following medium, cultures of *B. diphtheriae* were grown, and, after an incubation of 16 days, killed guinea-pigs in the course of 36 to 38 hours:

Glycerin	3.40 parts
Sodium chloride	0.60 "
Calcium chloride	0.08 "
Magnesium sulphate	0.32 "
Di-Potassium phosphate	0.23 "
Ammonium lactate	0.75 "
Glycol	0.10 "
Distilled water to make	100.00 "

4. In several instances there were obtained cultures of pathogenic, solid-staining varieties of *B. diphtheriae* (C², D², E²), which, upon inoculation, killed guinea-pigs in 37 to 60 hours.

5. Cultures of *B. diphtheriae* which will not at first grow upon proteid-free media, may be adapted to it by slow degrees; and whether during the process of adaptation, or after the adaptation, it is the solid-staining forms of the diphtheria organism which always manifest the most rapid and luxuriant growth.

6. A single morphological variety of *B. diphtheriae* is decidedly modifiable, and there are indications that there may be in the life of the diphtheria organism what may be roughly called a series of adaptive forms, each one of which is best suited to a certain condition of environment, where it may produce color, toxin, or change in form.

REGENERATION AND THE QUESTION OF "SYM-
METRY IN THE BIG CLAWS OF
THE LOBSTER"

BY VICTOR E. EMMEL.

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REGENERATION AND THE QUESTION OF "SYMMETRY IN THE BIG CLAWS OF THE LOBSTER"

IN view of several recent articles¹ on the phenomena of symmetrical chelæ in the lobster it seems desirable to offer a few further considerations on the subject of the origin of such structures.

Let us briefly present the nature of the problem. It is a matter of common observation that in the adult lobster the "great" claws are almost invariably asymmetrical with reference to each other; the claw on one side of the body being a "nipper" and the other a "crusher." In a few cases, however, a variation from this normal asymmetry has been discovered, in which the claws instead of differing from each other are very much alike and symmetrical in form. These variations fall into two categories: First, those in which both claws are of the nipper type, and second, those in which the similar claws are both crushers. Two theories for the origin of these relations of symmetry have been presented—first, that they are predetermined in the egg, and second that they may arise through regenerative processes and consequently, are not of necessity wholly determined by congenital factors. Let us consider first the variations from normal asymmetry.

¹ See especially: (1) Herrick, F. H., 1907, "Symmetry in the Big Claws of the Lobster," SCIENCE, Vol. XXV., p. 275. (2) Calman, W. T., 1906, in the "Proceedings of the Zoological Society of London," p. 633.

I. *Explanations for Abnormally Symmetrical Claws.*

(a) *Similar Nipper Claws.*—Until very recently in all the authentic cases of similar chelæ, the claws belonged to the first category of the nipper type. Out of over 2,400 lobsters² found only three had similar claws. In an examination of some 600 specimens as they came in from the traps at the Experiment Station of the Rhode Island Commission of Inland Fisheries the writer³ found only one lobster with both claws alike. The similar claws of these four cases were all nippers. Theoretically, it may appear quite plausible that a symmetry of this character might be congenital in origin. For in the early development of the lobster both chelæ are alike and similar to the nipper type. At about the sixth stage⁴ normally one of the claws begins to differentiate into a crusher. We might thus have an adult lobster with two nipping claws because they had failed to differentiate in the usual asymmetrical manner. On the other hand, the writer has elsewhere⁵ furnished evidence that this type of symmetry may also be brought about as the result of a process of regeneration.

(b) *Similar Crusher Claws.*—With regard to this second category, however, the con-

² Herrick, F. H., 1895, "The American Lobster," Bull. U. S. Fish Commission.

³ Emmel, V. E., 1907, "Regenerated and Abnormal Appendages in the Lobster," thirty-sixth annual report of the Rhode Island Commission of Inland Fisheries, special paper, No. 31.

⁴ Hadley, P. B., 1906, "Changes in Form and Color in Successive Stages of the American Lobster," thirty-fifth annual report of the Rhode Island Commission of Inland Fisheries, Special paper No. 19.

⁵ Emmel, V. E., 1906, "Torsion and other Transitional Phenomena in the Regeneration of the Cheliped of the Lobster," *Journ. of Exp. Zoology*, Vol. III., No. 4.

genital theory does not appear to apply so readily. For in this case the development must be conceived as starting in the normal way, and then instead of differentiating asymmetrically both chelæ have passed beyond the normal stages and developed into two crushing claws of the phylogenetically later (according to Stahr⁶ and Przibram⁷) type. With reference to this latter type of symmetry the following observations serve to emphasize the process of regeneration as a factor in the origin of such abnormal appendages.

Heretofore, a strong presumption has existed that a crusher claw would not be developed on each of the big chelæ, first because, as has already been indicated, the claws of the young lobster are alike and similar to the nipper type, and second, that in the adult lobster, the few cases of symmetrical claws were always of the nipper or embryonic type. Up to 1905 the only case recorded of two crushing claws on a lobster was in a foot-note to Herrick's⁸ description of variations in lobster chelæ: "I have heard of a single case reported by a fisherman where similar crushing claws were developed on both sides of the body" (p. 143). To Przibram writing in 1901⁹ this seemed such an incredible phenomenon that in view of the theoretical reasons indicated above, he concluded that "Der eine Fall von einer Hautung beiderseitigen" crushing claw "von dem Herrick nur vom Horensagen durch Fischer Kenntnis erhielt,

⁶ Stahr, H., 1898, "Neue Beiträge zur Morphologie der Hummerschere Jena," *Zeitschr. f. Naturw.*, Bd. 32.

⁷ Przibram, H., 1901, "Experimentelle studien über Regeneration, I.," *Archiv. f. Entw.-Mech.*, Bd. XI.

⁸ *Loc. cit.* (2).

⁹ *Loc. cit.* (7).

wird wohl in der Reich der Fischermythen zu verweisen sein" (p. 333).¹⁰

Since the year 1905 three authentic cases of lobsters with two crushing claws have been placed on record. One of these was reported by Dr. W. T. Calman,¹¹ of the British Museum. He exhibits the photograph of a lobster (*Homarus gammarus*, Linn.) "with symmetrically developed chelæ" which were both crushers (p. 634). Herrick, '07,¹² observes that "this case is, for the present, essentially unique in the literature of the subject" (p. 277), but in making this statement he has evidently overlooked my description,¹³ published in 1906, of the two other lobsters with similar crusher claws. The latter two cases of similar crushers were regeneration products, and they are, as far as I am aware, the only cases on record in which the origin of the two crushing chelæ is known, for in neither of the cases recorded by Herrick and Calman has the history of the abnormal chelæ been obtained. A brief restatement of the facts with regard to these regenerated crushers may, therefore, be in place here:¹⁴

One of these cases was obtained in the course of a series of experiments on regeneration made

¹⁰ I gladly take this opportunity, however, to correct the impression which might be drawn from this quotation. For Przibram in a recent letter has kindly informed me that he has modified his earlier opinion with regard to this matter as the result of his studies on other crustacea. See especially page 215 of his monograph on "Die Heterochelie bei decapoden Crustaceen," *Archiv. f. Entw.-Mech.*, Bd. XIX., 1905.

¹¹ *Loc. cit.* (1).

¹² *Loc. cit.* (1).

¹³ Emmel, V. E., 1906, "The Regeneration of Two Crusher-Claws following the amputation of the Normal Asymmetrical Chelæ of the Lobster," *Archiv. f. Entw.-Mech.*, Bd. XXII.

¹⁴ For a more detailed description with figures, see *loc. cit.* (3), (13).

during the summer of 1905, and the other during similar experiments in 1906. In both instances the lobsters had been recently taken from the traps near the experiment station, placed in floating cars and kept in as normal a condition as possible. Let us designate the former as specimen A, and the latter as specimen B.

Specimen A.—The original appendages of this specimen were all normally developed and the animal was in a healthy condition throughout the experiment. The lobster was a female and measured $8\frac{3}{8}$ inches in length. On July 26, 1905, both chelæ, and the second and third right walking legs, were autotomously removed. On September 23, sixty-four days after the amputation, the lobster moulted and then measured $8\frac{1}{2}$ inches. It had meantime regenerated both chelæ, and the second and third right thoracic legs.

The original left claw of this lobster was a completely developed crusher, characterized by the wide massive claws with an almost entire absence of tactile hairs, and by the presence of broad tubercle-like teeth. The right chela was of a characteristic nipper type with a relatively slender claw, pointed cutting teeth, and a fringe of tactile hairs along the jaws. The right and left chelæ measured 146 and 140 mm. in length, respectively.

Soon after the amputation of these limbs another pair of chelæ began to regenerate from the remaining stump or basipodite. July 18, twenty-three days after the amputation, the regenerating buds both measured 5 mm. in length. By the time the segments of the future limbs were well outlined, attention was drawn to the very similar appearance of the two regenerating structures. Usually, as the lobster approaches the culmination of the moulting period, the regenerating chelæ become so clearly differentiated that a distinction between the crusher and nipper can be readily detected. In the present case, however, no characteristic differences could be observed between the right and left regenerating buds, and, moreover, the general morphological appearance of each suggested that *both* were developing into the crusher type of claws.

After the lobster had moulted, the regenerated chelæ assumed their normal shape and each meas-

ured 63 mm. in length. But the regenerative processes had not reproduced the original asymmetrical type of chelæ. The regenerated left claw was a true crusher like the former claw; but the regenerated right claw had the general characters, not of the nipper, but of a typical crusher. A close analysis of the structural features of the regenerated right claw demonstrated that, in all its morphological characters, it corresponded point for point with both the normal and the regenerated crusher of the left side, with respect to the general form, size and proportion, in the shape and arrangement of the teeth, and even in the number and distribution of the tufts of tactile hairs.

Specimen B.—This specimen was an eight-inch male lobster. The original chelæ, as in the preceding case, were also of the normal asymmetrical type, except that in this lobster the right claw was the crusher and the left a nipper. Each chela measured 162 mm. in length.

On August 4, 1906, both chelæ and the second left leg were autotomously removed. Soon after the operation another pair of limbs began to regenerate. By the time the segments of the future appendages were well outlined, the two regenerating chelæ looked very much alike, and the fact that their external characters resembled those of a crusher, suggested that both limbs would develop claws of a crushing type.

By the middle of October, 1906, the lobster had moulted and regenerated both chelæ and the second right leg. Each chela measured 111 mm. in length; they were remarkably similar in structure, and each displayed the character of a typical crushing claw.

In these lobsters, therefore, we have two cases in which the regenerated claws were symmetrical in form and of the crusher type of chelæ.

With regard to the origin of similar crusher chelæ, Dr. Calman's case has been interpreted as discrediting the regeneration theory for symmetrical chelæ, for in his discussion he says: It has been supposed that this might be due to regeneration after in-

jury, since it is known that in *Brachyura*, on removal of the crushing-claw, a cutting-claw is regenerated. Przibram, however, failed to obtain such "heteromorphic" regeneration in the lobster, and the present specimen throws still further doubt on the regeneration theory, since it possesses a well-developed and quite typical crushing-chelæ on both sides of the body.¹⁵

Herrick in his earlier writing¹⁶ has evidently also favored the congenital theory, for in his discussion of symmetrical claws he states that "there seems to be about as much variation as regards the details here mentioned in normal symmetrical claws as in the abnormally symmetrical ones, and it is probable that in either case the conditions met with are to some extent congenital" (p. 244). In his recent article he discusses both theories without definitely favoring either, and in conclusion states that, "The explanation just offered is based on the assumption that regeneration, following loss, actually occurs in these cases. If there has been no regeneration, we must then fall back upon the view that asymmetry in the great forceps is normally produced by changes which take place in the egg, so the rare condition of symmetry in these appendages may be casually brought about in the same way" (p. 277). With regard to Dr. Calmans's case of two crusher claws, Herrick suggests the possibility of getting such a condition through a process of regeneration. But it is important to note that neither of these writers furnishes any experimental proof for the conclusion that symmetrical crushing chelæ have arisen either congenitally or as the result of regeneration. The two cases just described furnish such experimental proof, and *establish the fact that the process of regeneration is an*

¹⁵ *Loc. cit.* (1).

¹⁶ *Loc. cit.* (2).

important factor in the origin of the symmetrical chelæ occasionally found in the adult lobster.

At present it seems difficult to bring these cases which show the regeneration of two crusher claws under any definite principles of regulation or a developmental mechanics. Evidently they can not be explained as due to a retardation in the process of ontogenetic differentiation, nor does it appear that they can be regarded as a reversion to a phylogenetically older type of chelæ. It is apparently impossible to interpret such a regeneration as a case of "compensatory regulation" in Zeleny's¹⁷ sense, for the regenerated chelæ are almost identically similar in size and form. Nor is it clear that they both can be brought under the category of "reversal" phenomena, if by this term we mean a reversed order of asymmetry. At present, therefore, these cases must rather be described merely as the *substitution* by regeneration of the crusher claw in place of an original nipper chela.

II. *The Ontogenetic Origin of Normal Asymmetry.*

The main question here is, whether normal asymmetry is congenital and wholly predetermined in the egg, or whether it may be influenced by external factors during development.

With regard to this matter Herrick,¹⁸ on the basis of his experiments with the shrimp *Alpheus*, concludes that asymmetry in the lobster "is probably one of direct inheritance, all members of a brood being either right- or left-handed. That is to say, the normal position of the toothed or crushing claw is not haphazard, but is predetermined in the egg" (p. 225). But here again there is a necessity

¹⁷ Zeleny, C., 1905, "Compensatory Regulation," *Jour. of Exp. Zoology*, Vol. II., No. 1.

¹⁸ 1907, *loc. cit.* (1).

for evidence, for it still remains to be demonstrated that such asymmetry in the lobster is thus predetermined. The results of some experiments made in order to determine whether the crusher could be developed on either side of the body by making appropriate mutilations during the larval stages, *i. e.*, at a period when the chelæ have not yet differentiated into nipper and crusher—may be here introduced. Although these experiments are still in progress, some of the data is already significant because it tends to support a different theory than that of direct inheritance.

On July 24, 1906, two groups of second-stage larval lobsters were mutilated. In group A, the right chela was amputated, and in group B, the left chela was removed in each specimen. The lobsters were kept in

GROUP A: RIGHT CHELA REMOVED

Specimen	Stage	Date of First Mutilation	Number of Moults	Character of the Chelæ		
				Date	Right	Left
1	2d	July 24	Six	Sept. 29	Nipper	Crusher
2	2d	" 24	Six	Oct. 6	Nipper	Crusher
3	2d	" 24	Six	Sept. 29	Nipper	Crusher
4	2d	" 24	Six	Nov. 8	Nipper	Crusher*

GROUP B: LEFT CHELA REMOVED

1	2d	July 24	Six	Oct. 27	Crusher	Nipper
2	2d	" 24	Six	Sept. 29	Crusher	Nipper
3	2d	" 24	Six	Oct. 13	(?)†	Nipper
4	2d	" 24	Six	Oct. 19	Crusher	Nipper
5	2d	" 24	Six	Oct. 19	Crusher	Nipper
6	2d	" 24	Six	Oct. 19	Crusher	Nipper
7	2d	" 24	Six	Oct. 19	Crusher	Nipper
8	2d	" 24	Six	Oct. 19	(?)†	Nipper
9	2d	" 24	Six	Sept. 22	Crusher	Nipper

* This specimen was very late in displaying any asymmetrical differentiation, but by November 18 the left chela became somewhat broader, showed a characteristic crusher curve in the dactyl and tubercle-like teeth in the proximal region of each jaw.

† Up to date showed no evidence of having differentiated into a crusher.

separate compartments and precaution taken to keep a careful record of mutilations, moults, and regenerations for each individual. Such an experiment is especially difficult because the naturally great mortality of larval lobsters when kept in artificial conditions is greatly increased by the injury attending mutilation, but I succeeded in rearing beyond the fourth stage four specimens in group A, and nine specimens in group B. After each moult the regenerated chela was invariably amputated. The limb on the opposite side of the body was thus given every possible advantage with regard to growth, in order to see whether this chela could be made to differentiate into a crusher. The data so far obtained for these specimens is in the table given above.

From this table it will be observed that in over 90 per cent. of the specimens the chelæ have already differentiated asymmetrically, but in no case for group A did a crusher develop on the right side, or in group B, a crusher on the left side. The evidence for specimens Nos. 3 and 9 is at present neutral, for they still appear to retain their embryonic symmetry, and it remains to be seen at the next moult, which will occur during the spring, whether they too will finally develop a crusher on the right side or not. At any rate, this experiment clearly shows that *in all cases where the chelæ have differentiated far enough to display asymmetrical characters, the crusher has developed on the chela which was given the greater opportunity for growth; i. e., on the side which was not mutilated.*

The results so far attained, therefore, establish a strong presumption that the "right- or left-handedness" of the lobster may not be entirely predetermined in the egg. If these results are confirmed by further experiments,

it ought to furnish convincing proof that the asymmetrical relation of chelæ in the lobster may under certain conditions, at least, be determined by other than hereditary factors.

This result is especially interesting in view of the fact that in the adult lobster we do not seem to meet with the phenomenon of reversal or compensatory regulation which Zeleny¹⁹ and Przibram²⁰ have found in other crustacea. In the course of my experiments I have mutilated over 200 adult lobsters in which the normal asymmetrical limbs were autotomously removed and preserved for each specimen, but in no case did a crusher ever regenerate on the side which had originally carried a nipper and at the same time *vice versa* for the nipper. It has been suggested that possibly one reason why we do not get a typical reversal in the lobster is because the asymmetry of chelæ consists in a greater qualitative differentiation than in the case of the crabs and some other decapod crustacea, consequently, a true reversal in the lobster would involve more fundamental morphological transformations than in the case of these other forms. On the other hand, in the larval lobster the chelæ are very similar both qualitatively and quantitatively, and the results of our experiments seem to indicate that the symmetrical relations of the organisms are at this stage in a much more plastic condition.

We may summarize, then, this discussion of regeneration and the origin of symmetry as follows: First, positive evidence has been advanced that the process of regeneration is an important factor in the origin of symmetrical chelæ. Second, the results of the foregoing

¹⁹ *Loc. cit.* (17).

²⁰ *Loc. cit.* (7).

experiments on the larval stages establish a strong presumption that the right- or left-handed asymmetry of the lobster, instead of being entirely hereditary, may be influenced during ontogenetic development by external factors.

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THE PHYSIOLOGY OF THE DIGESTIVE TRACT
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BY MICHAEL X. SULLIVAN.

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DEPARTMENT OF COMMERCE AND LABOR
BUREAU OF FISHERIES

GEORGE M. EOWERS, *Commissioner*

CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE BUREAU OF FISHERIES AT WOODS HOLE, MASS.

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THE PHYSIOLOGY OF THE DIGESTIVE TRACT OF ELASMOBRANCHS.

BY MICHAEL X. SULLIVAN, PH. D.

INTRODUCTION.

The digestive tract in fishes has been studied quite extensively both from the histological and from the physiological standpoint. Most of this work has been done on European species, however, and has given rise to contradictory conclusions, especially from the viewpoint of physiology. Hence it seemed advisable to devote some attention to fishes found also in American waters, and I have accordingly undertaken the study of the digestive tract of elasmobranchs.^a

This group of fishes was chosen for investigation, first, because of the relatively simple structure of their digestive tract, and second, because they may, from their position in the scale of evolution, form the groundwork for an extensive comparative study of fish in general. Thus we may arrive at a unified view of the changes, structural and physiological, which have taken place in the alimentary canal of fishes from the lowest to the highest. The treatment of the subject is partly histological, but mainly physiological.

HISTORICAL DISCUSSION.

THE DIGESTIVE TRACT IN FISHES.

MORPHOLOGY.

As in higher animals, the digestive tract in fishes may be divided into the following portions: Mouth, esophagus, stomach, small and large intestine. In fishes, however, two or more of these divisions may coalesce and become indistinguishable. As a rule there is a complicated dentition, but no salivary glands. The buccal cavity opens directly into the esophagus, and this in turn into a large stomach.

^aThe work embodied in this paper was done at the laboratory of the U. S. Bureau of Fisheries, Woods Hole, Mass. during the summers of 1905 and 1906, when the writer was a salaried assistant of the Bureau. I am indebted to Dr. W. L. Chapman for making the photomicrographs of the rectal gland (plate I).

which is usually furnished with a valve at its posterior end. The digestive tract may be straight, U-shaped, or Y-shaped—straight in *Branchiostoma* and the cyclostomes; syphonal or U-shaped in the elasmobranchs and in some teleosts, where the stomach presents the form of a bent tube, of which one half is the cardiac and the other the pyloric portion; caecal or Y-shaped in most teleosts, where the cardiac division is a long, descending blind sac, with the cardiac and pyloric openings of the stomach lying close together. In most cases the pyloric tube is long and slender.

In many fishes, especially among ganoids and teleosts, a variable number of blind tubes open into the intestine immediately posterior to the pylorus. These tubes are termed the pyloric caeca and are often filled with the same material as is the intestine. When present in large numbers, the appendages often coalesce into a common duct. In the cyclostomes and dipnoans no pyloric appendages exist, and in the elasmobranchs pyloric caeca have been found by Turner (1873) only in the Greenland shark, *Lamargus borealis*, and by Gegenbauer (1892) in certain skates.

The duodenum receives the hepatic and the pancreatic secretions, and also the secretion of the pyloric appendages.

The intestine varies much in length, and in many fishes the absorbing surface is increased by folds of the mucous membrane, which wind spirally or are arranged in parallel lamellæ. These spiral valves are found in cyclostomes, selachians, ganoids, and dipnoans. In short, the digestive tract in fishes varies greatly, from a simple condition to a complex one, with valves, folds, and appendages.

The pancreas is the most constant of all digestive glands in vertebrates. In the lower fishes it occurs as a compact mass, while in the teleosts it is, as a rule, diffused and distributed about the pyloric caeca, hepatic duct, and in the liver. The presence of the pancreas in bony fishes in a widely diffused state was demonstrated by Legois (1873). In the elasmobranchs the pancreas is comparatively large, and pinkish in color. It empties by a single duct into the duodenum.

Caecal appendages at the end of the intestinal canal are of exceedingly rare occurrence in fishes. In the elasmobranchs, however, an appendage, the so-called rectal gland, exists near the end of the intestine. This gland varies from half an inch in length in the skate to three or four inches in the big sharks. According to Wiedersheim (1905, p. 422), cloacal appendages exist in the dipnoans and traces of a blind intestine may be found in certain teleosts, while in the Holocephali the place of the rectal gland is taken by glandular tissue within the walls of the rectum.

For a more detailed account of the gross anatomy of fishes the reader is referred to Home (1814), who described the intestines of thirty species, and to Rathke (1824), who described fifty-six species. General works on the intestinal canal of fishes are Siebold and Stannius (1854), Milne-Edwards (1860), Günther (1880), Oppel (1896, 1897, 1900, 1904), and Wiedersheim (1905).

HISTOLOGY.

Though Nehemiah Grew (Gangee, 1893) made mention, in 1676, of a glandular secretion in the stomach of the horse, it was not until 1836 that the gastric glands were actually discovered. In this year Boyd (1836) discovered gastric glands in mammals and noticed their presence in some fishes. Following Boyd, Bischoff (1838), one of the earliest workers on the histology of the alimentary canal in fishes,

studied the mucous lining of the stomach of a great many species. In Cyprinidæ he was unable to find gastric glands. In other species, however, he found them abundant. As we shall see later, the lack of gastric glands is not peculiar to the Cyprinidæ, since many other fishes have no functional stomachs.

Rathke (1841) found that the alimentary canal of *Amphioxus* (*Branchiostoma*) is composed of ciliated epithelium without glands, and Johannes Müller (1843), in his work on the myxinoids, arrived at the same results. By these investigators the simplicity and uniformity of the mucous lining of the alimentary canal in the lower fishes was fully established.

Vogt (1845) proved the existence of two kinds of cells in the stomach of the common trout, *Salmo fario*, i. e., cells of cylindrical epithelium, covering the surface, and round cells in the crypts. Vogt, however, did not recognize these crypts as gastric glands. Leydig (1852), on the other hand, clearly recognized the gastric glands in *Squatina augetus* and in *Torpedo galvani*, since he writes of the small round cells, containing highly granular protoplasm, as granular cells. In 1853 Leydig found such glands in the sturgeon, *Acipenser uasus*, but could not find them in the stomach of the loach, *Cobitis fossilis*. In a still later paper Leydig (1857) referred to these glands as "labdrüsen," thus signifying that they were like the gastric glands of higher vertebrates.

Since 1857 much work has been done on the histology of the alimentary canal of fishes, and especially on the histology of the stomach. Perhaps the best reviews of previous work are presented by Edinger (1877), Richet (1878), and Yung (1899). To the works of these authors I am greatly indebted.

One of the earliest workers on the glands of the stomach of fishes was Valatour (1861), who noticed the presence of gastric glands in various species and confirmed Bischoff's work in that he could find no functional stomach in Cyprinidæ. From 1861 to 1870 much advance was made in histological technic, and in 1870 Heidenhain discovered two kinds of granular cells in the mammalian stomach, and Rollet the same year confirmed his discovery. These cells are now known as chief and parietal cells. In fishes, on the other hand, Edinger (1877) could not find the two kinds of gastric cells distinguished by Heidenhain and Rollet in the mammalian stomachs. Of Edinger's work we may speak in detail.

Edinger (1877) made a detailed histological study of the entire digestive tract of fishes. According to his investigations, the stomachic crypts are only partly lined with gastric glands, for in the pylorus the crypts are functional merely as mucous glands. The pyloric appendages are simply evaginations of the intestinal wall and present the same structure as the part from which they arise. Properly speaking, no glands exist in the middle intestine, and the mucous cells are the only secretory part. The other epithelial cells are merely absorptive in function. Finally Edinger paid much attention to the question as to whether or not chief and parietal cells exist in fishes. He concluded that there is only one kind of cell in the gastric glands—a cell which is homologous to neither of these cells.

Edinger's conclusion has been generally accepted, although several authors have noted differences in the cells of the gastric crypts. Thus Cajetan (1883) called attention in the case of *Cobitis barbatula* to the fact that the cells of the stomach differ with respect to the dimensions of their granules and their staining reaction to osmic

acid. Pilliet (1894) also mentioned some differences between the gastric cells of *Pleuronectes* according as they are situated at the superficial or the deeper portions of the gland.

Pilliet studied principally selachians and *Pleuronectes*. According to him, the glands of the stomach of the selachians are long. In *Pleuronectes* he noted a difference in the extent of the distribution of the glands, in that they are fewer in young or undeveloped fish. He likewise claimed that the cardiac portion of the stomach of *Pleuronectes* is essentially peptic, while the pyloric portion is essentially mucous.

According to Cattaneo (1866), who studied numerous fishes, the fishes highest in the scale of evolution repeat in their development the structure of the digestive tract as found successively in adult acraniates, cyclostomes, selachians, and ganoids. The least differentiated part of the intestine of the higher forms has a structure like the most differentiated part of the lower forms. Like Edinger, Cattaneo found in all species of fishes that the stomach and middle intestine are the most differentiated parts, while the esophagus and terminal intestine preserve a primitive character. With Edinger, he concluded that only one kind of cell is present in the gastric glands of fishes.

In addition to the writers already mentioned, Macallum (1886) described the intestines of some ganoids, Decker (1887) studied fresh-water fish, while W. N. Parker (1889), Hopkins (1890, 1895), Mazza (1891), Mazza and Perugia (1894), Claypole (1894), and Haus (1897) have added to our detailed knowledge of the digestive tract in fishes. More recently Yung (1899) made a detailed study of the digestive tract of *Scyllium canicula*, while Oppel (1896, 1897, 1900, 1904), in his "Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbelthiere," has made a comprehensive review of the previous work on the microscopical anatomy of the digestive tract.

PHYSIOLOGY.

The first experiments on the digestion of fishes were made by Spallanzani (1783), who worked on eels, pikes, carps, and barbels. Previously, Réaumur (1752) and Stevens (1777) had worked respectively on birds and man. Réaumur, indeed, made the first decisive step in the physiology of digestion. He introduced into the stomach of a kite small metallic tubes with the ends covered by a grating of threads or fine wire. He found that the gastric juice is acid and that it would digest meats and bones, but not vegetable grains or flour. Stevens proved the same thing for man, and in addition proved that the gastric juice would digest *in vitro*. Spallanzani in like manner passed into the stomach of his fish tubes filled with flesh, and, having left them in the stomach forty-two hours, found them covered with mucus, but with little or no flesh within them. From this work Spallanzani concluded that digestion is carried on best in the fundus of the stomach. He believed, however, that the stomach is not the only part capable of digesting food, but that the esophagus, in a more feeble way, also has digestive power. He likewise believed that digestion is accomplished without trituration, for the thin tubes which he used did not show any trace of deformation.

Spallanzani also showed that digestion goes on *in vitro* as in the stomach; consequently, hypotheses regarding vital force, coction, and fermentation have no reason to exist. Digestion is, on the contrary, a chemical phenomenon, not a process

of putrefaction. Furthermore, this investigator saw that the acid is secreted by the stomach and that it might be seen exuding from the walls. He did not make mention, however, of digestion in the intestines or of the action of the bile. In his eyes, indeed, the stomach in all animals was the principal digestive organ.

Tiedemann and Gmelin (1827) made observations upon the contents of the intestinal tract of the trout, barbel (*Cyprinus barbus*), etc., and proved that in a fasting fish the mucus does not redden litmus, but that a stomach full of food contains free acid and coagulates milk. Tiedemann and Gmelin believed that the acidity is due to a mixture of acetic and hydrochloric acids. These workers also paid some attention to the liquid of the pyloric appendages. This liquid, they found, reddens litmus but slightly, and they believed that it mixes with the food dissolved by the stomach and accelerates assimilation.

In 1873 Fick and Murisier called attention to the fact that the ferment in the stomach of the trout and the pike differs from that of higher animals in that it digests food at a low temperature as well as at 40° C., while the higher organisms digest better at the higher temperature.

In the same year Rabuteau and Papillon (1873) recognized that the gastric juice of the skate is acid, and the former writer secured, by distillation, a colorless liquid which he considered hydrochloric acid.

A little later Homburger (1877) concluded from his researches upon *Cyprinus tinca*, *Chondrostoma nasus*, *Scardinius erythrophthalmus*, and *Abramis brama* that the bile and extracts of the liver of these animals, as well as extracts of the intestinal mucous membrane, digest fibrin, emulsify fats, and convert starch to sugar.

In 1877 Krukenberg carried on investigations upon the intestines, and then upon the glands connected therewith, of widely different species belonging to all classes of fishes except dipnoans. From this work he concluded as follows:

No fish possesses salivary glands, although some have a diastase in the mucous membrane of the mouth, as, for example, *Cyprinus carpio* and *Lophius piscatorius*.

The action of the stomach is variable. With some selachians, ganoids, and teleosts this organ secretes pepsin similar to that of mammals in that it acts only in an acid medium, but different in that it can act at a lower temperature. In some cases, as in certain teleosts (*Zeus faber*, *Scomber scomber*), the stomach produces pepsin only in its anterior part, while the fundus secretes a mixture of pepsin and trypsin or a juice capable of digesting fibrin in an acid or in an alkaline medium. With other teleosts (*Gobius*, *Cyprinus*) the stomach, or the organ, considered as such does not furnish any enzyme at all. Digestion in these instances is carried on exclusively in the middle intestines.

In the selachians and the ganoids pepsin is produced not only in the stomach, but also in the anterior end of the middle intestines, in the selachians to the place where the pancreatic duct empties, and in the ganoids to the pyloric appendages.

In the selachians the massive pancreas secretes trypsin, while in the ganoids and teleosts, which have a diffused pancreas mixed with hepatic tissue, a ferment similar to pepsin can be extracted from the liver. This ferment is absent from the liver of the selachians.

In the case of the Cyprinidae trypsin is found both in the liver and in the mucous membrane of the middle intestine. The middle intestine, indeed, should be regarded as the principal seat of digestion in these fishes.

As regards the function of the pyloric appendages in most fishes, they inclose only mucus and chyle and are absorbing organs, while in other cases they secrete either a trypsin-like ferment, as in the *Thynnus vulgaris*, a mixture of pepsin and trypsin, or sometimes a mixture of pepsin, trypsin, and diastase.

Finally, in many species the liver, or hepato-pancreas, and the middle intestine secrete a diastatic ferment, as does even the buccal mucous membrane.

The general tendency of Krukenberg's studies, therefore, is to establish the existence of an evolution of the digestive function from the invertebrates (molluses, crustacea, etc.) to the higher vertebrates. By the great variation in the distribution of the ferments, fish, according to him, show the principal stages of this evolution.

Luchbau (1878), by means of glycerin extracts of the mucous membrane of the stomach of the salmon, pike, and sandre, secured juices that would peptonize fibrin. Contrary to Fick and Murisier (1873), he observed that the peptonizing action is more rapid at 40° C. than at 15° C. Luchbau also examined the digestive activity of the juice of certain Cyprinidæ (*Cyprinus carpio*, *C. blicca*, *C. carassius*, *C. tinca*, *C. erythrophthalmus*, and *Abramis brama*), which do not have a functional stomach. In no case did he find an enzyme digesting in an acid medium—that is, pepsin; but he did find that fibrin is digested by the neutral or alkaline extract of the intestinal mucous membrane and that the digestive power is greater at 40° C. than at lower temperatures. Luchbau compared the ferment of the intestines of Cyprinidæ to the trypsin of mammals, and in addition to the trypsin-like ferment he found the diastatic ferment also. The trypsin-like ferment, he asserted, is secreted in the middle region, while the diastatic ferment is secreted along the whole length of the intestine. He did not find a fat-splitting ferment, nor, unlike Krukenberg, did he find any ferment which would digest albumen.

In researches upon the composition of the gastric juice, Richet (1878) analyzed the gastric juice of different fishes. He proved conclusively the presence of hydrochloric acid, free or combined with organic substances, such as tyrosin and leucin. He found the acidity to be high, in the case of *Scyllium canicula* even as high as 1.5 per cent hydrochloric acid. The digestive power of *Scyllium canicula* he found to be greater than that of *Lophius piscatorius*. In a later paper Mourrut and Richet (1880) found that the liquid in the stomach lost its digestive power by filtration. An acidity of 2.5 per cent was found by them to prevent peptonization, while moderate heat favored the action of the ferment. Mourrut and Richet did not observe that either *Lophius* or *Scyllium* produced a diastatic ferment in the stomach.

In a still later study of digestion in fish, Richet (1882) confirmed the facts previously given by him and declared that the gastric juice of sharks digests the chitin of crustacea. Further, the pancreas of *Scyllium* and of *Galeus* has no action on proteids but is limited to the transformation of starch to sugar and to the emulsification of oil.

Raphael Blanchard (1882) investigated the rectal gland of elasmobranchs and the pyloric appendages of teleosts. He found that the former organ produces both a diastatic and a fat-splitting ferment. The pyloric appendages, according to this investigator (1883), represent, in a certain sense, the pancreas, since they secrete a diastatic enzyme and a trypsin-like enzyme.

The presence of the trypsin-like ferment in the pyloric appendages has been proved also by W. Stirling (1884, 1885), who worked on the herring, cod, and hake, and made glycerin extracts of the stomach and pyloric appendages. In the stomach he found a ferment acting in acid and in the pyloric appendages one acting in an alkaline medium, from which observations he concluded that the stomach secretes pepsin, the pyloric appendages trypsin.

Decker (1887) found the stomach of fish to be sometimes neutral, sometimes alkaline, and he likewise found that the esophagus of the hake digested fibrin much more rapidly than the stomach did. He found in these species, moreover, that the esophagus, the intestine along its whole length, the cloaca, and the pyloric appendages all produced a ferment comparable to pepsin.

According to the researches of Knauthe (1898) all the intestinal mucous membrane of the carp, and especially the anterior portion of the intestine, produces a strong tryptic ferment, as does also the liver, or hepato-pancreas. The intestinal mucous membrane, except that of the mouth and the hepato-pancreas, produces amyolytic and fat-splitting ferments. The bile, he concluded, has of itself no digestive action on proteids or fats mixed with extracts of the intestinal mucous membrane or of the hepato-pancreas; it augments their action. The bile has, however, a diastatic action which is at the maximum at 23° C.

Bondouy (1899) investigated the function of the pyloric tubes in teleosts and came to the conclusion that they played an active part in digestion. They secrete trypsin and amylopsin, but no lipase. On the other hand, Bondouy believed the pyloric tubes have but little function as absorptive organs.

Yung (1899) in a very comprehensive and detailed work on elasmobranchs, including *Scyllium canicula*, *Acanthias vulgaris*, *Lamna cornubica*, *Galeus canis*, and *Carcharias glaucus* found that—

- (1) The buccal and esophageal membranes have no digestive action.
- (2) The stomach digests proteids.
- (3) The acidity of the stomach may be as high as 1 per cent.
- (4) The stomach may or may not convert the food into anti-peptone.
- (5) The gastric juice of *Scyllium canicula* acts better at 38° C. than at 20° C.
- (6) The formation of pepsin is limited to the stomachic sac.

Very little study has been given to the physiology of the pancreas of fishes. Bernard (1856) proved that the pancreas of the skate converts starch to sugar and acidifies fats. Krukenberg (1877), in his work on selachians, found that the pancreas of these fishes was secreting trypsin, the proteolytic ferment, but no amylopsin, the starch-splitting ferment, nor lipase, the fat-splitting ferment. Richet (1878), however, was unable to find trypsin in the pancreas of selachians, but did find the starch-splitting and fat-splitting ferments. Yung (1899), working on *Squalus acanthias*, found amylopsin and lipase, but only occasionally trypsin. Yung attempted to get the juice by a fistula, but had little success. His water glycerin extracts were only occasionally active. He found that extracts of the spleen aided the activation of the pancreas. More recently, Sellier (1902) found that the pancreas of several selachians studied by him does not of itself digest proteid, but must be activated by the juice of the spiral valve.

From this synopsis of the literature, it may be seen that there is by no means unanimity of opinion regarding the physiology of the digestive tract of fishes.

OBSERVATIONS AND EXPERIMENTS.

HISTOLOGY OF THE ALIMENTARY CANAL OF THE SMOOTH DOGFISH AND THE SAND SHARK.

The intestine of both *Mustelus canis* and *Carcharias littoralis* is bent twice upon itself: the first of these bends is between the stomachic sac and the pyloric tube, the second between the pyloric tube and the middle intestine. From an anatomical standpoint these two bends divide the alimentary tube into three portions, of which the first two constitute the anterior intestine, the third the middle and terminal intestine. As a rule the middle intestine, or what we might call the duodenum, is short. In *Mustelus canis*, indeed, there is almost no duodenum or valve-free portion between the pyloric tube and the spiral valve. On the other hand, in *Carcharias littoralis*, *Carcharhinus obscurus*, *Dasyatis centroura*, *Lamna cornubica*, and *Tetronarce occidentalis*, the middle intestine, or duodenum, is well marked off from the spiral valve and pyloric tube. From a histological standpoint the entire intestine may be divided into buccal, esophageal, stomachic, pyloric, duodenal, valvular, rectal, and cloacal mucous membrane.

Upon the digestive tract of European selachians, as Yung shows in his paper, "Recherches sur la digestion des Poissons" (1899), considerable histological work has been done. Yung himself made a thorough study of the alimentary canal of *Scyllium canicula*. The histology of *Mustelus canis* and *Carcharias littoralis* is practically the same and agrees in most respects with that of the European form *Scyllium canicula*. Histological study of the digestive tract of the American species shows the following facts:^a

BUCCAL MUCOUS MEMBRANE.

The mucous membrane of the buccal cavity is smooth, often covered with fine papillæ and moistened with mucus. Sections of the mucous membrane of the buccal cavity showed epithelium and connective tissue, but no glands. The epithelium is of the stratified pavement type. The epithelial cells next to the connective tissue are cylindrical, finely granular, and possess oval nuclei. Above this layer of cylindrical cells are several layers of large mucous cells, which are oval and contain a substance that stains with the ordinary mucus stains. The nucleus is very small, elongated, and pressed against the cell wall. Finally, the superficial epithelium consists of one or two layers of flat or oval cells which form a fine membrane.

MUCOUS LINING OF THE ESOPHAGUS.

Numerous papillæ and longitudinal folds occur in the inner lining of the esophagus. The folds are fine at their beginning, but thicken toward the cardiac end of the stomach. They vary in number and frequently anastomose. Transverse folds form a boundary more or less marked between the esophagus and the stomach. The mucous membrane of the esophagus is whitish, in strong contrast to that of the

^aAs fixing agent I used corrosive acetic, and as stain hematoxylin and eosin.

stomach, which is always reddish in color, especially noticeable when the stomach is full of food. In the beginning of the esophagus the epithelium is similar to that of the buccal cavity, but it is gradually replaced by an epithelium consisting of ciliated cylindrical cells and goblet cells.

MUCOUS MEMBRANE OF THE STOMACHIC SAC.

The mucous membrane of the stomach has a reticulated appearance, due to numerous folds. Some of these folds are continuations of the longitudinal folds of the esophagus, while others are transverse and oblique. In the pyloric tube the folds are extremely fine. Histologically, the mucous membrane of the stomachic sac differs from that of the esophagus by the absence of cilia and of goblet cells, and by the presence of true peptic glands.

The epithelium of the stomachic sac is of two kinds, superficial and glandular. The first is composed of a single layer of prismatic or pyramidal cells with oval nuclei. In these, two portions may be distinguished—one, finely granular, which incloses the nucleus and occupies four-fifths of the length of the cells; and another, the superficial part or the part nearest the cavity of the stomach, composed of a highly refractive, nonstaining, transparent substance. These two portions, as Yung (1899) has pointed out in his work on *Scyllium canicula*, corresponded to what Oppel (1897) called the protoplasmic portion and the upper portion. The refractive superficial portion of these cells has been called "Pfroph" or "plug" by Biedermann (1875), and is considered by Oppel as a substance comparable to mucus. The superficial epithelium, which is rather uniform in character, covers all the folds of the mucous membrane and the superficial portions of the glandular tubes.

The glandular tubes begin in the cardiac end of the stomach and extend to the pylorus, being most plentiful in the middle of the stomachic sac. Each gland is a cylindrical tube, with the canal narrow in the upper part but wider toward the bottom. The tubes in the middle of the stomach are longer than those of the cardiac end or the pyloric end of the sac. In every case they are separated from each other by a fine layer of connective tissue. The epithelium of the neck of the peptic crypts consists of cylindrical cells, like those of the superficial epithelium, which become little by little shorter and thicker. They are distinguishable from the superficial layer, however, by the absence of the mucous plug, and by the presence of a large round nucleus. They differ from the neighboring peptic cells by their clearer contour, smaller size, and the smaller amount of granulation. The body of the gland is occupied by cells which are irregularly polygonal in shape, highly granular, and closely packed together. These cells are all of one kind, and can not be differentiated into chief and parietal cells, such as Heidenhain and Rollet have found in the mammalian stomach.

PYLORIC TUBE.

In the long narrow pyloric tube we find crypts and the same superficial epithelium as in the stomachic sac. The crypts, however, are short and the polygonal peptic cells are absent.

INTESTINE.

The intestine of elasmobranchs may be divided into two portions—a small intestine or duodenum, and a large intestine. The former is short, varying from one-

half an inch to 2 inches in length. The latter is longer and very wide; it is divided into two portions—the colon, containing the spiral valve, and the rectum, which is short.

From the end of the pyloric tube to the cloaca the histology of the intestine is practically the same and consists essentially of cylindrical and goblet cells. No glands are present, but the villi project into the lumen of the intestine both in the duodenum and in the spiral valve. The epithelium which covers these villi is the same throughout and consists of cylindrical and goblet cells. Since the villi are more prominent in the spiral valve, it would be well to consider this part of the intestine in detail.

SPIRAL VALVE.

A spiral valve is present in the colon of cyclostomes, selachians, ganoids, and dipnoans. Its histological structure in *Mustelus canis* and *Carcharias littoralis* is like that of the duodenum. The villi stop abruptly at the point where the rectal gland opens into the intestines. The folds of the spiral valve are formed from the mucosa of the walls of the intestines. Through the middle of each fold passes the muscularis mucosa. From the center connective tissue extends into the villi. A cross section of a fold shows: (1) Epithelium of upper surface, (2) connective tissue, (3) connective tissue and muscular tissue, (4) connective tissue, (5) epithelium of undersurface.

RECTAL GLAND.

The rectal gland, glandula or processus digitiformis, is a compound tubular gland varying from one-half inch in the skate to four inches in the mackerel shark. It opens into the rectum by a duct, which, beginning at the central canal of the gland, runs forward along the edge of the mesentery to enter the dorsal wall of the lower end of the spiral valve or the top of the rectum. The gland consists of three layers: (1) an outer fibro-muscular layer, (2) a middle glandular layer, and (3) a central region consisting of ducts and blood vessels arranged round a central lumen.

The middle layer is composed of a number of branched tubules radially arranged and separated by capillaries which are usually gorged with blood. The high power shows mono-nucleated cubical cells not clearly defined from each other and of a glandular appearance.

The central layer begins at a varying distance from the periphery by the sudden transition of the gland cells into the epithelium of ducts which open into the central lumen. In many cases the more superficial cells have undergone a mucoid change and a band of clear cells is visible lining the duct. The microscopical appearance of the gland is shown in plate I.

PHYSIOLOGY OF THE DIGESTIVE TRACT OF ELASMOBRANCHS.

While studying the food of the dogfish, *Mustelus canis*, at the laboratory of the Bureau of Fisheries, Woods Hole, Mass., during the summer of 1904, Irving A. Field found that 16 per cent of the dogfish contained lobsters, 34.17 per cent rock crabs, and 20.1 per cent spider crabs. The carapace of these organisms consists of salts and chitin, the latter highly resistant to reagents. As the carapace was found in varying degrees of decomposition, and, further, since the carapace of crabs and

lobsters fed to the fish could not be found in the stomach after four days of digestion. the question arose as to whether the dogfish actually does digest chitin. I therefore began, during this summer, a physiological study of the alimentary canal of *Mustelus canis*. During the summers of 1905 and 1906 the investigation was extended to include *Carcharias littoralis*, *Squalus acanthias*, *Tetronarce occidentalis*, *Carcharhinus obscurus*, *Raja crinacea*, *Lamna cornubica*, and *Dasyatis centrura*. The work consisted of—

- (a) The preparation, for artificial digestion, of extracts of buccal, esophageal, and gastric mucous membranes.
- (b) The study of the normal content of the stomach.
- (c) The study of the acidity of the stomach.
- (d) Determining whether or not *Mustelus canis* digests chitin.
- (e) The preparation of extracts of the intestinal mucous membrane and of the pancreas.
- (f) The study of the activation of the pancreas.
- (g) The study of the rectal gland.

BUCCAL CAVITY.

The elasmobranchs as a rule swallow their food whole, without mastication. Naturally we should suppose that little digestion goes on in the buccal cavity. This probability is increased by the absence of glands. Since Krukenberg (1877) claimed, however, that the buccal mucus of some fish, especially of *Cyprinus carpio* and *Lophius piscatorius*, possesses a diastatic action, it seemed proper to test the action of various kinds of infusions of the buccal mucous membranes of selachians.

The buccal cavity of a number of these fish, freshly killed, was scraped. The mucus thus collected was white in color, neutral in reaction, and gave a good test for mucin, but showed no diastatic activity. Scrapings of the buccal cavity of all the elasmobranchs obtainable gave the same results.

The buccal cavity of elasmobranchs, then, as Yung has already shown for *Scyllium canicula*, secretes mucin comparable to that of the saliva of man, but with no diastase.

Water extracts of the buccal mucous membrane have no permanent emulsifying action on olive oil.

Five-tenths per cent hydrochloric acid extracts of the buccal mucous membrane filtered free of mucin have no peptonizing action on white of egg or pig fibrin. The buccal mucous membrane then contains no pepsin-like enzyme.

Conclusions: The buccal mucus of all the elasmobranchs examined contains mucin but no digestive ferment.

ESOPHAGUS.

The reaction of the esophagus of a fasting fish is neutral. Tested when the fish is in full digestion, on the other hand, the reaction of the esophagus is acid, due, undoubtedly, to regurgitation from the stomach.

Mucus was scraped from the esophagus of ten fasting smooth dogfish. This mass was divided into two equal portions and one portion was made slightly alkaline with sodium carbonate, while the other was acidified to the extent of five parts of

hydrochloric acid in one liter. To each portion thymol was added to prevent the action of microbes. Into test tubes containing the alkaline and acid solutions, respectively, fibrin was placed. In no case was the fibrin digested, whether the tubes were kept at 18° C. or at 37° C.

Therefore the esophagus produces neither trypsin nor pepsin. If the mucous membrane is scraped from the esophagus of a fish in full digestion, extracts of this mucus may have a slight digestive action on fibrin in acid solution. This digestive action, however, is due to some pepsin which has come from the stomach, for if the esophagus is well washed, before scraping the esophageal mucus is found to have no action on fibrin.

In like manner neither water extracts nor weakly alkaline extracts of the mucous membrane of the esophagus have any diastatic action on starch paste even after a lapse of ten hours. Yung (1899) in two cases found a diastatic ferment in the mucus of the esophagus. These cases were one *Scyllium canicula* in full digestion and one *Acanthias vulgaris*. He concludes from his experiments, however, that as a rule the epithelial elements do not produce a diastatic ferment.

Water extracts of the esophageal mucus have no action on olive oil.

Conclusion: The esophagus has of itself no digestive action.

MUCOUS MEMBRANE OF THE STOMACHIC SAC.

The mucous membrane of the stomachic sac was scraped and triturated in equal parts of glycerin and 0.5 per cent hydrochloric acid. Neutralized extracts did not coagulate milk. Therefore the rennet enzyme and its zymogen are absent from the mucous membrane of elasmobranchs.^a The acid extracts digested uncooked white of egg and fibrin rapidly, but acted very slowly on cooked egg. As a rule the products of digestion by the acid extracts were peptones. Alkaline extracts of the stomachic sac showed no digestive activity.

The only proteolytic ferment in the stomachic sac of elasmobranchs is, accordingly, pepsin similar to that of higher vertebrates. There is one great difference, however, between the pepsin of mammals and that of fish: The pepsin of fish acts at a low temperature far better than does that of mammals. Moreover, Fick and Murisier (1873) and Hoppe-Seyler (1877, cited by Yung, 1899) claimed that the fish pepsin acts better at 10° C. or 15° C. than at 37° C. Luchau (1878) and Yung (1899), on the other hand, observed that the peptonizing action of the stomach of fishes is greater at 40° C. than at 15° C.

While I should admit that the pepsin of fish acts rapidly on fibrin at 15° C., I must conclude from my experiments that the pepsin of *Mustelus canis*, *Carcharias littoralis*, and *Galeocerdo tigrinus* digested fibrin better at 37° C. than at 20° C. In this conclusion I am in exact agreement with Yung, who found in *Scyllium canicula* that the pseudopepsin of fish acted more rapidly at the higher temperatures. Before leaving the question as to the action of pepsin it must be said that the artificial digestion in no way approximates the natural digestion as carried on in the stomach.

^aCertain experiments have led me to believe that the rennin zymogen (pexinogen) may exist in the mucous of the stomachic sac of at least some of the elasmobranchs and may be extracted by appropriate methods as the active enzyme rennin (pexin). To this question I hope to return at another time.

because in natural digestion the products are rapidly carried off, the stomach is in constant movement, and the pepsin and hydrochloric acid are constantly being renewed.

In no case, whether the solution was acid, neutral, or alkaline, did I find that glycerin extracts of the mucous membrane of the stomachic sac of the various elasmobranchs had the power of converting starch to sugar. In concluding that the mucous membrane of the stomachic sac of elasmobranchs does not produce a diastatic enzyme I should be in exact agreement with Richet (1882), who studied *Scyllium* and *Acanthias*, and with Yung (1899), who extended his studies further—to *Galeus* and *Lamna cornubica*. Upon ethyl butyrate, likewise, I found that the watery extracts had no effect whatever.

MUCOUS MEMBRANE OF THE PYLORIC TUBE.

Peptic glands are absent from the pyloric tube. To study the physiology of this tube, I took 10 smooth dogfish (*Mustelus canis*) and 10 sand sharks (*Carcharias littoralis*). After carefully washing the inner surface of the pyloric tube I scraped off the mucus and macerated it in glycerin and 0.5 per cent hydrochloric acid solution. After twenty-four hours the liquid was filtered. To the filtered liquid small pieces of fibrin were added. In twelve hours the digestion mixture was tested and showed syntonin, but no peptones. Contrary to Krukenberg's (1877) results from work on selachians, we must conclude with Yung that the formation of pepsin is limited to the cardiac end of the stomach or the stomachic sac.

The pyloric tube has likewise no action on starches or fats.

Conclusion: The only active ferment secreted by the stomach of elasmobranchs is pepsin.

CONTENT OF THE STOMACH.

The study of the content of the stomach is really the study of the content of the stomachic sac. The content of the stomach varies greatly. Sometimes it is strongly acid and viscid; sometimes it is liquid and holds in suspension alimentary débris, more or less recognizable, oil, fish in various stages of decomposition, chitin, etc.

An analysis was made of the contents of the stomachic sac of *Mustelus canis*, *Carcharhinus obscurus*, *Carcharias littoralis*, *Squalus acanthias*, *Tetronarce occidentalis*, *Raja erinacea*, *Lamna cornubica*, and *Galeocerdo tigrinus*. The acid content of the stomach was neutralized and an abundant precipitate of syntonin occurred. The filtrate was boiled, and if a precipitate occurred was again filtered. The solution was boiled and again treated with an excess of ammonium sulphate. The precipitate showed albumoses. The filtrate was then tested with the biuret reaction. As a rule syntonin, proteoses, and peptones were found in the stomach content. Occasionally, however, no peptone could be found in the stomach content of *Mustelus canis* and *Carcharias littoralis*.

Conclusions: The stomach of *Mustelus canis*, *Carcharias littoralis*, *Squalus acanthias*, *Tetronarce occidentalis*, *Carcharhinus obscurus*, *Raja erinacea*, *Lamna cornubica*, and *Galeocerdo tigrinus* secretes pepsin and converts proteids partly to antipeptone.

Acidity of the gastric juice. - Richet (1878) found the acidity of the gastric juice of fish to be much greater than that of mammals. Thus he found the acidity of fish he studied to be as follows:

Fish.	Parts in 1,000.
Skate (<i>Raja clavata</i>)	14.6
<i>Lepidus piscatorius</i>	6.2
<i>Squalus squatina</i>	6.9
<i>Scyllium catulus</i>	6.9
<i>Scyllium canicula</i>	14.9
Pike	6.0

The acidity Richet found to be due to an acid not soluble in ether. He believed that the acid was hydrochloric acid combined with some organic substance, as leucin or tyrosin.

Yung (1899) in his study of the gastric juice of *Scyllium canicula* found the mean of four analyses to be 0.84 per cent.

The acidity of the stomach of elasmobranchs is greatest when the fish is in full digestion. Indeed, the fasting stomach is practically neutral. In order to study the acid, phenolphthalein, alizarin, and dimethyl-amido-azobenzol were used as indicators as recommended by Webster and Koch (1903) in their Laboratory Manual of Physiological Chemistry (p. 36), and experiments were made to determine: (a) The total acidity of the stomach content in terms of hydrochloric acid; (b) the physiologically active hydrochloric acid; (c) the free hydrochloric acid. The results are given in the following table:

Species.	Total acidity in percentage hydrochloric acid.	Physiologically active hydrochloric acid, average percentage.	Highest percentage free hydrochloric acid.
<i>Mustelus canis</i>	0.04-1.00. Average, 0.73. 50 individuals.	0.538. 6 individuals.	0.2.
<i>Carcharias littoralis</i>	0.1-1.2. Average, 0.87. 25 individuals.	0.614. 10 individuals.	0.31.
<i>Squalus acanthias</i>	Average, 0.67. 60 individuals.	No tests.	No tests.
<i>Carcharhinus obscurus</i>	Average, 0.55. 2 individuals.	0.493. 2 individuals.	0.254.
<i>Lamna cornubica</i>	0.275. 1 individual.	0.229. 1 individual.	0.172.
<i>Galeocerdo tigrinus</i>	0.93. 1 individual.	0.812. 1 individual.	None.
<i>Tetronarce occidentalis</i>	0.51. 1 individual.	No tests.	None.

In the case of *Carcharias littoralis* and *Carcharhinus obscurus* the physiologically active hydrochloric acid was determined as follows: (a) By neutralizing 10 c.c. of the stomach contents, evaporating, calcining, and finding the total chlorides by titrating with normal silver nitrate; (b) by evaporating, calcining, and finding, by titrating with the silver nitrate solution, the chlorides in a nonneutralized 10 c.c. of the stomach content; (c) subtracting (b) from (a). The results were as follows:

	Per cent.
<i>Carcharias littoralis</i>	1.1
<i>Carcharhinus obscurus</i>92

Physiologically active hydrochloric acid by $\text{AgNO}_3 = \text{C}$:

Carcharias littoralis	0.660
Carcharhinus obscurus525

Action of the gastric juice on chitin.—Lobsters and crabs form part of the food of several of the elasmobranchs. The shell of these crustaceans consists of chitin and salts. This chitin is very resistant to reagents. According to Hammarsten (1901), chitin, to which he gives the formula $\text{C}_{60}\text{H}_{100}\text{N}_8\text{O}_{38} + n(\text{H}_2\text{O})$, is insoluble in boiling water, alcohol, ether, acetic acid, dilute mineral acids, and dilute alkalis. It is dissolved without decomposing in cold concentrated hydrochloric acid. Since chitin is so resistant it is interesting to know whether the chitin-eating fish digest chitin or whether it passes through the body unchanged.

An analysis of lobster shells given by Herrick (1895) from the work of Albert W. Smith is as follows:

TABLE SHOWING COMPOSITION OF THE CARAPACE OF THE LOBSTER (3 SPECIMENS).

Composition, air dried.	1. 2. 3.		
	1.	2.	3.
Weight in grams.....	11.87	21.51	8.48
Calculated as calcium carbonate.....	43.68	32.83	32.93
Calcium phosphate.....	7.70	8.32	11.18
Calcium sulphate.....	.58	.53	.99
Magnesium carbonate.....	3.50	2.39	3.38
Sodium carbonate.....	1.51	1.80	2.31
Alumina.....	.68	2.04	1.04
Silica.....	.14	.29	.08
Organic matter and water.....	42.21	51.80	48.09

Richet (1878) believed that the chitin of the shell of crabs, lobsters, etc., is digested by dogfishes and sharks, although he recognized that it is extremely difficult to dissolve chitin by artificial digestion. Yung (1899), on the other hand, claimed that the selachians do not digest chitin, for he found pieces of chitin not only in the stomach but even in the spiral valve and rectum. More recently Zaitschek (1904) has proved quantitatively that the chitin in the wings of insects is absolutely undigested by hens.

To determine whether the elasmobranchs, and especially the smooth dogfish, digest chitin, the following experiments were made:

1. Several fishes were fed with crabs and lobsters and in the course of from one to five days were killed. In some cases the shells were found in the stomach in a macerated state. On the other hand, no compact chitin could be found after ninety hours of digestion, but in the spiral valve might be found a gritty dark-brown or reddish mud.

2. The gastric juice was drawn from several large dogfish. Into small quantities of this juice lobster shells were placed. The mixtures were kept at a constant temperature—some at 18°C ., some at 38°C . After twelve hours the only change found in the shell was that the edges were softened a trifle.

3. The mucous membrane of the stomach of five dogfish was scraped, triturated in glycerin and 0.5 per cent hydrochloric acid. This juice, although it acted quickly on fibrin, did not digest the chitin in forty hours.

4. Experiment 2 was repeated with the difference that at frequent intervals the gastric juice was renewed and the chitin was subjected to frequent grinding. In this

way there was formed a pulverized mass of a dark brown or dark red color, which approximated the granular mass found in the intestines of the chitin-swallowing fish.

5. Pieces of chitin were placed in acid of strengths varying from 0.5 to 35 per cent hydrochloric acid. Carbon dioxide was set free in each case, but in greater quantities with the stronger acids. The chitin became softened, pliable, but did not dissolve.

6. Crabs were fed to dogfish confined in small aquaria. The excrement of the fish was carefully watched, and in this excrement, known by its shape and color, some pieces of the softened but otherwise unchanged chitin could be found. No evidence was gathered that the fish ever regurgitated any of the chitin, though Yung believes that regurgitation might take place.

Conclusion: The conclusion to be drawn from the experiments is that *Mustelus étuis* and other chitin-swallowing fishes do not digest the chitin. The frequent change of the gastric juice, combined with the movements of the stomach, dissolves out the salts, softens the shell, and breaks it up into a fine mass, such as may be found in the spiral valve. The chitin is not regurgitated, but on the contrary is excreted in a finely divided mass.

MIDDLE INTESTINE.

Extracts of the middle intestine or duodenum of the various elasmobranchs show no digestive activity. Whether or not the cylindrical cells and goblet cells lining the mucous membrane of the duodenum play any part in activating the pancreatic juice will be discussed under pancreatic digestion.

SPIRAL VALVE.

Extracts of the mucous membrane of the spiral valve showed no digestive action on starches, fats, or proteids; nor indeed was it possible to demonstrate any inverting power, though we may presume that such power may exist in this mucus. The main function of the spiral valve is absorptive. Its further action in pancreatic digestion will be taken up in the discussion of the function of the pancreas.

PANCREAS.

As may be seen by reference to page 9, there has been but little experimentation on the pancreas of fishes, which fact is warrant for discussing the physiology of the pancreas of elasmobranchs. In order to get at the problem with the greatest clearness, it would perhaps be well for us to outline the growth of knowledge concerning pancreatic digestion, from the first experiments on the pancreas to the later researches leading to our present-day understanding of the action of this organ.

The pancreatic ducts, according to Haller (1764), were discovered by Wirsung in 1642. Although Wirsung appears to have observed the pancreatic juice, he did not pursue the subject further, and little was made of his discovery until Regner De Graaf took up the matter. In 1664, De Graaf, according to Foster (1901), made the first successful pancreatic fistula and collected the juice from a dog. But De Graaf did not obtain a definite grasp of the function of the pancreas. Eberle (1834), however, announced that a watery infusion of the pancreas when shaken with oil emulsifies it. In 1836, according to Corvisart (1857), Purkinje and Pappenheim discovered the proteolytic power of the pancreas, and nine years later Boucharlat and Sandras (1845) discovered and established with precision, by means of observation

carried on with the aid of pancreatic infusions as well as of small quantities of pancreatic juice obtained from hens and geese, that this secretion possesses powerful diastatic properties.

As pointed out by Gamgee (1893, p. 203), this discovery of the sugar-forming enzyme of the pancreas has been erroneously attributed to Valentin (1844). Valentin recognized that starch was changed, but did not say that the change was a conversion to sugar. His own words are: "Wie man sieht erlauben diese Erfahrungen noch keine irgend bestimmenden Schlüsse. Höchstens deuten sie darauf hin, dass vielleicht die Pancreasflüssigkeit die Fähigkeit habe die Stärke löslich zu machen und bewirken eine Umsetzung derselben einzuleiten." No further study of the pancreas seems to have been made until Bernard took up the work.

Bernard (1856), by means of a pancreatic fistula, proved that the secretion is an alkaline fluid with a threefold action on starches, fats, and proteids. He concluded, however, that the pancreatic juice alone has no action upon proteids, but that it is able to dissolve them either when they have been first of all subjected to the action of bile or when it acts in conjunction with bile. To this proteolytic function of the pancreatic juice, indeed, Bernard gave little weight.

In 1857 Corvisart called attention to the proteid-digesting power of the pancreatic juice, and although his observations were more or less discredited by some, they were confirmed by Meissner (1859), Danilewsky (1862), and Kühne (1867), the latter particularly contributing greatly to our knowledge of tryptic digestion.

The great interest awakened in the proteolytic activity of the pancreas by the researches of Kühne (1867) was intensified by the publication of a remarkable memoir by Heidenhain (1875). In this paper the author described for the first time those changes in the secreting cells of the pancreas which correspond to the different states of activity, and announced that the fresh pancreas does not contain the proteolytic ferment, but an antecedent body which he called zymogen. This zymogen he found could be extracted from the gland, and under suitable treatment would yield the proteolytic ferment. Since Heidenhain's discovery the antecedent bodies of other enzymes have been discovered. To the antecedent of the proteolytic enzyme of the pancreas, trypsin, the name trypsinogen has been given.

As a result of the study of the pancreas by the various investigators, this organ has long been known to secrete an alkaline juice and three enzymes or their zymogens, namely, trypsin, acting on proteids; amyllopsin, acting on starches; and steapsin or lipase, acting on fats. Notwithstanding all the study of the pancreatic juice, however, in many ways the knowledge of its action was somewhat uncertain. Sometimes the pancreatic extracts would show a little digestive power, while the juice collected by a fistula was, as a rule, inactive. To explain these variations, investigations were made on the correlation between the pancreas and other organs and juices. Heidenhain (1875) had observed that when an aqueous solution of dried pig's bile was added to a glycerin extract of the pancreas, the proteolytic power of the latter was increased. Chittenden (1885) noticed that bile in a pancreatic extract containing salicylic acid increased tryptic action. Martin and Williams (1890) and Rachford and Southgate (1895) also noticed the stimulating action of bile on tryptic digestion. Chittenden and Albro (1898), however, found that normal bile exerts very little influence on pancreatic proteolysis and may retard as well as aid. Bruno

(1899), on the contrary, found that the bile even doubled the action of the pancreas, and that this action was not lost by boiling, and Delezenne (1902) verified, in the main, Bruno's work, but declared that bile does not activate inactive pancreatic juice. What part the bile plays in activating the pancreas is not yet fully decided.

The spleen has also been claimed to play a certain part in digestion. Schiff (1862), Gachet and Pachon (1898), Bellamy (1901), and Mendel and Rettger (1902) have shown that the spleen when congested during digestion increases the proteolytic power of the pancreas. On the other hand, Heidenhain (1883), Ewald (1878), and Hammarstein (1901) do not find that the spleen had any action on pancreatic digestion, while Noel Paton (1900) has shown that there is not necessarily any difference in the nitrogenous metabolism of dogs before and after splenectomy. Frouin (1902) has demonstrated that the removal of the spleen from dogs with an isolated stomach does not interfere with their nutrition even during a meat diet. Further, Camus and Gley (1902), Bayliss and Starling (1903), and Hekma (1904) have shown that extracts of the spleen have no activating action. The influence of the spleen on pancreatic digestion is still open to debate.

An activating principle more easy of demonstration is that discovered by Dr. N. P. Schepowalnikow (1898) in the succus entericus, or the juice of the small intestines. This juice, though possessing no proteolytic action itself, has the power of augmenting the activity of the pancreatic ferment, and especially of the proteolytic ferment—trypsin. Indeed, it was found that the succus entericus would convert an otherwise inactive pancreatic juice into an active juice. To the ferment, since such the activating principle was found to be, Pawlow gave the name of enterokinase. Others have corroborated Schepowalnikow's work, and Delezenne (1902) found enterokinase not only in the duodenum, jejunum, and slightly in the ileum, but also wherever leucocytes abound. In other words, he claims that the activating principle is generated by the white blood corpuscle.

From the size of the pancreas in the elasmobranchs we should expect this organ to play a large part in the work of digesting food. Krukenberg (1877), in his work on selachians, found that the pancreas of these fishes was secreting amylopsin, steapsin, and trypsin. Richet (1878), however, was unable to find trypsin. More recently Yung (1899), working on *Squalus acanthias*, found amylopsin and lipase, but only occasionally trypsin. Yung attempted to get the juice by a fistula, but had little success. His water glycerin extracts were only occasionally active. He found that extracts of the spleen aided the activation of the pancreas. Sellier (1902) found that the pancreas of several selachians studied by him does not of itself digest proteid, but must be activated by the juice of the spiral valve.

To determine just what part the pancreas of selachians plays in digestion and what enzymes it secretes, my work comprised experiments as follows:

1. Pancreatic fistulæ were made to obtain pure pancreatic juice.
2. Water glycerin extracts and sodium carbonate extracts were made to extract the zymogens or enzymes.
3. Extracts of the pancreas were combined with bile, and with extracts of the duodenum, spiral valve, spleen, stomach, and rectal gland.
4. The fresh pancreas was used to determine the presence of lipase.
5. The content of the spiral valve was studied.

Pancreatic fistula.—In order to collect the pancreatic juice a slit was made in the abdomen and in the wall of the duodenum of *Carcharias littoralis* in such a way as to cut the pancreatic duct. Into the central end of the duct was fastened a small glass cannula. To the outer end of the cannula was fastened a small sterilized rubber balloon. After the sand shark had been sewed up it was set free in a large aquarium. In a few days the balloon was taken off and the juice collected with a pipette. As a rule the quantity of juice thus collected was small and had no digestive activity. Owing to the difficulties of keeping the fish alive for a prolonged period and of feeding them, I made but six fistulae and then abandoned this kind of work for the pancreatic extracts.

The proteolytic enzyme. Activation of the pancreas.—The pancreas was ground in a mortar with glass, and the comminuted mass was treated with water and glycerin. After twenty-four hours the mixture was filtered through cotton. To test the digestive activity of the extracts, at first I used Mett's tube and fibrin. Finding both of these media unsatisfactory, I employed Fermi's (1902) gelatin method, using 10 per cent gelatin and 0.6 per cent carbolic acid. The gelatin was placed in small test tubes and the upper layer of the gelatin marked on the tube by means of a blue pencil. The amount digested was measured in twenty-four hours if the experiment was carried on at the room temperature; in three hours if at 37° C. The pancreatic extracts had as a rule very little digestive activity. Accordingly, I added water glycerin extracts or water chloroform extracts of the mucous lining of the stomachic sac, pyloric tube, duodenum, spiral valve, rectal gland, and spleen to determine whether or not any of these extracts would activate the pancreas. Controls were made in each case. The results may be found in the table.

TABLE SHOWING THE ACTIVATING ACTION OF THE VARIOUS EXTRACTS UPON TRYPTIC DIGESTION.

Species.	Pancreas.	Pancreas duodenum.	Pancreas spiral valve.	Pancreas rectal gland.	Pancreas spleen.	Pancreas bile.
<i>Carcharias littoralis</i>	0 or +	0 + or ++	+++	0 or + ^a	+	+; — ++ ^b
<i>Carcharhinus obscurus</i>	0 or +	++	+++	0 or +	0 or +	0 or +
<i>Lamna cornubica</i> ^c	0 or +	?	++	?	?	?
<i>Mustelus canis</i>	0 or +	0 + or ++	+++	0 or +	0 or +; ++ ^a	—; ++ ^b
<i>Squalus acanthias</i>	0 or +	0 or +	++	0 or +	0 or +	0 or +
<i>Raja erinacea</i>	+	+	++	0 or +	0 or +	0 or +
<i>Dasyatis centrura</i>	0		++	0	0	0

Species.	Bile.	Duodenum.	Spiral valve.	Rectal gland.	Spleen.	Pancreas and stomachic sac.	Pancreas and pyloric tube.
<i>Carcharias littoralis</i>	0	0	0	0	0	+	+
<i>Carcharhinus obscurus</i>	0	0	0	0	0	+	+
<i>Lamna cornubica</i> ^c	0	0	0	0	0	0	0
<i>Mustelus canis</i>	0	0	0	0	0	0	0
<i>Squalus acanthias</i>	0	0	0	0	0	0	0
<i>Raja erinacea</i>	0	0	0	0	0	0	0
<i>Dasyatis centrura</i>	0	0	0	0	0	0	0

+ , quantity digested by pancreas.
 ++ , greater quantity.
 +++ , still greater quantity.
 0 , no digestion.
 — , less than pancreatic extract alone.
^a Only a few tests were made to determine the activating action of the rectal gland.
^b The bile often increased the proteolytic activity of the pancreas, but occasionally diminished this activity.
^c Only two sets of experiments were made.
^a The spleen occasionally showed activating action.

The conclusions to be drawn from the table are:

- (1) The pancreatic extracts may or may not show proteolytic activity.
- (2) The duodenum as a rule causes the inactive pancreatic extract to digest the gelatin and increases the digestive activity of an active pancreatic extract.
- (3) The greatest activation is produced by the spiral valve.
- (4) The spleen occasionally activates the pancreatic extract.
- (5) The bile sometimes activates, sometimes has no effect whatever, and sometimes slightly diminishes the digestive activity of the pancreatic extracts.
- (6) Extracts of the duodenum, spiral valve, and rectal gland have no digestive activity.
- (7) The bile alone has no digestive power.
- (8) Extracts of the rectal gland have no activating influence.
- (9) Extracts of the mucous membrane of the stomachic sac and pyloric tube have no activating action.

Amylopsin and Lipase.—Krukenberg (1877), Richet (1878), and Yung (1899) found amylopsin and lipase in the pancreas of European elasmobranchs. To determine the presence of these enzymes in the pancreas of the American elasmobranchs experiments were made (1) on the amylolytic activity and (2) on the lipolytic activity.

1. Water-glycerin extracts of the pancreas, slightly acidified with acetic acid, were made at different times from different lots of fishes. To 5 c. c. of a starch paste, free from sugar, was added 5 c. c. of the extract. After a short period the mixture was examined for sugar by Fehling's test. If negative, the tests were repeated at hourly intervals for six hours. In every case control tests were made. The results of the experiments are as follows:

Species.	Diastatic enzyme (amylopsin).	
	Number of tests.	Positive.
<i>Carcharias littoralis</i>	6	4
<i>Carcharhinus obscurus</i>	2	2
<i>Lamna cornubica</i>	2	0
<i>Mustelus canis</i>	10	6
<i>Squalus acanthias</i>	2	1
<i>Raja erinacea</i>	10	0
<i>Tetronarce occidentalis</i>	1	1
<i>Dasyatis centrura</i>	1	1

The table shows that the pancreas of elasmobranchs may secrete the diastatic enzyme or its zymogen. Even in the case where the tests were negative I should expect on further investigation to find that the pancreatic extracts have the power to convert starch to sugars.

2. To determine the presence of the lipolytic ferment of the pancreas, the fresh pancreas of *Mustelus canis*, *Carcharias littoralis*, and *Raja erinacea*, the only elasmobranchs available at the time, was used. The methods employed and the results obtained are as follows:

(a) The fresh pancreas of the three fish mentioned was cut finely and mixed separately with a little water to make a thin paste. To a small quantity an equal volume of olive oil and litmus solution was added, and this mixture was kept at 30° C. for

twenty-four hours. When a small quantity of a 1 per cent sodium carbonate solution was added to the oil mixture a permanent emulsion was formed in every case. When olive oil alone was treated with water and sodium carbonate the emulsion was not permanent.

(b) A neutral ethereal solution of butter was made and litmus added to a distinctly blue tint. This was placed in contact with a teased bit of fresh pancreas, as recommended by Gamgee (1893, p. 213). In a short time the liquid bathing the pancreas became faintly pinkish in spots, showing that a slightly acid reaction had developed.

(c) Aqueous extracts of the pancreas separated a small amount of butyric acid from a dilute solution of ethyl butyrate.

From these experiments it is to be concluded that lipase is secreted by the pancreas of *Mustelus canis*, *Carcharias littoralis*, and *Raja erinacea*, although its activity as demonstrated in vitro is not very great.

RECTAL GLAND.

Blanchard (1882) studied the function of the rectal gland, or digitiform gland, in *Acanthias vulgaris*, *Mustelus canis*, *Scyllium catulus*, *Scyllium canicula*, *Raja punctata*, and *Raja maculata*. In every case he found that extracts of the gland emulsified oil and converted starch to sugar, but had no action on white of egg or cane sugar. Extracts made by me of the rectal gland, or processus digitiformis, of *Carcharias littoralis*, *Carcharhinus obscurus*, *Lamna cornubica*, *Mustelus canis*, and *Raja erinacea* had no digestive action on fibrin or starch, nor did they hydrolyze ethyl butyrate. In the secretion of the gland I found considerable mucin. To the structure and physiology of the rectal gland I shall return in a later paper. At present, however, I should decide that the rectal gland has no digestive activity.

SUMMARY.

The results of the histological work in the present investigation may be summarized as follows:

1. The mucous membrane of the buccal cavity of *Mustelus canis* and *Carcharias littoralis* consists of stratified epithelium, with goblet and cylindrical cells, but no glands.

2. The mucous membrane of the esophagus possesses ciliated cylindrical cells and goblet cells, but no glands.

3. Gastric crypts exist in the stomachic sac of the elasmobranchs. There is no differentiation into chief and parietal cells. The epithelium of the crypts consists of cylindrical cells and polygonal cells.

4. The pyloric tube has the same kind of superficial epithelium as the stomachic sac and similar crypts. The polygonal cells, however, are absent.

5. The epithelium of the intestines from pyloric tube to cloaca consists of cylindrical cells and goblet cells.

6. The rectal gland is a compound tubular gland.

The physiological study and experiments produce the following conclusions:

7. In the elasmobranchs examined, neither the buccal mucous membrane nor the mucous membrane of the esophagus has any digestive activity.

8. The stomachic sac secretes pepsin and hydrochloric acid.
9. The total acidity of the stomach contents, in terms of hydrochloric acid, may reach as high as 1 per cent.
10. The physiologically active hydrochloric acid may be as strong as 0.6 per cent.
11. The gastric juice does not digest chitin.
12. The middle intestines and spiral valve have no digestive activity, but activate the pancreas.
13. The spiral valve possesses the greatest activating power.
14. The pancreas secretes trypsinogen as a rule, but may secrete trypsin.
15. The pancreas secretes amylopsin, the starch-splitting ferment, and lipase, the fat-splitting ferment.
16. The rectal gland has no digestive activity.

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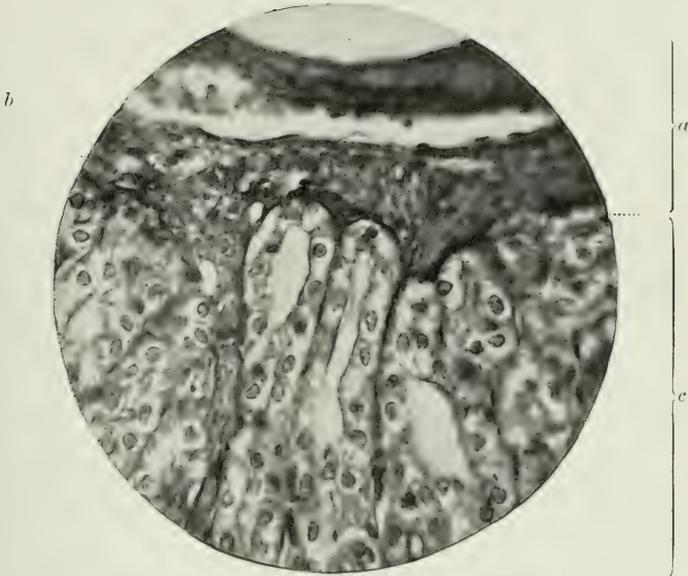


Fig. 1.—*a*, Outer fibro-muscular layer. *b*, Blood sinus. *c*, Middle glandular layer. $\times 200$.



Fig. 2.—Middle glandular layer. $\times 1000$.

PHOTOMICROGRAPHS SHOWING STRUCTURE OF THE RECTAL GLAND (PROCESSUS DIGITIFORMIS) IN THE SMOOTH DOGFISH.

THE REACTIONS OF PLANARIANS TO LIGHT.

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WITH FOURTEEN FIGURES

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I INTRODUCTION

Light is one of the physical factors which influence the behavior of organisms. The great majority of living things are normally subjected to regular periodic changes in the amount of light to which they are exposed during the alternation of day and night. In addition to these constant periodic changes, there are innumerable irregular gradations in both the intensity and the character of the light naturally acting upon any organism. An agent of such wide range and almost universal influence as light ought, therefore, when properly analyzed, to prove of material service in interpreting the behavior of animals and plants. The dependence upon light of animals provided with organs of sight, is self evident. The direct bearing, too, of light upon chlorophyllaceous plants in the manufacture of their food substance, is plain. But how far light plays a direct part in the life of non-photosynthetic plants and of animals which cannot "see," is less clear.

Although possessing eyes, it is very probable that planarians are unable to see in the sense of distinguishing shapes, and it is questionable how far they can distinguish between even large regions of different light intensity.

The object of the following paper is to examine the relation of light to animal behavior as applied to certain planarians.

II HISTORICAL

Our knowledge of planarians, as of most other animals, has passed through certain historical phases, during which emphasis has been laid first upon taxonomy and anatomy and latterly upon embryology and zoögeography. The results of these various forms of investigation are highly important since they make the foundation for all future work upon this group of animals. They have, however, only an indirect interest in the present connection and do not, therefore, require review.

Perhaps the most modern advance in our knowledge of planarians is represented by the school which treats of them as living objects whose individual behavior is to be intimately correlated both with their structure and environment. The most noteworthy contribution from this standpoint has been made by Pearl ('03), who has analyzed in considerable detail the reactions of fresh-water planarians (notably *Planaria maculata*, *Planaria dorotocephala* and *Dendrocœlum lacteum*) to various stimuli. He has not, however, discussed the effects of light except incidentally.

The earliest reference to the relation of planarians to light is by Dalyell ('14). In his interesting volume on planarians a great number of keen observations upon the general habits and structure of planarians are made, which have since been confirmed, together with certain statements which have not fared as well with the advance of scientific knowledge.

He makes the statement ('14, p. 9) that "most planariæ *court the light indeed*;¹ but *P. flexilis* rather inclines to shun it, less, we may conjecture, from being warned of its presence by the specks or eyes, than from some disagreeable sensation produced on the body." Again, referring to *P. felina* ('14, p. 46), "This planaria, like the rest of its genus, is powerfully excited to motion by the presence of light. If a number be confined in a glass vessel, the whole assemble in a quiescent state, *on the side next the light*.¹ It is a little surprising that Dalyell should have received the impression that the majority of planarians "court the light," since he clearly points out the nocturnal habits of these worms. He

¹ The italics are mine.

doubts whether the eyes are of service in finding food and says of worms under aquarium conditions ('14, p. 107), "If remaining a considerable time unchanged, the planariæ decrease more rapidly, they become languid, scarcely moving either by the influence of the light or heat, and at last adhere entirely to the side of the containing vessel, where they perish."

Dugès ('28) observed that when light is concentrated by means of a lens upon either *Dendrocœlum* (?) or *Planaria*, movement results which is most pronounced when directed toward the anterior end of the worm. He tested the effects of direct sunlight and of diffuse daylight as well as of candle-light, and concluded that the response increases with the intensity of the light. The non-dioptric character of the eyes he has described remarkably well for one working so long before the days of the microtome, and his conclusion, already suggested by Dalyell and later confirmed by Kennel ('88), and others, that the eyes play no part in the finding of food, is noteworthy. He also notes that planarians seek the dark.

Dalyell ('53, p. 99), in a later volume says, "On April 29 I procured a fine specimen of *Planaria cornuta*, which spawned soon afterward. The spawn had been breaking up for two or three days preceding May 24, when multitudes of extremely minute yellow specks were seen swimming in the water. Their motion was sufficiently active, without being very quick; it was pursued in all directions and the spawn being contained in a small cylindrical jar, the specks crowded to the sides next the light whereon numbers remained almost stationary." Again ('53, p. 104), "When withdrawn from the dark the young *Planariæ* rose in great numbers toward the surface of the water, congregating on the sides next the light." It is extremely doubtful whether the organisms here described were really young planarians. It is more likely that they were the young of some other aquatic animal. Dalyell correctly describes *Planaria lactea* (*Dendrocœlum lac-teum*?) as being nocturnal. He observed that numbers of this species, beginning activity in the evening, rose on the sides of the jar, although many had descended again by morning.

More recently attention has been specifically directed to the

light relations of planarians in various papers by Loeb, whose important contribution in 1890, "Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen," paved the way in general for all work on this subject. He found ('93b, p. 101) that *Planaria torva* is not "heliotropic" in the strict sense, but rather "unterschiedsempfindlich," that is to say, it did not always move away from the source of the light in the direction of the rays and remain as far removed as possible, but moved about more or less at random, coming to rest in some area of lessened light intensity.

In a later paper Loeb ('94, p. 255) states that when planarians are suddenly brought into the light they begin to move, an increase in light intensity leading to activity and conversely a decrease, to rest. The grounds for this conclusion are not made clear. He further confirms the view that planarians are active at night, coming to rest in situations of lowered light intensity in daytime.

In further experiments *P. torva* when decapitated was found to react to light precisely as normal worms do with the difference that the reaction required more time. *Thysanozoön brochii*, a polyclad, on the other hand, lost its power to respond to light when the eyes and brain were amputated, from which Loeb draws the conclusion that animals which are closely related morphologically may exhibit wide physiological differences.

Hesse ('97), in his classic study of the anatomy of the turbellarian eye, mentions some experiments and observations on the behavior of planarians and in addition makes valuable contributions to the morphological basis of light reactions. He observed that planarians become active at twilight and he also experimented upon decapitated worms, apparently without being aware of the previous work by Loeb, with whose results his own agreed. He found, as Loeb did, that worms deprived of eyes finally come to rest in areas of lesser intensity much as do normal worms but after a longer time. Hesse found, too, that *Dendrocœlum lacteum* came to rest in the dark 119 times out of a possible 120, whereas with *Euplanaria (Planaria) gonocephala* the same result was effected in only 88 out of 120 times, notwithstanding the fact that the latter has more highly developed eyes than *Dendrocœlum*.

This led him to state ('97, p. 552) that "die Stärke der Reaction auf Lichtwirkung nicht der Stärke der Lichtwahrnehmung entspricht," and he ascribes this difference in behavior to a difference in the "Gefühlston" of the two species. Among other observations described by Hesse, the two following are of importance in this connection, namely, that a sudden introduction of light caused an almost immediate *turning away* on the part of the worm, and, that worms with eyes could not be made to remain in the light when escape was possible. In his opinion this apparent perception on the part of the worm is due not to the animal's ability to distinguish light but rather to unpleasant chemical reactions set up within the organism as the result of light stimulation. And, lastly, Hesse showed that the general position of the eyes of a planarian, together with the arrangement of their sensory portion, partly enclosed as it is within pigment cups, affords a device whereby the worm can be oriented to light. By means of this simple apparatus it receives a localized stimulus, which enables it to distinguish the direction from which the light comes. If light, striking the eye of a worm, fell upon sense cells which were unscreened in any way by pigment, there would result a general stimulation without localization of the stimulus and consequently orientation could not be effected.

Parker and Burnett ('00) sought, by quantitative methods and with more accuracy than Loeb or Hesse, to establish the part played by the eyes in light responses of planarians. They came to the same general conclusion as these authors since they found that *Planaria gonocephala* without eyes reacts to light essentially as normal animals do, except that the reaction time is somewhat longer. They also showed that worms when pointed toward the source of light travel at a slower rate than when headed in the opposite direction. With regard to the mechanism of the light response they say ('00, p. 383): "We have seen nothing in our experiments that supports the opinion suggested by Hesse (p. 551) that reactions such as we have described are due to the direct influence of light on the internal parts of the planarians, and we are more inclined to the view that these reactions are initiated by the effect of light on the integument of the animal, *i. e.*, are

due to what Graber ('83, p. 229) has called a 'dermatropic' function."

Bardeen ('01a, p. 13), speaking of *Planaria maculata*, states that "susceptibility to light is apt to become lost if worms are kept in captivity," and he notes the fact, already brought out by Chichkoff ('92), that pigment becomes reduced in sunlight. Hesse had previously emphasized the point that the pigment of the eye of any organism has in itself primarily nothing whatever to do with light perception. Bardeen further found that small pieces of planarians capable of locomotion will respond to light in the same way as uninjured animals, and he notes ('01a, p. 13), that the worms seem "to move about more by night than by day." In a later paper ('01b) he speaks of the fact that when a dish containing planarians is brought into light the worms are commonly roused to activity, although how far such activity is due to light and how far to mechanical disturbances he does not make clear.

Lillie ('01), experimenting upon the regeneration of *Dendrocœlum lacteum*, discovered that posterior headless parts fail to give the typical reaction to light and are incapable of regeneration. He draws the conclusion ('01, p. 132) that "any symmetrical piece of *Dendrocœlum* capable of regeneration tends to come to rest in the shaded part of the dish precisely like a normal individual" and that parts incapable of regenerating "also become incapable, after a day or two, of performing the usual reactions to light." These results on *Dendrocœlum*, it will be seen, are similar to those Loeb obtained in experiments upon the polyclad *Thysanozoön*.

Curtis ('02) reports from laboratory observations 42 cases of fission in *Planaria maculata*, of which number 39 occurred between 10 p. m. and 6 a. m. He adds, however ('02, p. 524), that "this did not seem due to the amount of light to which the animals were subjected during the day, for some of the dishes were so shaded that there was practically no light, day or night, except when they were being examined, and the division was the same in these as in others which were exposed to full daylight." A case of division in *Bipalium* also occurring by night is described by Lehnert ('91).

In a contribution to the geographical distribution of *Planaria*

gonocephala, *P. cornuta* and *P. alpina*,² Voigt ('04) incidentally refers to the manner in which these animals come to rest in the darkest part of a dish. He affirms that when an aquarium is suddenly lighted at night only those that are hungry, *i. e.*, those with comparatively empty digestive tracts, are found in motion, and he notes that in certain conditions worms may remain quiescent for weeks. The statement made earlier by Dugès, that the eyes of planarians play no part in finding food, Voigt confirms. These organs he explains are an aid in distinguishing differences in light intensity as well as the direction from which light comes but are entirely incapable, owing to the simplicity of their structure, of discerning the form of objects. In his opinion worms crawl into hollow stems and similar sheltered places to escape light rather than for warmth, as Wilhelmi ('04) suggests. Neither author, apparently, considers the possible part played by thigmotaxis under such circumstances. Of the delicacy with which worms react to light Voigt says ('04, p. 173): "Die Empfindlichkeit der Planariden gegen plötzliche Belichtung tritt so scharf hervor, das sie für den Unterricht eines der anschaulichsten Beispiele zur Demonstration der Lichtflucht bei niederen Tiere darbieten." Notwithstanding this high degree of sensitiveness to light, he finds that the worms when seeking their food leave the shade and come out even into direct sunlight. And, finally, concerning the bearing which light has on the problem of distribution, he concludes ('04, p. 175): "Auf die Verbreitung im Allgemeinen hat die Belichtung der Bäche wenig Einfluss, da sich in der Regel genug dunkle Schlupfwinkel finden, in denen sich die Tiere verbergen können."

Darwin ('44, p. 242) observed that *land planarians*, "especially *Planaria tasmania*, had an immediate apprehension and dislike of light, which they showed by crawling, when the lid of the box was taken off, to the under side of pieces of rotten wood," and in his enumeration of the places where various species of land planarians were found, their avoidance of light is plainly shown.

A note by Leidy ('58) refers to finding *Rhynchodemus sylvaticus* crawling about on fences frequently at night, but rarely by day.

² *P. alpina* = *P. torva* according to Borelli ('93).

Moseley ('74, p. 111) states that "land planarians are probably all of them nocturnal in habit." Speaking of the Ceylon land planarians in particular he says: "They are found in dark places, such as under large fallen leaves, and in confinement they coil themselves up away from light." He mentions also the fact that *Planaria torva* and *Dendrocœlum lacteum* choose the dark side of the vessel in which they are contained.

As has already been mentioned, Lehnert ('91) found *Bipalium kewense* undergoing fission in the dark. Both *Bipalium* and *Geodesmus*, he says, seek continually to hide in shadowy places avoiding even diffuse daylight. Concerning the degree of light perception possessed by planarians, he offers the opinion ('91, p. 326) that "*Bipalium* scheint mit seinem Augen die Umrisse von Gegenständen in Lichte wahrnehmen zu können."

Hogg ('97) notes that *Bipalium* is nocturnal in habit, remaining sluggish during the day.

Only incidental references to the *polyclads* are found bearing upon the question of light reactions, as for example this sentence, which occurs in Lang's exhaustive monograph ('84, p. 641), "Die meisten Arten scheuen das directe Sonnenlicht." The behavior of *Thysanozöön* with reference to light has already been mentioned (Loeb, '94).

Concerning the light reactions of the rhabdocœles, especially certain green forms in which the green cells are probably symbiotic, a considerable literature may be found. The principal papers relating to these forms are as follows: On *Convoluta schultzei*, by Geddes ('79), Barthélémy ('84) and Delage ('86); on *Convoluta roscoffensis*, by Haberlandt ('91), Bohn ('03a, '03b, '03c), Gamble and Keeble ('03) and Fühner ('06). *Vortex viridis* and *Mesostomum viridatum* (?) are discussed by Schultze ('51), von Graff ('84) and Sekera ('03). A résumé of these papers is, however, out of place here, since the presence of green cells in the organisms involves an entirely different problem from that which is under consideration.

The foregoing historical sketch furnishes the basis of the following general summary of facts which have thus been established with more or less certainty regarding the reactions of planarians to light.

- 1 Planarians are nocturnal, seeking the dark when exposed to light.
- 2 The eyes are useless in finding food.
- 3 The anterior end of the body is the part most responsive to light
- 4 Decapitated worms act normally except for a slower reaction time.
- 5 Orientation to light depends largely upon the character of the pigment cups of the eyes.
- 6 The relative energy of the response is dependent upon the intensity of the light.
- 7 Pigment is reduced in sunlight.
- 8 Pieces of worms which are large enough to move or regenerate react to light.
- 9 Fission *may* occur more readily in the dark.
- 10 Different species respond differently to light.
- 11 Light reactions diminish during "captivity."
- 12 Planarians are "unterschiedsempfindlich" instead of "heliotropic."

III MATERIAL

The species principally used in the following investigations were *Planaria maculata* Leidy; *Planaria gonocephala* Dugès; *Phagocata gracilis* Leidy; *Dendrocoelum lacteum* Oersted; and *Bdelloura candida* Giard, all of which are inhabitants of fresh water except *Bdelloura*, a salt-water species, found living semi-parasitically on the horseshoe crab (*Limulus polyphemus*). Some observations also were made upon a cave planarian, that as yet has not been identified but which may belong to the genus *Phagocata*. This interesting worm was kindly placed at my disposal by Dr. A. M. Banta.

At any season of the year an ample supply of fresh material was easily obtained except in midwinter, when it was necessary to cut through the ice and dredge up from the bottom water-weeds to which the worms cling.

The source of supply for *Planaria gonocephala* was a small pond to the west of Fresh Pond in Cambridge, Mass., while Pla-

naria maculata, *Dendrocœlum* and *Phagocata* were chiefly obtained from a pond at Falmouth, Mass., where they are especially abundant. Twice, through the kindness of Professor Parker, aquaria were generously stocked with *Dendrocœlum*, from a spring on Mount Monadnock, N. H. *Bdelloura* was obtained from Wood's Hole, Mass., during the summer from freshly caught horseshoe crabs and, later in the year, from specimens kept in captivity.

The setting-up of balanced aquaria in which planarians would thrive did not prove to be a difficult matter. The following method, based largely upon suggestions by *Wilhelmi* ('04), was used. Jars were filled to the depth of two or three inches with cinders, dirt and dead leaves, over which was spread an equally deep layer of clean sand. Clear water was then poured into the remaining space and the whole allowed to settle, after which a few such plants as *Anacharis* or *Myriophyllum*, with whatever microscopic life might adhere to them, were added, together with a handful of large pebbles to diversify the bottom. The jars were kept covered from dust in a cool place and occasionally a crushed snail was dropped into each one to supply the worms with food.

Planarians require pure water. Whenever for any reason the water in which they are kept becomes foul they will desert their places of concealment and crawl up the sides of the jar, while water that has been standing in lead or iron pipes quickly causes them to disintegrate. Rainwater or water taken directly from some natural source, gives better results than that which has been conveyed through pipes. Naturally the least chemical disturbance takes place when the worms are kept in water dipped up at the time and place of their capture.

Planarians will live without being fed for over three months when isolated in jars containing nothing except pure water, but meanwhile they decrease regularly in size. It seems to be impossible to "starve" them in the sense in which higher animals may be forced to die from lack of food leaving behind a dead body. These worms instead simply consume their own substance almost to the vanishing point.

During a part of the summer of 1905 observations and experiments were carried on at the laboratory of the U. S. Fisheries

Bureau at Wood's Hole, Mass., and I wish here to express my thanks to the director, Dr. F. B. Sumner, as well as to others in authority there, for their uniform courtesies. The bulk of the investigation, however, was made at Harvard University. I am deeply indebted to Professor Mark for the privilege of having a place in his laboratory and particularly to Prof. G. H. Parker, under whose immediate direction the work was done and whose daily counsels and generous suggestions were indispensable.

IV CRITERIA FOR MEASURING BEHAVIOR

Both the form and the structure of an animal set a limit to the character and degree of its movements, which no combination of stimuli, external or internal, can force it to overstep. In estimating the influence of light upon planarians, therefore, it is necessary to know not only the normal behavior of the worms but also the possible range of their reactions under any circumstances. For example, the ordinary gliding locomotion of planarians is accomplished by means of cilia beating in a mucus track and augmented by muscular contraction. It is physically impossible for this sort of locomotion, even under the most favorable conditions, to exceed a certain rate. By the use of excessive stimuli, however, a worm may be forced to abandon this accustomed gliding for a somewhat faster method of progression known as "crawling" or "humping," in which the muscles are used more than the cilia. But when this is done the limit of possible rate of locomotion has been reached, at least for fresh water planarians, which cannot be urged to abandon entirely contact with some support and to swim freely in water, although the marine form, *Bdelloura*, does have this addition to its repertory of behavior.

The following observations may illustrate more specifically what is meant by range of behavior. *Planaria maculata*, when gliding on the bottom of a dish, was lightly touched on the anterior end with a hair mounted on a glass rod. During one hundred trials of this kind eight different responses resulted, which may be indicated as follows:

	Times
1 Contracted, and turned aside.....	32
2 Contracted, lifted up the anterior end, and turned aside.....	27
3 Contracted, lifted up the anterior end and went straight forward.....	17
4 Contracted momentarily and then went straight ahead.....	5
5 Did not contract but turned aside.....	2
6 Did not contract but lifted up the anterior end and turned aside.....	7
7 Did not contract but lifted up the anterior end and went straight forward.....	9
8 Did not contract but went straight ahead.....	1
Total.....	100

Animals which, like planarians, present a limited range of behavior are, therefore, more favorable subjects for experimentation than higher forms whose structural complexity increases their possible responses, making in consequence the analysis of cause and effect in their activities more difficult. It is evidently desirable, then, to have as many different ways for measuring behavior as possible, in order not to state these responses loosely from general impressions but in quantitative terms. The principal criteria of planarian reactions to light used in this study, follow:

1 *Rate of Locomotion.* Since the entire range of possible rates of locomotion depends upon the structure of the worm and is not very great, slight differences become significant.

2 *Amount and Character of Turning,* that is, whether persistent or irregular, decided or vague, clockwise or contra-clockwise.

3 *Change of Course.* A change in the character, but not necessarily in the direction, of the course is referred to here. "Circus movements," for example, would not be included under this heading because the curving path in such cases, although constantly changing in direction, does not change in character. Tangents to a circle, however, as well as angular and abrupt deviations from a straight line may properly be regarded as changes of course.

4 *Interval of Response.* The apparent effect of light is not immediate in all cases, therefore, the time elapsing between the application of the stimulus and the response to it is a valuable measure of reaction.

5 *Degree of Wandering.* In a sense the degree of wandering shown by a worm is a measure of its indifference to the stimuli acting upon it. It must be noted, however, that apparent indif-

ference may sometimes be due to a balance of opposing stimuli, in which case wandering or aimlessness is not a true measure of the effect of any single stimulus.

6 *Orientation.* This is a measure of behavior with reference to the source of the light. It is expressed by the degree of positiveness or negativeness which the worm exhibits.

7 *Duration of Movement.* The time it takes a worm to tire out when subjected to certain stimuli or, in other words, a measure of fatigue.

8 *Effect of Repetition.* A measure of response is here referred to which may be expressed quantitatively in units of time or qualitatively in manner of behavior.

9 *Wigwag Movements.* These are waving movements of the anterior end of the planarian, which appear to be a definite attempt on the part of the worm to become adjusted to the stimuli acting upon it.

10 *The Time Required to Leave a Unit Circle.* This is a rather unsatisfactory criterion because it may indicate in some cases a combination of several conditions as, for instance, latency of response, rate of locomotion and degree of wandering.

11 *Manner of Coming to Rest.* Included under this heading are such points as the position assumed, the locality selected, and the abruptness of the act.

Naturally some of the foregoing measures of behavior will be seen to have more application and value than others in the following study.

V OBSERVATIONS

I PHOTOKINESIS

The term photokinesis was introduced by Engelmann ('83) to denote the activities which are induced solely by the intensity of light when the directive or orienting factor has been eliminated.

In this section will be considered, (A) the behavior of planarians in the absence of light; (B) their behavior in different intensities of non-directive light, and (C) the effect of abrupt changes, both in time and space, in the intensity of non-directive light.

A Behavior in Dark

Darkness may be called the zero point in the scale of light intensities. That light is not essential to the activity of planarians is shown by their performances in its absence, as is demonstrated by the following facts.

Rate of Locomotion. The average rate of ten individuals of *Planaria gonocephala* was found to be 0.50 mm. per second in the dark while the same ten worms, subjected to a light from above of 38 c.m.,³ with all the other conditions unchanged, averaged 0.82 mm. per second.

Again, ten worms of the same species were allowed to travel in the dark ten minutes in one set of experiments and six minutes in another, when their average rates were found to be 0.42 and 0.57 mm. per second, respectively.

The method devised for obtaining the above records, previously used in experiments upon fresh water snails (Walter, '06), although tedious was comparatively accurate. A clean glass plate was submerged in a dish of water and the latter placed in a light-proof receptacle. A single worm was then allowed to travel on this glass for a unit of time, after which the plate was removed and "developed" by pouring over it powdered carmine shaken up in water. A sufficient number of the insoluble carmine particles adhered to the mucus-track left on the glass by the gliding worm to make it possible to wipe dry the reverse side of the plate and to trace thereon in ink the exact course taken by the worm. This permanent ink line was then measured by means of a map measurer such as is in common use for measuring sinuous lines.

A series of experiments, to be described more in detail later (Table III, p. 57), forms a basis of comparison with the foregoing records in the dark, and further shows that there is an increase in the rate of locomotion in the light.

Ten worms, subjected to various intensities of light projected from above and ranging from less than one to several hundred candle meters, showed rates which in all cases were greater than the rate traveled in the dark.

³ The abbreviation c.m. is used to denote candle meters.

Turning. That planarians do more turning in the dark than they do in various intensities of non-directive light is apparent from the following table of percentages.

TABLE I

Per cent of turnings of Planaria gonocephala in the dark and in various intensities of light

Light in candle meters.....	0 (dark)	0.94	11	39	78	126	155	217	431	Av. of all intensities
Per cent of turning.....	87	76	66	69	81	67	75	77	65	72
Per cent of straight paths.....	13	24	34	31	19	33	25	23	35	28
Number of observations.....	71	79	67	85	57	62	67	57	58	

Furthermore, out of a total of 46 cases of turnings made by different individuals of *Planaria gonocephala* in the dark 23 were clockwise and 23 contra-clockwise. This perfect balance in behavior did not recur when the same worms performed turning evolutions in the light.

Change of Course. As to what constitutes "definite" and what "indefinite" changes of path, an S-shaped course is to be regarded as an indefinite aimless wandering, whereas angles in a straight path or tangents in a curving path are classed as definite responses because they are what would normally occur if some directive stimulus were interposed. It was found that *P. gonocephala* made *indefinite* changes in its course more frequently in the dark than in any series of light intensities to which it was subjected for an equal length of time. On the other hand *definite* changes occurred oftener in the light, although the factor of directive light had been excluded.

Table II summarizes 350 records on 10 different worms with the results reduced to percentages.

It will be seen that the per cent of S-shaped ("indefinite") paths in the dark decidedly eclipses that which was made in any intensity of light, while the per cent of angular and tangential paths ("definite") laid in the dark is exceeded in every instance by that made in any intensity of light with one exception, viz: 11 c.m., which, however, is not sufficient to change the average result.

Summary. Planarians move about in the dark but at a slower rate than in non-directive light whatever the intensity. They

turn more in the dark than in the light, going clockwise or counter-clockwise with equal readiness. Finally, they make more indefinite changes in their paths in the dark, but fewer definite changes than in the light.

TABLE II

Percentage of definite and indefinite changes in the character of the course in dark and in light of different intensities

			Details of the several intensities employed							
Light in candle meters.....	o (dark)	Average for all in- tensities	0.94	11	37	78	126	155	217	431
Definite changes (angular or tangential changes), per cent.....	18	28.5	30	15	27	32	35	21	32	40
Indefinite changes (S-shaped paths), per cent.....	47	23	21	30	23	20	26	34	20	99
No change in character of course, per cent.....	35	48.5	49	54	50	48	39	45	48	51
Number of observations.....	34	316	49	35	48	37	31	48	35	33

B Non-Directive Light

a Apparatus

To test the effect of purely non-directive light, it is of course necessary to eliminate the possible influence of directive light. This may be done by projecting the light upon the moving worms in such a way that they are unable to go either toward or away from the source of the light. Whatever effect is obtained under such circumstances must be ascribed to the non-directive power of light.

The elimination of the directive influence of light can be accomplished by means of various devices. (1) The light may be made to fall vertically from above upon a horizontal field; (2) it may be reflected vertically from below so as to pass through a transparent field at right angles to the plane of the field; (3) methods 1 and 2 may be combined. The apparatus finally used in the majority of experiments with non-directive light, was based upon the method first mentioned.

Fig. 1 shows a diagrammatic vertical section of this apparatus. The light (*A*), an incandescent electric lamp, was mounted in a black sheet-iron hood (*B*) to prevent the escape of any lateral light. This hood was suspended from the ceiling of the dark room where the experiments were carried on and was arranged so that it could be easily raised or lowered, thus changing the height and consequently the intensity of the light with reference to any fixed point below. In the hood, beneath the light, was supported

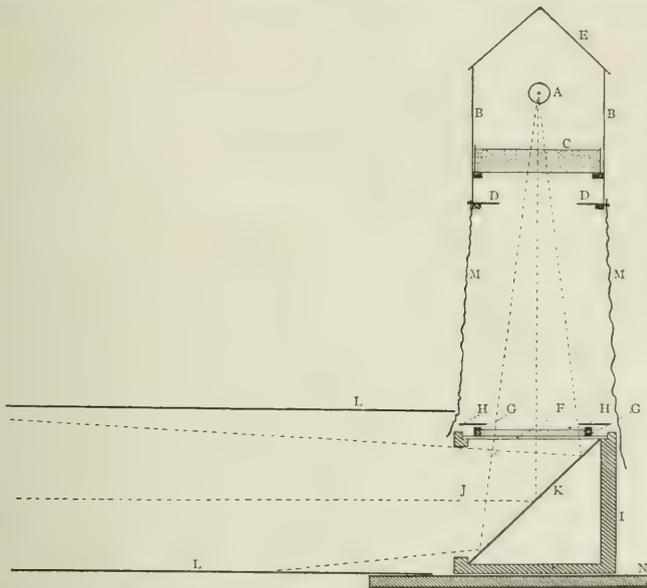


Fig. 1 *A*, light; *B*, walls of hood; *C*, heat screen; *DD*, diaphragm; *E*, roof of hood; *F*, plate-glass floor of aquarium; *G*, paraffine wall of aquarium; *HH*, diaphragm to cut off light reflections from paraffine wall; *I*, wall of reflector box; *J*, open side of reflector box; *K*, mirror; *L*, walls of tunnel; *MM*, black draperies; *N*, table.

a flat-bottomed, clear-glass dish (*C*) containing distilled water to a depth of about three centimeters. The heat screen thus obtained effectually filtered out the heat rays, allowing only the light rays to pass through. A few inches under the heat screen was inserted a diaphragm (*D*), painted black, the purpose of which was to aid in cutting out side reflections besides allowing only a central column of light to escape below. A black sheet-iron roof (*E*) con-

fined the upward rays to reflections within the hood itself, at the same time permitting the escape of heated air. On a table directly under the suspended light lay a horizontal sheet of plate glass (*F*), affixed to the upper surface of which was a circular ring (*G*) made of a mixture of paraffine and lampblack. There was thus formed a circular water-tight aquarium twenty centimeters in diameter and two centimeters deep, in which the worms could be observed. On the top of this circular ring rested a black diaphragm (*H*), the aperture of which was sufficiently small to exclude any side reflections which might come from the black paraffine wall.

The aquarium, it must be explained, did not rest directly on the table but was mounted as the cover of a box (*I*), the interior of which had been rendered largely free from reflecting surfaces by the use of black camera-paint. One side of the box was removed and, facing the opening thus made, a mirror (*K*) was placed at an inclination of 45° with the horizon. The end of a square tunnel (*L*), ten feet long and made of black cloth stretched upon a framework of wood, fitted close up to this opening. Suspended from the lower edge of the hood and surrounding the aquarium were adjustable black draperies (*M*) designed to shut out possible side light and at the same time to allow a hole for the eye of the observer. It will be seen that all light reaching the aquarium comes from the lamp above by passing through the heat screen.

After illuminating the field of observation the light passes through the glass floor of the aquarium and is reflected by the mirror into the black tunnel. Most of the light is absorbed in the tunnel, only an insignificant minimum being reflected back to the aquarium floor. Otherwise complications in the character and intensity of the light might arise.

By moving the hood (*B*) up and down and by using lamps of different candle powers a variety of intensities was obtained. The lamps used were tested by means of a Lummer-Brodhun photometer, the loss by reflection from the surface of the water both at the heat screen and at the aquarium being reckoned out in determining the different intensities employed.

By simple observation, data for such criteria of behavior as

amount of turning, changes in course, degree of wandering, interval of response and manner of coming to rest, could be obtained in this apparatus with approximate correctness. To determine the rate of locomotion, however, required a device which would measure accurately the distance traveled in a unit of time. The

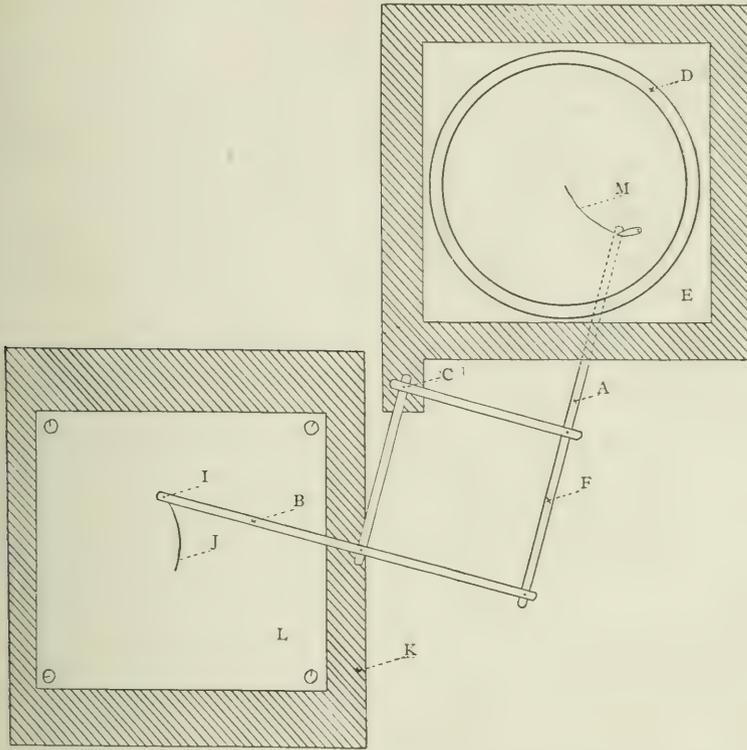


Fig. 2 *ABCF*, pantograph; *C*, fixed point; *D*, paraffine wall of aquarium; *E*, plate glass bottom of aquarium; *F*, place where the arm *A* is grasped by the operator. A style is located at end of arm *A*, in contact with under side of aquarium floor. *I*, style at end of tracing arm *B*, in contact with smoked paper; *J*, beginning of a course traced on the smoked paper; *K*, drawing board for attachment of smoked paper; *L*, sheet of smoked paper fastened to drawing board; *M*, actual course of the worm.

method already mentioned of measuring rate from mucus-tracks developed by means of powdered carmine, proved too tedious and uncertain except for the worm's maneuvers in the dark, when it seemed the only available way.

To avoid the inconveniences of this method an attachment was devised for directly duplicating the path of a worm by means of a style traveling over a sheet of smoked paper. The records thus traced were made permanent by immersing the smoked sheets in a weak solution of resin in alcohol and allowing them to dry, after which the paths could be accurately measured and the rates computed.

The arrangement of this attachment, as seen from above, is shown in Fig. 2. The diaphragm (Fig. 1, *H*) has been removed for the sake of clearness. At the tip of arm *AF* a style directed upward comes in contact with the under surface of the aquarium bottom (Fig. 1, *F*), while at the tip of arm *B* a similar style that is pointed downward traces a line on the sheet of smoked paper *L* at the left. After a little practice it was not difficult to keep the style of arm *A* directly under the posterior end of a gliding worm, thus duplicating its movements with considerable accuracy. The expiration of any time interval can be indicated on the smoked paper record by a crosswise scratch in the path.

Arm *A* was rendered as non-reflecting as possible by black camera paint as well as by being made triangular in cross section with the apex of the triangle upward. Thus whatever rays struck it from above were mostly either absorbed or reflected in a horizontal direction, so that they did not reach the worm under experiment.

b Results

Rate of Locomotion. *Planaria gonocephala* moves somewhat more quickly in non-directive light than it does in dark. Ten apparently normal and representative worms were selected and isolated in individual aquaria. They were kept in the dim light of the dark room in water of the same temperature as that of the experimental aquarium in which they were observed. At the end of thirty-four days of experimentation these worms showed practically the same average rates under the same intensities of light as they did at first. By alternating the individuals these trials were so made that fatigue effects had little part in the results, while the succession of light intensities was varied in such a way

that cumulative effects and the influence of previous exposures were largely avoided.

The results obtained in 259 trials are condensed in Table III.

TABLE III

Rate of locomotion in millimeters per second of Planaria gonocephala in various intensities of non-directive light

Candle meters.....	0	0.94	11	39	78	126	155	217	431
Average mm. per sec.....	0.57	0.66	0.69	0.75	0.64	0.66	0.69	0.70	0.63
Number of records	30	28	30	29	27	30	30	27	28

The mechanical stimulus resulting from the removal of the worms, by means of a camel-hair brush, from their individual aquaria to the observation aquarium was practically the same in all cases as were all the other external stimuli except light. The difference in the rate of locomotion appearing in these averages is, therefore, clearly due to differences in the light intensity employed.

It will be seen also that rate does not increase progressively with intensity. The series of rates and intensities under Table III, if plotted in a frequency curve would give two modes, one at 39 and the other at 217 candle meters, with a slight depression between the two. Still, as has been already pointed out, any intensity of light gives a faster rate than no light at all.

The slowest average rate was made under the highest intensity of light employed. Certain facts to be brought forward later favor the opinion that this was not an accidental result.

Under continuous exposure to one intensity of light the rate of locomotion decreases. The worms seem to "run down" gradually, so that at the end of ten minutes their rate is only about half that during the first minute. Data illustrating this point are given in Table IV.

The rate of locomotion depends not so much upon the intensity of light as upon other factors which tend to produce individual behavior upon the part of each particular worm. Stated in another way, there is greater variation between different individuals in the average rate of their locomotion under all intensities than there

is in the average rate of all individuals collectively under different intensities. The data for this latter point based upon the average rate of ten worms (259 observations) under different intensities has already been given in Table III (p. 57). The extremes in rate there shown are 0.57 mm. per sec. at zero intensity and 0.75

TABLE IV

Average rate of locomotion of Planaria gonocephala in successive minutes of exposure to 39 c.m. of non-directive light

Number of minute.....	1st	2d	3d	4th	5th	6th	7th	8th	9th	10th	11th	12th
No. of records averaged..	17	15	12	7	5	4	4	3	3	2	2	2
Rate in mm. per second..	.63	.625	.565	.55	.53	.55	.375	.39	.39	.29	.25	.29

mm. per sec. at 39 c.m. intensity, which makes a range of 0.18 mm. per sec. When the same data are rearranged to show the average rate for each individual for all intensities, as in Table V, the extremes are 0.49 mm. per sec. and 0.83 mm. per sec. with a range of 0.34 mm. per sec.

In fact the individual behavior of these ten worms, despite their apparent similarity, was sufficiently distinct to allow each one to be thereby identified.

Turning. Attention has already been called to the fact that there is less turning in light of various intensities than in the dark. A return to Table I will make plain that there fails to be any

TABLE V

Average rate of locomotion for each of ten worms (Planaria gonocephala) based on trials with non-directive light of various intensities

Identification number of worm.....	1	2	3	4	5	6	7	8	9	10
Average rate in eight intensities expressed in mm. per sec.....	0.79	0.57	0.68	0.64	0.83	0.70	0.72	0.58	0.49	0.62

definite correlation between the degree of intensity of the light and the amount of turning, although the least turning occurs under the highest intensity. This latter point, however, rests upon a very slight difference and may not be significant. It is nevertheless worth mentioning, since it is in line with the effect of the

highest intensity upon rate, as well as with certain other evidence to be discussed later.

The small excess of clockwise over contra-clockwise turnings is not explainable upon the ground of varying intensities of light. A distribution of the cases under the several intensities of light (Table VI) makes it plain that this peculiarity is due rather to individual causes than to light intensities. Indeed it would be difficult to conceive theoretically how varying intensities of non-directive light could influence a worm in such a way as to affect the direction in which it turns. The natural expectation according to chance would be an equal number of turnings in either direction. The excess of clockwise turns seems, therefore, undoubtedly due to internal causes which render certain worms more liable to go one way than another. In fact, when the records were arranged according to individual behavior it was found that of the ten worms seven averaged a majority of clockwise turns while only three fell in the contra-clockwise column.

TABLE VI

Character of turning of Planaria gonocephala in non-directive light of various intensities

Light in candle meters.....	0	0.94	11	39	78	126	155	217	431	Total
Clockwise turns.....	23	25	21	32	17	17	22	24	22	203
Contra-clockwise turns.....	23	23	17	20	17	18	17	17	14	166

Change of Course. A greater number of "definite" changes occur in the light than in the dark, but fewer "indefinite" changes. This point requires no further exposition as its corollary has already been given.

The behavior of the worm in this respect seems to be more closely correlated with the highest intensity (431 c.m.) than with any other. In the highest intensity employed there are indicated (Table II, p. 52) 40 per cent of definite changes, which is considerably in excess of the percentage of such changes made in any other intensity. On the other hand indefinite, or S-shaped, changes constitute only 9 per cent of all records taken at the highest intensity, which is less than half the number of indefinite paths made in any other intensity.

While the extremes of the series of definite changes indicate a general rise in the percentage of their occurrence with an increase of intensity, and while in the same way the extremes of the series of indefinite changes suggest in general a decrease of frequency with the increase of intensity, it can hardly be maintained that the character of the changes in course is definitely correlated in the majority of cases with changes in intensity.

Degree of Wandering. Wandering is not closely correlated with the intensities of light. In Table VII, which deals with the percentage of straight paths made by *P. gonocephala* under different intensities of non-directive light, this fact is expressed negatively, since it is held that a straight path is a good indication of the absence of aimlessness or wandering and may thus serve as a negative measure of such behavior.

TABLE VII

Percentage of straight paths made by P. gonocephala in the dark and also in non-directive light of different intensities

Light in candle meters.....	0	0.94	11	39	78	126	155	217	431
Percentage of straight paths.....	13	24	34	31	19	33	25	23	35

In this respect again the behavior of the worms under the highest intensity is more pronounced than under any other intensity since the greatest number of straight paths were laid at an intensity of 431 c.m.

Interval of Response. There seems to be some evidence that the interval of time elapsing between the reception of a light stimulus on the part of a worm and its consequent response, may be quite considerable. Three facts were established that may support this conclusion.

First, when two-minute records were made under various intensities, it was found that the worms averaged a faster rate during the second minute of exposure to the light than during the first, in spite of the facts that the mechanical stimulus due to placing the worm in the light machine had a more quickening influence during the first minute and that the fatigue effects were more likely to appear during the second minute. The actual figures

for the above statement, based upon 240 two-minute trials under various intensities, are 0.645 mm. per sec., the average during the first minute, as against 0.713 mm. per sec., the average during the second minute.

Secondly, in these 240 trials, the percentage of turning under all intensities is greater during the first minute than during the second, being 87 per cent and 57 per cent, respectively. This result may possibly be conceived to be due to a greater steadying influence of the light during the second minute than during the first and to a consequent greater turning than during the first minute. But on the other hand a similar decrease of turning, although not so pronounced, took place during the second minute when the worms were in the dark. It must be admitted, therefore, that the fact of less turning during the second minute may have nothing to do with the interval of response.

Thirdly, on several occasions a notable piece of behavior was observed, which may have a bearing on the interval of response. The phenomenon in question always occurred in connection with a modification of the experimental field within the light machine to be more fully described later. Briefly this modification consisted in making a field of two distinct intensities of light, the latter being projected vertically from above in such a way that a sharp line of demarkation formed a boundary between the two areas. Ordinarily when the worms reached this boundary line as they glided from one intensity to another, they responded promptly to the stimulus caused by the change of intensity. Several times, however, they were observed to travel indifferently exactly along this dividing line for a distance of several centimeters with half the body in one intensity and half in the other. This curious fact lends itself to various interpretations, one of which is that the response to a new intensity may not be, in all cases, immediate.

Manner of Coming to Rest. During the experiments made in the non-directive light apparatus previously described, normal worms could never be induced to come to rest in the light. If allowed to remain in the aquarium they would wander about until they reached the shadow under the diaphragm (Fig. 1, *H*),

where they finally stopped, usually in the angle formed by the paraffine wall and the bottom.

Loeb's conclusion ('93b, p. 101) that planarians subjected to directive light come to rest in regions of least intensity, seems therefore to be equally true of planarians in non-directive light.

Summary. In non-directive light *Planaria gonocephala* moves faster, turns less and makes more "definite" but fewer "indefinite" changes than in the dark. Rate of locomotion; amount of turning; changes in the character of the course, as well as the amount of wandering, do not appear to be correlated with varying light intensities, unless in the following instance. Under the highest intensity employed, namely, 431 c.m., occurred the slowest rate; the least turning; the greatest number of "definite" and the fewest "indefinite" responses, together with the straightest paths. The excess of clockwise over contra-clockwise turnings throughout the series of intensities is probably not attributable to light.

Continuous exposure to light results in a decreasing rate of locomotion, although in the second minute of movement as compared with the first an increase in the rate of locomotion takes place, while fewer turnings occur.

Rate of locomotion is less influenced by differences in light intensity than by certain internal factors which go to make up what may be termed the individuality of different worms. Individual worms may sometimes fail to respond for a considerable interval of time to light stimuli that ordinarily produce immediate effects.

Finally, planarians subjected to non-directive light come to rest in regions of lessened light intensity the same as they do in directive light.

C Abrupt Changes in Intensity

Abrupt changes in intensity may be of two kinds: either with reference principally to time or to space. First, those changes are abrupt *in time* in which light or dark is suddenly thrown upon the worm, and secondly, those changes are abrupt *in space* in which a moving worm passes immediately from an area of one intensity into a sharply defined area of a different intensity. This topic

will be discussed here only in its relation to non-directive light, the effects of sudden changes in directive light coming more properly in a later section.

a Abrupt Changes of Light Intensity in Time

Whenever worms were left over night in the experimental aquarium completely shut off from light, a large proportion of them would be found at rest in the morning when the light in the hood was again turned on. By removing the diaphragm (Fig. 1, *H*), under the edge of which near the paraffine wall the worms were usually collected, it was possible without any mechanical disturbance to subject resting worms to sudden non-directive light after a prolonged period of complete darkness. This sudden stimulus rarely had an instantaneous effect. The interval of response was often several minutes and frequently non-directive light alone proved insufficient to start the worms into activity.

No sudden increase of intensity ever proved powerful enough to throw a gliding worm into the more rapid method of crawling. Pearl ('03, p. 551) stated the same fact after subjecting planarians to much stronger intensities of light than were employed in the present experiments.

It was found that *P. gonocephala* showed a decided response—either some change in course or a wigwag motion of the anterior end—more frequently when suddenly subjected to dark than to light. By inserting a key into the electric circuit it was possible to control the light in the hood to a fraction of a second. Worms in complete darkness were by this means subjected to various intervals of sudden light and worms in light to intervals of sudden dark, the results being at once noted. While the worms were in the dark their behavior could not, of course, be directly observed, but by watching them closely just before the light was turned off and also the instant it was turned on again there was no great difficulty in determining whether a response had occurred during the interval. The results obtained from nearly a thousand trials are indicated in Table VIII.

It will be seen from this table that there are more responses than failures to respond and that the responses occur more fre-

quently when the worms are suddenly subjected to dark than to light.

It may be further noted that the excess of the responses in the dark over those in the light increases with the interval of exposure, indicating that the worm's adjustment to a change in the light stimulus affecting it is not in all cases immediate.

The effect of previous exposure, whether to several hours of dark or light, is a factor in these results which will be considered more properly later on.

TABLE VIII

Percentage of the responses of P. gonocephala in various intervals of time when suddenly subjected to dark and to light of 39 c.m.

Number of seconds exposed.....	5	10	15	20	25	30	Average
Percentage of responses in light.....	51	59	54	54	48	46	52
Percentage of responses in dark.....	63	66	73	75	71	71	70
Excess of responses in dark.....	12	7	19	21	23	25	18

It should be added that *Bdelloura* gives a remarkable response when enveloped in sudden darkness. It will frequently forsake its attachment under these circumstances and unattached in the water go through violent contortions. This striking response can be called forth by an exceedingly brief interval of dark, namely, the shortest time required to turn the electric light off and on. Nagel ('94, p. 387) speaks of animals thus affected by sudden shadow as "skioptic."

The relation of *Bdelloura* to light falls into a somewhat different category, however, than that of the fresh-water planarians, since *Bdelloura* is positive to light, while fresh-water flat-worms are negative.

b Abrupt Changes of Light Intensity in Space

Several devices were employed to test the behavior of planarians passing abruptly from an area of one intensity of non-directive light into another. The most successful device tried was that in which two lights of different intensities were mounted overhead

in the hood of the apparatus already described in Fig. 1, the mingling of their rays being prevented by the insertion of a vertical diaphragm (Fig. 3, *C*), which extended from the region between the lights down to the surface of the aquarium. In order to place the diaphragm in position it was, of course, necessary to remove the heat screen (Fig. 1, *C*), the presence or absence of which, however, would not have affected the results sought since the water in the aquarium itself was nearly 2 cm. deep and thus

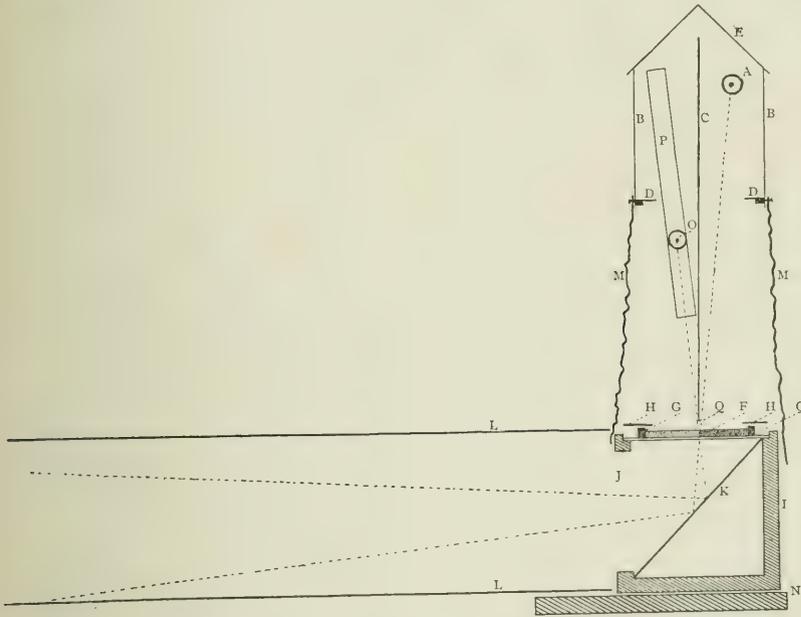


Fig. 3 *A*, stationary light; *B*, sheet iron walls of hood; *C*, vertical diaphragm separating the two lights; *D*, horizontal diaphragm; *E*, sheet iron roof of hood; *F*, plate glass aquarium floor; *G*, paraffine wall of aquarium; *HH*, diaphragm to shut off reflections from wall of aquarium; *I*, wall of reflector box; *J*, open side of box; *K*, mirror; *L*, black tunnel; *M*, black draperies cutting off side light; *N*, table supporting reflector box and end of tunnel; *O*, movable light; *P*, track for movable light; *Q*, narrow, horizontal diaphragm attached at right angles to the lower side of the diaphragm *C*, in order to prevent the light rays from the two sources of light, *A* and *O*, from overlapping.

constituted an efficient heat screen. By keeping the hood stationary and causing one of the lights (Fig. 3, *O*) to slide up and down at will, it was possible to bring about various contrasts of

intensity in the field below. The complete plan of the apparatus is given in Fig. 3.

The principal variations in the behavior of *Dendrocœlum* and *Phagocata* upon reaching the critical line separating the areas of two intensities are indicated diagrammatically in Fig. 4.

The dotted line represents the boundary separating two areas of different light intensities. The arrows represent the types of paths made by *Dendrocœlum* and *Phagocata*. For the sake of simplicity the worms are represented as going in one direction; that is, into one of the two contrasting intensities, but the same types of paths resulted as well when the opposite direction was taken. The angles made in crossing the critical line were also more varied than those represented in the diagram.

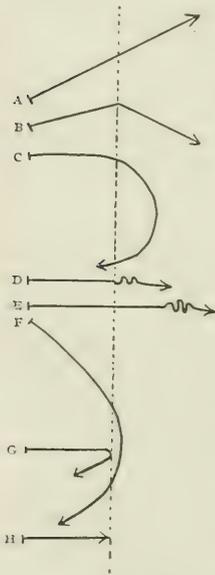


Fig. 4

Type *A* represents a passage without response; *B*, an angular change of course made at the critical line; *C* and *F*, a loop-like return effected after a short excursion into the new intensity, and *G*, a sharp turning aside, while *H* indicates a halt at the critical line, as if a barrier had been encountered. Finally *D* and *E* represent a temporary pause on the part of the worm accompanied by wigwag movements of the anterior end of the body. In the case of *D* the wigwagging is immediate, but *E* typifies a case when there occurred in the response an interval of such a nature that the significant movements were not made until the worm had advanced at least its own length into the new area.

Of these types all, with the exception of *A*, are to be regarded as reactions to differences in intensity encountered. The most questionable are the infrequent types *C* and *F*, which may be otherwise explained as arcs in a curving course which might have occurred in a field of uniform intensity. By far the commonest type was *D*, plainly the least doubtful of the series.

As a result of over 3000 observations on the manner in which the critical line separating the two intensities was passed, three facts become evident. First, responses were considerably more

TABLE IX

Kind and percentage of responses of *Dendrocoelum* and *Phagocata* in passing from one intensity of non-directive light to another

Character of course	No responses (Type <i>A</i>)	Wigwags (Types <i>D</i> and <i>E</i>)	Turn-backs		Angular courses (Type <i>B</i>)	Total responses
			and full stops (Types <i>G</i> and <i>H</i>)	Loops (Types <i>C</i> and <i>F</i>)		
Going into greater intensity, per cent.	79	11	6	2	2	21
Going into lesser intensity, per cent.	50	36	5	8	1	50
Average responses, per cent.	64.5	23.5	5.5	5.0	1.5	35.5

frequent when the worms were passing into the lesser intensity than they were when entering the greater intensity. Secondly, lack of response is more frequent than a visible response of any kind since 64.5 per cent of the crossings made over the critical line were of the type *A*. Thirdly, the responses at the critical line were more frequent when the worm was upside down, *i. e.*, moving on the surface film, than when it was on the floor of the aquarium. This latter point was illustrated most fully by *Phagocata*, which, being an active worm, takes quite readily to the surface film, so that it was possible with this species to get a series of observations in which the behavior when crossing the critical line on the bottom of the aquarium could be compared with that when the same line was encountered at the surface film. Table X contains the results of these observations.

The doubling of responses when the worm is on the surface film is probably not due to an unequal receptivity of light stimulus by the dorsal and ventral surfaces of the planarian as might at first thought seem possible. As will be shown further on, the worm's rate of locomotion on the bottom of the aquarium is nearly the same whether the light comes from below or from above, pro-

vided the amount of light in both cases is equal. Planarians, as Pearl has emphasized, are strongly thigmotactic. Naturally, then, their response to contact is much greater when they are on the glass bottom of the aquarium than when they are suspended on the less resistant surface film. In other words, the less the worm is influenced by the stimulus of contact the freer it is to respond to the stimulus of light.

TABLE X

Percentage of the responses made by Phagocata at the critical line separating two intensities of non-directional light either on the bottom of the aquarium or on the surface film

	Number of observations	No response per cent	Response per cent
On the surface film.....	740	45½	54½
On the bottom.....	1664	76	24
Total.....	2404	60¾	39½

Finally, a series of experiments was tried in which the contrast between two intensities was varied by raising or lowering one of the lights in the hood. It was found that the responses made by Phagocata under these circumstances increased with the increase in contrast between the two intensities as shown on the bottom line of Table XI, where these contrasting intensities are expressed in a ratio between the constant light taken as unity and the movable light.

The fact that responses by no means invariably occur when bright light and complete darkness are suddenly substituted for each other (see Table VIII) rendered a further extension of this series unnecessary. The contrasts here used form probably a much greater range of intensity contrasts than the worms ever encounter in nature.

Attention to the details presented in Table XI brings to light the fact that, although the number of responses is correlated in a general way with an increase in the contrast between the two illuminated areas, as shown in the bottom line of the table, yet the percentage of the responses is further influenced by the actual degree of the intensities employed. For example, when the two

areas of light were respectively 33.16 and 68.18 c.m. the ratio was practically the same as when the two intensities were 16.3 and 33.16 c.m., yet the percentage of responses in the two cases is decidedly different, being 10.5 per cent in the former, and 56 per cent in the latter case. When the lesser of the two lights was 33.16 c.m. there were invariably fewer responses than when the lesser light was 16.3 c.m. The latter intensity is undoubtedly nearer the planarian's optimum intensity, and the apparently inhibitive action of the higher intensities agrees perfectly with certain facts already detailed, as, for instance, that the activities of *Planaria gonocephala* were less pronounced at 431 c.m. than in lesser intensities; and, again, that all planarians show more responses on going into a lesser than when going into a greater intensity.

Attempts were made in some other ways to subject planarians to areas of contrasted intensities and, although the results were less satisfactory in general than those obtained by the method of using two overhead lights of different intensities just described, yet certain facts were brought out that may be worth recording.

In the first of these attempts two concentric rings of white paper, each about two centimeters wide and having between them a space of a couple of centimeters, were fastened to the under surface of the aquarium floor. The white paper thus arranged reflected the light upward and made areas of gradually increased intensity as compared with the remainder of the aquarium floor through which the light passed without reflection. Worms placed in the center of these circles would consequently be obliged to pass from one intensity of light directly to another, whatever the direction of the radius they might be taking. When worms were actually tested, it was found that they exhibited considerable modification in their movements, particularly when approaching the edge of the paper backgrounds.

Owing to the considerable thickness of the plate-glass floor of the aquarium as well as to the fact that white paper is a surface which scatters the light falling upon it, it was found that there was formed, not a sharp line of demarkation between two intensities, but rather a penumbra-like margin of intermediate light. This apparatus was therefore abandoned as unsatisfactory.

The difficulties presented by paper as a reflecting surface largely disappeared by the substitution of a plain mirror in its place, since the surface of a mirror is such that all the light striking it at right angles is reflected at right angles. When, therefore, an unmounted mirror was brought into contact with half of the under surface of the aquarium floor the whole field was thereby divided into two regions sharply separated from each other. Of these one was supplied with light from above only, while the other received the same light plus nearly an equal amount reflected from the mirror below. With the aid of this device an increase of 11 per cent was gained over the responses obtained when white paper instead of a mirror was used as a reflector. Both *Phagocata* and *Dendrocœlum* were tried by this method. In 76 per cent of the trials made, *i. e.*, in 125 cases out of 165, the worms showed a visible modification in their behavior on reaching the boundary of the two areas of light. It was nevertheless decided that this method was an uncertain test of behavior, since the body of the worm, although fairly translucent, would by no means allow all the light that fell upon it to pass through and be reflected, and consequently the difference of the two intensities to which it was being subjected could not be easily estimated.

Summary. When sudden light or dark envelops planarians (*Dendrocœlum*, *Phagocata* and *Planaria*) the response, if any occurs, is often not immediate.

No one of the intensities of light which were employed in these experiments when introduced suddenly was sufficient to make the worms forsake gliding for crawling.

Sudden dark calls out more responses than sudden light, while the number of responses increases with an increasing interval of exposure to the stimulus. *Bdelloura* is decidedly "skioptic."

Worms encountering the edge of a reflecting area which increases the intensity of the light without introducing any other barrier, show a marked degree of response. The percentage of response is considerably larger when a mirror instead of white paper is used to produce the reflecting surface. If worms are allowed to pass from one intensity to another sharply separated from it, their responses are more frequent upon passing into the lesser intensity

than when going into the greater. The average number of failures to respond to these contrasts of intensity reaches about two out of three.

Phagocata, at the critical line separating two contrasting intensities, responds oftener when on the surface film than when gliding over the bottom of the aquarium.

The number of responses increases with the increase in the contrast between the two intensities employed, but the percentage of response is greater, regardless of ratio, when one of the lights is of low intensity (13.6 c.m.) than when both are of higher intensity (33 + c.m.)

2 PHOTOTAXIS

The term "phototaxis" was introduced by Strasburger ('78) in a study of certain swarm-spores, to indicate movements which were parallel with incident light rays. The term has since been extended by several authors to include similar movements on the part of animals. Any organism is said to be positively phototactic when it moves toward the source of light in the direction of the rays and negatively phototactic when it goes in the opposite direction.

The purpose of this section is to consider the phototactic movements of planarians, as distinct from their photokinetic behavior, (A) when the light remains constant, (B) when the light is changed either (a) in intensity or (b) in direction, and (C) when phototaxis is combined with responses of a different kind.

A In Constant Directive Light

Orientation. With the exception of *Bdelloura* all the planarians studied are, under normal conditions, negatively phototactic so far as their first movements in directive light are concerned. To obtain quantitative data for this statement it was necessary to construct an apparatus in which the worms to be tested could be placed quickly and with as little mechanical disturbance as possible in the center of a unit circle with the long axis at right angles to the direction of incident light. The circle was marked off into degrees so that by noting the place at which a worm made its exit a quan-

titative measure of the amount of turning toward or away from the source of the light under the given conditions was obtained.

The apparatus finally utilized for this experiment was based upon a device employed by Parker and Burnett ('00) in testing the relative behavior of normal and eyeless planarians when subjected to directive light. Its arrangement is shown in Fig. 5.

On the top of a table (*A*) in the dark room was placed a rectangular aquarium (*BCDE*), the ends of which (*BE* and *CD*) were

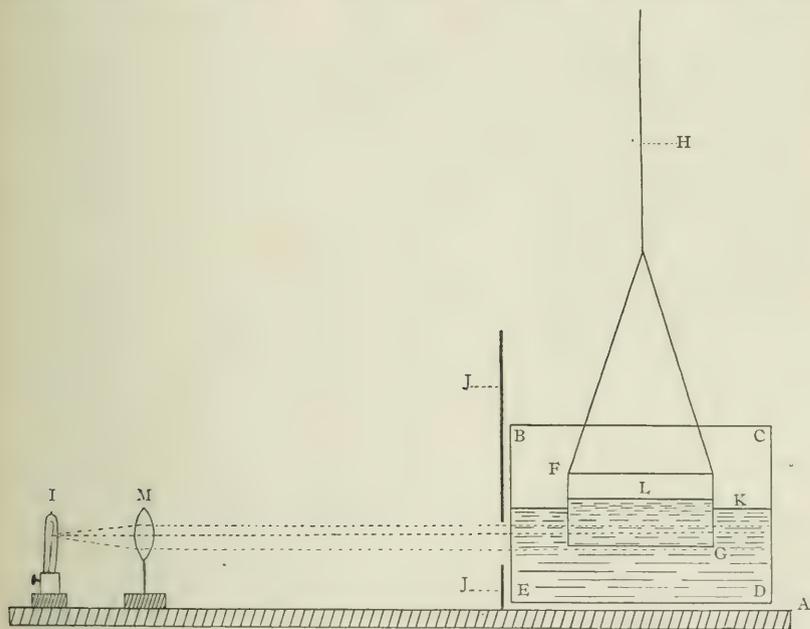


Fig. 5 *A*, Top of table; *BCDE*, rectangular aquarium; *BE*, glass end; *FG*, round swinging aquarium; *H*, copper wire attached to ceiling and supporting the swinging aquarium *FG*; *I*, movable light; *J*, diaphragm; *K*, surface of water in outer aquarium; *L*, surface of water in inner aquarium; *M*, lens.

made of glass while the floor and sides were of wood painted with camera-black. Within this aquarium a second cylindrical one (*FG*), made entirely of thin glass and measuring 20 cm. in diameter, was suspended from the ceiling by means of a fine wire (*H*) attached to a swivel to allow turning. On the floor of the outer aquarium and directly beneath the inner one was drawn a circle

10 cm. in diameter and marked off plainly into arcs measuring 5 degrees each. An incandescent lamp (*I*), placed on the table at approximately the height of the inner aquarium floor, could be manipulated at any desired distance, while a diaphragm (*J*) prevented much of the light from reaching either the upper surface of the water contained in the two vessels or the floor of the outer aquarium whence it would be reflected. A biconvex lens was then so interposed as to make the light rays practically parallel upon their emergence from it. Their course through the inner aquarium was kept parallel by means of the medium of water on both its inner and outer sides. A nearly uniform intensity over the entire floor of the swinging aquarium was thus obtained and the objection arising when the inner aquarium is used in air, viz: that it acts as a converging lens, was obviated. Side reflections were eliminated by enclosing the light (*I*), together with the intervening space between it and the diaphragm, with black screens.

When a worm introduced into the inner aquarium began to glide, it could with slight mechanical disturbance be quickly rotated, by means of moving this inner aquarium, into any desired position with reference to the light, and then swung so as to bring its posterior end exactly over the center of the stationary circle below.

Various species of planarians were started in this manner at right angles to the light. Out of 386 cases, 371, or 96 per cent, emerged from the 10 cm. circle at a point farther away from the light than that toward which they were originally directed. This is taken to mean that 96 times out of a hundred the worms were negatively phototactic. If, however, the method of reckoning negativeness employed by Parker and Arkin ('01) on the earthworm is used, the foregoing per cent would be somewhat less. These authors assume ('01, p. 28) that the apparently positive responses of a normally negative animal, such as the earthworm, may be due to causes other than light, in which case an equal number of responses of like nature might be expected to occur on the negative side as well as on the positive. A number equal to the sum of these apparently positive responses should therefore be subtracted from the total of the apparently negative responses

in order to obtain approximately the amount of unquestionable negativeness. By following this method in the case just given, the per cent of negativeness would be 92 instead of 96, but since this method assumes that normally negative worms are never positive, which is contrary to the evidence to be given later, the most accurate estimate of negativeness would probably fall somewhere between these two percentages.

Bdelloura, on the other hand, behaves in the same way only three times out of ten, therefore showing itself to be positively phototactic.

This difference in orientation becomes more marked if the total number of degrees, that is, the *amount* of positiveness and negativeness of emergence from the circle is used as the basis of reckoning, instead of only the number of times of emergence. Such a quantitative computation is shown in Table XII.

TABLE XII

Amount and kind of orientation to directive light exhibited by various species of planarians in 396 trials

	Number of trials	Total degrees positive	Total degrees negative	Percentage of degrees neg.	Percentage of degrees pos.
Negative worms (<i>Dendrocoelum</i> , <i>Planaria</i> , <i>Phagocata</i>)...	386	566	10157	94.7	5.3
Positive worms (<i>Bdelloura</i>)...	10	397	50	11.2	88.8

Although the actual number of trials for *Bdelloura* in this table is small, they are characteristic of what was observed in a large number of unrecorded instances.

The amount a planarian may deviate from the direction in which it is pointed, depends upon the direction of the light impinging upon it. A negative species deviates from a straight course least when headed away from the source of the light and most when headed toward it, while an intermediate degree of deviation occurs when the direction of the light is at right angles to the long axis of the worm. In the case of *Bdelloura* the converse is true, as shown in Table XIII.

Rate of Locomotion. In obtaining the rate of locomotion of worms subjected to directive light, the double aquarium apparatus

just described was used. After the worm to be tested had been placed in the inner aquarium and had begun gliding, it was so oriented that the tip of its posterior end came precisely over the center of the subjacent circle 10 cm. in diameter. The exact time of its departure from the center of the circle was then noted and the instant thereafter that the tip of the posterior end passed over the circumference of the circle was again taken and the worm's course plotted at once on a duplicate circle sheet. Each worm was given four trials in this manner, being started in four different directions, toward the light, away from the light, and with the long axis of the body at right angles to the light, first with one side to the light and then with the other.

TABLE XIII

Amount of average deviation in 2400 trials expressed in degrees of a circle, exhibited by negative planarians, (Dendrocoelum, Planaria and Phagocata), and a positive one (Bdelloura) when pointed toward, away from, and at right angles to the source of light

Direction in which the worm was pointed with regard to the light	At right angles	Toward	Away from
Negative planarians, degrees.....	48.1	128.7	27.3
Positive planarians, degrees.....	49.	39.3	132.1

The time of the worm's emergence from the circle was not taken with a stop-watch because the observer's hands were otherwise occupied. Instead a small clock, ticking half-seconds, was placed conveniently near. By counting the number of ticks during the interval of the worm's transit from the center to the circumference of the circle the time consumed could be determined within less than a half-second. After tracing the worm's course on a duplicate circle sheet and measuring the same by means of a map measurer, a unit of distance was obtained, which together with the known unit of time consumed in covering this distance, furnished all the data necessary for computing the rate of locomotion.

Ten representatives of *Dendrocoelum lacteum*, *Planaria maculata*, *Phagocata gracilis* and *Planaria gonocephala* respectively were given four trials apiece by the method just explained. The results are presented in Table XIV. From the 160 records thus obtained it becomes evident that the average rate of locomotion

is greatest when the worms are pointed toward the light, and least when they are pointed in the opposite direction, while an intermediate rate occurs when they are started at right angles to the light.

This result is at variance with the findings of Parker and Burnett ('00, p. 381), who incidentally reported that *Planaria gonocephala* when started away from the light traveled faster than when started toward the light.

TABLE XIV

Average rate of locomotion, expressed in mm. per sec., of various species of planarians when started toward, away from, and at right angles to the source of directive light of 27 c.m. intensity.

Species	Dendrocœlum lacteum	Planaria maculata	Phagocata gracilis	Planaria gonocephala	Total average
<i>Direction in which the worm was pointed with reference to the light</i>					
At right angles	0.855	1.475	1.445	0.980	1.19
Toward.....	0.910	1.505	1.430	1.205	1.26
Away from	0.795	1.440	1.310	1.090	1.16

It was further found that, regardless of the direction in which the worms were started, there was a gradual decrease of the rate during the four successive trials. The order in which different worms were oriented during the four trials was arranged so as to neutralize the possible effect of the sequence in the direction started. In Table XV the data for 200 trials are arranged to express this slowing down of the rate.

TABLE XV

Average decrease in rate of locomotion for 50 planarians during four successive trials while subjected to directive light of 27 c.m.

Number of trial.....	First	Second	Third	Fourth
Average rate in mm. per sec.....	1.140	1.130	1.075	1.070

Various factors influencing the rate of locomotion, such as the intensity of light, the size and species of the worm, the amount of pigment present in the body and the general physiological state of the animal under experimentation, will be more suitably discussed in other connections.

Change in Character of Course. When several specimens of Phagocata were placed in a square aquarium which received light solely from one side, their first movements were plainly negative, that is, away from the light. After a brief interval, however, it was seen that apparently as many worms were going toward the light as in the opposite direction. In fact an actual count showed that in a certain interval of time 43 worms passed a central point going toward the light while 44 passed the same point in the opposite direction. This apparent change in the character of the course was probably due, not to any change in the degree of negativity of the animal, but rather to the fact that the impulse to keep moving in some direction is stronger than the impulse to negative phototaxis. Consequently when the limit of the aquarium in a negative direction is reached a worm, since it normally travels in straight lines or sweeping curves and does not turn around and around in one spot, continues its locomotion in the direction of least resistance, namely, back toward the light. It will be remembered that Loeb ('93b) has called attention to this fact by saying that planarians are not negatively "heliotropic" in a strict sense because they do not remain as far away from the source of light as they can get.

Among various observations made with other ends in view, there were numerous incidental cases of a normally negative worm making an unexpected positive response even from the first moment of being subjected to the light stimulus. This occasional positiveness is clearly apparent from the general fact already noted that four times out of a hundred the average negative planarian turns toward the light.

Two definite instances of a reversal in the character of response may be cited.

The first was the case of a Phagocata in the double aquarium, which became increasingly positive through twelve successive trials. Its average emergence from the circle for the first four trials was 45° , which is a normal negative result, since 90° represents complete indifference. In the next four trials, however, the average was 100° , that is, slightly positive, and in the last four, 124° , which is decidedly positive, as shown diagrammatically in Fig. 6.

In the other instance an individual worm, *Planaria gonocephala*, made the erratic average emergence from a circle of 145° , just 35° short of absolute positiveness. This worm was carefully isolated and tested again four days later under identical external conditions when it was found to have returned to a normal negative condition by showing an average record of 56° .

Accuracy of Orientation. It was found to be frequently the case that when negative worms were subjected to directive light their first movement instead of being directly away from the source of light formed a path in a diagonal direction. This tendency to

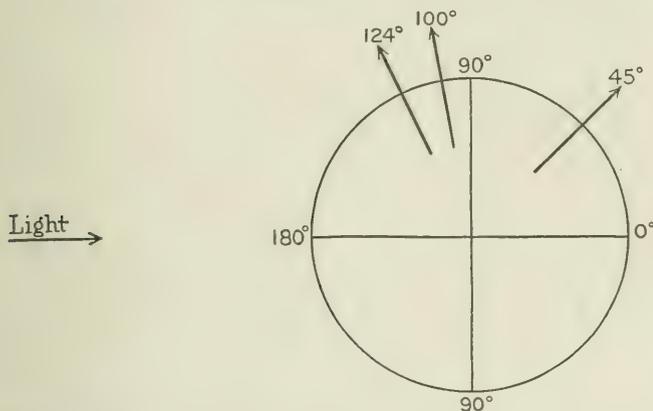


Fig. 6 The arrow at the left represents the constant direction of the light. In each of the three sets of trials each worm was headed successively toward 0° , the upper (in the diagram) 90° , 180° , and the lower 90° . The point of average emergence for the first set of trials—supposing the records of the lower semicircle to have been transferred to the upper semicircle—was at 45° , of the second set, at 100° , and of the third set, at 124° .

travel diagonally away from the light has also been noted in the case of the earthworm by Smith ('02, p. 469).

If the negative phototaxis of planarians is to be explained on the theory of tropisms, and if, moreover, the eyes, as Hesse ('97) maintains, are the principal organs which, when unequally illuminated, cause the directive response, it may be shown that possibly the arrangement of the crescentic pigment shields around the sensory cells of the eyes is such that equal stimulation of both eyes is just as certainly received by the worm when it is in a position diagonal to the light as when it is pointed directly away from the light.

By reference to Fig. 7, in which the relative size of the eyes is somewhat exaggerated and made diagrammatic for sake of clearness, it will be seen that no more light reaches the sensory cells of either eye from position *A*, the diagonal position, than from position *B*, and that it is only when the light comes from some source more lateral than *A* that the left eye receives more illumination than the right.

This view may furnish a possible explanation of the diagonal paths representing imperfect orientation among planarians, but it can in nowise apply to the case of earthworms since in them direction eyes are absent.

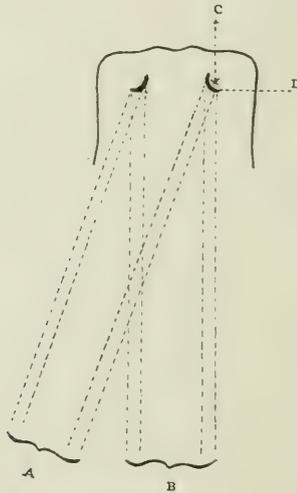


Fig. 7 *A*, diagonal direction of light; *B*, posterior direction of light; *C*, location of sensory cells; *D*; pigment shield.

Degree of Wandering. The degree of wandering decreases with an increase of intensity. It may be found approximately through the degree of error in orientation in a unit space under different intensities of light, for perfect orientation signifies the minimum of random wandering and, conversely, the greater the error of orientation the greater the probable wandering.

The error of orientation expressed in percentages was computed as follows. With a negative worm emergence from the circle at

a point directly opposite the light was reckoned as 0 per cent of error, whereas emergence at a point directly toward the light was reckoned as 100 per cent, or a maximum of error in orientation. The orientation value at these two extremes having been established, the percentage of error which occurs when the worm emerges at any intermediate position on the circumference of the circle may be easily determined.

TABLE XVI

Average degree of error in orientation made by various species of planarians during 360 trials in directive light of different intensities

	Percentage of error in orientation		
	When started toward the light	When started away from the light	Average
3.3 candle meters.....	34	11.5	22.7
27.0 candle meters.....	32	12	22.0
53.0 candle meters.....	31	10	20.5
Average.....	32	11	

From this table it appears that there is three times as much wandering, or error of orientation, by worms headed toward the light, as by those headed away from it. This doubtless indicates that orientation is a more complicated process in the former case than in the latter.

Duration of Activity. Superficial observation is sufficient to establish the fact that different species of planarians when set into activity in directive light show decided differences with regard to the length of time they normally continue in motion before coming to rest. Among the forms experimented upon, *Bdelloura* came to a stand-still in light soonest and *Phagocata* latest. Fatigue in itself is by no means the inevitable result of continued activity on the part of an organism. For instance, Hodge and Aikens ('95) observed a *Vorticella* continuously for 36 hours, during which time its regular ciliary and contractile movements continued uninterruptedly, while Rádl ('01) found that the eye of *Daphnia* when

light was flashed upon it vibrated as vigorously after the experiment had been repeated 410 times in close succession as it did at first.

An attempt was made with *Planaria maculata* to see how long activity would continue in a succession of trials in directive light. The worm was started on the middle of an aquarium floor and allowed to glide in any direction. As soon as it stopped and assumed the relaxed contour of the resting worm, the time required for the journey being noted, it was immediately returned to the starting point. Subjected to this treatment, the worm made 39 trips, which in general occupied an ever decreasing length of time, ranging from 18 minutes to $1\frac{3}{4}$ minutes, or an average of 5 minutes and 53 seconds each. When returned to the starting point the fortieth time the worm refused to start. Although in this experiment, which lasted $4\frac{1}{2}$ hours, the worm became gradually less responsive to the mechanical stimulus of the brush by means of which it was transferred to the starting point, its fatigue did not materially affect the negative character of its response to light.

Time Required to Leave a Unit Circle. In obtaining the data on this point, the apparatus and method already described (p. 73) were employed. It was found that when worms of different species were subjected to three different intensities in immediate succession the degree of intensity did not prove to be as important a factor as fatigue in determining the average number of seconds necessary for the worm's exit from a circle 10 cm. in diameter.

During the series of experiments upon this point care was exercised so to vary the succession of intensities that the effect obtained could not be attributed to any cumulative increase or decrease of intensity. Thus, on one day the order of intensities was 1, 2, 3, on the next 2, 3, 1, and on the third, 3, 1, 2. In Table XVII the data obtained are arranged on the left with reference to the actual intensities employed and on the right with reference to the succession of trials made upon the various species which are designated in the middle column. The averages in the table are each made up of four records.

It will be noted that *Phagocata gracilis* and *Planaria gonoccephala* are, according to these figures, less subject to fatigue than *Dendrocœlum lacteum* or *Planaria maculata*.

Manner of Coming to Rest. Loeb ('93b) and others have shown that planarians under the influence of directive light generally come to rest in regions of lessened intensity. A few experiments were made bearing on this point. By means of screens and backgrounds, both black and white, a rectangular glass aquarium was arranged so that the area of least intensity was plainly localized and could be varied in different ways. In Fig. 8 are shown (1) the places where worms (*P. gonocephala*) which had been started together in the middle of the dish finally came to rest; (2) the number of worms in each locality; and (3) the different combinations of backgrounds and screens used in each of the experiments.

TABLE XVII

Relative effect of fatigue (at right of table) and change in intensity of light (at left of table) as shown by the average number of seconds required for individuals of various species of planarians to leave a circle 10 cm. in diameter

INTENSITY			SPECIES	GROUPS OF TRIALS		
3.3 c.m.	27.0 c.m.	53.0 c.m.		First	Second	Third
<i>seconds</i>	<i>seconds</i>	<i>seconds</i>		<i>seconds</i>	<i>seconds</i>	<i>seconds</i>
63	65	64	<i>Dendrocœlum lacteum</i>	54.5	63	72.5
40	43	41	<i>Planaria maculata</i>	37	42	45.5
40	38	46	<i>Phagocata gracilis</i>	38	44	42
52.5	47	49	<i>Planaria gonocephala</i>	46	52.5	50
65	64	67	Average	58.5	67	70

Wherever shaded borders are indicated the aquarium was surrounded on five sides by black screens and likewise on the sixth side except for a narrow space admitting the light, the direction of which is indicated by arrows; in a similar fashion, where unshaded borders appear, light-reflecting screens enclosed five sides.

It will be seen at a glance that the great majority of the worms placed in directive light come to rest as far from the light as possible. That this is due to the directive power of light is at once apparent by comparing *A*, *B* and *C* with *D*, where the light was non-directive. The darkened area was selected whenever the directive force of the light did not prevent, as in *A*, *C* and *D*.

The five worms coming to rest on the lighter side of *D* were carefully examined and found to be mutilated or fragmented individuals, while the same was not true of the others.

The reason why the worms in *B* failed to arrive in the darkened area is probably that, being started near the middle boundary line, their first movements were normal, *i. e.*, away from the light, and carried them into the area of greatest intensity, whence they were unable to escape. In this case the effect of the directive light seems to have more than counterbalanced the locomotive

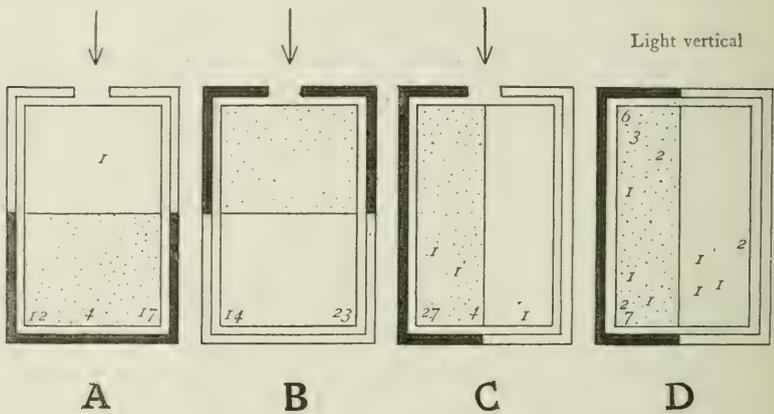


Fig. 8 *Planaria gonocephala*. The arrows represent the direction of the light. The dotted areas were surrounded by black backgrounds, except for a space on the side toward the light, and the clear areas similarly by white backgrounds. The figures represent the number of planarians that came to rest in any particular locality.

energy exerted by the worms. Had the species experimented upon been *Phagocata gracilis*, instead of *Planaria gonocephala*, the result might have been different, for in the former species, as already shown (p. 78), the phototactic response is secondary to the tendency to a general wandering.

It was frequently observed that worms when fatigued after a period of activity apparently lost their phototaxis, with the result that the final movements of a tired worm would sometimes be made toward the light. Such behavior is probably not to be considered as a reversal of phototaxis, but rather as indifference to

photic stimuli, due to the worm's lowered physiological state and a chance turn toward the light. In fact the final position taken by 49 fatigued worms with reference to the source of light, showed that only five of them, or 10+ per cent, pointed away from the light while 15 (30+ per cent) were headed toward the light and 29 (59+ per cent) stopped indifferently at right angles to it. It is quite probable that among the external factors that influence a worm to come to a halt, light plays an exceedingly insignificant rôle, as compared with the stimulus of contact or some stimulus, probably chemical, given out by other worms in close proximity.

One curious instance was observed, however, in which light was apparently of more importance than contact or other stimuli in determining the place of coming to rest. A large crystallizing dish half full of water was left over night with a few planarians in

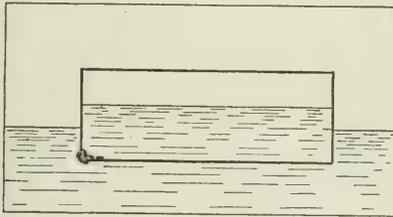


Fig. 9

it. Floating on the surface of the water in this dish was a small Petri dish, in which a few more planarians were isolated. In the morning the worms in both vessels were found grouped at the same region on the outside and inside of the smaller dish, as shown in Fig. 9.

This curious distribution on both surfaces of the Petri dish could not be due to chemical stimulus exerted by one group of worms on the other, and there seems to be no particular reason why a thigmotactic reaction should have caused them to assemble in such a way. The locality chanced to be one, however, where the intensity of the light was considerably reduced; this seems to offer a reasonable explanation of the observation.

Bdelloura in coming to rest shows an entirely different behavior. When left over night free to wander in an aquarium half of which

had been previously covered with black cloth to exclude most of the light, this species was found in the morning in the light area, a behavior exactly the reverse of that shown by fresh-water planarians. Another peculiarity of this species is that individuals in coming to rest arrange themselves in compact rosettes with the anterior end of the body pointed toward the circumference of the rosette, while the sucker-like posterior end remains attached near the center of the group. They are so delicately responsive to mechanical stimuli that any slight disturbance of one member of such a rosette is sufficient to throw the whole group into activity. The advantage to the individual worm of such a habit of arrangement in coming to rest, is evident.

Finally, *Bdelloura* was repeatedly seen on taking the resting position to point directly toward the light with the anterior end of the body raised and the posterior end flattened out into a sucker-like expansion.

Summary. Fresh-water planarians (*Dendrocœlum*, *Planaria* and *Phagocata*) are negatively phototactic while *Bdelloura* is positively phototactic.

Negative planarians deviate most from the direction in which they are started if pointed toward the light and least if pointed away from the light, an intermediate deviation occurring when they are pointed at right angles to the light.

The rate of locomotion is greater when worms are headed toward the light than when they are headed away from it.

During successive trials the rate of locomotion decreases.

Negative planarians frequently take an apparently positive course because the impulse to move in any direction is greater than the phototactic impulse.

The normal negative phototaxis of a worm may change temporarily to positive by reason of some physiological state which is not obviously referable to external stimuli.

The greater the intensity of the light the less worms wander in their course. When they are headed away from the source of light, there is less error in the precision of their orientation than when they are started toward it.

Planarians frequently travel away from the source of light diagonally instead of directly.

Bdelloura continues activity in the light for a much shorter time than *Phagocata*.

When subjected to successive trials the period of a planarian's activity decreases.

Change in the intensity of light is less important than the effects of fatigue in determining the time required for a worm to leave a unit circle. When fatigued, worms often become indifferent to light, coming to rest less frequently in an oriented position with reference to the light than in an unoriented one.

Fresh-water planarians come to rest as far away from the source of light as possible and, if the directive stimulus does not prevent, in the region of least illumination.

Bdelloura candida, on the contrary, comes to rest in regions of greater rather than of less illumination; usually worms of this species arrange themselves in compact rosettes with the anterior ends pointed outward.

B In Changing Directive Light

The light acting upon planarians in their natural habitat must necessarily be a variable factor of great complexity, since its intensity changes constantly throughout the day, while the position of the sun relative to various surfaces which reflect light is also continually shifting.

The fact that planarians, to a great extent, keep out of the light, does not diminish the force of this statement, for whatever the part played by light in their behavior, it must always be an exceedingly varied and complex one.

Changes in the Intensity. When a worm is gliding away from a source of light it shows a more marked response to change of intensity when the change is made *suddenly* than when it is made gradually. In fact, it is possible by exercising patience and care to change the intensity of directive light to a considerable degree so gradually as to produce no corresponding response on the part of the worm, whereas a comparatively slight change, if abruptly effected, immediately results in the animal's performing some one or more of the acts in its repertory of behavior, such as halting, wigwagging, etc.

In all the experiments made upon the effects of change of intensity in directive light, more responses were found to occur when the intensity was decreased than when it was increased. This is in agreement with the experiments already described relating to the critical region between two intensities, in which it was found that worms show a greater number of responses when going from a higher into a lower intensity than vice versa.

Bdelloura is particularly sensitive to changes in intensity. It is necessary to throw a shadow on a moving worm only momentarily to cause it to perform vigorous wigwag movements or to change the direction of its course.

Whitman ('99), writing of Clepsine, suggests that the extreme agitation of this animal when a shadow is thrown upon it may be the result of natural selection, since any sudden shadow cast upon it in its natural environment may be caused by a turtle swimming overhead, to which the leech, if it is quick enough, may become attached. It may be that Bdelloura, which is also an ecto-parasite, has developed this extreme responsiveness to sudden decrease of intensity in a similar way.

Changes in Direction. The precision with which all the planarians in a dish may be made to pass back and forth by shifting a directive light from one side to another is a striking phenomenon, which is sure to impress anyone who sees it. By careful manipulation of the light, it is possible even to make an individual planarian follow a predetermined path in the most undeviating manner. For example, when two lights, placed near the ends of an aquarium, are alternately turned on and off, the worm will zigzag across the field, at right angles to the direction of the lights, while under a moving light it may be made to turn around and around, almost as if its posterior end were a pivot, to trace figure 8's and curves of various patterns, or to turn abruptly at right angles an imaginary corner.

Unlike the changes in intensity previously described the degree of abruptness in any change in the direction of the light made no apparent difference in the quality of the reaction, since any change in direction, however gradual, met with an immediate response on the part of the worm. Indeed it was necessary to abandon an

attempt to illuminate one side of the worm alone because the animal invariably turned faster than it was possible to regulate the light.

The quickness with which this delicate response to any change in the direction of the light occurred was found to increase upon successive trials. A square aquarium was arranged so that it could be illuminated instantly at either end, in a room otherwise dark. With one light on, a planarian was allowed to move until it had assumed the characteristic negative direction, whereupon the source of illumination was instantly changed 180° by turning this light off and the one at the other end of the aquarium on. The time required for the worm to become headed about was noted and then a reversal of lights repeated and the interval necessary for re-adjustment again recorded. In a typical experiment of this kind the number of seconds required by the worm, *Planaria maculata*, to accomplish re-orientation were for 16 successive orientations as follows: 260, 70, 100, 60, 65, 110, 60, 85, 70, 105, 80, 60, 50, 40, 45, 35. The sum of the first eight is 810 sec., that of the last eight, only 485 sec.

Summary. Planarians show a greater response to sudden change of intensity than to gradual change. This response is more pronounced when the intensity is lowered than when it is raised.

Bdelloura is particularly affected by sudden changes of intensity.

Planarians respond with great precision to changes in the direction of the light, and as promptly when the change is gradual as when it is abrupt.

The period required for re-orientation to changes in the direction of light, diminishes upon repetition.

C In Combination with Other Responses

It is impossible to subject planarians to the influence of light alone. The best that can be done is to render extraneous factors as uniform as possible. For example, so long as a moving worm is kept upon a horizontal surface there can be no directive geotactic stimulation, because the worm is moving in a plane at right angles

to the force of gravity. The moment the worm begins to glide up the sides of an aquarium, however, the relation of the axes of its body to the center of the earth changes and directive geotaxis results.

No systematic attempt was made to analyze compound stimuli, for such a study would overstep the boundaries set for the present inquiry. Nevertheless certain facts bearing on this point were incidentally noted and these may properly be detailed here.

Geotaxis. In a majority of cases, *Planaria gonocephala* seems, after several hours of exposure to the dark, to be positively geotactic, and after several hours of exposure to light, negatively geotactic, as shown in the following series of observations.

A cylindrical aquarium jar 20 cm. in diameter and 40 cm. high was placed before a moderately lighted window and stocked with a freshly obtained supply of about 300 worms. No stones, sand, or water-weeds, which would afford places of concealment, were introduced. At intervals during the next 10 days the distribution of the worms was recorded and these records are brought together in Table XVIII.

TABLE XVIII

The distribution of about 300 planarians (Planaria gonocephala) in an aquarium, as observed forenoons and afternoons during 10 days. The figures express percentages

PLACE IN THE AQUARIUM	TOP		SIDES		BOTTOM	
	a. m.	p. m.	a. m.	p. m.	a. m.	p. m.
Time of day						
April 26.....		51		11		38
April 27.....	61		13		26	
April 28.....	74	3	11	15	15	82
May 1.....	72	29	6	7	22	64
May 2.....	63	39	12	20	25	41
May 3.....	43		16		41	
May 4.....	50		16		34	
May 5.....		31		13		56
Average.....	60.5	30.6	12.3	13.2	27.2	56.2

The forenoon census was taken about 8 o'clock, when the worms were re-arranging themselves after the darkness of the night, while the afternoon records were made about 4 o'clock, when the worms

had been all day in the light. The average at the bottom of the table indicates, first, that an approximately equal percentage of worms was found on the sides of the aquarium at both times of day, which may therefore be left out of the reckoning, and, secondly, the occurrence of a significant migration during the interval between 8 a. m. and 4 p. m., demonstrated by the distribution of the worms at the top and bottom of the jar respectively. According to the data obtained, at least 30 per cent of the worms in the top group must have become positively geotactic and gone to the bottom during the day.

A later set of experiments in which an aquarium was kept swathed in black cloth during the day showed less migration. The conclusion naturally follows that geotaxis is more likely to occur in the presence of light than in its absence. Whether there is a regular diurnal vertical migration among planarians in nature, as Birge ('97) and Schouteden ('02) found to be true for freshwater entomostraca, and various authors⁴ for different forms in marine plankton, remains unknown. It is probable, however, that planarians ordinarily remain quiescent on the under sides of stones or in other shaded places for considerable intervals of time, coming under the influence of light only when started into activity through some other stimulus.

A worm placed in an aquarium with square sides and left free to travel undisturbed on the bottom or the sides occupies the sides more frequently than the bottom.

In a trial to test this point, an aquarium was used, the bottom area of which measured approximately five times that of the sides. The course pursued in this aquarium by one worm (*P. gonocephala*) in directive light and covering 1340 cm., was plotted and the percentage of distance traveled on the sides was found to be practically equal to that traveled on the bottom, notwithstanding the fact that the animal was started in the middle of the bottom, where it had five times as much available territory to travel over as on the sides. Other things being equal, therefore, this worm showed itself five times as ready to travel on the sides of the aquarium as on the bottom.

⁴Groom and Loeb ('90), Loeb ('93a), and Parker ('02).

The existence of such a decided geotactic tendency should not be forgotten when trying to determine the part light plays in planarian behavior.

Again, it was found that there was less accuracy of orientation to directive light while the planarians were on the sides of the aquarium in a position parallel to the light rays than while they were on the bottom.

Their behavior in the former case was the resultant of at least two known stimuli, gravity and light, whereas gravity was practically eliminated when they glided on the floor of the aquarium. In the experiment cited under the preceding paragraph 92 per cent of the distance traversed by the worm on the bottom of the aquarium was in a direction in general away from the light, as contrasted with only 79 per cent when it was traveling on the sides of the aquarium. This difference of 13 per cent may represent roughly the necessary correction for geotaxis, in order to ascertain the influence of light alone.

Thigmotaxis. Contact with the substratum is an almost constant condition of planarian activity. Occasionally worms may be seen dangling free at the end of a mucus-thread, as commonly occurs among many fresh-water snails; sometimes they may fall helplessly from the surface-film to the bottom, but definite contact with something firm is the rule during their ordinary locomotion.

A change in the degree of this contact, and consequently a production of thigmotactic stimulation, may come about in two ways: the surface on which the animal glides may present irregularities, such as increased roughness or a different degree of solidity, or the worm itself may vary in the extent of body-surface which it brings into contact with the substratum. This latter method of causing thigmotactic stimulation applies especially to *Bdelloura*, which has the habit of frequently alternating a leech-like looping movement with ordinary gliding, thus changing its contact relations and probably producing a thigmotactic stimulus in consequence.

As already mentioned, *Bdelloura*, when subjected to sudden dark, usually detaches itself from its support and wriggles vio-

lently in the water. It is uncertain how far this behavior is attributable to light alone or to some combination of light and thigmotaxis.

This phenomenon of compound stimulation occurs in a less pronounced way whenever a change of light intensity results in the "wigwagging" response common to planarians. The same uncertainty prevails as to how far the subsequent behavior of the worm may be due to the direct stimulation of light and how far to thigmotactic stimulation primarily and to light stimulation secondarily. It is evident, then, that under any circumstances there is such a close interrelation of stimuli that an accurate analysis of the consequent behavior is difficult.

Further evidence of the close relation between different kinds of stimuli is afforded by the fact that planarians are more responsive to the mechanical stimulus of a slight jar when the entire ventral surface of the body is in contact with the substratum than when the anterior end is lifted up and waving about. Apparently the greater the degree of contact the greater is the effect of a jarring mechanical stimulus.

This point was demonstrated by means of a small aquarium mounted on a turntable, such as is used in "ringing" microscopic slides, in such a way that it could be rotated with great ease and delicacy. A light from one direction only was projected upon the single planarian placed in the aquarium. Any attempt to change the angle of light by rotating the aquarium ever so slightly resulted instantaneously in a momentary halt on the part of the worm, provided it happened to be gliding with its ventral surface entirely in contact with the floor of the dish. If, however, the rotation was made when the anterior end of the worm was lifted, the halt did not so readily occur. This response was of such delicacy that with a little practice it was possible to halt the anterior end of a worm without disturbing the continuous progress of the posterior end! That this halting was due to thigmotaxis rather than to any rheotaxis induced by the movement of the animal against the relatively stationary water particles, is shown by the fact that the reaction was more pronounced when the anterior end of the body was held flat than when it was raised and so brought more under the possible influence of a water current.

Finally, it may be recalled that in a preceding section data were given (Table X, p. 68) to show that there is more response to light while worms are upside down on the surface-film than when they are in contact with the bottom of the aquarium, a difference probably referable in large measure to the different thigmotactic relations in the two cases.

Goniotaxis. Goniotaxis is a term introduced by Pearl ('03, p. 561) to define a particular kind of thigmotactic response in which the "different parts of the body are brought into such positions that they form unusual angles with each other," as when a planarian occupies the angle formed between a side and the bottom of an aquarium.

There is no doubt that the peculiar movements resulting from the goniotactic stimulus directly modify the phototaxis of the worm. Once in the angle of an aquarium a planarian becomes increasingly indifferent to light. In one series of records, showing how a considerable number of planarians came to rest, it was found that the majority came to rest in an "angle" and that out of this number 78 per cent failed to orient to the light. The stimulus of the "angle" was greater apparently than the stimulus of light.

Furthermore, it is to be noticed that goniotaxis is always more effective if the worm is in a lowered rather than in a heightened physiological state, for whenever a planarian is freshly introduced into an aquarium and is in an aroused condition on account of the mechanical stimulation necessarily given it in transference, it will pass over angles and crevices with total indifference, all the while responding plainly to light. As soon as it has become fatigued, however, if its path chances to cross an angle or crevice it exhibits goniotaxis at once by slowing down and remaining in the new situation, as if caught in a trap, with complete disregard of the continued action of directive light.

Chemotaxis. Pearl has made an extensive study of this phase of planarian behavior and suggests that the well-known planarian habit of collecting in groups may be explained on the supposition that a resting planarian is surrounded by a halo of chemical ema-

nations which serve as a direct stimulus to other planarians, attracting them and causing them to come to rest in groups.

In this connection it is worth mentioning that several times when *Dendrocœlum lacteum* was put in an aquarium with other species of planarians, the individuals of this species would later be found gathered into a separate group by themselves. This manner of isolation was also repeatedly noticed in examining on the under sides of stones taken from the pond at Falmouth, Mass. A similar segregation of species in the case of *P. alpina* and *P. gonocephala*, was noted by Collin ('91). He says ('91, p. 180) "Iijima fand diese beiden Arten zusammenlebend, während sie im Harz stets getrennt vorkamen; auch in der Gefangenschaft schien die *P. alpina* die grössere *P. gonocephala* in demselben Behälter zu meiden und ihr ängstlich auszuweichen." It would be difficult to explain how these planarians avoid each other so as to fraternize in this fashion, except on the basis of some delicate chemotactic response which caused them to halt when they entered the chemical halo of their own kind, but not to do so in the different chemical halos of other species. As in the case of goniotaxis, the manifestations of phototaxis may be entirely superseded by the effect of feeding (Chemotaxis). When once a hungry planarian, driven by directive light into the neighborhood of a crushed snail, becomes subjected to the chemical stimulus arising from the fluids of that object as they are disseminated through the water, it seems to become suddenly indifferent to the light, owing to the greater influence of the chemical stimuli.

The same inhibition of the influence of light by a chemotropic response to food has been observed by Parker ('03) on the mourning-cloak butterfly, *Vanessa antiopa* L. He says ('03, p. 457) "when a butterfly alights on a bough, it orients in the sunlight with the usual precision. Should the sap be running from a near stem, the insect is very soon attracted to the spot, begins feeding, and moves about from that time on with no reference to the direction of the sun's rays. Thus, when feeding or near food the butterflies do not respond phototropically." Furthermore Darwin ('81, p. 23) observed that earthworms are less disturbed by light while feeding or during copulation than at other times.

The foregoing examples illustrate only a few of the many modifications of light responses due to the interference of some other stimulus.

Summary. In judging the effect of any stimulus upon an animal it is necessary to have constantly in mind the accelerating or inhibiting effects of other stimuli which may be influencing the organism at the same time. In the case of planarians some of the responses known to be intimately connected with phototaxis are geotaxis, thigmotaxis, goniotaxis and chemotaxis.

Planaria gonocephala shows itself to a certain extent negatively geotactic after several hours of dark and positively geotactic after a similar interval of light.

When given horizontal and vertical surfaces of equal extent, worms travel more on the vertical surfaces.

Their accuracy in orienting themselves to light while subjected to geotactic stimulus on a vertical surface is less than when they are traveling on a horizontal surface, where the directive geotactic stimulus is eliminated.

Thigmotactic stimulus may result either from an environmental change in the substratum, or a change in contact caused by the worm itself whereby its relation with the substratum is varied.

There is a close interdependence of the various stimuli which may be acting on an animal at the same time.

Behavior may be the direct consequence of light or the indirect result of light combined with the direct effect of a thigmotactic stimulus indirectly brought about by some change in the intensity of the light.

The greater the degree of contact with the substratum the more responsive a planarian becomes to the mechanical stimulus of jarring, but the less to the stimulus of light, as shown by comparing the behavior of worms on the surface film with their behavior on the aquarium floor.

Goniotaxis has an inhibitive effect on phototaxis; this effect becomes more apparent as the worm reaches a condition of fatigue, phototaxis meanwhile becoming less apparent.

Dendrocœlum lacteum exhibits a remarkably delicate response (Chemotaxis?) in frequently coming to rest in the neighborhood of its own kind.

Hungry planarians in the presence of food have their phototaxis entirely obscured.

3 KINDS OF BEHAVIOR

In the two preceding sections, treating of Photokinesis and Phototaxis, respectively, animal behavior, as illustrated by the effect of light upon planarians, has been taken up from the point of view of the stimulus. In the two following sections, on the other hand, the reactions of planarians will be dealt with from the standpoint of the animal rather than from that of the stimulus.

To this end a classification of the behavior of planarians in light is here presented based upon (A) generic and specific differences, and (B) individual differences.

That there are morphological differences which fall naturally within the lines of this classification has long been recognized, indeed, the criteria used in classification by systematists are based almost exclusively upon such differences, while relatively little importance has been attached to differences in the behavior of animals.

As already mentioned in the historical review, Loeb ('94), in dealing with the differences of behavior which characterize the two genera, *Planaria* and *Thysanozoön*, pointed out that decided physiological variation may appear in forms closely related morphologically. The same fact had been previously emphasized for the case of the pulmonates by Willem ('91). Obviously such physiological variations do not furnish reliable criteria for the systematist, since they are so largely dependent upon environmental causes, and furthermore the work of the systematist is usually done upon dead animals. Nevertheless some interesting relations between behavior and systematic position await the student who approaches the study of animal behavior from this direction.

Strictly speaking, all behavior is individual behavior. In this sense it is manifestly incorrect to speak of the behavior of a genus or of a species *per se*.

The behavior of individuals may, nevertheless, be classified into responses which are characteristic of all the members of a genus,

or again into responses which are characteristic of only one species of a genus and not necessarily of other species of the same genus, and, finally, into those peculiar to the individual as such, which may not in all particulars be shared by other representatives of the species to which the individual in question belongs. It is in this sense of the terms generic, specific and individual, that behavior will be taken up in the present section.

A Generic and Specific Behavior

In the present inquiry a basis for generic comparisons is afforded by a study of the behavior of individuals of four different genera, namely, *Planaria*, *Dendrocœlum*, *Phagocata* and *Bdelloura*, while some idea of specific differences is made possible by comparing the behavior of individuals of the two species *Planaria maculata* and *Planaria gonocephala*. In the cases of *Dendrocœlum*, *Phagocata* and *Bdelloura* it is obvious that the conclusions drawn are based in each instance upon the behavior of representatives of a single species under each genus. The question may be properly raised as to how far such conclusions indicate generic behavior and how far specific behavior. Conceding that from the data obtained exact deductions may not be drawn, the fact still remains that the three species, *Dendrocœlum lacteum*, *Phagocata gracilis*, and *Bdelloura candida*, are separated from each other by generic gaps, such that the differences exhibited by these species may be regarded as generic in degree. The point unestablished, then, is whether other species of the genera in question if examined might not show that the behavior, which in these single representative species seems generic in nature, is not characteristic of other species of the same genus as well.

It will be convenient to present the data of both generic and specific behavior at the same time.

Percentage of Negativeness. The manner of obtaining this criterion of behavior has been explained in the section on Phototaxis (p. 72). It will be remembered, too, that in Table XII a comparison was made between positive and negative worms, showing the degree of their orientation to directive light. The

data there used are rearranged for the present purpose in Table XIX.

TABLE XIX

Percentage of generic and specific negativeness in worms started at right angles to incident light, as determined at the circumference of a circle 10 cm. in diam. by the average amount of their deviation from the directions in which they were started

	GENERIC DIFFERENCES				SPECIFIC DIFFERENCES	
	Dendrocœlum	Phagocata	Planaria	Bdelloura	Planaria maculata	Planaria gonocephala
Number of observations.....	78	80	158	10	78	80
Total number of degrees positive...	155	238	165	397	5	160
Total number of degrees negative...	2112	1964	4070	50	2102	1968
Percentage of negativeness.....	93.1	89.6	96.1	11	99.9	84.6

Comparing the figures given in this table, a greater range of difference is seen to obtain between the two species of *Planaria* (*P. maculata* and *P. gonocephala*) than between the genus *Planaria* and either of the other negative genera, namely, *Dendrocœlum* and *Phagocata*. Although not indicated in this table, similar results appear when the number of times the worms went in a negative direction is used as a basis of comparison, instead of the total number of degrees of negative deviation.

Character of the Course in Directive Light. When worms were placed on the middle of a rectangular aquarium floor and subjected to a directive light their movements showed both generic and specific differences. By experimenting with one worm at a time it was possible to plot on a sheet of paper with sufficient accuracy for general comparison the entire course of the worm during a considerable period. This was done many times and typical records of such observations are given in Figs. 10-14. In such instances the worm was exposed to a light of approximately 147 c.m., placed so as to correspond to the right side of the figures. The central rectangular area bounded by the broken lines indicates the limits of the floor of the aquarium, while the smaller exterior adjacent areas represent its vertical sides so rotated as to

bring them into the plane of the floor. The course taken by a planarian is indicated by the tortuous line. The full line shows the course taken on the solid surface of the aquarium; the dot-

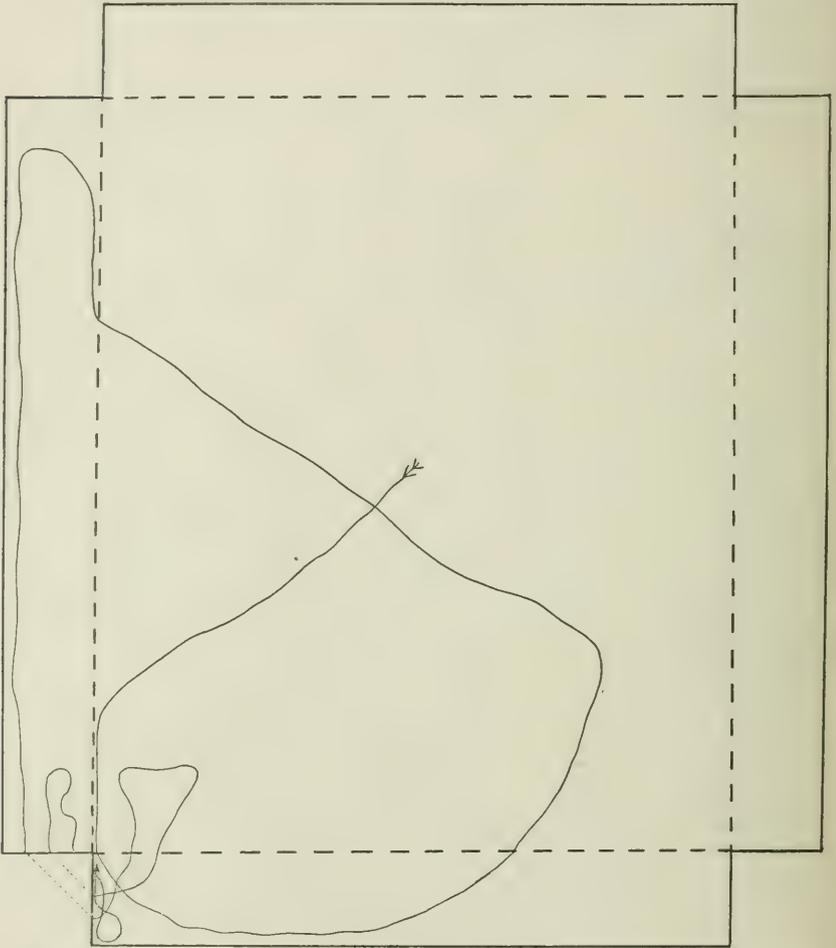


Fig. 10 *Dendrocœlum lacteum*. The shortness of the path shows comparatively little persistence in locomotion, and the direction, considerable indifference to the source of light.

and-dash lines, the course of the worm on the surface film. The dotted line indicates a hiatus in the path, made necessary by the attempt to represent on a flat surface a continuous line which traverses vertical as well as horizontal surfaces. A succession of

abrupt kinks in the line signifies that at that point the worm executed decided wigwag movements with its anterior end. The figures are reduced in size from the original records.

In Fig. 10 is given a specimen record of a *Dendrocœlum* which

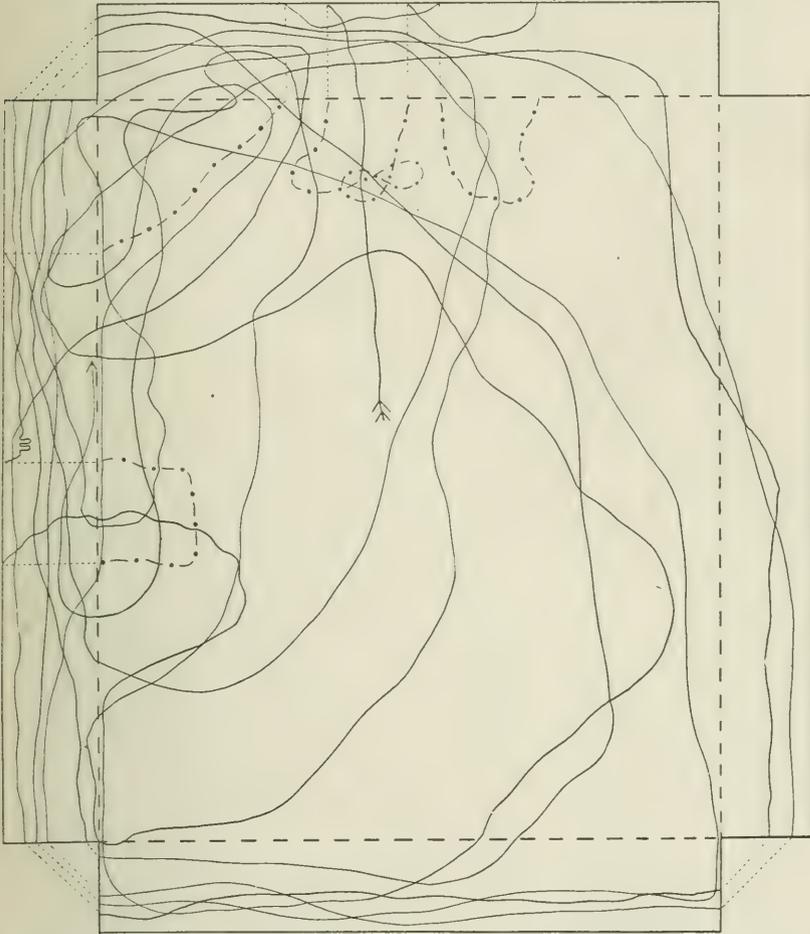


Fig. 11 *Phagocata gracilis*. This path shows great activity on the part of the worm, and, although it is mostly laid down away from the source of the light, it shows that the worm experienced no great difficulty in moving toward the light.

came to a standstill after 18 minutes of locomotion. The first movement of this worm was diagonally away from the light, but it soon came back toward the light traversing almost the entire

width of the aquarium and in doing so showed considerable indifference to the directive influence of the light. Its susceptibility to goniotactic stimulus is plainly shown by its behavior upon reach-

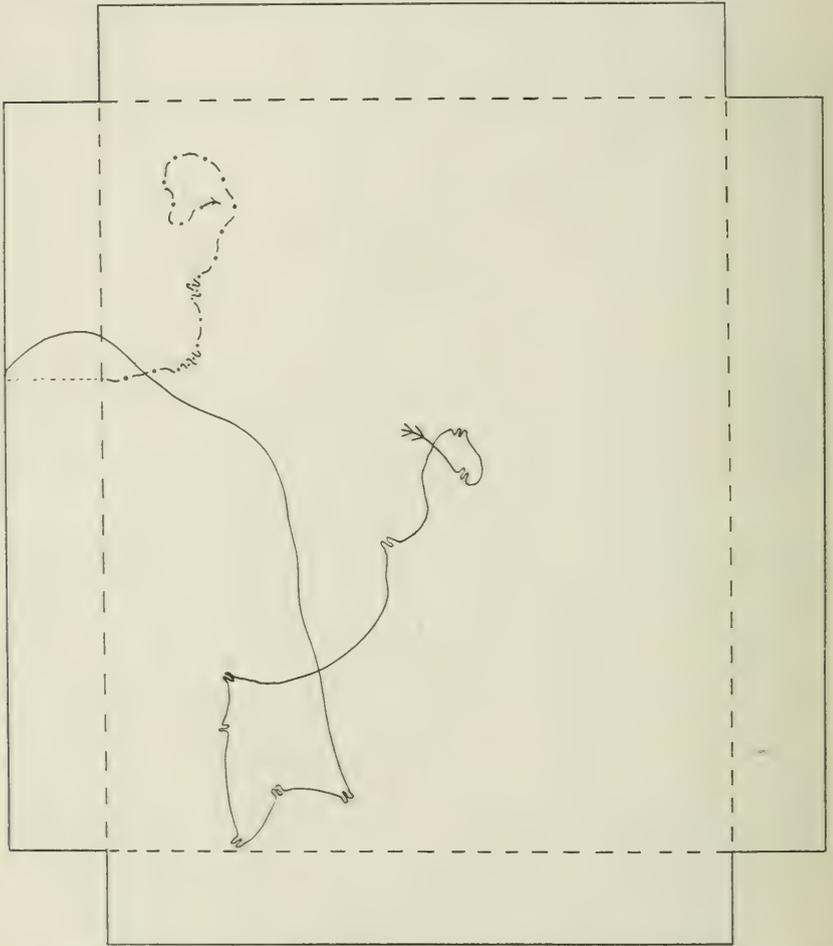


Fig. 12 *Bdelloura candida*. This path was traversed with much "wigwagging;" there was indifference to the source of light and locomotion was not of long duration.

ing the angle formed at the junction of the sides and floor of the aquarium, as well as by its manner of finally coming to rest.

A typical *Phagocata* (Fig. 11), on the other hand, exhibited

almost no goniotaxis, although the worm repeatedly crossed the line of the angle. The response to the directive influence of the light, too, was in this case even less than that of the

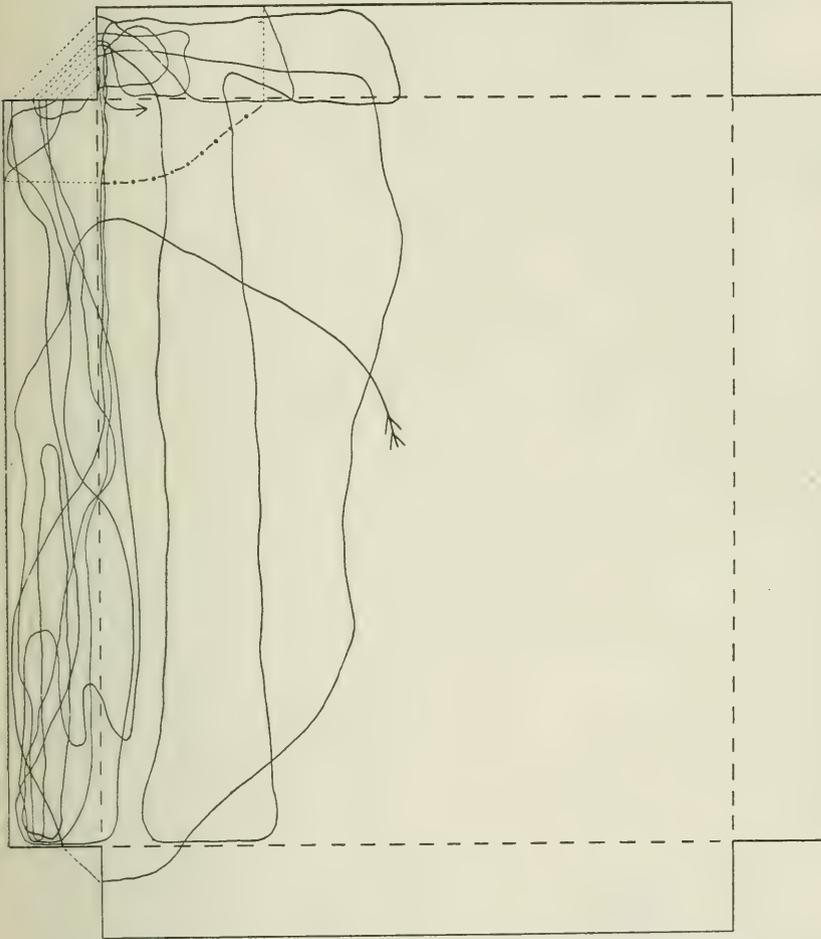


Fig. 13 *Planaria maculata*. Considerable activity was shown over this course and a decided inability to approach the source of the light beyond about the middle of the aquarium.

Dendrocœlum just described, as is evident from the general wandering character of the course. Although the Phagocata in question frequented both sides of the aquarium—that which was toward

the light, as well as the opposite side—its wanderings were in the main on the side away from the light. An hour's activity is chronicled in the record, at the close of which the worm was apparently as energetic as ever.

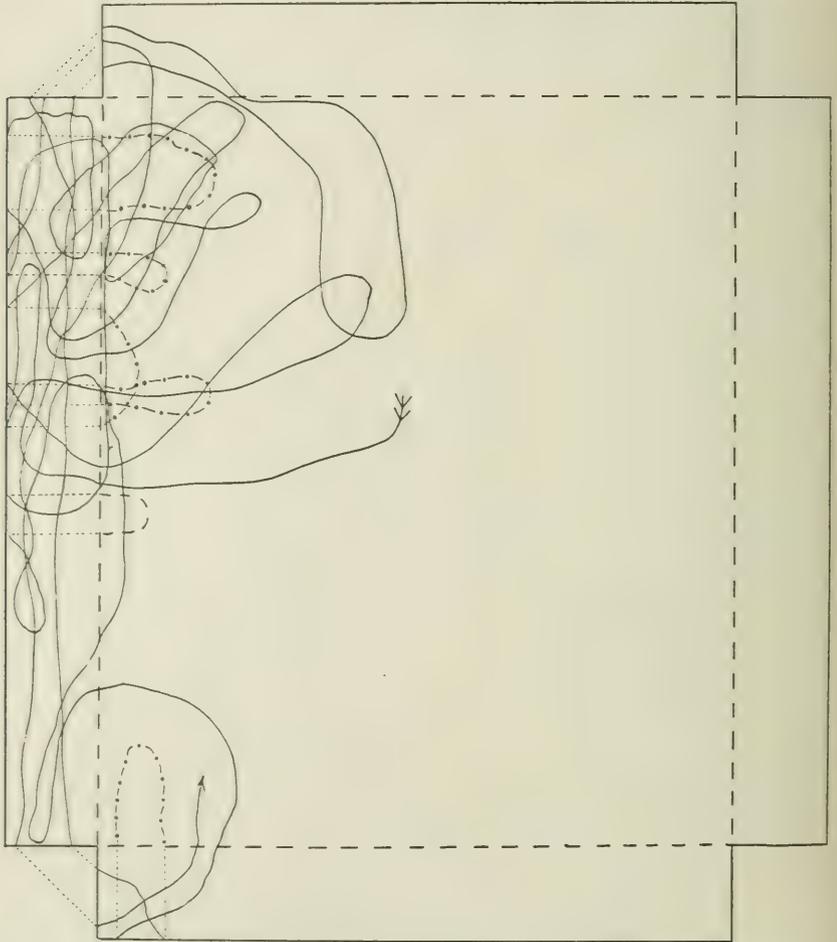


Fig. 14 *Planaria gonocephala*. The path is of the same generic type as with *Planaria maculata* (Fig. 13), and is easily distinguishable from those of *Dendrocoelum*, *Phagocata* and *Bdelloura*.

Fig. 12 gives a characteristic record of the way in which *Bdelloura* behaves. The first movement of this specimen was more

toward than away from the source of the light, but very soon wig-wagging motions set in, and after every exercise of these movements, which were apparently in the nature of explorations, a change in the direction of the course was effected. As might be expected, such abrupt changes in direction were more difficult of execution when the worm was on the surface-film.

Characteristic movements of individuals of the genus *Planaria* are shown in Figs. 13 and 14. From these two typical records it would be difficult to select any diagnostic points which would distinguish the behavior of *P. gonocephala* from that of *P. maculata*. There is no doubt, however, that taken together the behavior of representatives of these two species presents a distinct (generic) difference from that of the representatives of the other genera studied. The most striking feature of the *Planaria* records (Figs. 13 and 14) is the high degree of response exhibited by members of this genus to the directive action of light. Although many attempts were made by the individual worms to penetrate the half of the aquarium nearer the light, yet they seemed as unable to keep to that direction as they would have been had a solid barrier been interposed between them and the light. This characteristic responsiveness to directive light helps to explain why (as shown in Fig. 8, B, p. 84) *P. gonocephala* was unable to come to rest in the area of lessened illumination as it would naturally have been expected to do.

From the cases cited in this section, at least, it may be affirmed that the generic differences are so pronounced that one could take a miscellaneous, unidentified assortment of such records and correctly assign the great majority of them to the proper genera.

Duration of Movement. When worms of different genera are subjected to the same light intensity there is considerable variation in the time required to bring them to a standstill. *Bdelloura* is usually the first to stop, followed in order by *Dendrocœlum*, *Planaria* and *Phagocata*. Of the two species of *Planaria*, *P. gonocephala*, although averaging somewhat smaller in size, usually keeps in motion for a longer time than *P. maculata*. The individual records of the duration of movement given in Figs. 10-14 may be taken as a typical set of records. They were as follows:

- Fig. 10. Dendrocœlum, 18 min.
 Fig. 11. Phagocata, 60 min. (still moving).
 Fig. 12. Bdelloura, 15 min.
 Fig. 13. Planaria maculata, 47 min.
 Fig. 14. Planaria gonocephala, 60 min. (still moving).

Woodworth ('97) in contrasting the activity of *Planaria maculata*, *P. gonocephala* and *P. dorotocephala* states that individuals of the latter species remain in motion longer than individuals of the other two—an observation confirmed by Pearl ('03).

Degree of Wandering. If a worm is started at the center of a circle parallel to the direction of the light and pointing away from its source, then the more devious its course the more it may be said to wander. Both generic and specific differences were obtained bearing upon this phase of behavior. Selected instances of such differences are given in Table XX, expressed in average degrees of deviation upon emergence from a circle 10 cm. in diameter.

TABLE XX

The average generic and specific differences between individuals of four genera and two species of planarians expressed in degrees of deviation upon leaving a circle 10 cm. in diam. In every instance the worm was started away from the source of the light

	GENERIC DIFFERENCES				SPECIFIC DIFFERENCES	
	Dendro- cœlum	Phago- cata	Planaria	Bdelloura	Planaria maculata	Planaria gono- cephala
Average degree of deviation.....	9.4	30.0	24.6	132.0	21.6	27.7
Number of observations.....	56	46	92	10	46	46

The remarkably large deviation shown by *Bdelloura* is due to the fact that it is a positive worm. When pointed toward the light its deviation was only 39.3° , a number which would perhaps be more justly comparable with the other records in this table. But even so, it will be seen that *Bdelloura*, of all the forms observed, is the least oriented by directive light. Specific differences in the degree of wandering are in general less marked than the generic differences, according to the records in Table XX.

Rate of Locomotion. As regards rate of locomotion the records of specific differences exhibit a wide range, although not as great as that of the generic differences existing between Dendrocœlum and Phagocata.

TABLE XXI

The average rate of locomotion expressed in millimeters per second

	GENERIC DIFFERENCES			SPECIFIC DIFFERENCES	
	Dendro- cœlum	Phagocata	Planaria	Planaria maculata	Planaria gonocephala
Rate in mm. per sec.....	0.850	1.395	1.272	1.470	1.075
Number of observations.....	40	40	80	40	40

It is interesting to note in this connection that Parker and Burnett ('00, p. 385) give the average rate for *Planaria gonocephala* as 1.08 mm. per sec., while Pearl ('03, p. 546) records for *P. maculata* 1.48 mm. per sec. in the case of a worm 11 mm. in length and 1.23 mm. per sec. for one 6 mm. in length. An average of these two records, that is, 1.355 mm. per sec., might perhaps be comparable with the average (1.272) given in Table XXI, since an equal number of large and small worms from each genus formed the basis on which these averages were calculated.

Time Required to Leave a Unit Circle. If planarians invariably took a straight radial path in going from the center to the circumference of a circle, the time required to leave a unit circle might be used in computing the rate of locomotion. Such a path, however, is not taken. Nevertheless, records of this kind, although untrustworthy for purposes of accurate calculation, furnish a reliable criterion for the comparison of generic and specific behavior. The differences in behavior in the representatives of three genera and two species are given in Table XXII. *Bdelloura* failed so frequently to emerge from the circle that it is excluded from the list. Each genus and species was tried an equal number of times in light of three different intensities.

As might be expected, Table XXII presents a close parallel to Table XXI. The only difference in the relative values of behavior, expressed by the averages of rate and time in these two tables, appears in the case of *P. maculata*. This species, though first in the scale as regards actual rate of locomotion, is second as regards the time required to leave a unit circle, a condition indicating relatively more wandering on its part than was shown by any of the other worms.

TABLE XXII

The average time in seconds taken in passing from the center to the circumference of a circle 10 cm in. diameter in directive light

	GENERIC DIFFERENCES			SPECIFIC DIFFERENCES	
	Dendro- cælum	Phagocata	Planaria	Planaria maculata	Planaria gonocephala
Average number of seconds...	62	40	54	47	60
Number of observations.....	120	120	240	120	120

The Effects of Fatigue. To obtain an idea of generic and specific differences in the effects of fatigue, two sets of averages have been combined. First the average rate of ten worms of each kind, when subjected to four successive trials, was first ascertained and the difference between the first and the fourth rate was then expressed as a percentage of increase or decrease in rate, as the case might be. Secondly, the time required to leave a unit circle in twelve successive trials was next recorded and the average percentage of increase or decrease in time of the last four trials, as compared with the first four trials, was computed. By combining these two kinds of percentages the relative differences in the effects of fatigue upon the individuals of the various genera and species, are clearly brought out.

If the results of this computation be compared with the conclusions reached in another way under the preceding paragraphs on "duration of movement," it will be seen that there is a complete agreement in the relative behavior of the different genera and species. That is, the worms most subject to fatigue are the

first to come to rest and those least affected by fatigue continue longest in motion

TABLE XXIII

The average generic and specific difference in fatigue

	GENERIC DIFFERENCES			SPECIFIC DIFFERENCES	
	Dendro-cœlum	Phagocata	Planaria	Planaria maculata	Planaria gonocephala
Percentage of change in rate of the fourth trial as compared with the first.....	-11	+9.5	-9	-13	-5
Percentage of change in time required to leave a unit circle of the last four as compared with the first four of twelve consecutive trials.....	-33	-10	-15.8	-23	-8.7
Average percentage of fatigue	-22	-0.25	-12.4	-18	-6.8
Total number of comparisons	30	20	40	20	20

Responses to Changes in Intensity. When worms in non-directive light pass from a given intensity to one $2\frac{1}{2}$ times as great, decided differences appear in their behavior, the generic differences being plainly of wider range than the specific.

TABLE XXIV

Average differences in response at the critical line separating two areas of non-directive light of which one (82.50 c.m.) is approximately $2\frac{1}{2}$ times as great as the other (33.16 c.m.)

	GENERIC DIFFERENCES			SPECIFIC DIFFERENCES	
	Dendro-cœlum	Phagocata	Planaria	Planaria maculata	Planaria gonocephala
Number of observations.....	45	202	206	50	156
Percentage of responses.....	17	37	52.5	55	50
Percentage of failures to respond.....	83	63	47.5	45	50

In this table Dendrocœlum is shown to respond in only 17 per cent of its passages across the critical line separating the two different intensities of light, while Phagocata responds in 37 per cent

and *Planaria* in 52.5 per cent of the cases. These are differences in degree of response that are great enough to be of unquestionable significance. When, however, *Planaria maculata* and *Planaria gonocephala* are compared in the same way, only a slight difference in the degree of response, namely, that between 55 per cent and 50 per cent, is to be observed.

Manner of Coming to Rest. Although little attention was paid to this point during the series of observations taken up for the present study of planarian behavior, still a few indications of generic difference in the manner of coming to rest appear from the foregoing data. *Bdelloura*, it will be remembered, has a distinctive manner of coming to rest in close rosettes within an area of increased illumination, while *Dendrocœlum* shows a considerable tendency to collect in exclusive companies during periods of inactivity. With regard to the two species of *Planaria* studied, nothing at all definite was observed in this connection which could be called a true specific difference in behavior. Between *Dendrocœlum* and *P. gonocephala*, however, a decided generic difference seems to exist, as several series of records on orientation in directive light show. *Dendrocœlum* according to these records came to rest in an unoriented position in 70 per cent of the cases observed, while *P. gonocephala* failed to take up an oriented resting position in only 59 per cent of the observations. In other words, *P. gonocephala* is more liable to come to rest in a position oriented with reference to the light than *Dendrocœlum*.

Summary. The essential points brought out in the foregoing section are condensed for the sake of brevity and clearness in Table XXV.

In certain instances, namely, in changes in the character of the course (2), the influence of fatigue (7), and the percentage of responses to change in light intensity (8), specific behavior shows a more intimate correlation than generic behavior, otherwise the range between the behavior of *P. gonocephala* and *P. maculata* is greater than the generic differences separating *Planaria* from the other genera under observation.

It might be expected *a priori* that generic differences would exhibit a greater range than specific differences and that similarly,

specific behavior would include more phases of action than individual behavior.

In the present series of records hardly enough representatives of different genera and different species were under consideration to establish any convincing generalization on this point.

TABLE XXV
Comparisons in behavior, generic and specific

CRITERION OF BEHAVIOR	GENERIC DIFFERENCES				SPECIFIC DIFFERENCES	
	Dendrocoelum	Phagocata	Planaria	Bdelloura	Planaria maculata	Planaria gonocephala
(1) Percentage of negativeness	93.1	89.6	92.2	11	99.9	84.6
(2) Character of course in directive light						
Turns toward the light	without much difficulty	with great indifference	with much difficulty	with ease	No	contrast
Shows goniotaxis	plainly	slightly	slightly	none	slightly	slightly
Wigwag movements	few	few	few	many	few	few
(3) Average duration of movement	18 min	60+ min.	?	15 min.	47 min.	60+ min.
(4) Amount of wandering (Av. deviation in degrees)	9.4	30.	24.6	39.3	21.6	27.7
(5) Rate of locomotion (In mm. per sec.)	0.85	1.395	1.270	?	1.470	1.075
(6) Seconds required to leave a 10 cm. circle	62	40	54.	?	47	60
(7) Comparative influence of fatigue, per cent.	22	0.25	12.4	?	18	6.8
(8) Percentage of response to change in light intensity.	17	37	52.5	?	55	50
(9) Manner of coming to rest.	in dark in exclusive groups	in dark	in dark	in light in rosettes	in dark	in dark

B Individual Behavior

The analysis of specific behavior leads to the study of individuals, since it is the average activity of different individuals that makes up the behavior typical of the species. In biological litera-

ture animal behavior, particularly among the lower forms, is ordinarily referred to in its specific or even generic aspect. The distinctive actions of individuals, as such, it seems, have usually been outside of the purpose of the observer.⁵

Individuals, however, even among such comparatively simple forms as planarians, do not always act with machine-like uniformity. Until it is possible to predict with exactness what behavior will result under any given set of conditions, an accurate knowledge of the behavior of any kind of organism must be based upon repeated observations of individuals as such rather than as representatives of species and genera.

Individual variations in behavior constantly appeared throughout the course of the present investigation. It will be sufficient, however, for the purpose of making clear their importance to cite only a few instances of such variations.

It should be noticed that whenever "exceptions to the rule" of behavior occur, as in the case of negative planarians coming to rest in the light or becoming positively phototactic for a time (see the two cases cited on p. 78), they are ordinarily simply abnormal cases of individual behavior standing out against the background of average specific or generic behavior. Exceptional cases of this kind, however, are not so typical of what really constitutes individual behavior as the less aberrant actions making up the majority of the movements which the animal performs.

The main point to be recognized, then, is that the individual presents unknown factors, which, even in the simplest forms of life, where the range of variation is least, have never yet been reduced entirely to chemico-physical terms, a fact which impairs somewhat the conclusions of those writers who would draw a complete parallel between an organism and a machine.

Rate on Successive Days. When the rate of locomotion of certain isolated individuals is averaged from four trials, for example, and the same experiment is repeated on the following day with the same individuals, thereby eliminating the effects of fatigue, under as nearly identical conditions as possible, the two sets of figures

Frandsen ('01), who was impressed by individual differences in the phototaxis of *Limax*, and Smith ('02), who worked with the earthworm, are exceptions to this generalization.

thus obtained show more variation than would be expected if the organisms experimented upon responded in a machine-like way. If not all, at least a part of this variation may, then, be due to differences in individual behavior.

TABLE XXVI

The differences among isolated individuals of different species in the average rate of locomotion, based on 4 trials each on each of two different days, expressed in mm. per sec.

	Dendrocelum lacteum	Phagocata gracilis	Planaria maculata	Planaria gonocephala
First day	1.52	1.22	1.76	0.67
Second day	0.70	0.96	1.11	0.73

The Relative Value of Individual Behavior. In the three following tables individual behavior will be compared with light intensity with respect to (1) rate of locomotion, (2) range of rate and (3) manner of turning.

First, the individual behavior of 10 worms belonging to the species *Planaria gonocephala* under all intensities of non-directive light showed greater range in the rate of locomotion than the average behavior of the same ten worms showed under any single intensity of non-directive light.

TABLE XXVII

The relative effect on rate of locomotion of individual behavior and light intensity. The averages are expressed in mm. per sec.

A VARIATION OF INDIVIDUAL BEHAVIOR

Identification number of worm	1	2	3	4	5	6	7	8	9	10
Average rate in all the intensities given in B.	0.79	0.57	0.70	0.64	0.83	0.70	0.72	0.60	0.49	0.62

Range = 0.34 [0.83 (No. 5) — 0.49 (No. 9)]

B VARIATION IN DIFFERENT LIGHT INTENSITIES

Light in candle meters	0	0.94	11	39	78	126	155	217	431
Average rate of the 10 worms given in A	0.57	0.66	0.69	0.75	0.64	0.65	0.69	0.70	0.63

Range = 0.18 [0.75 (39 c.m.) — 0.570 (0 c.m.)]

Secondly, the range between the maximum and minimum rates of ten individuals in all intensities of non-directive light was greater than the average range of rate of the same individuals under different intensities of non-directive light.

TABLE XXVIII

The relative effect of individual behavior and light intensity on the range of rate of locomotion, expressed in mm. per sec.

A VARIATION OF INDIVIDUAL BEHAVIOR

Identification number of worm.....	1	2	3	4	5	6	7	8	9	10
Maximum rate in all intensities given in B.....	2.58	1.67	2.00	1.67	2.17	2.08	2.20	1.78	1.82	1.58
Minimum rate in all intensities given in B.....	0.92	0.67	0.92	0.83	1.03	0.42	0.67	0.28	0.28	0.75
Range of rate	1.66	1.00	1.08	0.84	1.14	1.66	1.53	1.50	1.54	0.83

Range 0 83 = [1.66 (No. 1 or 6) — 0.83 (No. 10)]

B VARIATION IN DIFFERENT LIGHT INTENSITIES

Light in candle meters	0	0.94	11	39	78	126	155	217	431
Maximum rate for all worms given in A	1.58	1.93	1.92	1.77	1.92	1.79	1.87	2.00	1.55
Minimum rate for all worms given in A.....	0.71	1.07	0.74	1.04	0.77	0.62	1.15	1.03	0.79
Range of rate	0.87	0.86	1.18	0.73	1.15	1.17	0.72	0.97	0.76

Range 0.46 = [1.18 (11 c.m.) — 0.72 (155 c.m.)]

Thirdly, with respect to clockwise or contra-clockwise turnings, individual factors were found to be of more importance than differences of intensity of non-directive light in determining the direction of turning.

It should be added that the ten worms concerned in the three preceding tables were as similar in size and external appearance as it was possible to select.

A Cave Planarian. This specimen came from an Indiana cave, where it probably had always lived in darkness up to the time of its capture. When first made the subject of experiment, it could be briefly described as a white worm, about 6 mm. in

length, devoid of any dark pigment except in the two eye spots. Although most nearly resembling *Dendrocœlum lacteum* in color, it showed some differences from this species in the contour of its body and particularly in its behavior. It was thought probable, therefore, that this was a representative of some species peculiar to a dark habitat. The absence of sexual organs made its exact identification impossible. In the present connection it will be referred to simply as "the cave worm." As a unique subject for the study of individual behavior, it proved to be very

TABLE XXIX

The relative effect of individual behavior and light intensity on the direction of turning, expressed in a ratio of contra-clockwise to clockwise movements

A VARIATION OF INDIVIDUAL BEHAVIOR

Identification number of worm.....	1	2	3	4	5	6	7	8	9	10
Ratio of contra-clockwise to clockwise turn-ings in all the intensities given in B	1 to 1.52	1 to 1.40	1 to 0.42	1 to 4.00	1 to 2.08	1 to 4.21	1 to 2.23	1 to 4.02	1 to 0.85	1 to 0.93
Range = 1 to 3.60 [1 to 4.02 (No. 8) — 1 to 0.42 (No. 3)]										

B VARIATION IN DIFFERENT LIGHT INTENSITIES

Light in candle meters.....	0	0.94	11	39	78	126	155	217	431
Average ratio of contra-clock-wise to clockwise turnings of the 10 worms given in A...	1 to 1	1 to 1.10	1 to 1.24	1 to 1.65	1 to 1	1 to 0.93	1 to 1.32	1 to 1.40	1 to 1.58
Range = 1 to 0.72 [1 to 1.65 (39 c.m.) — 1 to 0.93 (126 c.m.)]									

interesting. A comparison of its activities with those of other planarians is given in Table XXX, where it will be seen that this cave worm was considerably more active than any other kind of worm under observation, both with respect to locomotion and to the average time required for it to leave a unit circle. Regarding the degree of negativeness which it presented, no new feature appeared, though its average in this point was rather higher than that of all the other worms studied. However, its degree of wandering quite exceeded anything shown by planarians which had been reared in the light.

If the relationship of an animal could be determined by behavior alone, there need be no hesitancy in saying that this unidentified planarian should not be classified under the species *Dendrocœlum lacteum*, since in all the criteria mentioned in the foregoing table it stands at an opposite extreme to *Dendrocœlum*. In point of fact its behavior more closely resembled that of *Phagocata gracilis*, a species which, according to Dr. A. M. Banta, who kindly furnished the cave planarian for this study, is common in the streams in the vicinity of the cave where the latter was found.

TABLE XXX

The behavior of a cave planarian compared with that of planarians accustomed to light.

CRITERIA OF BEHAVIOR	THE CAVE PLANARIAN		OTHER PLANARIANS			
	Number of trials	Average record	Average record	Maximum	Minimum	Range
Average amount of negativens, expressed in the percentage of deviation upon leaving a circle 10 cm. in diameter when started at right angles to incident light	70	99.6	91.8	99.9	84.6	15.3
Average rate in mm. per sec.....	60	2.00	1.203	1.473	0.853	0.62
Average seconds required to leave a circle, 10 cm. in diam.....	90	27.8	52.2	62.2	39.7	22.5
Average deviation in degrees when pointed away from the light. (Amount of wandering)	46	47°	25°.6	39°.3	9°.4	29°.9

Summary. Average individual behavior constitutes typical specific behavior. Variations in individual behavior make accurate predictions of responses to stimuli under given conditions, impossible. The rate of locomotion of the same individuals varies from day to day even under apparently identical conditions. Individual variations in the rate of locomotion, in the range between maximum and minimum rates, and in the percentage of clockwise turnings, are more variable than the average behavior in these particulars under different light intensities.

An unidentified cave planarian showed greater activity and more inclination to wander than any of the other planarians under observation.

(To be continued)

THE REACTIONS OF PLANARIANS TO LIGHT

BY

HERBERT EUGENE WALTER

WITH FOURTEEN FIGURES

(Concluded)

4 BASIS OF BEHAVIOR

In the sections on Photokinesis and Phototaxis certain conditions of illumination were shown to be variable factors in influencing the movements of planarians. Following this treatment of the subject an attempt was made under "Kinds of Behavior" to classify the effects of light according to the way in which the responses of planarians become manifested in a generic, a specific or an individual sense. It now remains to consider the nature of the factors which cause different individuals to present characteristic differences in behavior. There are at least three ways of approaching the matter. These may be roughly indicated as the point of view of the morphologist, the physiologist, and the psychologist.

A Morphological Basis of Behavior

The structure and shape of a planarian, its muscular and ciliary equipment, together with the kind and distribution of its light-receiving apparatus, are some of the morphological factors definitely restricting the kind and range of its reactions to light. These morphological factors may be grouped into, first, those which determine the general form of the body and consequently influence the animal's activities in a broad sense, and, secondly, those directly concerned with the reception of the light stimulus, the photoreceptors.

a General Form of the Body

A normal, full-grown planarian may be expected to give typical reactions to any stimulus. Fragments of a planarian, on the other hand, whether occurring from natural or artificial causes, would not be expected to behave as perfectly developed worms do, and observation shows that they do not.

As previously mentioned, Loeb ('94), and later other investigators, established the fact that planarians with eyes and brain removed are still able to give characteristic reactions to light, while Lillie ('01) found that any fragment capable of regeneration would respond to light.

In all cases of mutilated worms, however, the response to light is slower and less precise than that exhibited by normal individuals, and therefore different in degree if not in character from that of the latter. It has been repeatedly observed that worms mutilated unilaterally perform circus movements regardless of the light. This seems to be a plain case of morphological limitations on the part of the crippled animal, whereby the cilia and musculature of one side, on account of injury, are less efficient than those on the other side. Since it is practically impossible in nature to select at random a dozen planarians of which at least one specimen does not show some sort of mutilation, the modified behavior of morphologically imperfect animals becomes a factor of considerable importance in any general analysis of planarian activities.

Again, with regard to the general form of the body, it seems reasonable to suppose that a mature planarian loaded down with sexual products, or one gorged with food, must encounter mechanical difficulties in responding to light, so far at least as locomotion is concerned, which the same animal when unencumbered would not experience. A few experiments were performed to test this supposition, in which a comparison of the behavior of large and small worms was attempted. Pearl ('03, p. 546), it will be recalled, has shown that in the case of *Planaria maculata*, a worm 11 mm. long travels at a faster rate than one 6 mm. long. This experiment was repeated with a confirmatory result but, as will be seen

upon examining Table XXXI, the same result did not occur when *Dendrocœlum lacteum* was used.

TABLE XXXI

The average rate of locomotion in mm. per sec. of 5 small and 5 large individuals of each of four species, subjected to identical light conditions

SPECIES	LARGE		SMALL	
	Size mm.	Average rate	Size mm.	Average rate
<i>Dendrocœlum lacteum</i> (first trial).....	11	0.695	4	1.01
<i>Dendrocœlum lacteum</i> (second trial).....	11	0.74	4	0.77
<i>Phagocata gracilis</i>	9	1.58	4	1.21
<i>Planaria maculata</i>	13	1.57	8	1.37
<i>Planaria gonocephala</i>	10	1.17	5	0.98

The worms selected for the experiments detailed in Table XXXI were carefully chosen as to length and did not vary more than a millimeter in any case from the size recorded in the table. The result obtained with *Dendrocœlum* was so unexpected that the same ten individuals were put aside and tried a week later under as nearly identical conditions as possible. As will be seen by the table, the result of the second experiment was in general the same, though not so pronounced, as that obtained in the first set of trials. In the cases of *Phagocata gracilis*, *Planaria gonocephala* and *Planaria maculata*, the larger worms traveled faster than the smaller ones. Why the factor of size should give a different result in the case of *Dendrocœlum lacteum* from that common to the dark-pigmented planarians is by no means clear. It is conceivable that a planarian with undeveloped sexual organs or one whose size was reduced through starvation might have a better ciliary equipment *in proportion to its mass* than a normally adult animal and that in consequence it could travel faster. This supposition explains the behavior of *Dendrocœlum lacteum*, but it does not throw light on that of the other species, of which the smaller individuals, instead of traveling faster than their larger associates, moved at a slower rate. It is possible that in the case of the dark-colored worms reduction in size is accompanied by a

corresponding reduction in the photoreceptive elements, which, according to the experiments of Loeb ('94) and of Parker and Burnett ('00) seem to be in some degree at least distributed over the entire body. If this is true, there would result less stimulation from the light and consequently a slower rate. That Dendrocœlum lacteum when reduced in size does not suffer a similar reduction of its photoreceptive apparatus is probable. The work of Lillie ('01), wherein he showed the inability of headless individuals of Dendrocœlum lacteum either to regenerate or to respond to light, suggests that the photoreceptive apparatus of this species is not scattered over the entire body, but is rather concentrated anteriorly, in all probability consisting of the eyes only. If this is true, a reduction in the size of the body would not necessarily cause a proportionate reduction in the photoreceptors, and, indeed, the proportion of the light-receiving elements as compared with the mass of the body might increase as the worm became smaller. In this connection it is interesting to note that Gissler ('82) pointed out that in the case of *Bdelloura candida* increasing size of the body is accompanied by a decrease in the size of the eyes, and so far may this inverse ratio be carried that the eyes sometimes disappear entirely in large individuals. If there actually exists some such inverse ratio between the size of the photoreceptors and the mass of the body in the case of Dendrocœlum lacteum, it is easy to see why the smaller worms travel faster than the larger ones.

By another series of experiments it was found that the smaller worms of all four species, with the possible exception of Dendrocœlum lacteum, orient with less accuracy than the larger worms under the same external conditions. In these experiments, as in the previous ones already described dealing with orientation, each worm was placed at the center of a circle 10 cm. in diameter and headed successively toward, away from, and at right angles in both directions, to the incident light. The average amount of deviation at the circumference of the circle from the direction in which the worms were started, reckoned in degrees, gives a criterion of their accuracy in orientation. The averages of behavior obtained are indicated in Table XXXII.

The lessened accuracy in orientation among the smaller worms, as compared with the larger ones, helps to support the hypothesis that reduction in size entails proportionate reduction in the photoreceptive apparatus. The fact that *Dendrocœlum lacteum* forms an apparent exception to this general rule may also be taken as evidence that in this case the photoreceptive apparatus is more localized than in the other worms studied and conse-

TABLE XXXII

The average deviation (expressed in degrees), at the circumference of a circle 10 cm. in diameter, of large and small worms, each lot consisting of 5 individuals. Each worm was headed successively toward, away from and at right angles in both directions to incident light. The actual sizes of the worms were the same as in Table XXXI

SIZE OF WORMS	DENDROCŒLUM LACTEUM			PLANARIA		Phagocata gracilis	Total average
	First trial	Second trial	Average	maculata	gonocephala		
Large, degrees...	67	70	68.5	57	64	63	63
Small, degrees...	57	85.5	68.5	61	69	72	67.4

quently does not suffer a proportionate decrease when the size of the body becomes less. It is furthermore quite possible that a sexually mature planarian may on that account behave differently in light than an immature one. For instance, Yerkes ('03) states that in the case of the hydromedusa *Gonionemus murbachii*, the sexually mature individuals are the ones most sensitive to light, and Schouteden ('02) found the young of *Daphnia* positive, while the adults were negative to light.

Finally, Harper ('05) has shown that in the case of the earthworm the degree of sensitivity to light depends upon the degree of contraction or expansion of the body, since the photoreceptor cells—which in the earthworm lie interstitially at the bases of the epithelial cells—are more exposed to stimulation when the worm is expanded and conversely more shielded when it is contracted. It is more than likely that planarians offer a parallel instance and that their comparative indifference to light stimulation when in the relaxed resting position is due to the fact that then they present a more rounded contour and consequently their photoreceptors

are more deeply buried from the light than when they are in the expanded position assumed while gliding.

b Photoreceptors

What is the photoreceptive apparatus of the planarian? Is it made up of the eyes only, or partly of nerve-endings or of some special morphological elements homologous perhaps to the photoreceptor cells in the integument of the earthworm as described by Hesse ('06). Or does the central nervous system, the ciliary apparatus, or the musculature receive the stimulus directly without the mediation of special sense organs?

Although these questions were not made the subject of particular investigation in the present study of planarian behavior, certain facts incidentally appear from the observations made for other purposes which bear directly upon these inquiries and may serve as a basis for a brief discussion of the nature and location of the photoreceptive apparatus of planarians. The presence of eyes in the anterior part of the body, together with the wigwag movements which often take place in the same region when a variation occurs in the light conditions, point directly to the conclusion that the anterior end of the worm is more responsive to light than the posterior end. The fact that many planarians continue to react to light with considerable definiteness after the whole anterior end of the body is removed, indicates that this region does not necessarily contain the entire photoreceptive apparatus. Decapitated individuals of the species *Dendrocoelum lacteum*, it should be noted, seem to be exceptional in this respect since, according to Lillie, they fail to react to light.

In further support of the supposition that the anterior end of the planarian is the portion most sensitive to light it was found that the skioptic response of *Bdelloura candida* is confined not only to the anterior end but particularly to the region directly including the eyes. Observations repeatedly showed that if *Bdelloura* was allowed to come to rest in a field illuminated from above only, a sharp narrow shadow thrown across its body produced no visible response unless the shadow included the eyes.

The moment, however, that the eyes were in shadow the worm would elongate and frequently begin strikingly active movements.

It has already been shown (Table XIV, p. 77) that all the different species of planarians upon which experiments were made, traveled at a faster rate when they were started with the anterior end pointed toward directive light than when away from it. A reason may be offered for this characteristic increase in rate on the ground that the anterior end was plainly subjected to stronger stimulation when directed toward the light than when pointed away from the source of the stimulus. In the latter instance it was not only turned away from the source of the stimulus but was shielded also from the light to a considerable extent by the shadow formed by the posterior part of its own body.

Again, when a small beam of sunlight passing through a pin-hole in an opaque screen was directed locally to different parts of a gliding *Planaria maculata*, it was found that tropic response would occur in case one side of the anterior end was illuminated, and that it was not necessary for the eye itself to be included in the illuminated area to obtain such responses. However, when the middle of the body or the posterior end was similarly stimulated the worm could not be made to turn.

From the foregoing observations it seems probable that the photoreceptive apparatus of planarians is mainly but not exclusively located in the anterior end of the body and that considerable specific or generic difference may exist with respect to the extent of the distribution of additional light-receiving organs over other parts of the body. It is interesting to note in passing that Gamble and Keeble ('03) found that in the case of the green rhabdocœle *Convoluta roscoffensis* the sensitiveness to light was at the anterior end of the body only.

Concerning the relative sensitiveness to light of the dorsal and ventral surfaces of planarians, a set of experiments was performed on *Planaria gonocephala* in which the results show an absence of any marked differentiation in this regard. It is well known that in the matter of response to a thigmotactic stimulus the dorsal and ventral surfaces of a planarian show a very striking difference. Indeed, the dorsal surface is negatively thigmotactic to

such a degree that it is practically impossible to make a worm remain with its dorsal surface in contact with any surface, while its ventral surface is just as strongly positive in its thigmotaxis.

In contrasting the receptivity of these two surfaces to light stimulation a field of two adjacent intensities, similar to that used in the experiments on abrupt spacial changes in light intensity (Fig. 3, p. 79), was arranged in such a way that, in the first instance the source of the two lights was below, and in the second above, the field in which the worms were placed. The intensities of the light in each case were approximately 66 and 33 c.m. By this means the responses of the worms could be tabulated as they glided from one intensity of light to another and those given when the light impinged on the dorsal surface compared with similar responses made when the light struck directly on the ventral surface. It will be seen in Table XXXIII that the results do not indicate any particular difference for the dorsal and ventral surfaces with respect to the distribution of the photoreceptors. This condition of affairs, however, may be largely due to the translucency of the planarian's body, which would render light-receiving organs accessible from whatever direction the light primarily comes.

TABLE XXXIII

A comparison of responses made by Planaria gonocephala to a change in light intensity, tabulated with reference to the source of the light and its relative degree of stimulation upon the dorsal and ventral surfaces of the worm respectively

Position of light	Number of observations	Percentage of total responses	Percentage of wigwag movements
Above.....	101	50	42
Below.....	156	53	36

An exact determination of photoreceptors other than the eyes was not made. Both Iijima ('84, p. 438) and Carrière ('82, p. 167) in their histological researches upon planarians found "Neben-äugen" frequent and these occasional accessory eyes have also been described by Jäninchen ('96, p. 259). Such structures may

possibly be interpreted as the connecting link between undifferentiated light-receiving organs and the normal eyes of the planarians.

The part that pigment plays in the reception of light is not as yet clearly defined. It is not probable that pigment in itself constitutes a photoreceptor, though it is usually found associated with sensory cells which are directly concerned with light reception. That it is not an essential factor of a photoreceptor is evident, inasmuch as it is absent from the eyes of albino animals. The secondary rôle of pigment in the reception of light by organisms is admirably pointed out and discussed by Beer ('01).

The presence of pigment in a planarian may, however, modify the animal's response to light stimulation by shielding the sensory cells from light, and since its distribution in general is near the exterior, it may afford some clue to the relative receptivity of internally and externally situated photoreceptors. In other words, if pigmented and non-pigmented worms, for example, exhibited the same behavior in light, it might reasonably be assumed that the photoreceptors were not located internally, since they would be partially shielded from light in the case of the pigmented forms and consequently would give rise to a different response.

It is of interest, therefore, to contrast the behavior of dark-pigmented worms with those in which the dark pigment is absent except in the eyes. This is done in Table XXXIV, but it by no means follows that the contrasts there given between the behavior of dark and light worms are due to the presence of dark pigment in the one case and its absence in the other. Other factors than pigment may very probably have been influential in bringing about variations in the light reactions tabulated. Furthermore, it is inaccurate to refer to a white worm as being non-pigmented, since in that case it would be entirely transparent. The question, then, so far as planarians are concerned, is confined not to differences between pigmented and non-pigmented but to differences between dark-pigmented and light-pigmented forms.

It will be seen from Table XXXIV that when subjected to light stimulation dark-pigmented worms in general show more activity than light-pigmented forms. A single exception to this rule occurred in the case of the cave planarian experimented upon.

This marked difference in behavior might possibly be explained on the hypothesis that the direct effect of light on the deeper lying nervous system is inhibitive; that is, so excessive as to produce a sort of light rigor. Thus the more the central nervous system is shielded from light by pigment the less the inhibitive effect becomes apparent. Certain it is that *Bdelloura candida*, which has dark

TABLE XXXIV

The behavior of dark-pigmented worms contrasted with that of worms not possessing dark pigment distributed over the body. The number of observations in each case is not given since the details of this table have already appeared elsewhere

	DARK PIGMENTED				LIGHT PIGMENTED			
	<i>Planaria maculata</i>	<i>Planaria gonocephala</i>	<i>Phagocata gracilis</i>	Average	<i>Dendrocelum lacteum</i>	<i>Bdelloura candida</i>	<i>A. cave planarian</i>	Average
Duration of movement in a typical set of experiments, minutes	47	60+	60+	56+	18	15		16+
Percentage of orientation to light upon coming to rest.		41		41	30			30
Wigwag responses at the critical line separating two intensities of non-directive light, per cent		39		39	8.5			8.5
Average number of seconds required to escape from a circle 10 cm. in diameter	48.8	59.6	39.6	49.3	62.2		27.6	44.9
Precision of response								
Deviation in degrees upon emerging from a circle 10 cm. in diameter when headed away from the light.	24.4	25.3	29.1	26.3	10.1		11.4	10.7
Rate of locomotion in mm. per sec.	1.47	1.075	1.395	1.28	0.85			0.85

pigment in its eyes only, may be brought to a standstill very readily by means of light stimulation. With the exception of the eyes it may be possible that the photoreceptive apparatus is not differentiated to such an extent that it could fairly be said that any part of the translucent planarian body is entirely free from the direct stimulation of light. The relation of pigment to light reactions

is, however, by no means settled in the foregoing observations. This matter should be finally tested by comparisons in the behavior of different individuals of the *same species* showing variation in pigmentation or of identical individuals at different times when their phases of pigmentation are unlike, rather than upon individuals of different species.

It has proven impossible to include such a consideration in the present paper, but the preliminary steps toward attempting an analysis of the function of pigment with reference to light reactions have already been made and it is expected that a discussion of this phase of planarian behavior will be presented later. It may be stated here that when *Planaria maculata* is fed with a drop of human blood, a decided increase in pigmentation makes its appearance within a few days, due probably to the oxidation of the hæmoglobin in the blood corpuscles with which the planarians have become gorged. This single observation suggests an experimental means for controlling the amount of pigment in a single individual and it may reasonably be supposed that tests of behavior before and after excessive pigmentation will contribute direct evidence upon the part played by pigment in reactions to light.

Summary. Mutilated planarians in general respond to light with less accuracy than normal individuals.

Small worms move more slowly than large ones in the case of those species whose photoreceptive apparatus is not solely confined to the anterior end of the body. In the case of *Dendrocœlum lacteum*, whose photoreceptive apparatus is relatively greater in small individuals than in large, the rate of locomotion is faster among the smaller than among the larger.

Small worms orient with less accuracy than large ones. Planarians in the relaxed, resting position are less responsive to light than when they are stretched out in the act of gliding, a result probably of the greater exposure of the photoreceptors to light in the latter instance.

The anterior end of the body is the chief photoreceptive region and in certain worms, such as *Dendrocœlum lacteum* and *Bdeloura candida*, the anterior end is apparently the exclusive seat of this function.

No marked difference in response to light is shown between worms stimulated on the ventral surface and those equally stimulated on the dorsal surface.

Aside from the eyes, which form at least a part of the photo-receptive apparatus, no definite light-receiving organs were recognized.

Planarians possessing dark-colored pigment distributed over the body show in general greater activity when subjected to light than forms in which there is no dark pigment except in the eyes.

The central nervous system, as well as the more exterior parts of the planarian, may possibly be stimulated directly by such light as passes through the translucent body.

B The Physiological Basis of Behavior

The continually changing adjustment in any organism between the incoming and the outgoing energy gives rise to varying phases of metabolic balance, which may be designated as different "physiological states." Such physiological states form a noticeable factor in the behavior of any animal, a fact to which Jennings ('04b, p. 109) in particular has called attention.

That the difference between such states is great may be readily demonstrated. A planarian's response to directive light when it is in a relaxed, quiescent condition is plainly different from that exhibited after it has been vigorously disturbed by a brush. In fact, it is extremely difficult to get two animals that are in precisely the same physiological condition, or the same animal in precisely the same state at two different times, since the exact adjustment of physiological states is too delicate a matter to be controlled by the present gross experimental methods.

The attempt is ordinarily made to eliminate from experiments, so far as possible, the disturbing element of changing physiological conditions, that is, to keep constant all the factors except the one which is being subjected to test, and those results are counted as most successful in which such disturbance is reduced to a minimum.

It is the purpose of this section first, to give a possible classification of the different physiological states in which a planarian may

be, and, secondly, to pass briefly in review some of the many ways in which light may change the physiological state of such a worm.

a Classification of Physiological States

It is by no means easy to define even a simple physiological state, since the subtle changes form a continuous series of conditions which pass imperceptibly into each other.

An arbitrary classification for convenience may, however, be made as follows:

- 1 Relaxation, or rest.
- 2 Slight activity, without locomotion.
- 3 Normal activity.
- 4 Violent activity.
- 5 Rigor.
- 6 Exhaustion.

In the first of these states there is a minimum expenditure of energy caused by the ebb of the katabolic processes.

The second and fourth states indicate what are often referred to as conditions of low and high "tonus," but as this term has a technical significance with reference to muscle reactions, it will not be used in this classification. The third state, that of normal activity, is the average condition; it is the most desirable one to maintain in testing the animal's responses to different stimuli. By rigor is understood a state wherein there may be an excessive outgo of energy, but unaccompanied by movement, while under exhaustion is included the condition when energy is not being released because there is none to release.

That excessive or continuous light stimulation may go beyond the point producing rigor or exhaustion and may actually cause death, has been repeatedly proven in the case of bacteria by a long line of observers.⁶ The inhibitive effect of excessive light upon other organisms than bacteria has been pointed out by Berger ('00) with reference to *Cubomedusæ*; by Pearl and Cole

⁶ Tyndall ('78), Downes and Blunt ('77, '78), Jamieson ('82), Duclaux ('85a, '85b, '90), Arloing ('87a, '87b), Roux ('87), Dandrieu ('88), Raum ('89), Pansini ('89), Janowski ('90), Buchner ('92), and Ward ('94).

('02) in the case of various infusoria as well as Hydra, Hyallela, Clepsine, Stichostema and Physa; by Yerkes ('03) for Goniomemus and by Carpenter ('05) for Drosophila.

b Changes in Physiological States Induced by Light

A variety of stimuli besides light may cause an animal to pass from one physiological state to another. For example, the sense of phototaxis was reversed through mechanical stimulation by Towle ('00) in *Cypridopsis* and by Holmes ('01, '05b) in *Orchestia* and *Ranatra*.

The following typical illustration of the manner in which changes from one physiological state to another succeed each other is offered as a basis of comparison with the responses to light itself, which are about to be described. In the absence of mechanical stimuli a planarian may be in a state of relaxation. Very gentle mechanical stimulation causes the worm to lift its anterior end and move it cautiously about, bringing the animal into a state of slight activity without locomotion. If, now, the mechanical stimulus is prolonged or increased in intensity, enough energy is released to put the animal into gliding locomotion, when it may be fairly said to have passed into the state of normal activity. Provided the stimulation is made still more pronounced, the worm can next be forced to forsake gliding for crawling or humping, so passing into the state of violent activity. Further, it is possible by vigorous shaking to throw the worm, temporarily at least, into a condition of inactivity through excessive stimulation, during which the animal would remain quiet, not because it is failing to release any energy, but because it is unable for the time to set free its energy in the form of locomotion. In other words, it is in the state of rigor. Last of all, if mechanical stimulation is repeatedly applied a condition of exhaustion will appear when the worm has no more available energy and so is unable to move at all.

Effect of Different Intensities. As already pointed out, no intensity either of directive or non-directive light was found sufficient to change the condition of normal gliding into crawling.

Moreover, light of any intensity or direction frequently proved ineffective in arousing a quiescent worm into any state of apparent activity, particularly if the worm had but recently passed into the state of rest after a prolonged period of exercise.

Effect of Excessive Light. In the experiments with non-directive light it appeared that *Planaria gonocephala*, when subjected to an intensity of 431 c.m., showed somewhat less activity than at lower intensities, both with respect to rate of locomotion (Table III, p. 57) and to the number of turnings made (Table VI, p. 59); yet, so high a degree of intensity of the light stimulus was apparently not sufficient to cause a change into the physiological state of light rigor. It was comparatively easy, on the other hand, to transform *Bdelloura candida* by means of excessive light from the state of normal activity into that of light rigor.

Effect of Sudden Change in Light Conditions. A sudden change in light intensity either by increase or decrease is more effective in producing a new physiological state than an equal gradual change. The sudden withdrawal of the lamp to a considerable distance, for example, is usually sufficient to throw a worm from a normal state into violent activity, that is, from a gliding movement into a disturbed state in which the anterior end is waved actively about. But if the light is gradually withdrawn the same distance the worm will usually not pass into a different physiological condition.

The sudden introduction of complete darkness was never found sufficient to reduce an active worm more than temporarily to the resting position. Sudden dark might temporarily halt a moving worm, but it would not cause it to come to rest and assume the relaxed contour. In *Bdelloura candida* sudden dark, instead of checking the animal's movements, threw it into violent activity.

Effect of Continued Exposure to Light. Continuous exposure to light results in fatigue, which finally causes planarians to change from the state of normal activity to that of relaxation. The tendency toward such a change is shown in Table XXXV, where the responses of a number of worms newly subjected to light stimulation are contrasted with the responses made by the same worms after they had been moving about for several hours in the light.

The fresh worms show more activity than the fatigued worms do. Otherwise expressed, the worms have a tendency to change into a lowered physiological state upon continued exposure to light.

TABLE XXXV

Fatigue effects due to continuous exposure to non-directive lights forming adjacent fields of different intensities, as shown in the behavior of Phagocata gracilis

RATIO OF THE TWO INTENSITIES	1.96 : 1			13.45 : 1			Average		
	Going into greater intensity	Going into lesser intensity	Average	Going into greater intensity	Going into lesser intensity	Average	Going into greater intensity	Going into lesser intensity	Average
Fresh worms.....	10.5	21	16	45.5	47.5	46.5	28	34.4	31+
Fatigued worms....	2.5	9.5	6	32.5	33.5	33	17.5	21.5	19.5

It may be incidentally noted in Table XXXV that, as has already been pointed out in another connection, the percentage of responses is greater when the contrast between the light intensities is greater, and that both fresh and fatigued worms respond oftener upon going into the lesser intensity than when going into the greater intensity.

The time required for a worm placed in directive light to come to rest; that is, to run the gamut from the state of normal activity to that of rest, becomes gradually shorter with continuous exposure. As fatigue increases the worm shifts down the scale of physiological states in less time than when freshly subjected to directive light. A specific case of this kind has already been described in the paragraph on "duration of movement" (p. 105), where in 39 consecutive trials the change from normal activity to relaxation was first made in 18 minutes, but the thirty-ninth time in $1\frac{3}{4}$ minutes, while the fortieth time even mechanical stimulus failed to arouse the exhausted worm from the resting position.

Effect of Previous Exposure to Dark. Worms kept several hours in complete darkness make a larger percentage of responses to changes in their light environment than those which previous to experimentation have been several hours in light. Individuals removed from the stimulus of light for any consider-

able time are more responsive when subjected to it, for the reason that they are in a physiological state farther removed from fatigue than those worms which have remained a long period in the light. This point is brought out in Table XXXVI.

TABLE XXXVI

Percentage of reactions of two worms, Planaria gonocephala, to a sudden change in light intensity both when previously kept several hours in the dark and also when previously exposed for several hours to light

	Percentage of responses	Number of observations
After several hours in the light.....	54	100
After 48 hours in the dark.....	66	100

Summary. Physiological states grade imperceptibly into each other, but may be tentatively divided into: 1, relaxation; 2, slight activity; 3, normal activity; 4, violent activity; 5, rigor; 6, exhaustion.

Various stimuli besides light may induce a change from one physiological state to another.

No light intensity lower than 431 c.m. is sufficient to throw a worm into a higher state than that expressing normal activity, nor is the absence of light sufficient to bring a planarian to rest.

Excessive light intensity shows a tendency to carry *Planaria gonocephala* from a state of normal activity to one of rigor. *Bdelloura candida* is easily changed into a condition of rigor by light.

A *sudden* change of light intensity acts more immediately than a *gradual* change in causing planarians to pass from one physiological state to another.

Continuous exposure to light induces fatigue, finally resulting in the passage of the worm into a state of continuous relaxation, in which condition it becomes practically indifferent to light. Repeated trials of the time required in constant light to come to rest show that a progressively shorter interval occurs between the state of normal activity and that of relaxation until a point of complete inactivity is reached, the worm finally remaining in the latter state for a prolonged period.

Planarians kept for some time in darkness pass into a state in which they are more responsive to light than individuals exposed for a similar length of time to light.

C Psychological Basis of Behavior

Among the first questions that naturally arise concerning the behavior of planarians in light are those which approach the matter from a psychological point of view. How much can planarians actually see, and can they, by repeated experience, "learn" to adapt themselves to changes in the light surrounding them?

To this kind of inquiry it is most difficult to give a satisfactory answer, for the reason that it is impossible to go beyond conjecture and inference in judging what any animal, aside from man, can see or know or experience. It is only possible to state, in more or less definite terms, the responses which animals make to light, since it is beyond man's power ever to experience how animals "feel" under any circumstances.

a. How Much Can Planarians See?

Broadly speaking it may be said that planarians can distinguish light from darkness. The experiments described on pp. 84, *et seq.*, relating to planarians placed in aquaria so surrounded by backgrounds as to produce regions of different light intensity, point to this conclusion, since when subjected to such differential environments the worms come to rest in the darkened areas.

Again, the numerous responses made at the critical line separating two light intensities may be regarded as evidence of some power of discrimination on the part of the worm between different intensities of light.

It is probable, furthermore, that planarians can distinguish a moving object when that object is of sufficient size and contrasts with its surroundings in its degree of illumination, for the reason that a moving object from which light is reflected, means the same to a worm coming into the vicinity of the object as any other change in the direction of light, such as might be caused by moving a

lamp from one position to another. To changes in directive light planarians are known to respond very definitely, and consequently they may be said to distinguish the motions of objects.

With regard to true seeing, however, in the sense of distinguishing the forms of objects, it is safe to assume that planarians have almost no power whatever, since their eyes are optically unable to form images even if the central nervous system were highly enough developed to interpret images when formed. In the case, therefore, of *Planaria alpina*, which, according to Collin ('91, p. 180), "shuns" *Planaria gonocephala* when the latter has been put into the same aquarium with it, seeking "strenuously to escape" from its larger relative, the conclusion does not necessarily follow that *P. alpina* sees an enemy and experiences the sensation of fear. As previously pointed out (p. 95), the whole matter is probably explainable on the basis of negative chemotaxis alone. To attribute fear, therefore, or any other similar complex sensation, to an organism whose responses are so plainly of a simple reflex nature, is to go quite beyond the evidence.

In the performance of the two great life processes of nutrition and reproduction, light is apparently in no way a direct aid to planarians, since they thrive in situations from which light is entirely excluded, as in caves, and since they habitually frequent places where this factor is reduced to a minimum. Light cannot, then, be regarded as a directly essential factor in the life of planarians.

That light is not essential to the activity of protoplasm has more than once been demonstrated. Engelmann ('79), for example, showed that the streaming protoplasm of plant cells occurs normally in darkness, while Maupas ('87) found ciliates multiplying as rapidly in the dark as in the light.

b Are Planarians Able to "Learn"?

With regard to the ability of these worms to acquire upon repetition an abbreviated form of response; that is, to "learn," a few suggestions may be drawn from experiments already described in other connections.

It will be remembered (p. 93) that when a small aquarium

was delicately mounted upon a turntable, such as is used in "ringing" microscopic slides, a very slight rotation was sufficient to bring to a halt momentarily a gliding worm in this aquarium. It was possible to control this momentary response to such a point of nicety that the anterior end of the worm could be made to halt for an instant without interfering with the onward locomotion of the posterior end. If this slight rotation was repeated at intervals of a second it was found that the worm under observation halted with less and less certainty, until after a dozen or more trials it continued to glide on without halting at all. In ordinary phraseology the worm had learned by experience not to be alarmed by a sudden mechanical shock. The lesson, however, was always very soon forgotten, for after an interval of less than a minute, during which the aquarium remained stationary, the worm responded exactly as it did at first, whenever a slight rotation was made. In a similar way the skioptic response of *Bdelloura candida* became less pronounced upon repetition, until it was possible to throw a shadow upon the animal without obtaining any response at all.

Again, when worms were placed in a field of non-directive light, parts of which were of two different intensities, the number of wigwag responses made at the critical line separating the two intensities grew less after the animals had repeatedly crossed the line. At first the new condition of sharply contrasted light intensities in the worm's field of locomotion called out a large percentage of wigwag responses. Later, however, by repeated experiences the worm became familiar with this feature of its environment and made fewer wigwag motions. A definite instance of such a decrease in response is given in Table XXXVII.

TABLE XXXVII

Responses of Planaria gonocephala on crossing the line separating two intensities of non-directive light

	Wigwag movements	No response	Percentage of response
First 25 crossings.....	21	4	84
Second 25 crossings.....	19	6	76
Third 25 crossings.....	12	13	48
Fourth 25 crossings.....	8	17	32

It will be seen that when *Planaria gonocephala* was first introduced into a field of contrasted intensities, it made the wigwag response at the critical line marking a change of light intensity, in 84 per cent of the first 25 crossings, while during the second, third and fourth sets of 25 crossings, the per cents uniformly decreased until at the fourth 25 crossings the number of wigwag responses fell to 32 per cent. It may be objected that the instances thus far cited in this section find a more reasonable explanation upon the hypothesis of fatigue, but the same surely cannot be said of the following case.

It was found that *Planaria maculata* oriented itself to directive light at successively shorter intervals when the position of the light was suddenly changed. To produce such a series of responses there was placed in the dark room a shallow aquarium with an electric lamp at either end, under the control of the right and left hand, respectively, of the experimenter. A planarian was placed in the middle of the aquarium and the right-hand light turned on. As soon as the worm was fairly oriented to this light and gliding away from it, the right-hand light was turned off and at the same instant the left-hand light turned on. The time in seconds required for the worm to orient to the new light; that is, to turn 180° and begin to glide away, was recorded. On p. 89 a typical series of records of such responses is given, in which the number of seconds required for re-orientation when the source of light was reversed, varied from 260 seconds, at first, irregularly down to 35 upon the sixteenth trial. It will be seen from this series that the worm acquired by experience some degree of facility in adapting itself to certain variations in its environment which it would never be liable to encounter in nature, and that this adaptation cannot be explained as due to fatigue. Davenport and Cannon ('97, p. 32) found similarly that "Daphnias respond more quickly and accurately to light after having made several trips to it."

It is quite certain, however, that any educative attainment which a planarian may experience, or which a planarian may acquire, is exceedingly evanescent and also that there is no evidence that the worm emerges from reflex behavior into responses connected with consciousness.

Summary. The existence of feeling or consciousness among planarians is a matter of pure conjecture.

From their responses it may be inferred that they are able to distinguish dark from light, as well as objects in motion, but it is not clear that they can distinguish the forms of objects.

The knowledge which planarians have of objects in their immediate environment, such as food, enemies, etc., depends largely upon chemical and tactile means. They are, therefore, as well able to go through the entire range of their activities in the dark as in the light.

Upon repetition planarians may in some instances become accustomed to, or acquire greater facility in, responding to stimuli, but this result of experience is almost instantly lost, so that it is doubtful whether these animals possess more than the merest rudiments of the primary criterion of consciousness, namely, the ability to learn.

VI GENERAL CONCLUSIONS

Probably the questions which have occupied the greatest share of attention throughout the literature dealing with the reactions of organisms to light, are the following:

- 1 Is the direction or the intensity of light of more importance in orientation?
- 2 Which theory best explains orientation and phototaxis, the theory of trial and error or that of the tropisms?
- 3 How far is behavior with respect to light, adaptive?

I DIRECTION OR INTENSITY

Before the part played in the behavior of planarians by either the direction or the intensity of light can properly be discussed, it will be necessary to present a brief historical résumé of certain general conclusions reached by investigators along this line.

A Historical

Cohn ('53), Strasburger ('78) and Loeb ('90, '93a) attributed the directive effect of light to the action of the rays. In a later

paper Cohn ('64) abandoned his first position and came to regard intensity as the important element in light, a position also maintained by Famintzin ('67), Engelmann ('83), Oltmanns ('92), Verworn ('01) and even by Loeb ('93b) in the case of *Planaria torva*, which he found came to rest in accordance with the intensity, and regardless of the direction, of the light. Davenport and Cannon ('97) modified this point of view by attempting to show that direction and intensity may each operate independently, producing, respectively, "phototaxis" and "photopathy." Holt and Lee ('01) followed with an excellent summary of the whole controversy, emphatically maintaining, in opposition to Davenport and Cannon, that intensity alone is the only possible operative factor in light stimulation and that direction of the rays has no effect whatsoever except in determining a greater intensity of light with reference to one part of an organism as compared with other parts.

Among more recent investigations Holmes ('03), experimenting with the same organism that led Oltmanns to ascribe the greater importance to intensity, namely, *Volvox*, declares himself in favor of direction, while Zeleny ('05), on the other hand, gives an instance of *Serpulid* larvæ going both toward the source of the light and away from it; that is, moving regardless of direction, in order to arrive in regions of increased intensity.

Carpenter ('05) found that the pomace fly, *Ampelophila drosophila*, will orient to the direction of light after it has first been sufficiently aroused by the intensity of the light, while both Yerkes ('99) and Towle ('00) maintain that direction and intensity are by no means mutually exclusive, and that each may play a part simultaneously in determining the behavior of an organism.

Lastly, it has been made clear by Parker ('03) that, besides direction and intensity of light, the size of the source of illumination may determine the orientation. This theory explains why butterflies alight upon a patch of reflected sunlight which produces a large but faint retinal image instead of flying toward the sun itself, which forms only a small but intense retinal image. In the case of planarians, however, this phase of light stimulation is not operative, since the eyes of these animals are incapable of forming retinal images.

B Conclusions with Reference to Planarians

The behavior of planarians may in general be more satisfactorily explained by regarding, with Loeb, the intensity rather than the direction of the light as the principal operative factor in light reactions. At the same time there is much evidence that the intensity utilized by the organism, is intimately associated with, and powerfully modified by the direction of the light. As a basis for these conclusions the following points will be considered. First, the distinction between direction and intensity; secondly, the way in which directive light modifies the intensity with reference to planarians; thirdly, the action of intensity without the modifying effect of direction, and finally, modifying effects of factors other than light.

a. The Distinction Between Direction and Intensity

Theoretically it is plain that light *per se* with respect to any fixed point, may be regarded in two distinct aspects, namely, that of intensity and that of direction. The intensity of light under ordinary circumstances varies inversely as the square of the *distance* and is independent of the position of the source of light. That is to say, at any points equidistant from its source, light has the same intensity, but the more remote the less is the intensity at any given point. The direction of light, on the contrary, is dependent solely upon the *position* of the source of the light and in no way upon the distance. When intensity and direction are considered with reference not to a fixed point but to an organism presenting three dimensions and made up of differentiated protoplasm, the basis of light relations becomes more complex. Light cannot here be treated as a phenomenon *per se* but must be considered in relation to a differentiating organism.

It is true that intensity in the case of the organism, as in the case of a fixed point, varies with the distance from the source of the light. A decided difference, however, appears in the case of the organism inasmuch as, owing to its structure, *the intensity received by it varies also in accordance with the position of the light.* This

second form of variation in intensity is directly due to the fact that the organism has a solid form and is not homogeneously photo-receptive.

The direction of light with reference to the organism, presenting as the latter does a structurally diversified form, is influential only as regards the position of the source of light, just as in the case of a fixed point.

Any change in the position of the source results, then, in a redistribution of the intensities falling upon the organism, so that again the intensity received varies in accordance with the position of the light.

It is this factor of *position* in light that has been termed the directive influence of light and it is seen to be due to variations in the intensity of light with reference to the organism, and not to any peculiar property of light itself. By "non-directive light," on the other hand, is understood those conditions which secure for the organism equalized or symmetrical intensity with respect to the parts stimulated. If this interpretation is correct there can be no response, strictly speaking, to the *direction* of light *exclusive of intensity* although the factor of intensity may be continually modified by that of direction in the light relations of organisms.

b The Modifying Influence of Direction

It is undeniable that the planarians experimented upon exhibited without exception a definite characteristic phototaxis, that is to say, they habitually go either toward or away from the source of light according as they are respectively positive or negative. In analyzing this phototaxis it seemed desirable to eliminate so far as possible the factor of intensity, but the attempt to do this was only partially successful owing to physical limitations. A step was made, however, toward subjecting worms to directive light without at the same time exposing them to a variation in intensity by inserting a biconvex lens between the source of the illumination and the aquarium, thus making the diverging rays of light parallel throughout their course in the aquarium. By this means was formed a field equal in its amount of illumination at

the two ends of the aquarium, the one opposite and the one next to the source of light, with the exception that there was a slight difference at the two ends due to the fact that light in its passage through water is partially absorbed. But modification of light in any degree results in producing less intensity at the farther end of the aquarium, though this difference is less pronounced when a lens is employed. Therefore, although worms placed in this apparatus went with considerable precision in the direction of the propagation of the light, there is no certainty that their behavior was not due simply to differences in intensity. Worms which are thus apparently traveling directly in accordance with the direction of the light, are meantime being subjected to different intensities at the anterior and posterior ends of the body, for the reason that the anterior end is more or less shadowed by the rest of the body, since the latter cuts out a certain portion of the light received at the posterior end.

That direction of light is a factor by no means to be disregarded, even if it cannot be proven to be the immediate cause of phototaxis, is apparent when it is recalled that slight changes in direction call out corresponding changes in the course of the gliding planarian, whereas considerable changes in intensity when the direction remains constant and particularly when such changes are gradually made, may fail entirely to produce corresponding changes in the worm's behavior. This is due to the fact that slight changes in direction may cause considerable changes in the asymmetry of illumination. When a worm, for example, is receiving horizontal light from behind, its head is more or less in shadow, the sides of its body being at the same time equally illuminated. The moment the light is shifted in even a small degree to one side, one entire side of the animal may receive an increase of illumination and the opposite side be thrown into shadow. Thus a slight change in position initiates a fundamental change in the distribution of intensity over the planarian's body.

c Instances of Behavior Due to Intensity Alone .

The effect of intensity as a separate factor from the directive influence of light is clearly demonstrable in certain phases of

light reactions. To isolate intensity by excluding the possibility of directive light; that is, to secure equalized intensity with reference to the organism, is not difficult and the manner in which this was done, with non-directive light falling upon a horizontal field from above, has been sufficiently detailed in the body of the paper.

It may be briefly recalled that planarians experimented upon by this method showed a certain unmistakable degree of response which could be referable only to differences in equalized intensity. For example, the rate of locomotion was found to be faster in any non-directive intensity up to 431 c.m. than in darkness, although light in itself was not always sufficient to start a worm into activity, nor was its absence sufficient to check an animal already in motion. Again, though no close correlation between behavior and the degree of intensity was found to exist, there appeared certain general results which were plainly referable to intensity differences only. Instances of such results are the behavior of *Planaria gonocephala* (which was modified in several particulars at 431 c.m. as compared with its behavior at lower intensities); the coming to rest in regions of diminished intensity of individuals of all species except *Bdelloura*; and the increase of wigwag responses corresponding to an increase of intensity differences when a field of contrasted intensities was used.

It is interesting to observe that increase in the intensity of non-directive light, and continued exposure to non-directive light of constant intensity, both tend to produce the same behavior that would result in directive light. Under any of the three conditions just mentioned there resulted by actual experiment fewer turnings, fewer "indefinite changes" and more nearly straight paths on the part of planarians than occurred when the worms were (1) placed in non-directive light of lower intensity, (2) subjected a short time to non-directive light of constant intensity, or (3) left in darkness. Now, fewer turnings, fewer "indefinite changes," and more nearly straight paths are ordinarily characteristic results of directive light, so that here is a case of reactions, which if resulting from the employment of directive light would be termed phototaxis, occurring in non-directive light as the result of intensity alone. Mast ('03) experimenting upon the reactions of planarians to thermal

stimuli obtained a similar result. He observed that apparently "negative" as well as "positive" responses resulted when the animals were subjected to non-directive thermal stimuli.

Another noticeable phenomenon with reference to responses to intensity is, that more wigwag responses occurred at the critical line separating two different intensities when the lesser of the two intensities was 16 c.m. than when it was 33 c.m. (Table XI, p. 69). Similarly responses were more frequent when planarians were subjected suddenly to dark than when they were flooded suddenly by light, and, throughout a large number of series, responses were invariably more frequent when the worms were passing into a region of diminished intensity than when they were entering an area of increased intensity. It is to be inferred that all these phases of behavior are due to the probable fact that the lower intensities compared are nearer the worm's optimum as regards light than the higher ones, since the latter apparently have a tendency to inhibit activity.

Lastly, the relative part played by intensity of light varies decidedly in different species of planarians. The relative intensity in different parts of an aquarium, when no lens is used to lessen the contrast, has comparatively little influence upon *Phagocata gracilis*, as its extensive wanderings (typically reproduced in Fig. 11) toward and away from the source of light, indicate. *Planaria maculata* and *Planaria gonocephala*, on the contrary (Figs. 13 and 14), notwithstanding their ability to come toward the light in the direction of the "rays" throughout the farther half of the dish, seemed invariably to encounter an impassable barrier as soon as they approached within a certain intensity, thereby showing a more delicate responsiveness to intensity differences.

d The Modifying Effect of Other Factors

In attempting to analyze the relative bearing of the intensity and of the direction of light upon the behavior of planarians there must be constantly kept in mind two general sources of error which are always present when these factors of light are in operation. These

are (1) the physiological state of the organism at the time of observation, and (2) the simultaneous effect of other stimuli.

A physiological state may be directly traceable to known causes, such as previous exposure to other stimuli or the condition of metabolic balance in which the animal chances to be at the time of observation, or, again, it may be the result of factors at present unknown, which consequently, although in active operation, are not susceptible of analysis. In any case it is certain that the uncontrolled factors comprehended under the term "physiological state" prove individual planarians to be not identical mechanisms, but organisms possessing a more or less definite individuality. Moreover, it has been shown that differences in physiological state play a greater part in the determination of behavior than do intensity differences in the light stimulus. When a planarian is approaching a state of fatigue, for example, it becomes indifferent to differences of intensity.

With regard to the simultaneous effect of other stimuli acting in conjunction with light, it has already been pointed out that behavior is the resultant of all the factors, external as well as internal, which may be acting upon an organism at a given time, and that consequently the effect of any one of the operating factors, such as that of light, for example, cannot be determined unless the value of the other factors involved is also taken into account. In support of this view, which is so self-evident, it will be recalled that some of the ways in which the responses of planarians to light may be modified by geotaxis, thigmotaxis, goniotaxis and chemotaxis, were touched upon.

Summary. Direction and intensity are separable qualities of light. Direction is dependent upon the relative positions of the light and the organism, whereas intensity depends upon the distance between the light and the organism as well as the initial intensity of the light.

When applied to living organisms intensity may act independently of direction, or in conjunction with it. Direction cannot act independently of intensity upon organisms, since the latter possess definite form and consequently cannot receive the light at a single point.

With reference to an organism, directive light is resolvable into unequalized intensity and non-directive light into equalized intensity.

Asymmetrical intensity in directive light is largely due to the partial shadowing of that part of the body farthest away from the source of the light. Slight changes in the position or direction of the light may cause considerable changes in the symmetry and the degree of the shadow effects and consequently in the relative intensity of the light on different regions of the body of an organism.

To different degrees of equalized or symmetrical intensity planarians show considerable response, but the correlation between their behavior and the degree of intensity is not so close as it is in the case of asymmetrical intensity.

Increase in intensity of non-directive light, continued exposure to non-directive light of constant intensity, and change from darkness to non-directive light, all tend to bring about apparent phototaxis similar to that occurring in directive light.

Responses are more frequent on the part of planarians in intensities approaching the optimum than in higher intensities, where there is a tendency to inhibition.

Relative differences in responses to various intensities are due to specific differences between planarians.

The physiological state of an organism together with the influence of known stimuli other than light are constant sources of error in estimating reactions to light. These factors taken together play a more important part in planarian behavior than light stimulus.

Finally, the action of light upon planarians is a function of its intensity, which, under certain conditions, is emphasized by the direction of the light.

2 TRIAL AND ERROR OR TROPISM?

It is apparent from the preceding section that light may have two effects upon organisms. Of these, one is a kinetic effect, arising from the intensity of the stimulus and resulting in a gen-

eral activity termed photokinesis, while the other, connected indirectly at least with the direction from which light impinges upon an organism, is called phototaxis. In the case of planarians these two phases of light stimulation have been shown to be intimately associated and both operative. Carpenter ('05) pointed out in the case of the pomace fly that phototaxis occurs only when preceded by photokinesis or some other reaction, and such an interrelation of the two is undoubtedly of wide occurrence. The object of this section is to inquire into the causes underlying phototaxis. Loeb ('93b) has shown that phototaxis is the result of orientation. It does not necessarily follow, however, that orientation invariably results in phototaxis. In fact Dearborn ('00) found that crayfishes would orient to an electric light introduced into the water near them without making any considerable locomotor movements in consequence.⁷

To the question of how orientation of organisms to light is caused, three possible explanations may be presented: 1, Chance result of photokinesis; 2, reflex response to directive stimuli; 3, voluntary action. Since the first hypothesis seems entirely inadequate to account for the uniformity of orientation in planarians, and the third alternative is out of the question with reference to these animals, a consideration of the reflex responses to directive stimuli may be taken up at once.

There are two general theories which attempt to explain the way in which orientation occurs through reflex responses to stimuli. These theories are first, the *trial and error theory* of Jennings and Holmes, and secondly, the *tropism theory* of Verworn and Loeb. By the trial and error theory orientation, with its consequent phototaxis, is interpreted as the result of repeated attempts on the part of an organism to become adjusted to any given stimulus. Those attempts which fail to result in adjustment to the stimulus are "errors," and as such are followed by other attempts until finally some one secures the necessary adjustment. Trials of this kind may be made in different ways according to the organism

⁷ Throughout the following discussion orientation will be understood as a *position* assumed with reference to the light while phototaxis will be made to include motion *toward* or *away from* the source of the light.

in question. Among the infusoria and rotifera, as Jennings has shown in a masterly series of papers,⁸ such attempts at orientation are made by means of a "motor reflex," consisting in (1) a sudden withdrawal from the stimulus, (2) a rotation toward a structurally defined side of the asymmetrical organism, and (3), lastly, an advance in a new direction.

In the case of organisms which do not possess marked asymmetry the trial and error method, as pointed out by Holmes ('05a), resolves itself into a series of "random movements;" that is, a number of apparently experimental movements are made, which finally result in the best adjustment to the stimulus.

In both of these methods the organism acts as a unit and not in response to localized stimulation received asymmetrically.

The tropism theory, on the contrary, is based upon asymmetrical action as the result of asymmetrical stimulation. If an organism receives a stronger stimulus on one side of its body than on the other, the result, whether direct or indirect, is that it moves in such a way that this asymmetrical stimulation becomes symmetrical. In other words, orientation occurs.

It is unfortunate that the tropism theory was made to apply to the behavior of the infusoria, since it has been shown beyond doubt by Jennings that exact observation of the behavior of these organisms and an analysis of its details does not admit of the tropic interpretation, but is, on the other hand, explained by the trial and error theory of motor reflexes. It is also to be regretted that the unquestionable rout of the tropism theory, as applied to certain protozoa and other asymmetrical forms, should have led to an attempt to exclude it from the remainder of the animal kingdom.

In a paper on the tropism theory Jennings ('04a) names as an essential criterion of tropism the direct unilateral stimulation of the motor organs. After showing how inadequate such an assumption is to explain the orientation of animals, *particularly that of Infusoria*, he continues ('04a, p. 104), "We should perhaps con-

⁸ See bibliography in Contributions to the Study of the Behavior of Lower Organisms. Carnegie Inst. of Washington. Publication No. 16. 256 pp. 1904.

sider here a modification of the original form of the tropism theory that has been proposed by some authors. This is in regard to the assumption that the stimulating agent acts directly on the motor organs upon which it impinges. For this it is sometimes proposed to substitute the view that the action of the stimulating agent is directly on the sense organs of the side on which the stimulus impinges and only indirectly on the motor organs through their nervous connection with the sense organs. When thus modified the theory of course loses its simplicity and its direct explaining power, which made it so attractive. In order to retain any of its value for explaining the movements of organisms, it would have to hold at least that the connections between the sense organs and the motor organs are of a perfectly definite character so that when a certain sense organ is stimulated a certain motor organ moves in a certain way. When we find, as we do in the flatworm (see the following paper), that to the same stimulus on the same part of the body, under the same external conditions the animal reacts sometimes in one way, sometimes in another, the tropism theory, of course, fails to supply a determining factor for the behavior."

It seems to me that the mechanism by means of which the asymmetrical response is brought about is immaterial, so long as that response can be shown to be the result of asymmetrical stimulation. Asymmetrical response might occur either from direct stimulation of the motor organs as was implied in the earlier papers on the infusoria, or by means of a more complex method, consisting of stimulation of the sense organ, transmission to the central nervous system and thence to the motor organs.

The outcome in either case would fulfill the demands of the tropism theory, if asymmetrical response to asymmetrical stimulation be taken as its criterion. In the quotation just cited, the objection that such transmission compels stereotyped behavior is hardly valid, since stereotyped reaction is by no means the only alternative of asymmetrical stimulation. That flatworms do not respond uniformly to directive stimuli cannot be disputed, but that fact does not exclude the possibility of all tropic reaction on their part. The imperfection of response may be simply the result of imper-

fections in the worm's nervous circuit, assuming that planarian reactions are due to indirect rather than to direct stimulation of the motor organs. In fact, repeated evidence of the failure of a constant and perfectly invariable orientation on the part of planarians has been given in the preceding pages. Such failure, moreover, is quite as likely to occur in the application of the tropism theory to behavior as it is in the case of the trial and error theory, since stereotyped reactions and forced movements, as Holmes ('05a, p. 112) has emphasized, are no more characteristic of tropisms, which depend upon a differentiated stimulation and response, than they are of trial and error movements, resulting from a single motor reflex given in response to all kinds of stimulation.

Furthermore, it has been urged that tropism indicates a simpler form of reaction than trial and error for the reason that it involves only a local part of an organism while the motor reflex of trial and error requires that the organism act as a whole. Consequently, since motor reflex has been indisputably demonstrated as the method of infusorian phototaxis, Jennings ('04a, p. 95) asks, "Should we conclude that the reactions in the higher metazoa are simpler and less unified than in the protozoa?"

That the motor reflex, which occurs with machine-like uniformity, regardless of the point where the stimulation is received, is more complex in character than the stimulation of an asymmetrical part of an organism which *may* depend for its response upon sense-organ, nervous transmission and motor apparatus is an assumption difficult to sustain. It seems more reasonable to agree with Harper ('05) in placing tropism higher in the evolutionary scale than trial and error.

The fallacy that "tropism leads nowhere; it is a fixed final thing like a crystal" (Jennings, '04c, p. 251), while trial and error alone offers possibilities of the higher evolution of phototaxis, has already been answered by Holmes, who points out that trial and error, at least that phase of trial and error depending upon motor reflex, is even more fixed and stereotyped than the reactions occurring in accordance with the tropism schema. To quote: "The end result of both methods is the same, *i. e.*, to get the organism away

from the stimulus. In the one case it is accomplished by direct reflex without more ado; in the other, only after a considerable waste of energy in inconsequential vermiculations" (Holmes, '05a, p. 110).

It is at least conceivable that under the tropism schema, as the nervous differentiation of an animal becomes more complete, the ability of the organism to interfere with and modify its machine-like responses to external stimuli might also increase, resulting in a flexibility of behavior which would present quite as much variation for natural selection to act upon as that evolved by the trial and error method. This point of view by no means denies that trial and error is the usual "method of intelligence" (C. L. Morgan '00, p. 139). It is simply an attempt to recognize in the method of tropism also one of the possibilities of evolutionary progress in behavior and as such holding a higher position in the scale of evolutionary methods than trial and error by motor reflexes.

It has been shown (p. 143) that planarian responses of an apparently asymmetrical character may occur as a result of symmetrical stimulation. Similar instances in the case of planarians have also been demonstrated by Mast ('03) with reference to thermal stimuli. This, however, is no exception to the validity of the tropism theory, in which asymmetrical responses result from asymmetrical stimulation. Because a planarian *may* make an apparently phototropic response when subjected to symmetrical stimulation, is not evidence against the supposition that the usual phototropic response is due to asymmetrical stimulation.

The "wigwag" movements of planarians, to which repeated reference has been made in the preceding pages, resemble superficially the "random movements" of the earthworm as described by Holmes. They do not, however, ordinarily appear to be the basis of trial and error selection resulting in orientation, since in a majority of cases, after a worm halts and makes wigwag movements it continues on its way without a change of direction. The movements of *Bdelloura candida*, as shown in Fig. 12, form an exception to ordinary planarian behavior in this respect.

As a rule wigwag movements are probably occasioned by a general disturbance arising from some stimulation which throws

the worm into a different physiological state. Exploring movements, such as these seem to be, may bring about asymmetrical stimulation, in which case the worm makes a tropic response.

It was particularly noticed that when planarians received light from below, the anterior end of the body was frequently tilted back and forth as if to make it possible for the light when coming from such an unusual direction to enter the pigment cups of the eyes. The phenomenon suggested the craning of necks and bobbing of heads among a crowd of people who are all trying to see the same object at once.

Wigwag movements seem to be oftener connected with changes in the intensity of light than with changes in its direction. When the latter occur, tropic response is immediately the result.

In the course of the experiments previously described wherein the worms glided from an area of one intensity of non-directive light into another it was noticed that in a majority of cases when the critical line was not crossed at right angles, no change in course occurred, even when the worm halted and made wigwag movements. Of course at a certain instant of any diagonal crossing of the critical line one eye must receive more stimulus than the other, in which case according to an inflexible tropism theory asymmetrical response ought to occur. But such a response does not frequently appear and the reason for this becomes clear when it is remembered that a considerable number of responses were shown to occur which were called "latent wigwags" (Fig. 4, *E*), because they failed to make their appearance until in some instances the worm had passed more than the length of its body beyond the critical line. Since, therefore, latency of response to intensity is by no means uncommon, it is evident that the brief interval of asymmetrical stimulation occurring when a worm glides diagonally into an area of different intensity is not sufficient to result in an asymmetrical response.

Two conclusions, then, seem reasonable, namely, that phototaxis as related to planarians is primarily due to asymmetrical response resulting from asymmetrical stimulation, and that wigwag movements, together with similar apparent trial and error forms of behavior, contribute chiefly to this end, *i. e.*, to phototaxis.

Summary. Orientation may occur without phototaxis.

Two theories have been advanced to explain orientation and phototaxis in lower organisms, namely, the trial and error theory and that of the tropisms. The former may be based upon "motor reflexes" or upon "random movements" according to the symmetry of the animal.

The tropism theory rests upon asymmetrical response to asymmetrical stimulation. It does not necessarily depend upon the direct stimulation of the motor organs, nor is it essentially stereotyped in its character any more than are trial and error responses by motor reflex or random movements.

The tropic form of response may, and probably does, require a more complex mechanism than that which causes the motor reflex, consequently it is the form of response to be logically expected among planarians, since the motor reflex has been proven to be the form utilized by the protozoa.

Tropisms, as well as trial and error movements, provide, through the modifying control of an evolving central nervous system, sufficient latitude of variation for natural selection to work upon in the evolution of higher forms of behavior.

Asymmetrical response may, in certain cases, result from symmetrical stimulation, but ordinarily its cause is asymmetrical stimulation.

Wigwag movements are occasioned most frequently by changes in intensity, and they may result in orientation and phototaxis by assisting an organism to secure asymmetrical stimulation.

Latency of reaction accounts for some of the failures in orientation which often occur even when asymmetrical stimulation is acting upon an organism.

Finally, the orientation and phototaxis of planarians is more consistently explained by the theory of tropisms than by the theory of trial and error.

3 ADAPTATION.

It remains, finally, to inquire how far the reactions of planarians to light are adaptive; that is, how far the response to light is "of

such a kind that it better insures the existence of the individual, or of the race" (T. H. Morgan '03, p. 1).

It is evident that the generally negative character of the reactions of planarians to light indicates a tendency on the part of these worms to reduce as much as possible the amount of light stimulation received or to avoid it altogether. The rigor effects of excessive stimulation furnish evidence also that light is a factor in a planarian's environment which it finds unavoidable and unwelcome and to which it is adapted only in a negative fashion. In fact the vague distinction separating "lower" from "higher" animals consists largely in the ability of higher animals to assume an active aggressive rather than a passive defensive relation toward the factors making up their environment. For example, the evolution in animals of the visual organs, which in the planarians is only inceptive, enlarges the possible range of photic responses until light becomes an essential factor in an animal's environment, contributing largely to its welfare by enabling it to see its food, to avoid its enemies and to select its mates. It is plain that light plays no such important part in the activities of planarians, for, as has already been pointed out, light *per se* is not essential to planarians, since they are known to live successfully in dark caves. Moreover, so far as known, light does not influence the regenerative or reproductive processes of planarians in any way whatsoever. The formation of pigment may perhaps be regarded as an adaptation to light conditions, inasmuch as animals possessing pigment are thereby shielded to a certain degree from excessive stimulation.

With reference to activities connected with nutrition and reproduction, planarians are not dependent upon light stimulation. They are otherwise equipped, since they doubtless find their food by chemotactic means and avoid whatever enemies they may have, not aggressively nor actively by retreating from visible foes but rather in a passive way by remaining concealed from enemies that might see them. They have no organs of defense but survive by escaping attention. In this sense their negative phototaxis may be regarded as of protective value and consequently adaptive.

Furthermore, the geographical distribution of fresh water pla-

narians has been shown by Borelli ('93) and Wilhelmi ('04) to be chiefly dependent upon temperature and almost not at all upon the amount of illumination to which they are subjected. Voigt ('04) noticed that worms when hungry may be seen wandering about even in patches of bright sunlight with apparent disregard of light. This seems to be a case of the light reactions becoming over-balanced by other responses.

Summary. Light is not an essential factor in planarian activities, since the behavior necessary to the welfare of the individual and the race is mainly referable to other factors.

A planarian's response to light is of a passive character, which may have an adaptive significance only in so far as its phototaxis tends to conceal the worm from its enemies. The presence of pigment may also be regarded as an adaptive condition induced by the animal's relation to light.

The evolution of the photoreceptive apparatus of the planarian has not reached the degree of differentiation necessary to enable it to secure for itself such adaptations to the factor of light in its environment as would make aggressive activity possible to it in a manner characteristic of higher animals.

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E. L. MARK, *Director.*

. Abbreviations used:—

B. M. C. Z. for Bull. Mus. Comp. Zoöl.
P. A. A. for Proceed. Amer. Acad. Arts and Sci.
P. B. S. N. H. for Proceed. Bost. Soc. Nat. Hist.

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THE REACTION OF BLINDED LOBSTERS
TO LIGHT.

BY PHILIP B. HADLEY.

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THE REACTION OF BLINDED LOBSTERS TO LIGHT.

By PHILIP B. HADLEY.

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I. INTRODUCTION.

IN an earlier paper¹ the writer has considered at length some points in the behavior of the American lobster in the larval and early adolescent stages.² The investigations here reported were incidental to a more extensive study of the reactions to light of normal lobsters. They are not assumed to be complete or conclusive, and it is merely the aim of the present paper to present briefly some characteristics of the behavior of the larval and early adolescent lobsters when one or both eyes have been blinded. The experiments were conducted at the Wickford Experiment Station of the Rhode Island Fish Commission, where, through the kindness of the director, Dr. A. D. Mead, facilities for work were placed at the disposal of the writer, and where it was made possible to secure large numbers of young lobsters in all of the early and some of the later stages.

The investigations of the writer upon the behavior of the larvæ and early adolescent lobsters have led him to believe that their reactions to light are determined by two conditions of illumination:

¹ HADLEY: Report of the Rhode Island Commission of Inland Fisheries for 1906.

² Briefly stated, these results, so far as they deal with reaction to light, showed that lobster larvæ in the first three stages reacted to light by placing the longitudinal axis of the body parallel to the direction of the light rays, with the head directed away from their source; and then by swimming, by means of the exopodites of the thoracic appendages, either toward or from that source. Any change in the direction of the light rays, striking the eyes of the larvæ, determined a new direction of swimming; and any change in the intensity of light might determine a change in the index of the reaction. Thus an intensity of light, which brought about a negative reaction, might, if increased, produce a positive response.

first, the purely directive influence, so called, which, by conditioning different degrees of illumination on each eye, may cause a definite body orientation; secondly, a tendency to select, in varying intensities of light striking both eyes equally, areas of optimal illumination, and to remain therein. Experiments to date do not lead the writer to believe that the reactions of the larvæ to the intensity of light (photopathy) are produced by means of many slight responses to the directive influence of the light, as was assumed by Yerkes³ to be the case for *Daphnia pulex*. In consequence of this view the following experiments will be found to deal with three features of behavior: (1) the phototactic reaction, (2) the photopathic reaction, and (3) the method of reaction or the mechanics of orientation; and each of these points will be discussed in relation to three groups of larvæ: (1) Normal larvæ, (2) those with one eye blinded, and (3) those with both eyes blinded.

Technique. — The experiments, which were conducted with lobsters of the first five stages, were performed chiefly by daylight, in a room receiving light from the north and south, but so screened by dark curtains that the direction of the light rays could be accurately regulated. The larvæ, one or both of whose eyes had been excised by small scissors or blinded by a hot needle, were placed, as the experiments required, in one of two receptacles. — one a rectangular glass compartment $6 \times 3 \times 2$ inches; the other a wooden box $12 \times 6 \times 3$ inches, fitted with a glass bottom and a light-tight cover and painted black on the inside. During the experiments this box was set over a so-called light-shaft, which was built up from the laboratory table in such a way that parallel rays of light from a mirror, set at the base of the shaft, could be reflected up to the glass bottom of the box, which was placed 18 inches above the table, over the top of the shaft. By this contrivance all except nearly parallel rays of light were excluded, and these alone could influence the behavior of the larvæ swimming in the salt water, which was, seldom more than 12 mm. deep.

The quality of light entering the bottom of the box was further modified by plates of red, orange, green, blue, or white glass, which were laid in linear series over the top of the light-shaft, and at the same time directly under the glass bottom of the box. These plates

³ Reactions of *Daphnia pulex* to light and heat, Mark Anniversary volume, 1903, pp. 359-377.

of colored glass served to determine the intensity of light which was brought to bear on the larval lobsters, as they swam through different regions of the box. In other instances the light at opposite ends of the glass-bottomed box was regulated by graded wedge-shaped screens of gelatine which had been darkened with india ink. The resulting reactions of the larvæ were so similar and constant under both these conditions of illumination that any tendency on the part of the larvæ to gather at any particular part of the box

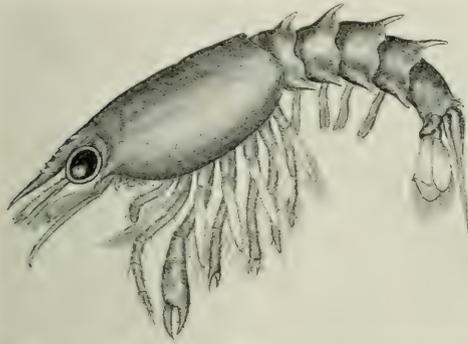


FIGURE 1.—Third-stage larval lobster, showing the position of the eyes and of the thoracic exopodites as they appear at the end of the downward stroke; also the abdominal swimmerets, which will become functional in the fourth stage.

was assumed to represent a reaction to the degree of light intensity in that area.

Since blackening the eyes of the larvæ seemed impracticable, the operation of blinding the young lobsters was performed by one of two methods,—either by searing the surface of the eye with a hot needle, or by excising the whole eye by cutting the eye stalk with a pair of small scissors. The former method gave, as a rule, better results; for, while “excising”

appeared to weaken the young lobsters, the “searing” seemed to disturb in no great measure their activity. In some groups of larvæ the left eye only was blinded, in other cases the right eye, and in still other cases both eyes. Such groups—or, in some instances, individual larvæ—were subsequently put in the rectangular glass container, which was placed in a large box blackened on the inside. This box was also fitted with windows of various sizes, and rested on the laboratory table in such a way that light was admitted to the glass container by means of such windows only. With this arrangement the aim was to ascertain either the index of reaction of groups of larvæ to the directive influence of the light, or to study the characteristic behavior of single blinded larvæ when subjected to similar light influences.

II. REACTION OF NORMAL LOBSTERS.

About one hundred first-stage larvæ, from forty-eight to fifty-four hours old, were transferred from one of the large hatching-bags to a crystallization dish. When this was set within the dark box and submitted to light coming from one direction through the side window, every larva oriented with the head away from the light and swam backward toward the window side of the dish (Fig. 2).

When twenty of these larvæ were transferred to the glass-bottomed box, which was mounted over the light-shaft and overlying the colored glass plates, the reaction showed that the majority of larvæ grouped themselves in the most brightly illuminated area, as represented below :

Time	Red.	Orange.	Green.	Blue.
3 10	0	1	1	18
3 15	1	2	4	13
3 20	0	0	2	18
3 25	1	0	2	17
Totals	2	3	9	66

Between each trial the position of the box was reversed. In the next instance the order of the glass plates was changed, and the results, which were as follows, show that the majority of larvæ still oriented in the brightest area of the box :

Time.	Green.	Red.	White.	Orange.
3.35	1	2	17	0
3.45	3	2	15	0
3.50	0	2	17	1
3 55	0	1	16	3
Totals	4	7	65	4

In the preceding lists it was observed that many of the larvæ which gathered over the white glass became oriented with the back downward, a position never favorable to progressive orientation. Since it was believed that this factor might be to some extent responsible for the gathering in the areas of the greatest illumination, in the next case the glass-bottomed box was set over a black background, the colored glass plates ranged in linear series over the top of the box, and the light admitted from above. The position of the glass plates was frequently changed, and the records of several tests, which were made at five-minute intervals, and which show that the larvæ still persisted in gathering in areas of greatest illumination, are as follows:

Red.	Orange.	Green.	White.
0	1	2	17
2	0	2	16
White.	Green.	Orange.	Red.
17	2	1	0
17	1	2	0
Green.	Orange.	White.	Red.
0	2	15	3
0	1	16	3

Experiments similar to the foregoing were conducted with fourth-stage and fifth-stage lobsters. Since the exopodites or thoracic appendages, by means of which the larval lobsters of the first three stages swim, are lost in the moult from the third to the fourth stage, some change in the type of reaction in the fourth and later stages might be expected. The differences which were found to exist are not of great importance to present considerations, but may be briefly outlined as follows: The normal fourth-stage lobsters, which for the greater part of the stage swim freely by means of the abdominal swimmerets, manifest throughout the stage-period a

negative phototactic reaction, which is accentuated towards the close of the stage. The photopathic reaction, which at the beginning is usually positive, gradually changes by the close of the stage-period to negative in the majority of fourth-stage lobsters. Generally speaking, the reactions of the fifth-stage lobsters are typical of the adult form, and are chiefly characterized by the light-shunning instinct. The phototactic and photopathic reactions are negative from the beginning of this stage to the end of it. As in the earlier stages, so in the fourth and fifth, the eyes play a most important rôle in determining the nature of the reaction to light, although the invariable tendency to "head" away from the light is never again, in the later life of the lobster, so strongly manifested as during the first three larval stages.

The results of the foregoing experiments show, first, that the normal first-stage larvæ react to the directive influence of the light rays by placing the longitudinal axis of the body, parallel to them, with the head away from the source of light, and by swimming toward that source. Lobsters in the later larval stages may at times, however, gather in the darker areas. Fourth-stage and fifth-stage lobsters do not manifest so strongly the tendency to place the axis of the body parallel to the direction of the incident light rays, although they do undergo definite progressive orientations.

III. REACTIONS OF LOBSTERS WITH ONE EYE BLINDED.

From the group of first-stage larvæ which, as has been shown above, were reacting positively to light, ten were selected and blinded, by means of a hot needle, in the left eye. Subsequently, these ten larvæ were put in the glass container, and this placed in the dark box. When the light was admitted through a small window to the side of the glass container, the larvæ underwent both a body-orientation and a progressive orientation. Both these orientations, however, usually occurred only when the intensity of light was not great, and both differed in their nature from the reaction of normal larvæ under similar conditions. The body-orientation was not characterized by placing the longitudinal axis of the body exactly parallel, but slightly oblique, to the direction of the light rays, as shown in Fig. 3; the progressive orientation took place as in normal larvæ, except that the reaction was less definite. The latter may be outlined as follows:

Positive.	Neutral.	Negative.
7	3	0
6	3	1
4	4	2
3	5	2
7	2	1
4	3	3
31	20	9

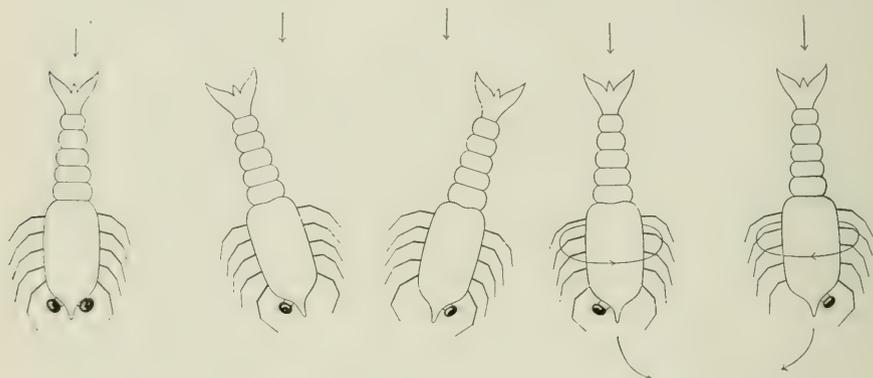
Next, these same larvæ were transferred to the glass-bottomed box mounted on the colored glass plates over the light-shaft. Records of the position of the larvæ were made at five-minute intervals, between which the box was reversed, and resulted as follows:

Red.	Orange.	Green.	White.
2	2	1	5
1	2	2	5
0	0	4	6
0	0	2	8
3	4	9	24

Similar experiments to ascertain the effect of blinding one eye upon the definiteness of reaction of fourth-stage and fifth-stage lobsters gave much the same results as in the case of the larvæ. The index of response was the same as that of normal lobsters from the same group, but the small number which at any one time would give a definite reaction, either positive or negative, showed that blinding had seriously disturbed the functions of some organs through which orientation to light is brought about.

These general results depend upon a large number of experiments on lobsters in all stages of development. Only a sufficient number of instances can be here reported to give a general idea of the reactions.

The methods of reaction. — There remains to be mentioned the method of body-orientation in larvæ having one eye blinded. The writer has already called attention⁴ to the fact that, in the case of normal larvæ, the behavior from one minute to another is made up of a large number of strange movements, — rotations, revolutions, swingings, turnings; furthermore, that these peculiar gymnastics are dependent upon the relative intensity of the light striking the eyes of the larvæ: light from one side determines a quick turning in the opposite direction; light from above precipitates



FIGURES 2-6.

the larva head first, or at least causes the assumption of a new swimming-position with the head downward; while light from below causes the larva to assume a body-position with the head directed slightly upward.

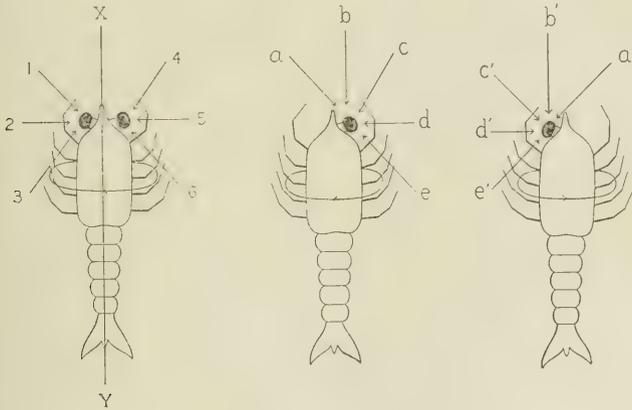
In the case of larvæ with the left eye blinded the results were found to be quite different. The swingings and rotations were invariably in a definite direction. Very frequently the most common reaction directly following the removal or blinding of the left eye was a long series of rotations on the longitudinal axis of the body. These rotations occurred with great rapidity, often at the rate of 150 per minute, and took place, moreover, in a determined direction, as shown in Figs. 5 and 6. Usually these rapid rotations soon subsided, although they might for an hour or more re-occur at intervals. When the larvæ attempted forward swimming, the line of progress invariably became an arc curving toward the side of

⁴ HADLEY: Annual report of the Rhode Island Commission of Inland Fisheries for 1906.

the injured eye, as shown in Figs. 5 and 6, and often the larvæ swam for several moments in small circles, about 3 c.c. in diameter.

If the right eyes of the larvæ were blinded, the resulting reaction was reversed. The body rotations were now in the direction indicated in Fig. 6, while in the case of straightforward swimming the progression took place in the direction of an arc curving as shown in Fig. 6.

It is not difficult to find the reason for these types of reaction in larvæ with blinded eyes. Any rotation of the larvæ on the longitu-



FIGURES 7-9.

dinal axis of the body is caused by unequal forces exerted by the thoracic exopodites on opposite sides of the body. In instances where rapid and continued rotations occurred, the vibration of the exopodites on the side of the blinded eye was reduced to a minimum, while in some cases the stroke of the exopodites on the side of the injured eye appeared to be correspondingly accelerated. Under natural conditions of eye stimulation the forces exerted by the exopodites on opposite sides of the body exactly counterbalanced one another. But when, for any reason, one set beat more rapidly than the other, there resulted either a single rotation, or a series of rotations on the long body axis, or a swing of the long axis toward the right or toward the left, according as the greater intensity of light was brought to bear on the right or the left eye of the larva.

In this connection one other point regarding the direction of light striking the injured eye and the localization of the stimulus is of

interest. If the light was introduced to a normal larva from direction designated 1 (Fig. 7), the head of the larva would swing toward the right; while, if the light was introduced in the direction 6, the head of the larva would swing toward the left. The reason for this is that the greater intensity of light on one eye causes a stronger action of the exopodites on that side, with a consequent interruption of the equilibrium, and the larva swings toward the opposite side, or, under certain conditions, undergoes a rotation on the longitudinal body axis. In other words, the direction of turning of the larva is invariably determined by the direction from which the light comes, and the consequent inequality of illumination of the two eyes. It is, therefore, easy to understand why, in the case of the normal larvæ, the turn is always in the direction of the shortest path by which the head may come to face directly away from the source of light.

Here, again, is a great difference when we attempt to contrast with the above-mentioned type of reaction that of larvæ with a blinded eye. When the left eye was blinded and the light was allowed to strike the uninjured right eye, the reaction was the same, from whatever direction the light might come. If, for instance, the larva was represented as in Fig. 8, and the light entered from the direction designated by arrows *a, b, c, d, e*, upon the right uninjured eye, the direction of movement was toward the left in every case; or if rotations on the longitudinal axis took place, these were invariably in the direction represented by the arrow passing around the body of the larva, as in Fig. 8.

If, on the other hand, the right eye was blinded and the rays of light came from the direction represented by the arrows in Fig. 9, then the turning of the larva was toward the right; or if rotations on the longitudinal axis occurred, these rotations were in the direction indicated by the arrow passing around the body of the larva, as in Fig. 9.

It thus becomes clear that the mechanics of orientation in the case of larvæ with one injured eye does not involve a swinging which brings the body by the shortest path to lie parallel to the direction of the light rays, as is the case for larvæ with normal eyes. The typical reaction is a swinging in a single direction; yet this direction may not be, at first, away from the source of light, but even more fully toward it than before. This point is represented more clearly by Figs. 7, 8, and 9. Let Fig. 7 represent a

larva with both eyes normal, Fig. 8 one with the left eye blinded, and Fig. 9 one with the right eye blinded. When, now, the light coming in the direction of the arrow 1, Fig. 7, struck the eyes of the larva, the reaction was an immediate swing toward the right, so that the long axis ($x - y$) of the larva came to lie parallel to the direction of the incident light rays, and the head pointed as represented by arrow 1. If, again, the rays impinged in direction of arrow 4, then the swing was toward the left and the longitudinal axis of the body assumed the direction of the incident rays, and with the head pointing as shown by arrow 4. The same method of reaction obtained in the orientation to light coming from the directions indicated by the arrows 2, 3, 5, 6. In all these instances the swing of the larva was by the shortest path that would bring the head to face away from the source of light, and the longitudinal axis of the body to lie parallel to the direction of the incident rays.

In Fig. 8 the conditions represented were different. When the light rays came from the direction indicated by the arrow a , the direction of swinging of the body-axis was invariably the same; the larva would swing to the left and through the supplement of the angle, through which it naturally would swing if both eyes were normal and the light came from the same direction. This method of orientation invariably took place, notwithstanding that in this swing the head of the larva must face directly, though momentarily, the source of light,—a condition of affairs quite unknown in the behavior of normal lobster larvæ. Here there are no conditions known that can cause a larva to face the source of light, even for an instant. Every movement serves to one end,—to bring the head away from the source of illumination. Yet, under the conditions represented in Fig. 8, if the light came from any of the directions indicated by arrows c , d , e , the resultant reaction was the same as that in the case of larvæ with both eyes normal.

In the conditions indicated by Fig. 9 the principle of the reaction was the same, but the results were reversed. In this case the right eye was blinded. If now the incident light rays took the direction represented by arrow a' , the larva would swing, not toward the left (as in the instance of normal larvæ, Fig. 7), but toward the right. In other words, the longitudinal axis of the larva would pass through the supplement of that angle through which it would naturally swing if both eyes were normal and the light came from the same direction. In case, however, the light came from the

direction designated by the arrows c' , d' , e' , then the reaction is the same as that of larvæ with both eyes normal. In other words, when in both the last cases (illustrated by Figs. 8 and 9) the light struck the larvæ from the side of the normal eye (Fig. 8 c , d , e ; Fig. 9 c' , d' , e'), then the resulting reaction was similar to that which occurred in larvæ with uninjured eyes: the larva would swing directly away from the light by the shortest path that would bring the uninjured eye to face away from the source of light (Figs. 2 and 3). Yet in this instance the long axis of the body was never brought exactly parallel to the direction of the light rays, but at a slight angle to them, so that the uninjured eye received the least possible stimulation. But even this body-orientation was seldom long maintained, since the tendency to manifest circus movements or to progress in an arc curving toward the side of the injured eye was ever present, regardless of the direction of the light rays. It is presumable that, for this reason, when larvæ with one eye blinded were placed under the influence of light from different directions, they might be observed to invariably progress by swingings or by rotations toward the side of the blinded eye. This aspect of behavior is to be seen in blinded larvæ of all the early stages, but most definitely during the first-stage period.

Observations on the behavior of fourth-stage and fifth-stage lobsters having one eye blinded gave similar results, although the tendency to assume body-positions with the head directed away from the light was not so prominent in these and later stages. In the fourth-stage lobsters with one eye blinded, the definiteness of both photopathic and phototactic response was lessened. The effect of illumination upon the good eye, moreover, was similar to that obtained in larvæ in earlier stages, except as it was modified by the difference in the manner of swimming which obtains between lobsters of the fourth and earlier stages. The free swimming of the fourth-stage lobsters having one blinded eye was invariably in an arc which curved away from the side of the uninjured eye. But while in the first-stage larvæ this arc of turning was usually one of small radius, the swimming-curve of the fourth-stage lobsters was one of much greater latitude; so that, for instance, when such lobsters were confined in a crystallization dish having a diameter of 150 mm., they swam in a circle about the rim of the dish and always in the same direction: if the right eye was blinded, clockwise; if the left eye was blinded, counter-clockwise. Often the

operation of blinding acted as a temporary stimulus to more energetic swimming. In such cases the larva would swim actively for a brief time in a circle of large radius. As fatigue increased, the radius of the circle decreased, with the result that a spiral-like course of progression was generally produced. The amplitude of the spiral gradually diminished, and eventually the lobsters would come to rest and fall to the bottom of the dish. It may here be noted that the rotations on the longitudinal body-axis, characteristic of larvæ in the first three stages blinded in one eye, never occurred in lobsters of the fourth or later stages. This is of course determined by the loss of the thoracic exopodites, by which in the early stages this rotary motion is produced.

In the fifth-stage lobsters the tendency to crawl over the bottom rather than to swim at the surface modified to no great extent the nature of the reaction in individuals having one eye blinded. Here also was manifested the same tendency to crawl in a circle and always away from the side of the good eye, and with the injured eye looking toward the centre of the circle.

IV. REACTIONS OF LARVÆ WITH BOTH EYES BLINDED.

From the same large group of larvæ from which the blinded lobsters mentioned in the last section were taken, ten others were selected, and their reactions tested in the rectangular container and in the glass-bottomed box. In both instances a definite positive

Positive.	Neutral.	Negative.
2	5	3
3	4	3
4	3	3
5	5	0
14	17	9

reaction resulted, and the mechanics of orientation was found to be similar to that observed in all previous cases.

Next, these larvæ were blinded, by means of the hot needle in both eyes. After the operations it was observed that blinding the

second eye, although it diminished the activity, appeared rather to re-establish the equilibrium than to cause a complete cessation of swimming movements in both the right and left sets of thoracic exopodites. When these fully blinded larvæ were transferred to the rectangular compartment, and this placed in the dark box, the reaction was as recorded in the preceding table.

Subsequently these larvæ were placed in the glass-bottomed box over the light-shaft, and submitted to the influence of the monochromatic lights. Many tests were made at five-minute intervals, and the position of the box was reversed between each test. The following record is characteristic of all:

Red.	Orange.	Green.	White.
3	2	2	3
2	2	2	4
2	1	3	4
3	2	4	1
10	7	11	12

When these larvæ were submitted to the influence of lights coming from many different directions, as in a room illuminated by several windows, no particular body orientation to the light could be observed, and the mechanics of orientation involved a turning, now in one direction, now in another. In other words, the reactions determined by the conditions of light were at a minimum, — as much so as the reactions of larvæ in deep twilight or darkness.

These records are typical of the results of many tests, the details of which cannot now be presented. In sum, they appear to demonstrate that the larval lobsters blinded in both eyes underwent no definite orientation to light, but became scattered homogeneously through the area of their confinement. Similar results, moreover, were obtained with fourth-stage and fifth-stage lobsters. Here also no definitely positive or negative phototactic or photopathic reaction was observed, but a homogeneous scattering, such as took place in the case of the larval lobsters.

V. CONCLUSIONS.

Perhaps the most important issue to which the foregoing observations lead involves, primarily, a consideration of the very intimate connection between the optical stimulation and the definite muscular reactions, which in the larval lobsters invariably follow. And co-ordinate with this point is the question of the degree to which the method of "trial and error" may enter into the behavior of the young lobsters, normal or blinded.

In the light of the experiments which have been recorded, it appears that stimulating with light one eye of a young lobster has its effect—depending upon the stage of the larva—upon three different sets of appendages which serve the purpose of locomotion; and that such stimulation is effective only on that side of the body which corresponds with the uninjured eye. In the first three larval stages the means of locomotion are the exopodites of the thoracic appendages. In the fourth stage, which is the free swimming stage *par excellence* of the lobster's existence, the means of swimming is found in the swimmerets, the paired, paddle-like abdominal appendages; while in the fifth-stage lobster, which is essentially a crawling animal, the usual means of progression is limited to the thoracic ambulatory appendages,—the legs proper, although in this stage also there may be brief and infrequent periods of swimming. In each of these cases it has been demonstrated that a very intimate connection exists between the eye, on one hand, and, on the other, the exopodites, the swimmerets, and the legs proper, on the same side of the body. A slight change in the intensity of light striking one eye is immediately followed by a succession of muscular extensions and contractions which concern alone that side of the body, and which determine, through medium of the nervous system and the appropriate appendages, the immediate assumption of a new body-position, which may be one of rest or one of continued movement.

Nothing can be farther removed from the orienting reaction of the larval lobsters to light than the method of "trial and error." The larval lobsters are, to all practical purposes, mere machines, upon which the forces of light act through the medium of the eyes, nervous system and appendages, and produce a constant and invariable result. There is no random movement, no evidence of "choice." The turning of the larval lobster in a certain direction

is dependent upon the vibration of the exopodites of the thoracic appendages: the vibration of the exopodites is dependent upon nervous excitation; this excitation is produced and regulated by the stimulation of the eyes of the larva. If one side of the larva receives more light than the other side, the eye on that side receives more stimulation. In consequence, the exopodites on that side beat the water more strongly and rapidly, and the larva "comes around" like a skiff to a position in which the equal stimulation of the two eyes determines an equally strong vibration of the exopodites on each side of the body, and consequently the re-establishment of a balanced equilibrium. In this instance the light impinging upon the eyes of the larva regulates the activity of the exopodites as regularly and as definitely as an electric current the movement of a magnet bar. That the movement of the exopodites causes the larva to head away from the light is not difficult to explain. The centre of the force exerted by the exopodites is anterior to the centre of equilibrium of the larva. When one eye is directed more nearly toward the light, the force of the vibrating exopodites is so applied as to swing the anterior end of the body. As soon as this end has assumed such a position that the eyes are no longer stimulated, or equally so, then the movements of the exopodites cease, or the vibration of the right and left sets counterbalance each other.

When one eye is blinded, the stimulus needful to maintain the vibratory movements of the exopodites on that side of the body is absent, and, in consequence, the anterior or head end of the larva is swung out of line as a result of the stronger action of the exopodites on the opposite side, whose activity is still sustained by stimulation through medium of the uninjured eye, until, by the turning of the larva, this eye comes to lie in the shadow. When both eyes are injured, the equilibrium has a tendency to become re-established by reason of an equal lessening of stimulus on each eye. That, under these conditions, some other factor than stimulation by light is operative in maintaining the vibration of the exopodites is clear, for these swimming movements, although much diminished in rapidity and force, still keep the larva in a kind of equilibrium, minus either body-orientation or progressive orientation. This continued action of the swimming appendages may be attributed to imperfect blinding, but more likely to mechanical irritation resulting from the operation of searing the eyes or of cutting the eye stalks.

The point of concise localization of function of different areas

of the relatively large compound eyes, as investigated by Holmes,⁵ was not undertaken in connection with the present work. Holmes ascertained that if only the lateral surface of one eye of *Ranatra* was exposed to light, the action of the flexor muscles on the same side, and of the extensor muscles on the opposite side, of the body was increased. The tendency to produce circus movements was checked and followed by a turn in the opposite direction. Holmes attributed this turn to the diminished amount of light received by the eye as it turned away from the source. This diminution, he concluded, acted as "a stimulus to a movement in the opposite direction." In the larval lobsters the lighted area of the eyes was never mechanically restricted, and it is not known what effect such limitation of the surface illuminated would have had upon the behavior. It was clear, however, that in the lobster larvæ with one eye fully blinded there was no such conflict of impulses as described by Holmes.⁶ No other tendency, nor any influences, save that of diminishing the light, hindered the continuance of the circus movements; and even in the latter case there was no inclination to turn in the opposite direction, but merely a tendency to remain unresponsive in the same body-orientation. Regarding the mechanics of this reaction, moreover, the stimulation of one eye by light was not observed to cause an increase in the action of the flexor muscles on the same side and of the extensors on the opposite side. Such stimulation increased the action of *both* the flexors and extensors on the same side, whether these muscles were associated with the thoracic exopodites, the abdominal swimmerets, or the legs proper; moreover, both phases of muscular action in the corresponding appendages of the opposite side of the body were proportionately diminished.

Although those results correspond, in a degree, with those obtained by Holmes⁷ from experiments with blinded amphipods, certain exceptions are to be noted. His general conclusion was as follows: "Blackening over one eye of the terrestrial amphipods and in several positively phototactic species of insects causes the animal to perform circus movements with the unblackened eye looking toward the centre of the circle. Blackening over one eye in negatively phototactic amphipods causes circus movements to be

⁵ HOLMES: *Journal of neurology and psychology*, 1905, xiv, p. 305.

⁶ HOLMES: *Loc. cit.*

⁷ HOLMES: *This journal*, 1901, v, p. 211.

performed in the opposite direction." This statement of the case indicates that in positive animals the light acts as an inhibiting agent producing lesser movement on the side of the body upon which it acts through the medium of the unblackened eye, while in negatively phototactic animals, on the other hand, the light acts as a stimulating agent on that side of the body which it influences through the medium of the unblackened eye.

In the lobster larvæ all the progressive reactions which took place immediately following the blinding of one eye were positive. In certain cases it appeared that either the operation itself or the effects of blinding changed the index of reaction from negative to positive. In all these instances, whether the previous reaction had been negative or positive, the resulting behavior was the same: a series of revolutions, of circus movements, or a progression in which the direction of turning indicated that the influence of light on the unblackened eye was to cause greater activity of the swimming appendages on that side of the body, while blinding invariably had the opposite effect. In other words, the reaction of the blinded positively reacting lobster larvæ corresponds with those of Holmes's negatively reacting amphipod, *Hyaella dentata* (Smith), but not with his positively reacting amphipods.

The reactions which have been described in the foregoing pages were characteristic of the larval lobsters, whether they were, at the time or previously, reacting positively or negatively to light. As the writer has shown in other papers,⁸ the index of the phototactic response depends upon the intensity of the light which strikes in equal degree the two eyes of the larva, and determines whether the exopodites shall beat forward and downward or backward and downward. This difference in stroke (especially the "posterior" or "negative position") is not manifested to so great an extent in larvæ with one blinded eye, and it is perhaps for this reason that such larvæ manifest so slightly the definitely negative progressive orientation. The writer hopes at a later date to study more fully the method employed by blinded larvæ in their continuous progression toward the light or away from it. It has been the aim of the present paper merely to give the general results of such reactions, and to describe, more in detail, the immediate changes induced by light upon the body-orientation with respect to the direction of the light rays.

⁸ HADLEY: *Loc. cit.*; also, This journal, 1906, xvii, p. 326.

VI. SUMMARY.

1. **Reaction of normal larvæ**—(a) The normal first-stage larvæ, within forty-eight to sixty hours after hatching, react to the directive influence of the light rays by placing the longitudinal axis of the body parallel to the incident rays, and then, with the head directed away, approaching their source. After the second day negative reactions may be manifested.

(b) If submitted to the influence of non-directive light, the larvæ usually congregate in the areas of brightest illumination. These reactions are definite and strongly manifested.

(c) The mechanics of orientation involves direct motor reflexes, due to the unequal stimulation of the two eyes, and accomplished through medium of the nervous system and thoracic exopodites, whose action causes the larvæ to place their longitudinal axes parallel to the direction of the light rays. In the fourth stage the swimming is accomplished by the abdominal swimmerets, while the fifth-stage lobster crawls with the true legs.

2. **Reaction of larvæ blinded in one eye.**—(a) The larvæ of any of the first three stages, when one eye is blinded, react to the directive influence of the light and to differences in intensity like normal larvæ, except that the reactions are much less definite, and are seldom negative except in fourth and later-stage lobsters.

(b) The immediate results following the destruction of photo-reception in one eye are: (1) The production of rapid rotations (often at the rate of 150 per minute) on the longitudinal axis of the body, which are invariably in a determined direction,—that shown in Figs. 5 and 6; (2) A type of progression in which the larva continually performs “circus movements,” or turns toward the side of the injured eye.

(c) The mechanics of orientation in such cases involves direct motor reflexes dependent upon the over-stimulation of one set of thoracic exopodites through the medium of the uninjured eye, and the lack of stimulation of the opposite set of exopodites as a result of destroying the photo-receptors in the blinded eye.

3. **Reaction of larvæ blinded in both eyes.**—When both eyes of the larvæ are blinded, there is no reaction, either to the directive influence, or to differences in the intensity, of light. In such cases the progressive swimming is weak, but more balanced than in larvæ

with one blinded eye, since the photo-receptivity in both eyes is the same.

4. The reactions of blinded fourth-stage and fifth-stage lobsters correspond to those of the larval lobsters, except as the former are modified by the swimming and crawling methods of progression respectively characteristic of lobsters in the fourth and fifth stages.

5. The direction, *per se*, of the light rays (unless it be because of a certain course through the body) has no influence in bringing about a reaction: If approximately the same area of the right eye is stimulated by light coming from any direction, the resulting reaction is the same.

6. The evidence gained from observation on the behavior of blinded and of normal lobsters demonstrates that many of the complexities of behavior (especially in the body-orientations) in the larval and early adolescent lobsters can be reduced to, and explained on the basis of, simple motor reflexes, which show no trace of random movement or of "choice" and have nothing in common with the method of "trial and error."

THEORIES OF BIRD MIGRATION.

BY HERBERT E. WALTER

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THEORIES OF BIRD MIGRATION.

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Migratory Route of the American Golden Plover

The American Golden Plover is known to travel in the neighborhood of 15,000 miles a year. Its breeding grounds are well within the arctic circle far beyond the northern tree line. In fact Gen. Greeley, the arctic explorer, found it nesting at 81° N. latitude within 600 miles of the north pole. These remarkable birds arrive in the far north about June 1st, remaining there approximately ten weeks. By the latter part of August, nesting duties completed, they have already traveled as far south as Labrador where a rich temporary feeding ground supplies them while the crowberries, common to that region, are ripening. From Labrador they move further south to Nova Scotia, and thence straight out over the open ocean 1,800 miles to the islands that lie east of Cuba and Porto Rico, sometimes breaking the journey at the Bermudas 800 miles south of Nova Scotia but more frequently passing by to the eastward. From the Eastern Antilles to the continent of South America is a flight of 600 miles more and after this mainland is reached they press on to the pampas region of Patagonia where they remain for the winter months, 8,000 miles from their nesting grounds. March finds them on the move again as far north as Guatemala and Texas. During April they are traversing the Mississippi valley, in May the vast territory of Canada, while early in June they are nest-building again in the land of the midnight sun, having completed the 15,000 mile circuit.

What explanation can be given to account for such astonishing behavior? How is a bird, who weighs only a few ounces and whose brain can easily be packed in a thimble, able to find its way over such vast reaches of land and sea, and what are the laws which impel it to carry out such a colossal undertaking in the face of all sorts of perils, not only once in a lifetime but every year so long as it lives? The American Golden Plover is an extreme case, but the laws which govern its behavior are doubtless the same as those which cause the lesser, but quite as noteworthy, migratory movements so generally observed among bird kind.

Early Mention of Migration

The migrations of birds have been recognized by man from the earliest times. Mention is made in the book of Job of the hawk that "stretches her wings toward the south." Homer observed the mighty rush of the water

fowl northward in the spring and Anacreon, in classic lines, welcomed the returning swallow five centuries before Christ.

Schlegel

Serious attempts to ascertain the facts of migration in any detail have been attempted only within the last century. For instance in 1828 Schlegel of Harlem made an analysis of the accounts of travelers in various lands upon 130 different journeys. After compiling all references which these travelers made to the birds which they saw he concluded from these heterogeneous statistics that, for any given locality, birds might be divided into three groups; first, *residents*, who remain all the year in one locality; second, *erratic wanderers*, who appear irregularly, and third, *migrants*, who pass through the locality at regular times. Since Schlegel's time there has followed many years of faunistic work by various observers who have catalogued the birds known to occur in different localities. This extremely useful kind of work is still being done in both hemispheres, since, until the general distribution of birds is more accurately known mere speculation upon their movements is productive of few results.

von Middendorf

In 1855 von Middendorf of St. Petersburg combined all the faunistic data then available in an attempt to find out the manner of bird movements by means of what he termed isopeptic lines. The isopeptic lines were arbitrarily formed by connecting the points of first arrival of certain species over as large an area as possible for any one date. By constructing a series of such isopeptic lines upon the map of Russia for succeeding dates he obtained a graphic representation of the kind of advance made during migration, throughout that region, drawing therefrom the general conclusion that birds move forward during migration in a broad front. Furthermore, the direction of the main European migration routes he determined theoretically by extending lines at right angles to the isopeptic lines.

**Sundevall and
Peters**

It soon came to be seen, however, that only general results could be hoped for so long as particular instances were not known. The first attempt to obtain detailed data concerning the movements of any single species of birds was the outcome of a correspondence about the migration of storks begun during 1862 between Sundevall in Sweden and Peters in Berlin. These two naturalists called upon their colleagues to aid them in making observations at various localities. Thus in a short time a large amount of data was collected concerning the migratory movements of storks, a species particularly favorable for study by reason of their being so conspicuous and

everywhere well known. As the result of this collaboration, the migratory route of the stork in Europe has been established with considerable accuracy.

Palmen

The efforts of Sundevall and Peters were followed in 1876 by the masterly work of Palmén of Sweden who determined the migratory route of nineteen species of European birds. Palmén emphasized the fact that birds do not travel in a "broad front" as suggested by von Middendorf but that instead each species moves in a definite path or route of its own.

Cooke

About 25 years ago the U. S. Biological Survey began a systematic collection of data concerning the movements of migratory birds in North America and already several most valuable papers, based upon the abundant data thus being collected, have appeared from the pen of Mr. W. W. Cooke, who is in charge of these admirable investigations.

Meanwhile speculations have multiplied far in advance of facts. It goes without saying that satisfactory explanations of the laws governing bird migration can only be hoped for after a far greater basis of facts has been established. However, speculations and theories of bird movements, unsatisfactory as they are, possess a certain interest, not to say value, as indicating the progress of science along this line of investigation. These guesses at the truth may accordingly be grouped as the answers to two questions: first, how do birds find their way in migration, and second, why do birds migrate?

I. How do Birds Find Their Way in Migration?

Instinct Theory

To say that birds find their way instinctively is only a roundabout method of acknowledging that we do not know what the mechanism of migration is. The term "instinct" is a vague generalization which, being made to apply to many diverse phenomena, loses its value in any particular case. Moreover the instinct theory not only does not explain anything but, since it does not admit of experimental test, closes the door upon the hope of ever reaching a satisfactory explanation of the phenomena to which it is applied.

Magnetism Theory

In 1855 von Middendorf, to whom reference has already been made, advanced the novel theory that birds are guided by lines of terrestrial magnetism which cross in the body after some such fashion as in a solenoid. This speculation is interesting because there is no known fact whatever in support of it. There are, however, facts against it. In North America, for example, birds do not go toward the magnetic

pole as they appeared to von Middendorf to do in Russia. So far as I am aware there is among plants and animals no known case of response in any way to magnetic force.

Semi-circular

Canal Theory

The attempt to locate some organ within the bird to which this function of path-finding might be referable resulted in the Mach-Breuer theory of the semi-circular canals which was elaborated particularly to explain how the carrier pigeon finds its way home. This theory rests upon the supposition that the semi-circular canals of the inner ear form an organ of equilibration by means of which an animal can orient itself in any of the three planes of space. Each of these three canals, which are situated at right angles to each other, enlarges at one of its ends into an ampulla, within which, surrounded by endolymphatic fluid, are located delicate nerve endings coming from the eighth cranial nerve. In whatever position the ear is held the endolymphatic fluid within the semi-circular canals presses more upon the nerve endings within one ampulla than upon those of the other two, and the particular stimulation thus received, upon being transferred to the brain, records for the animal its position in space. Along with this sensory registry of positions in space it is assumed that there has been developed the ability to record intervals of time upon the brain automatically. It is interesting in this connection to notice that the recognition of time intervals is a basic principle of music and birds are notably musical. Besides a registry of position in space and of time intervals there may be developed a registry of the distance traversed, in case a uniform speed is maintained. Thus when a pigeon going away from home travels at a given speed, for example, east twenty minutes, north thirty minutes and east again ten minutes, all these changes in direction, together with the time occupied in making them and consequently the distance traveled in following each direction, are recorded upon the brain as sounds are recorded upon the cylinder of a phonograph. To accomplish the return journey it is only necessary to reverse the record made upon the brain in order to get back to the starting point.

A theory of this kind has the advantage of being capable of experiments to test its soundness, and such a test was made in 1893 by Professor Sigmund Exner in Vienna. Exner attempted to find experimentally whether the brain of the carrier pigeon records automatically the direction and distance taken in the outward journey in such a way as to be equipped to make the journey home. He first took two covered cages of pigeons several miles away from home to a locality unknown to the birds and out of

sight of all familiar landmarks. During the journey one cage, which was suspended on a wire, was rotated hundreds of times at every point where the direction of the route was changed, while the other cage, containing control pigeons, was borne with great care in order to introduce as little confusion in the stimuli received by the semi-circular canals as possible. When released at the journey's end one at a time so that they could receive no aid from seeing each other, Exner found that, out of the entire number, the first pigeon to arrive home was one that had been whirled! In further experiments Exner produced galvanic dizziness in half of his pigeons during the outward journey by means of a portable dry battery with which he repeatedly sent a slight galvanic shock through the ears. This operation causes a dizziness which is referable to a failure in the semi-circular canals properly to function. Thus in the case of his "galvanized" pigeons the semi-circular canals had been unable to make records with any completeness during the outward journey but, notwithstanding the fact, such pigeons found their way home as quickly as the control individuals which had not been so treated.

Finally, Exner narcotized pigeons in order to destroy their power of recording stimuli, with similar results. He accordingly concluded it is impossible so to confuse the sensory impressions received by a carrier pigeon upon its outward journey as to interfere with its ability to find its way home. Therefore, although the semi-circular canals undoubtedly assist very largely in equilibration and orientation as a mechanism to guide the homing pigeon they are inadequate and, taken alone, they certainly cannot account for the much more extensive journeyings of migrating birds.

Sense of Direction Theory · Certain investigators have attempted to attribute to migrating birds a sixth sense, namely of direction, without going into embarrassing details as to what the physical basis of such a supposed sense might be. It has been repeatedly noticed that animals other than birds have an apparent sense of direction. Everyone can tell, either from experience or hearsay, the uncanny way in which a cat, tied securely in a bag and taken ten miles away and deserted, is found on the doorstep waiting to be let in when its unappreciating master returns home. But seriously after all the discounts rendered necessary by the accounts of the nature fakirs have been made, there remains in the behavior of animals a considerable residue of fact which seems to have its only explanation in the assumption of a sense of direction.

An instance is given by members of the Harriman Expedition in Alaska of the remarkable flight of murrelets in a dense fog between Unalaska island and their feeding ground upon another

island about 60 miles away. These birds were seen repeatedly looming up in the fog behind the steamer then passing on ahead out of sight, flying as steadily and surely as if by compass although it was possible to see hardly more than a boat's length ahead. Such cases strengthen the conviction of many that there must be present in birds an unknown sense which serves them in some such way as the compass serves the mariner. This view, however, is hardly better than the instinct theory since it gives the answer to the problem in unknown terms.

The Landmark Theory

The landmark theory has rather more to recommend it. Exner came to the conclusion that carrier pigeons find their way home by seeing familiar landmarks and when such landmarks are not visible the birds explore until landmarks are found. This explains how his pigeons, whether whirled, galvanized or narcotized, were quite as well able to get home as those which had not undergone such interference with their sensory impressions upon the outward journey. Anyone who has observed swallows hawking for insects upon a summer afternoon or who has seen a hawk swoop down upon a field mouse from a dizzy height in the sky, must be convinced that the sight of birds is very acute. This is proven not only by their behavior but by anatomical evidence as well. The eye of the hawk is perhaps the most perfect optical instrument in nature. So far as the sense of sight goes it may be admitted that birds are well endowed to observe landmarks from a distance, while those birds that habitually migrate during the twilight, as nighthawks, bitterns, woodcock and certain sandpipers, being accustomed to feed at this time of day, have no difficulty in seeing objects in semi-light.

The objection must be raised to the landmark theory, however, that many birds do not follow river valleys, coast lines or mountain chains in the way they might be expected to do if they were guided by what appear to us to be the most obvious landmarks. Furthermore, migratory birds leave Cuba for Florida without hesitation upon cloudy nights when no landmarks are possibly visible and the stretch across the Gulf of Mexico, which is also regularly traversed by birds, is so great that even if migrants rose to a height of five miles, which is beyond reason, they could scarcely see one third of the way across to the other shore on account of the curvature of the earth. Sight alone, then, although it is an important factor, cannot be the only resource of the migratory bird.

The Follow-the-Leader Theory

Still another theory with a large element of probability in it may be briefly described as follows. Birds are social animals and fly in company with each other. The total migratory stream is a vast straggling army, spreading

out or narrowing according to the character of the country over which it is passing. Dispersion over a wide area is the surest method of finding the way for in this manner a larger area of landmarks is visible to the migrating flocks. According to the best vantage point of vision, temporary leaders are continually created whom the others may follow. It is well known that when the leader in a harrow of wild geese becomes disabled the others are, for a time at least, thrown into confusion, showing that they were keeping to the path by following a leader. While certain species fly in comparatively close array, as cowbirds for example, others may be straggling far behind the pioneers so that all the members of any one species may occupy over a month in passing a given point. Thus it is possible for any individual bird to have companions constantly to guide it on its way when it might be unable to proceed independently. It is not necessary, however, to assume that the same birds are always the leaders in the flight or that the leaders themselves depend upon landmarks which they can see. It seems reasonable to believe that sound serves to keep the individuals of migrating hosts in communication with each other when sight fails for it is commonly observed that bird-calls during migration are much more frequent upon foggy than upon clear nights.

In the case of carrier pigeons the successful individuals are those who have been trained over the course, that is, those who have learned the way either by seeing landmarks for themselves or by following a trained companion. There is no mysterious sixth sense of direction, no crossing of imaginary magnetic lines, no intricate automatic registry of distance and direction by means of the semi-circular canals. It is simply a case of a home-loving animal away from home putting its wits and senses and experiences together to get back to its home and in this case these known resources are sufficient for the task. Why may not this also be the true explanation of the manner in which birds find their way on those greater pilgrimages which we call migration? The murre flying in the fog, the migrants striking out from Cuba for invisible Florida or across the Gulf of Mexico toward an unseen shore, are all either traveling a course they have learned by experience or following within sight or call of others who know where to go. It does not seem any more impossible that a bird should learn to travel a familiar distance without landmarks than that a blind man is able to walk in a familiar path. What causes the migration movement is another problem entirely but, once given the incentive for this wonderful exodus, it seems reasonable to believe that the manner in which it is carried out, the way in which the path is fol-

lowed, may find an adequate explanation in the temporary leadership of some individual within sight or hearing of the others, who knows at least a fraction of the way by experience or who strikes out a safe path by means of landmarks.

Finally, it must be remembered that all who start upon this winged crusade do not reach the holy land. The annual loss of bird life during migration is unquestionably enormous. Birds are not driven by an unfailing instinct that carries them all automatically to their destination. The blunderers and the stupid ones are relentlessly eliminated in countless numbers. The more resourceful ones, the quicker witted, the more vigilant, accomplish the grand tour amid perils innumerable with many a hair-breadth escape and the survivors are those choice spirits who, having thus won their spurs by noble effort, or because they possess the birthright of a superior endowment over their fellows, become the ancestors of other birds. So it is that winning qualities are grafted upon the race by hereditary transmission. It is to be greatly wondered at that, after ages of such rigid selection, we should at last have birds to-day whose performance is so remarkable that we are tempted to attribute it to powers uncanny and unknown?

II. Why Do Birds Migrate?

Theories to Account for the Fall Migration

Having discussed some of the theories advanced in explanation of how birds find their way during migration let us consider some of the reasons which have been given to solve the origin of the migration habit. Why do birds migrate at all? At once it is seen that the fall migration seems to present fewer difficulties than the spring migration.

The Temperature Theory

It has been maintained by some investigators that the approach of cold weather causes birds to go south in the fall and it is quite true that if all birds attempted to remain in northern latitudes during the winter many would doubtless succumb to the cold. The main factor in such a disaster, however, would not in all probability be low temperature in itself but rather scarcity of food dependent upon low temperature during the winter months. The fact that there are repeated instances of birds, such as robins, song sparrows, etc., which ordinarily migrate south, remaining occasionally in their summer habitat throughout the entire winter, demonstrates that these birds are able to endure low temperature when they have a plentiful food supply. In this connection two well known facts are significant. First, the ordinary bodily temperature of a bird is always several degrees warmer than in the case of man, and secondly, the fall migration begins and is largely completed before the weather becomes cold.

The Premonition Theory Years ago Brehm attempted to account for the fall migration by assuming that birds have premonitions of severe weather, or in other words that they are endowed in some mysterious way with a meteorological sense. This theory, which at first thought seems entirely fanciful, in reality contains a large element of probability but not exactly in the way that Brehm intended. Birds with their large lungs, pneumatic bones and numerous internal air sacs, are, to a remarkable degree, living barometers, responding with great delicacy to changes in barometric pressure. The uneasy behavior of robins and the repeated calls of cuckoos before a storm are familiar illustrations of this fact. That birds can anticipate winter, however, and as a result make an effort to avoid its disastrous effects, is beyond demonstration and seems quite unlikely.

The Short Day Theory Another alternative has been suggested, namely, that toward the fall of the year the days become too short for the bird to complete its daily task of feeding. When the enormous activity of birds is brought to mind and one remembers how rarely a resting bird is seen, particularly among seed and insect eaters, the hardship resulting from shortened working hours can be readily appreciated. The migration south, however, begins before the days are perceptibly shorter and so this theory suffers, as does many another, because of a few obtrusive incontrovertible facts!

The Food Supply Theory Still other theorists have assumed that the factor of greatest importance in causing the fall migration is a diminished food supply but here again it must be admitted that a large per cent. of migrating species leave for the south in the very height of the seed and insect harvest. It may be pointed out, however, that upon the ground of food supply, natural selection would promptly eliminate those who did not go south and would tend at the same time to favor the perpetuation of those who varied in the direction of southern migratory habits, whatever the cause of those variations might be.

Theories to Account for the Spring Migration Turning now to the spring migration, the factor of food supply seems to be of much less immediate importance since in many cases birds, as for instance the water fowl, push their way out of a land of plenty into a region of scarcity.

The Instinct Theory That it is a bird's *instinct* to go north in the spring is no better an explanation of the origin of migration than it is of how a bird finds its way during migration.

The Homesick Theory

Another attempt at an explanation is based upon the fact that in the spring migration birds are returning home to the place where they were born. May it not be then that they are overtaken by a strong desire to revisit their birthplace as the changing seasons duplicate the climatic conditions which existed when they formerly dwelt there? May they not be driven by a kind of home-sickness to fly north to the scenes of their early life? This is a favorite theory with those who are accustomed to endow birds with semi-human attributes upon a sentimental rather than upon any anatomical basis. The theory suffers somewhat when it is remembered that most birds forsake the home they make such strenuous endeavor to revisit, the moment their nesting duties will allow which would hardly be expected if they possessed such an overmastering affection for a particular locality as the homesick theory implies.

The Desire to Disperse Theory

Again, to say that birds have a "desire to disperse" in the spring of the year, as Dixon suggests, simply begs the question as to what actually causes the dispersal.

The Nestling Food Theory

Alfred Russel Wallace, whose biological opinions are certainly entitled to respect, points out that the food upon which many nestlings are fed consists of soft bodied insects and other materials that become relatively rare in the tropics during the dry season. It is so customary to think of the tropics as a region continually teeming with all sorts of life that testimony to the contrary by one who has spent many years there, comes at first as a surprise. It is, however, undoubtedly true that food of a quality suitable for nestlings would not be present in sufficient quantity if all the migratory species remained there to nest. Consequently in this sense, the spring migration may primarily depend upon food supply. Omnivorous birds whose food supply is to a lesser extent affected by the changing seasons, migrate less than those who feed upon a restricted diet.

The Safe Nesting Site Theory

Another theory has been presented by Professor Brooks of Johns Hopkins University, namely, that birds go north in the spring in order to find safer nesting sites than are available in the over populated tropics. It is natural that all animals during the breeding season should seek retirement and a place of security in which to rear their young and this seems to be the universal rule among all those animals which in any active way care for their offspring. But is it a fact that there are more safe nesting sites in the north than in the tropics? Surely in the luxuriant tropical vegetation there are more nooks for concealment, acre for acre, than in our open

northern forests! In both regions only a small number of the sites available for nesting are utilized. If the reason for nesting in the north was for increased safety it would be expected that those birds which do remain behind to contend with the perils of tropical nesting, would develop greater skill in building nests inaccessible to enemies than those going north who would presumably be exposed to fewer perils. Such, however, is by no means the case. Tropical nests cannot be distinguished from northern nests by any such criterion of efficiency against enemies. Some of our best nest builders, the Baltimore Oriole for example, are also notable migrants. In the case of both of these latter theories it would seem as if Nature, who always works along the lines of least resistance, would have found it easier to adapt migrating birds to a different sort of nestling food or to perfect in them the skill necessary to build securer nests in the tropics before evolving the intricate machinery incident to annual migration.

The Vacuum

Theory

A theory proposed by Allen seems more reasonable. It rests upon the idea that "Nature abhors a vacuum" and, therefore, any accessible territory from which animals have been temporarily excluded will not long remain unpopulated after the cause of temporary banishment has been removed. During the winter birds are forced to abandon the northern latitudes for the tropics because of cold and the consequent shortage of food. When spring comes this entire vacated area is again thrown open for habitation at the very time when the birds, temporarily crowded into the tropics, are beginning to seek nesting places. It is quite as inconceivable to imagine that birds, with their active powers of flight, should fail to reinvade the territory, from which they had been temporarily driven by winter, as soon as it is again available for habitation, as that an expansible gas should remain in a flask after the stopper which confined it there had been removed. This theory, then, explains spring migration as a logical expansion consequent upon the compression into the tropics during winter of a large per cent. of the bird population of all latitudes.

The Over-population

Theory

Another factor has been emphasized by Taverner. This may be called the over population theory depending as it does upon the circumstance that whenever the breeding season opens there is suddenly a great increase in population within a given feeding area. Such a condition must result in a keener competition for food and those birds who are stronger or who are the earliest to mate and produce young drive out the weaker and tardier ones into the surrounding region. This dispersion would not be towards the south, neither toward the east nor the west, because in

all these directions the territory would be equally preempted, but rather toward the north where there are fewer birds. Thus migration from the tropics might have had its origin. The direct result of such a movement would be that those individuals that were forced to become explorers in search of an adequate food supply would come to a halt only when compelled to do so by lack of food or when harrassed by superior competitors or, finally, by the demands of that period in their life cycle when the physiological impulse to nest-building can be no longer delayed.

Taverner explains the fall migration in the same way. That is, an overpopulation occurs in the nesting region at the north. The old birds drive away the young ones, or the first nestlings to mature become better established than those hatched later, driving the latter out. These being thus forced to migrate, on account of unfavorable conditions in the north find relief only by moving south and this constitutes the fall migration. This theory assumes that it is among weaker birds, those unable to hold their own, that the wonderful and complex habit of migration has developed, a habit demanding apparently far greater qualities of courage, persistence and resourcefulness than would be required by competition for a livelihood with their fellows in a neighborhood already familiar to them.

Ancestral-Habit Theories

All of the theories thus far mentioned to explain migration, namely, instinct, homesickness, dispersal, quality-of-nestling food, safe nesting sites, vacuum and overpopulation, seek to find an explanation in factors now operative. It is possible that a key to the puzzle may be found by regarding the performance as an inheritance of habit whose origin depends upon factors which have now ceased to act.

Graser's Theory

One of the most recent theories embracing this point of view was proposed in Germany by Gräser in 1904 and is based upon the supposition that the ancestors of modern birds, living in Tertiary times were very vigorous flyers who passed freely from one Tertiary island to another across immense stretches of water in order to find food and nesting sites. As the widespread tropical environment of the Tertiary times gave place to modern climatic conditions with changing seasons, and, as the present distribution of land and water gradually developed from the immense Tertiary seas with their numerous islands, birds more and more found suitable conditions of life in restricted areas wandering less and less until finally these ancestral wanderings have become limited to the regular fall and spring migrations, while many species are practically stationary. The logical conclusion of Gräser's theory is that birds are constantly becoming less

migratory and in time will become so well adapted to local conditions that migration will cease. This bold conception of the case loses significance when it is remembered that all the evidence from embryology, comparative anatomy and palaeontology points unmistakably to the conclusion that birds have arisen from reptile-like ancestors of the crawling or lizard type and not from the flying or pterodactyl type, and, moreover, that the art of flying was a gradual acquisition which had by no means reached the perfection in Tertiary times which Gräser's theory presupposes.

The Deichler-Jäger Theory

Another ancestral-habit theory, known as the Deichler-Jäger theory after its proposers, lays particular emphasis upon the rôle played by the glacial period toward the end of Tertiary times. There is geological evidence that during the pleistocene period at least three distinct glacial ages occurred one after the other, during which the present temperate regions of the earth were slowly invaded by an encroaching polar sheet of ice until they became quite uninhabitable except by arctic organisms. Before and between these glacial ages modern temperate regions swung to the tropical extreme in character which is proven by the discovery of fossil ferns as far north as Greenland. The Deichler-Jäger theory assumes that birds as a class in all probability arose from reptile-like ancestors during Tertiary times and that their original home was in the north. So long as the climate remained essentially tropical throughout the year there was no occasion for deserting this area. With the gradual advent of the first glacial age, however, the climate of the north slowly changed from being tropical the year around to a condition of seasonal changes somewhat similar to that obtaining today. When these seasonal changes became extreme tropical conditions were interrupted and the first winter occurred. There is no reason to believe that this first winter was either sudden or severe but, in the course of time, it became an established annual occurrence and was finally much more severe than our winters at present, as has been demonstrated by the occurrence of fossil reindeer bones in France and arctic musk-oxen as far south as Kentucky.

Now when organisms of any locality are overtaken by winter one of these results may occur; first, they may simply perish; second, they may hibernate through the cold weather in a semi-torpid condition, or finally, they may migrate to a more favorable environment. Birds, being endowed with the power of locomotion through the air pursued the latter alternative and thus the fall migration had its origin. Every spring as the advance of the glacial sheet relaxed for a season the birds which had been driven south into crowded quarters by the rigors of winter temporarily

reoccupied the ground they had lost, and these annual oscillations becoming greater and greater as the glacial age gradually gave way to an interglacial or post-glacial age, the conditions of migration which we observe today became established by long repeated practice.

The Dixon-Braun Theory A third ancestral-habit theory was developed independently in 1900 by Braun, who observed migrating birds extensively for several years in Constantinople and in 1892 by the English ornithologist, Dixon. The Dixon-Braun theory postulates that the center of distribution of birds, that is, their original home as a class, was not in the north as the Deichler-Jäger theory assumes, but in the tropics. The reason for this conclusion lies in the fact that many genera of our migratory birds are most largely represented by tropical species which do not migrate at all. For example, there are many more species of flycatchers remaining throughout the year in the tropics than migrating north, indicating that the original distribution-center from which flycatchers in general have spread must have been in the tropics where they are now most at home. As a result of overpopulation or famine in times past these tropical birds have been forced to travel to less crowded and more favorable localities for food. Relief could be found only toward the north since overpopulation is most likely to occur during the spring breeding season at a time when the northland is just released from the rigors of winter. Thus, according to the Dixon-Braun theory the first migration was a spring migration while according to the Deichler-Jäger theory the first migration was a fall migration. The Dixon-Braun theory further supposes that the original spring migrants, having been forced north by over-population are in turn compelled as winter comes on to retreat south into the overcrowded tropics or perish, only to repeat the experiment of finding relief in the north as soon as the advent of spring allows. In this way the old birds perform again what in their experience had proved to be a successful experiment, while the young birds go along with them and learn the habit.

The Kobelt-Duncker Theory A recent attempt has been made by Duncker in Bresslau (1905) to combine elements of the two theories last mentioned. Duncker accepts the classification of birds made by Kobelt (1902) into *summer-excursionists* (Sommerfrischler) and *winter-wanderers* (Winter fluchter). The former are birds whose home was originally in the south but who now make an annual excursion (Badereise!) north in order to breed returning home again as soon as this function is accomplished, while the latter comprise those whose home was always in

the north and who are temporarily driven abroad in the fall by stress of temperature and lack of food, only to return home again as soon as physical conditions allow. The summer excursionists go into a foreign land far away from their ancestral home or point of origin as a species, to perform the highest act of their lives, that is, the production of offspring. The winter-wanderers breed, as good conservatives should do, upon their ancestral acres but are obliged to be wanderers therefrom during many months of the year.

The Marek Theory

In the *Ornithologisches Jahrbuch* for 1906 there appeared still another theory to explain why birds migrate. It was put forward by Professor Marek of Hungary and emphasizes the factor of barometric pressure as being of the greatest importance in determining the migratory movements of birds. Marek's conclusions are entitled to serious consideration for they are based upon many years of painstaking investigations concerning the correlation between bird migration and barometric conditions. He began by comparing known migrations of the woodcock in Europe with the weather charts of the same dates and found that, aside from minor deviations, these birds migrate from anti-cyclonic areas of high barometric pressure to cyclonic areas of low barometric pressure. This coincides in general with the direction of the wind but Marek would not say that it is the wind which causes the movements of birds,—rather that both wind and migration are caused by the same conditions, namely, the proximity of two areas of unequal barometric pressure. During the winter the polar regions form an anti-cyclonic area of high barometric pressure with low temperature and clear air relatively free from moisture while in the tropics there is a corresponding area of low barometric pressure with high temperature and much humidity. The prevailing winds are from the north because the air always flows "down hill" from high pressure areas to those of low pressure. When spring comes there is a relative shifting in position in the barometric maxima and minima. In the north the temperature rises, humidity, cloudiness and precipitation all increase and an area of low barometric pressure becomes gradually established while the reverse conditions are occurring in the south. The result is that southerly winds become the prevailing ones and, at the same time, birds who are extremely sensitive to barometric changes unconsciously begin their spring migration. In the same way the fall migration is initiated by the shifting of the barometric maxima and minima.

Irregularities in migration, such as remarkable flights of birds

and unusual delays in the migration movement are all directly traceable to the barometric conditions prevailing at the time.

Marek's observations begun upon the woodcock were extended to very many other species. In fact, the paper referred to is a summary and generalization of 43 papers bearing upon migration, which this industrious investigator has published. It must be admitted that Marek's theory has the great advantage of dealing with known factors which may be made the object of further investigation. From his point of view there is no necessity for referring the habit of migration to hypothetical ancestral behavior, nor for endowing birds with such human attributes as love of home or the memory of previous successes. The streaming northward of birds in the spring and their return southward in the fall are both primarily dependent upon the same observable external factors as those which cause the flow of the air in the form of prevailing winds, northward in the spring and southward in the fall

Conclusion Yet the riddle has by no means been solved.

There still remains an immense halo of mystery around bird migration because there are so many things we do not know. We not only do not know *why* birds migrate but as yet we do not know *how* they migrate except in a general way.

What becomes, for instance, of the swallows, has been a conundrum for 2,000 years. Aristotle thought that swallows passed the winter buried in mud or in the bottom of ponds. Linné credited the hibernation idea. Dear old Gilbert White, in spite of his observing eye, died in doubt. Finally, a few decades ago an Italian naturalist thought it worth while to submerge a few swallows under water to see how long they would survive. These feathered martyrs to science of course promptly died, and thus at least there was delivered the death blow to the hibernation-under-water theory, but to this day no one knows the complete migratory route of the swallows nor where they pass the winter. Mr. Wells W. Cooke, our American authority upon bird migration, writes: "Upon leaving the Gulf of Mexico did they drop into the water and hibernate in the mud as was believed of old, their obliteration could not be more complete."

The meagerness of our knowledge concerning the migration of swallows is repeated to a large extent in the case of almost every other species when we seriously attempt to winnow out fact from fancy. It may, therefore, be said in conclusion that, until the store of facts as to how birds migrate has been greatly increased, we can only delight ourselves with interesting speculations as to *why* birds migrate, acknowledging the problem unsolved.

JOHANNES MÜLLER

BY PHILIP B. HADLEY

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John Müller.

See the article by Dr. Philip B. Hadley in the June issue.

JOHANNES MÜLLER¹

BY DR. PHILIP B. HADLEY
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IN the present day when the individual laborer in the fields of biology is so often lost in the flood of new facts which is continually being poured into the archives of the science; when a narrow specialization and very definite concentration of activity are the primary condition and means for furthering the highest interests of the science as a whole, and when the difficulty is ever increasing, to hold in the foreground the larger and more general problems of biological significance, it may not be altogether inappropriate to recall—we might almost say revive—at times, some of the monumental figures whom the history of every science, at rare periods, brings forth, and to learn once again our debt to them.

That the times are past when it is permitted a single individual to survey, in full understanding, the broad fields of activity in the realm of general biology must assuredly be considered as a sign of advance. We may even remark that the gradual expansion which physiology alone has undergone during the last half century, in passing beyond the confines of a unitary science and in trespassing—perhaps with right—upon the fields which had at one time belonged to other realms, is a necessary consequent to the death of the last great ruler of the science. For these reasons alone it may be of interest and of profit to recall the single instance of a man who, during his years of activity, so deeply influenced the drift of physiological thought; and after whose death, the overgrown and no longer self-containing science of physiology burst like a great stream at its mouth, by many and devious channels to reach the sea.

Johannes Müller was born in the city of Coblenz on the fourteenth day of July, 1801, the son of Mathias Müller, a shoemaker. Although a man of small means, the father determined not to deny his son the advantages of a fair education, and accordingly the young lad was sent to the Jesuit school in the place of his birth, then under French control. Here he remained for eight years, pursuing a study of the classics and mathematics and gaining the foundation of that knowledge of Greek used so brilliantly in after years in the translation and

¹On the above subject the writer would acknowledge the especial value of two German works from which he has freely borrowed: A comprehensive treatise by DuBois Reymond, "Gedächtnissrede auf Johannes Müller"; and a brief paper by Max Müller, in *Westermann's Monatshefte* for July, 1901. The present paper was first presented in a course of biological seminars at Brown University.

commentation of Aristotle. A few years later we find him at the Gymnasium, where, in spite of the old scholastic system of teaching, he took a deep interest in the study of the animal and plant worlds—an interest which was no doubt stimulated by the reading of Goethe, whose works were a source of great delight to young Müller. During this period there also appears to have developed in him that rich gift of imagination which, as one of his biographers says, is so necessary not only to the poet, but also to the natural investigator. In his later work on the “Phantasmal Phenomena of Vision,” Müller tells us how, as a boy, he perceived in the crumbling walls of a neighbor’s house all sorts of odd and fantastic figures and faces.

At the age of seventeen, Müller left the Gymnasium and, having served one year in the army—as was customary with the youths of his station—he entered, at the age of eighteen, the University of Bonn, which had just been founded. As has been the case with so many natural scientists, here Müller at first hesitated in making his decision between the church and medicine. Born as he was of Roman Catholic parents and nurtured in the Catholic faith by a strongly believing mother, it is not strange that, even as a child, he manifested a desire to enter the priesthood. But the decision was soon made. For three days, so we are told, young Müller closeted himself in his room in order that he might deliberate. At the expiration of this time he made known his decision to a friend in these words: “I am determined. I shall study medicine; for I know what I have and whom I serve.”

While at the University of Bonn, Müller’s career was characterized by an intense application to study. He maintained, however, a constant exercise of independent thought, and manifested a keen relish for original investigation. Here he initiated, even in the first year of his studies, a series of experiments upon the “respiration of the fœtus,” a subject in which a prize had been offered by the university. This prize Müller secured when at the age of nineteen. In connection with the work, a story which a friend of Müller has made known, is characteristic of the young investigator at this time. He had once started upon a journey on horse to Arrthal and was but a short distance on the way when, by the roadside, he espied a pregnant cat. He immediately gave chase, captured it and, for the time being postponing his journey, carried the animal back to the university, where, by Caesarian section, he deprived it of its young in order that he might consequently solve some point in his first problem of investigation.

During the early part of his period at Bonn, although as a student he was most intent upon his work, he was not wholly indifferent to the general yearning for constitutional freedom which was pervading the thought of the middle and lower classes throughout the German

states after the expulsion of the French. The movement towards a student alliance was then at its height, and this seized strongly upon Müller, who, as we learn, took a leading part in that rather enthusiastic association in which the academic students still cherished hopes of a German unity.

Even these early investigations of Müller were bringing him to the notice of many of the scientific men of his time. On the occasion of the publication of his work on the "Laws of Animal Motion," Oken, the then famous natural scientist, expressed his high approval together with the wish that Müller might be permitted to devote himself purely to natural science. Of this course of action, however, there seemed at that time little prospect. After the death of Müller's father, the small family inheritance lasted but a short while; and from this time until the dawn of his European fame Müller appears to have been constantly troubled with the distressing problem of obtaining the necessary funds for the continuance of his labors; and often even with the question of obtaining food. But in spite of the difficulties which his financial condition enforced upon him, this was on the whole a gay time. The thoughts of the wide possibilities of his chosen vocation appear to have maintained the spirit of the youth, and the unquenchable thirst for knowledge and recognition was gratified at every spring which philosophy, literature, theoretical natural science and careful observation offered. It was also here and during these early years of his study that Müller contracted the spirit of the *Naturphilosophie*, from whose grasp he was freed at a later date through his contact with Rudolphi at Berlin.

When we consider the trying conditions which surrounded Müller in this period of his life, it must be considered most fortunate that there stood at the head of the Prussian ministry a man who, more than any other, appears not only to have recognized Müller's genius, but also to have had the ability to loosen the fetters which bound up Müller's great gifts. This man was the Minister von Altenstein; and it was he who, by securing a generous government stipend, made it possible for Müller to spend two years—from the spring of 1823 to the autumn of 1824—in furthering his scientific studies at Berlin, where Müller shortly passed his examination for the license to practise his profession of medicine.

It was here that Müller had the great good fortune to become the favorite pupil of Rudolphi, who at that time was the most formidable enemy to subjective speculation in biological science, and who already had begun to base physiology—rather exclusively, perhaps—on the actual study of animal structure. It was Rudolphi, moreover, who had the liberality to place at Müller's disposal his laboratory, his apparatus, his library, and what was still more advantageous, his constant oversight and advice. Of the encouraging aid which he received

from that excellent master, Müller afterward spoke in the most grateful terms, and declared that it was through the influence and example of Rudolphi alone that his own scientific pursuits were afterwards turned so fully in the direction of comparative anatomy.

At the expiration of his two years of labor, and immensely enriched in all the fields of natural science, Müller again returned to Bonn, and in 1824 was enrolled as academic lecturer in comparative anatomy and physiology. Two years later, when but twenty-five years old, he was made professor extraordinary in the same branch of science.

The epochs in his activity in investigation which immediately followed upon his return to Bonn have well been called by DuBois Reymond the *subjective physiologico-philosophical period*. The literary landmarks of this period in Müller's career are two works: First, "On the comparative physiology of the sense of sight in men and animals, with researches on the motions of the eyes and on the sight of man"; second, "Concerning the phantasmal phenomena of vision: a physiological research dealing with the physiological evidence of Aristotle concerning dreams, the philosophies and the arts."

In the former of these two works we find recorded that excellent discovery that the sight of insects (which possess facet-eyes) must be conceived of as a mosaic interpretation of objects; that is, the pictures which the insects themselves see are placed together as in the form of a mosaic. In the second work regarding the "Phantasmal Phenomena of Vision," Müller took up a study, the idea of which reached far back into his earliest youth, when he was accustomed to give free play to his fancy in imagining strange shapes and figures on the plaster-scarred walls of the old buildings. These fanciful appearances, which thus early became so familiar in the imaginings of his boyhood, he submitted in maturer years to searching philosophic scrutiny; and the work in which they are described and discussed is a charming yet masterly application of experiment in anatomy, physiology, physics and psychology. Through the medium of these scientific principles Müller explained the seeing of devils and spirits; the friar, who, after long hours of supplication, sees the desired consecration in the form of a shining cloud; the superstitious, to whom the tempter appears as an evil spirit: these phenomena were for Müller only the results of the passion-aroused conditions in the material substances of their sight.

Of all Müller's labors at this time, greatest importance must be attached to his work in elucidation of the laws of the specific energy of the sense organs. With ingenious experiment he worked out the general law that, in whatever manner a sense organ may be stimulated, it always answers to our consciousness by the method peculiar to it. It was from these and other related investigations that Müller deduced many of his philosophical principles: For instance, that we can not

understand truly the things of the world outside of ourselves, but are cognizant only of the changes brought about in the sense-substance by the thing itself. From these considerations we can readily understand how Müller was led to adopt the view of subjective idealism.

During this period at Bonn, however, the duties which, as a teacher, Müller imposed upon himself, together with the unremitting employment in the lines of his original investigations with all its concomitant labor and thought, had induced, soon after his marriage in 1827, a state of mental and physical exhaustion. Upon the eve of a nervous break-down he secured a leave of absence from the university and with this a recompense of two hundred thalers which made possible for him a journey up the Rhine and through southern Germany. On this trip he was accompanied by his newly married wife. Soon, however, with bettered health he returned to Bonn, where in 1830 he was made professor ordinary.

This event marks the end of what we may term Müller's fiery subjective period, and the beginning of his great *objective physiologico-anatomical period*, which covered the years of his most brilliant achievement. He was now devoting himself to many branches of scientific work, especially to his morphological studies. Through his anatomical and systematic researches on the scorpion and spiders, he showed himself worthy to be ranked among the first zoologists of his time. In his work, "On the Development of the Reproductive Organs," which appeared a few years later, Müller traced the development of these organs in man and in animals. Coincident with this he was pursuing his researches into the development of other organs, and produced his treatise on the secreting glands. In this excellent work the phylogenetic and ontogenetic development is considered in both man and the lower animals.

In the latter part of Müller's life at Bonn occurred two significant physiological discoveries: First, he definitely proved, through a convincing series of experiments on the frog, the view which had been first announced by the Englishman, Charles Bell, in 1811: that the anterior roots of the spinal cord are motor, and that the posterior roots are sensory in function. In reality this experiment was simple enough. In a frog Müller cut on one side the anterior and on the other the posterior nerve roots of the spinal cord. On the side on which the posterior roots were cut the frog was wholly insensible, while the side on which the anterior roots were cut remained quite paralyzed. This experiment awakened in the scientific world of that time a storm of applause. The fortunate experimenter journeyed to Paris in order to demonstrate the fact before Alexander von Humboldt and Cuvier. Versalius in Stockholm had the experiment performed by Retzius. Hardly a year later, Müller announced his discovery of

the lymph hearts in amphibia; and also the results of his investigations on the coagulation of the blood.

Just and prompt recognition did not fail to follow in the train of these excellent results, and the consequent advancement and improvement in his material condition made possible for him other interesting journeys. In 1828 he visited Goethe. The spring of 1831 he spent in the Leiden Museum in Holland. In the autumn of 1831 we find him in Paris in the company of several of the great natural scientists, as Humboldt, Cuvier, Milne Edwards and others who were there at the time. One significant anecdote of this Paris trip should not be omitted. When for the first time Müller went to call upon Dumereil, the latter was very busy, and, since he did not know whom he had to meet, somewhat peevishly directed Müller to the door. Müller, however, as he was almost thrust out, pushed in his head and called out to Dumereil, "Yes, but the *Coecilien* in the young stages *do* have gill openings in their necks!" This thrust, it is needless to say, worked as a magic word to gain a long and pleasant interview between these two investigators.

In the year 1832 Rudolphi died at Berlin, thus leaving vacant the foremost position in anatomy and physiology in Germany. Negotiations were already in progress to secure as Rudolphi's successor Dr. Tiedermann from Heidelberg; but at this point in the proceedings Müller determined upon a unique step. He sent to his old friend and former benefactor, the Minister von Altenstein, copies of his works together with a letter in which he ("believing that the importance of the affair would furnish its own excuses") brought himself prominently into the proposition. He said, in part, that it was no more than right that the first and highest position of the kind in Germany should belong to the greatest among scholars; furthermore, that if this man were not Johann Friedrich Meckel, then he believed himself to be the foremost zoologist and physiologist in Germany.

This letter had results: the Minister von Altenstein at once ordered Müller's nomination; and on Easter, 1833, Müller, not yet thirty-three years old, entered upon his duties as "professor ordinary of anatomy, physiology and pathological anatomy, and director of the Anatomical Museums" in the University of Berlin.

The first fruit of Müller's residence in Berlin was the completion of his "Handbook of Physiology," which he had begun long before he left Bonn. Appearing in three parts, it was at last completed in 1840. These volumes represented a piece of work unparalleled in the field of physiological literature. The only work which could be compared with it was Haller's "Elementa." Müller's labors in preparation for this work included an immeasurable number of single observations with reference to the physiology of the voice, of speech, of hearing, of nerve physiology, of teachings on the blood—all of these rest.

to a very great extent, upon Müller's own discoveries. The "Handbook of Physiology" was accepted with almost universal accord as the most valuable treatise on general physiology that had appeared in the long interval since the time of Haller. It is perhaps of interest to observe that these two writers have much in common, for in both we perceive the fundamental desire of placing the doctrine of physiology upon a basis of fact. Anatomy, human and comparative, experiments on animals, chemistry and physiological science in its various departments, are all called in to bear upon the investigation of the truths of physiology. As one of his commentators has remarked, Müller in this work, as in his others, takes nothing on trust; every statement, whether matter of fact or of doctrine, is thoroughly tested; difficulties, however perplexing, are never evaded or slurred over; defects, however much they may deface the picture to be presented, are never disguised. The result of each quest, whether success or failure, is honestly told and there is no yielding to the temptation, so powerful with writers of systems, "to round off a ragged subject with smooth plausibilities." The influence of the "Handbook" was immense, and the judgment of it appears to have been conditioned not alone by the physiological data it contained, but also by the collected facts of importance to the medical profession.

With the completion of the "Handbook," Müller's activity in this particular line of work seems to have practically ended. From this time on he engaged himself to a greater extent in the fields of comparative anatomy and zoology; and in these subjects, as also in his physiology, Müller excelled both in the abundance of his observations and in the wide range of his discoveries. In his work on the comparative anatomy of the myxinoid fishes, Müller lays down the morphological plan of the vertebrates in their simplest form. The title conveys but a faint notion of the scope of this work. Although it treats chiefly of the anatomy of this particular family of fishes, it is rich in new and original matter in which the structure is compared with that of other families of fishes, and the facts sagaciously applied to the elucidation of greater questions in animal morphology. Regarding Müller's study of the Echinoderms, we may quote from an address by the president of the Royal Society of London:

Professor Müller early applied himself to the study of the structure and economy of the Echinoderms. After describing in a special memoir the anatomy of *Pentacrinus*, so interesting as a living representative of the extinct *Crinoidea*, and publishing, in conjunction with M. Troschel, a systematic arrangement and description of the *Asteridea*, he was at length happily led to investigate the embryo life of this remarkable class of animals. The field of inquiry upon which he entered had scarcely been trenched upon before, and he has since made it almost wholly his own by persevering researches carried on at the proper seasons of the last nine years, on the shores of the North Sea, Mediterranean and Adriatic. In this way he investigated the larval conditions of four out of the five orders of true Echinoderms, and has successfully sought out and determined the commonplace followed in their development, amidst

remarkable and unlooked-for deviations in the larval organization and habits of genera even of the same order. His inquiries respecting these animals have made us acquainted with the larval forms, with relations between the larva and future being; and with modes of existence, such as nature has not yet been found to present in any other part of the animal kingdom. Finally with the light thus derived from the study of their development, Professor Müller has subjected the organization of the entire class of Echinoderms, both recent and fossil, to a thorough revision, and has added much that was new, as well as cleared up much that was obscure in regard to their economy, structure and homologies. It is to their researches, which occupy seven memoirs of the Royal Academy of Sciences of Berlin, that more special reference is made in the award of the medal.

It was not long after his arrival at Berlin that Müller established the *Archiv für Anatomie und Physiologie*. Of this he continued the publication until the time of his death. This journal, during the period of its existence, formed a principal medium of publicity for the labors of the leading physiologists of Germany; and the establishment and continued superintendence of it by Müller, in the midst of other laborious employments, must be regarded as an important service rendered to science.

About this time, independent of Müller, his pupil Schwann, following apparently in the footsteps of Schleiden, made the discovery that the animal organism, just as the plant organism, was composed of elementary cells. Müller appears to have been the first to recognize the great significance of this discovery. He immediately employed the new fact for the explanation of certain disease phenomena and clearly pointed out the agreement between tumors and pathological and embryological development. His excellent work on the finer structure of morbid tumors signifies the beginning of all microscopical investigation in pathological anatomy, and here we see the fountain-head of that stimulus which, brought to bear upon the young investigator Virchow, gave rise to that well-known and comprehensive work on "Cellular Pathology."

Concerning the other events of Müller's life, during the Berlin period, it takes little time to relate. The routine work in the Berlin Anatomical Museum was interrupted only by the scientific expeditions which the desired investigation of the sea fauna afforded. The East and North Sea, Sweden, Norway, the coast of the Adriatic and Mediterranean, from Trieste to Messina and Marseilles, formed the territory of Müller's scientific explorations. On one of these trips, in 1855, Müller experienced a serious danger. He was returning with two pupils from a journey to the coast of Norway, when at night the steamer *Norge* on which he sailed was rammed by another and speedily sank. Nearly fifty people lost their lives; and among them one of Müller's young companions. In a letter to a friend in England, in which Müller gives an account of the disaster, he says that upon finding himself in the water at first he kept himself up by swimming. But having his clothes on, he soon became exhausted and would have

perished had he not caught hold of a ship's ladder which was floating by. For a long time he held on, and had nearly given up all hope of assistance when he was picked up by a boat from the other vessel. His remaining companion, Dr. Schneider, saved himself in a similar way. This event seems to have had a deep effect upon Müller, and although he still resorted to the seaside, ever afterwards he dreaded to trust himself on shipboard.

When, for a second time, Müller was chosen director of the Berlin Museum, it was certainly most unfortunate that his directorship fell in that memorable year of the revolution, 1848. Although Müller felt himself to be truly German, he was apparently no more of a politician than Goethe. He could experience no sympathy for the democratic rashness which on all sides of him was now being manifested. It was a time of civil commotion when political agitation distracted the whole academic being, and both students and professors were deserting the laboratory and lecture room to equip themselves as soldiers of the revolution. Müller, whose quick spirit had led him, in the olden days of the Student Alliance, to take so active a part in the threatened political eruption, had become a sober conservative. His situation was now one of difficulty, and not without peril. He strove manfully to maintain authority, and even those who took a different view of passing events paid willing tribute to his honesty of purpose and to the personal courage he displayed in the most trying circumstances when the university buildings had become the center of the intense revolutionary movement. Müller naturally feared the destruction of the priceless treasures of his collection. Regarding the state of his mind we can obtain some conception from the words of his distinguished scholar, Rudolph Virchow, who upon Müller's own request became his follower as professor of anatomy and physiology at Berlin University. Regarding these days of the revolution, Virchow has written as follows:

He trembled for the safety of the university, for whose treasures he felt himself to be personally responsible. Day and night he remained at the museum, ever on guard. He tore down agitating placards. He ventured with personal danger among the students. On the day of the great citizens' parade, with his own hand he seized away the black banner which was stretched across the balcony of the university building. But the movement more and more escaped the authority of the academic jurisdiction. In the teaching body of the university grew the voicing of disharmony. The professors and the private lecturers made diligent efforts to be heard and some of them (appointed as a committee, to which I also belonged) argued the matter with the director and the senate in a very unpleasant conversation.

Thus it is apparent that Müller was asked in the most kindly spirit to give up, at least temporarily, the position as director; for Virchow continues:

Thus all agreed, in order to relieve the at least exposed position of the director, to a painful duty; and it was an actual deliverance when, at the closing of the university year, he could give into other hands the office which he had taken upon himself.

This was, perhaps, the most unfortunate directorship since the

founding of the university; for the man who possessed the least political inclination was called upon to display, in that time of agitation, the abilities of the politician and statesman.

From this time on Müller worked as hard as ever, but with sadly altered spirits. The nervous strain of overwork was beginning to tell. He suffered much from sleeplessness and this condition he fought with larger doses of opium, which in turn led to a more serious trouble of the heart. In the winter of 1856-7 his health received the first open shock when a gastric fever, the first serious illness since 1827, necessitated the giving up of his lectures. In these days he worried much about himself, feared typhoid fever and wrote to his son, Max Müller, at Cologne. He set in order all his private affairs and engaged, in the case of his death, Dr. Diffenbach to open his body. At this time, however, he developed only a slight trouble in the joint of one foot, and the next summer found him again in fair health. The following winter, however, he again overburdened himself with work, suffered even more than ever from lack of sleep, and again resorted to large doses of alkaloids. For some time he had suffered from moments of dizziness, but had become accustomed to attribute them to the long hours he spent bending over his microscope. These attacks now became so frequent that he dared not venture even on his library ladder. In the evening one would see him sitting listless in his easy chair; or, as if driven by a deep inner anxiety, and gloomy foreboding, pacing restlessly at night through the secluded streets of Berlin.

Easter of the year 1858 did not bring him the accustomed feeling of satisfaction at having completed a period of uninterrupted scientific work. At the end of the summer semester he fully realized, but all too late, the necessity of taking the most energetic measures to bring about an improvement in the condition of his health. He again called his son from Cologne, and, after a consultation, decided to give up all his work and lectures in physiology. He planned an early consultation with his physician in order to decide more definitely regarding his future work; but the end came suddenly. On the morning of the day when this consultation was to have taken place, Müller was found in his bed, lifeless, April 28, 1858. It is needless to say that the tidings of the sudden end of his laborious and valuable life caused profound sorrow in every part of the world where science is cultivated.

II

Having now considered the more prominent events of Müller's life and his career as a man among men, let us now consider more in detail the nature of Müller's work, its fullness and its limitations. Let us attempt to discover wherein it has proved so substantial a foundation for the later development of modern physiology; and lastly let us make ourselves better acquainted with Müller's strong person-

ality, as it was manifested in the home and among the ranks of his students and associates.

In the estimation of a man's prominence it is hardly necessary to remark that the importance which he may assume is always a relative quantity. It is first roughly drawn from a direct comparison of this individual with other individual workers. It is then tempered, as we may say, by a consideration of the relation of the individual activities to the whole field of knowledge existent at that time. There may be great physiologists, great morphologists and great systematists, but the criterion invariably to be used to determine the highest rank must ever be that comprehensive vision which, as Verworn remarks, is able to grasp in a single *Weltanschauung*, the whole breadth and depth of natural scientific inquiry—that comprehensive analytic and synthetic quality of mind which brings isolated unities of fact into concrete principles. It is from this point of view, and by these standards that we must judge the extent and quality of the work of Johannes Müller: first examine into the relation of his activities to the field of natural science of his day; and, secondly, ascertain the relative value of his work when compared with the labors of other men whom posterity has been accustomed to hold as leaders in the rank and file of natural scientists. And yet, before we can fully understand—much less appreciate—the intrinsic worth of any phase of Müller's many-sided activity, we must first take time to examine briefly the condition of the biological science just previous to the period of Müller's greatest work.

We have already in the course of our discussion made mention of the scope and value of Haller's work in physiology; yet we may be pardoned, perhaps, if, in the present connection, we again make reference to some of the more important characteristics of his period, which extended from 1708 to 1777, and closed something over half a century before Müller's began.

As Galen, in the second century, had shown his recognition of the practical value of physiological data and had laid as a basis of medicine, the practical knowledge of vital phenomena; as Harvey, by his brilliant discovery of the circulation of the blood, temporarily revived, after a sleep of thirteen centuries, the exact experimental method in physiology; and after many other investigators had made important, though isolated, contributions to the budget of physiology, we find Haller bringing together the extensive mass of facts and theories and establishing thereby physiology as an independent science which should pursue not only practical lines for the aid to medicine, but also undertake theoretical aims for their own merit. We find many theories and speculations in the air during the period from 1750 to 1830, the latter date marking the beginning of the period of Müller's greatest activity. As a result of the microscopical observations made in last part of the seventeenth century on the development of the ovum, the theory

of preformation was attracting wide interest. This had stimulated Caspar Friedrich Wolff to the production of his *Theoria Generationis*, which was unfortunately held in the dark by the opposition of Haller who could not accept the principles which led, at a somewhat later date, to the conception of Epigenesis. The theory of irritability was also a bone of contention, and though it was materially furthered toward the true conception by Haller's own researches, these last, unfortunately, served also to further a doctrine which thoroughly permeated and confused the development of all physiology down to the middle of the nineteenth century. This was due chiefly to the following fact: That the seeming impossibility of explaining the phenomena of irritability led to the welcoming of the theory of vitalism, or vital force, which asserted a distinct dualism between living and lifeless nature. The vitalists at this time (and nearly all the natural scientists, except perhaps Rudolphi at Berlin, were vitalists in a greater or lesser degree) were discarding the mechanical and chemical explanation of life phenomena, and were introducing such mysterious and inscrutable explanatory principles as *la force hypermécannique* and the *visus formativus*. In this acute and exhaustive manner were explained even the most complex of vital phenomena.

Toward the end of the eighteenth century, however, some twenty years before the birth of Müller, a new note was being sounded from the ranks of German scientists, especially from Reil, whom we may well call the censor of German vitalism. In his work "Ueber die Seelenskraft," he was forcing upon unwilling hearers not only the conception that the life phenomena of living organisms are regulated by chemico-physical laws, but that there were higher principles in control which were present only in living matter. The few adherents to the chemico-physical hypothesis were, during the last years of the eighteenth century, receiving fundamental support from such men as Ritter, Galvani and Humboldt. Through the work of these men the notion was becoming popular that the galvanic current was the cause of all vital phenomena.

Among the chemical and physical discoveries of this time we can mention the advance of vegetable physiology through Ingenhaus (1730-99), who developed the theory of the consumption of carbon dioxide by plants; the discovery of oxygen by Priestley (1733-1804) and Lavoisier (1743-94), and the further discovery in this line by Girtanner, who showed that the venous blood is aerated in the lungs. Thus the existence of the mystical "pneuma," which had clung with a peculiar persistence to centuries of physiological thought, had now become a reality. The anatomical researches of this period were characterized by one discovery in particular, announced by Charles Bell in 1810; that is, the fundamental law of specific nerve physiology, to be later experimentally proved by Johannes Müller. In microscopy,

Spallanzani, Treviranus and others were dealing what we may call only the first of a long series of death blows to the hydra-headed theory of spontaneous generation, which was not eventually disposed of until the excellent work of Pasteur, over half a century later, and even now is often found lingering in popular scientific lore.

A consideration of these foregoing facts demonstrates to us that the greater number of these exact researches had been carried on in France and England. When now we turn with special interest to Germany, we find that her scientific thought had been fermenting in that powerful intellectual narcotic, the *Naturphilosophie*, which, under the great influence of Hegel at Heidelberg and Berlin, was stupefying every branch of accurate scientific research throughout Germany. Of the tendency of this movement to avoid the deductive method of research and to build up a conception of nature upon theoretical and speculative conclusions, we shall speak further. For the present, however, having gained some understanding of the condition of natural science, especially physiology, previous to the period of Müller's greatest activity, let us now consider more in detail Müller's relation to these movements, philosophical and otherwise.

Müller, as nearly every other investigator of his time, was a vitalist; but, as Verworn has said, "Müller's vitalism had an acceptable form." Although to him vital force was different from the forces of lifeless nature, its administration nevertheless followed certain physico-chemical laws. In this, Müller's conception seems to be modeled after the idea of Reil, the leader, as we have said, of the most rational form of the doctrine of vitalism in Germany. Müller maintained his position as a vitalist to the very end. He cherished to the last the thought of the existence of a "life energy." We well know how the activity of his pupils has apparently disproved forever this conception for natural science; and how it has led to the opposite extreme, the rather one-sided materialism of the present day.

When we turn to consider Müller's relation to the *Naturphilosophie*, we recall how he contracted this spirit while he was at Bonn, and how he was rescued, at least from its extreme influences, by Rudolphi at Berlin. Throughout his Berlin period, Müller devoted much of his thought to freeing natural science from the influence of the *Naturphilosophie*. The result was that not long after the death of Hegel, in 1831, the dangerous play with mystical words became gradually eliminated from the consideration of life phenomena. From this time on, the problems of living substance were furthered, especially by Müller, with the implements of comparative anatomy, of physics and of chemistry. In bringing about this condition, and in establishing the deductive scientific method as alone admissible in the realm of natural science, we must look upon Müller as a reformer whose work has been of enduring benefit to science. The nature of

his vitalistic hypothesis did not prevent him in the least from directing his labor to establish life phenomena on a physico-chemical basis. Even the vitalistic principle, as it appertains to the philosophy of the present day, is largely a matter of man's personal and ultimate view of his own life and his own destiny.

In our consideration of the relation of Müller's thought to the *Naturphilosophie* of his time, we must not deny the fact that Müller did recognize a grain of truth in the general philosophic tendencies of that day. As Verworn says: "While keeping constantly in mind the large problems and the goal of science, he regarded critically the special methods and questions only as means to an end—as means for arriving at a harmonious conception of nature." Throughout his whole life he remained steadfastly true to this philosophical conception of science which he had set forth in his inaugural address, "Concerning the Need of Physiology for a Philosophic Consideration of Nature." Verworn further laments that modern science has now so largely lost this element of philosophy, which it had gained as a result of Müller's treatment.

Having dealt thus far with the more abstract phase of Müller's activity and thought, let us now consider more concretely, for a few moments, first the extent of the realm over which Müller exercised so marvelous a command.

When we examine the list of 260 and more complete publications which have come from Müller's pen, we are better able to comprehend the universality of his activities; and it must be understood in this connection that in this great number there are few which represent merely a superficial dalliance with a possible line of investigation. They demonstrate, in almost every case, that Müller plunged boldly into the very heart of the matter which at the time received his fullest consideration. The main subjects to which his contributions appertain, include the following:

1. The Physiology of Motion.
2. The Life of the Fœtus,
3. The Sense Organs.
4. Dissection of Invertebrates; also
 - (a) their development,
 - (b) the histology of their tissues.
5. Nerve Physiology.
6. Animal Chemistry.
7. Human Anatomy.
8. Ethnography.
9. Comparative Anatomy of Vertebrates.
10. Physiology of the Voice and Speech.
11. Pathological Anatomy.
12. Systematic Zoology.
13. Paleontology.

It is clear that such an extent and variety of undertakings could not result from a single line of investigation, but required a universal activity which it is safe to say has never been equaled by any investi-

gator since Müller's time. A better conception of the degree of this extraordinary activity may be gained when one considers that Müller, from 1821 (when he was nineteen years old) to the time of his death, thirty-seven years later, produced, year in and year out, an average of one scientific article of from three to five pages, and with from one to three plates, every three weeks. And in none of these do we find the spirit of his work dictated by the desire to show that he could get some sort of a result out of this or that kind of investigation; but rather by the burning desire to survey and to understand the interrelation of all life phenomena.

It would seem that an unconquered field of knowledge left him no rest, and was for him a stimulus to activity just as much as was the knowledge of the existence of an unconquered people to Alexander the Great. At the first opportunity his attention would be directed to it, and never would the field be abandoned until its truths and its principles were at last incorporated in Müller's own system. This, for Müller, meant no simple undertaking. It included the universal proof, the definite transformation, the deepening, the enriching, the building up and the ordering of every detail of the work; so that from each such acquisition the greatest value to science invariably resulted.

This capability of Müller's is shown especially well in his work on the Echinoderms. He early applied himself to the study of the structure and habits of a single group of this interesting branch of animals. From this study he was led to consider the embryonic development, and, finally, having pursued his investigations in this line into four of the five orders of true Echinoderms, he culminated this great work by subjecting the organization of the entire class of Echinoderms, both recent and fossil, to a thorough revision. In this same thorough and exhausting manner, Müller attacked all possible points in the illimitable field of anatomical and physiological knowledge; and the insight into nature, gained through his own exhaustive researches, yielded to him a sureness of judgment which seldom failed him in the decisive moments of his career. An accurate personal knowledge lay at the bottom of his every work.

In the period of his greatest activity, when he was working simultaneously upon "The Development of the Reproductive Organs," "The Development of the Glands," and also the first volume of his "Handbook of Physiology," together with papers on "Osteology" and "The Myology of the Myxinoid Fishes," he must have possessed the ability to profitably divide his interest and to oscillate with a remarkable ease between these several objects of thought and investigation. The result is perhaps still more marvelous when we realize that, as a rule, Müller went over the same line of investigation three times: the second time while he was writing his results, and the third time when

the article was in the hands of the printer. Müller's manuscripts are said to have been the "terror" of all typesetters.

There was one peculiarity of this man of genius which, though perhaps a fault, no doubt favored the high degree of productiveness which Müller manifested throughout his life. This was his indifference to the formal completion of his written works. At the culmination of a certain line of investigation, in which he had arrived at definite, and usually important, results, he found too attractive the conclusions and speculations dependent upon these results, to spend his precious moments preparing or finishing his manuscript for the general reader.

Although Müller took, in the earlier part of his life, a certain interest in art, literature and music, it was usually the practical alone which was of consequence to him; and if this phase of the subject were once assured, he went forward in his work without much regard for the polishing or the agreeable rounding-off of his subject. And yet, had Müller lived under different influences and if he had dedicated to the superficial side of his work the same carefulness, we are bound to say that, like Cuvier, he too would have been a master of scientific style. But in spite of this tendency, in what Müller did write he was usually most thoughtful of the manner of his expression. He would sometimes read to members of his department, without disclosing the object, descriptions of certain forms to see whether or not he could awaken in his hearers the conception which it was his desire to implant. He was accustomed to enhance the value of his descriptions by forceful comparisons wherein the wealth of his imagination is readily recognizable. The dredging apparatus which worked before his laboratory window, the hood-like cap of Frau Martha, the little dagger of Cornelius, the sketch of Faust—all these common objects of his sight while hanging on the walls of his study were employed, as much else, for the elucidating of certain phases of the problems which occupied him at the time.

When we come to consider the nature and actual value of Müller's scientific work, it appears that in general he has more developed the principles set in motion by others, than himself given to the world epoch-making discoveries. In his teachings of the glands, of the voice, of the sense of sight and of the tumors, he has, with a tremendous power of work, heaped up an amount of raw material which not only became united in his own system, but has furnished a basis for much of the work in physiology since his time. It was Müller who first clearly recognized the interrelation of psychology and physiology. We remember that in his doctor's thesis he defended the position: "Psychology is nothing without physiology." In this regard Müller's own investigations, wherein he formulated his doctrine of the specific energy of the sense organs, demonstrated how fully dependent psychology might be upon physiology—a conception which in more recent times

has been developed so far as to arouse in many the belief that psychology should be taught as but a branch of physiology. That Müller saw so clearly the interrelation of these two branches of knowledge is decidedly a point in his favor. His theories were upheld, moreover, by the many facts presented in his works, "Concerning the Comparative Physiology of the Sense of Sight in Man and the Lower Animals," "Regarding the Phantasmal Phenomena of Vision," also "Concerning the Life of the Soul"; and many other references in his "Handbook of Physiology."

Another, and perhaps the greatest, debt which the world of science to-day owes to Müller is for his establishment of physiology upon a comparative basis. This conception did not first arise in Müller, however, but was previously expressed by his teacher, Rudolphi, who had already emphasized the motto: Comparative anatomy is the surest support of physiology. Grasping the fuller significance of this thought, Müller worked throughout his life to uphold the view that physiology can be only comparative; and among the vast number of his physiological works, there are few in which this comparative principle is not more or less clearly expressed.

A further consideration of the nature of Müller's work shows to us the evident necessity of making one concession; and yet one which, under careful examination, may not, after all, detract from the fame which the world accords to him. This is the fact that in spite of his varied activities Müller was never able to make what we may call a scientific discovery of the first rank. We can find issuing from his hand no single observation which, as has often been the case with other so-called great natural scientists, carries down with it through the ages the name of the fortunate discoverer. With the names of Priestley and Lavoisier will ever be linked the discovery of oxygen. The mention of the name Harvey immediately brings to mind the thought of the circulation of the blood, as with the name of Newton we invariably associate the statements of the laws of gravity. But discoveries of equal or even lesser importance can never distinguish the name of Johannes Müller. Even his excellent work on reflex action and the function of the anterior and posterior spinal nerve roots—these do not belong to him alone, for Charles Bell some years before had already promulgated the theoretical law; yet it remained for Müller to prove this law, and by nice experimentation to establish its universal application as a fact. Schwann presented to the world of science that noteworthy discovery that the animal tissue, just as plant organization, is composed of elemental cells; but it remained for Müller to show the highest importance attaching to this discovery, and to lay down the law of the correspondence between embryonic and pathological development.

This failure of Müller's to make a discovery of the first order can not, with justice, however, be made to count against him. As DuBois Reymond has said, "The most important discoveries can, and often do, play into the hands of insignificant investigators." "That Müller has no such discovery to his credit," continues DuBois Reymond, "can be called as little a failure as that a merchant, who becomes rich through industry and perseverance, should never have been visited by a great fortune." If, in the time when his productive strength stood at its maximum, instead of loosing his great power against a group of widely-extended activities, Müller had undertaken a course in a single definite direction, according to the view of Schiller, that strong stimulus would have been lost to the development of physiology.

Like Müller, Haller also, though he manifested an all-comprehensive knowledge of the field of physiology, failed in yielding an epoch-making discovery. Between these two men, as we have already noted, many points of similarity exist. But, notwithstanding the immense value which Haller rendered to science by his collection and ordering of the tag-ends of physiology up to his time (1775), his work as a whole is excelled by that of Müller with his over-weighing power of judgment and the massive comprehension which took in the whole realm of biological science. While Haller rendered an immense service by uniting the facts of physiology into a certain order and system, Müller took that system as he found it, worked it over, did away with every vestige of the false *Naturphilosophie*, deepened by his own exhaustive researches every channel of it, and turned into those channels the fresh spirit of a new physiology of comparative anatomy.

We come now, in closing, to a consideration of Müller's personality. From his father Müller inherited the strong and active body characteristic of the Müller line, which is traceable far back into German history. We can picture him a man of medium height; in his youth somewhat slim and of an elegant appearance; the breadth of his shoulders in good keeping with the well-shaped head, which was always held erect with a certain attitude of determination. Lithographs and photographs, pencil, pen and brush drawings presenting Müller's appearance at different times in life, have been given to the world; but, as one of his biographers has said, no picture could accurately repeat, now the sad, now the illuminating, splendor of that dusky countenance, with the dark locks of hair and brilliantly glowing eyes.

While we know that Müller received his physical characteristics from his father, it was from his mother that he appears to have inherited his mental qualities. Among these we may distinguish chiefly the strongly-developed sense of order and method, and the deep spirit of enterprise and of indefatigable activity. To these were added a thorough knowledge of men, a great gift of observation, a conscientious punctuality, and a firmness of purpose together with a knowl-

edge of the appropriate both in speech and in action. In his domestic life Müller appears to have been a true husband and to his son and daughters a good father. His home life was of the pleasantest—at least until the misfortune of ill-health in his later life.

As Müller's work as a whole is most comparable to Haller's, so we can say that his personality must have had much in common with that of Pasteur. In both we see the fine sensitiveness of mind, the same modesty in self-assertion, the same love of simplicity, the tenacity of purpose, the scrupulousness for details and the same religious devotion to the hardest labor: these attributes make up a character not altogether common in the general biography of the older school of natural scientists.

Müller's address was characterized by that stiff formality peculiar to the old school type of German professor; and yet with this he combined the dexterity and activity of the more modern scholar. His conversation was never productive. The constant consideration of the various problems of his activity was usually uppermost in his mind and, although he would talk pleasantly and interestingly of many varied subjects, as art, architecture and music, it was to some phase of his labors that the further discussion of these subjects almost invariably led back. And yet, in the circle of his own family, in a group of personal friends, or on his vacation and outings with his nets and microscopes, he could be the most congenial fellow, entering with enthusiasm into whatever duty, sport or pastime presented. Recreation for its own sake, however, Müller seems never to have desired. Yet in his earlier years at Berlin, he was seldom seen exhausted. In his later life, however, the intense nervous strain under which he worked was a source of much regret to his many friends; and the knowledge of his frequent use of opium and other alkaloids to bring him sleep a deeper source of sorrow to those who knew and loved him best.

As a teacher in the anatomical theater and in the class room, as also a guide of young investigators in the laboratory, Müller possessed an extraordinary ability. And yet, in the beginning he had no natural gift of speaking, no eloquence and no talent for foreign languages. Indeed, his early years as academic lecturer at the University of Bonn were, in this particular respect, not in the least promising. With constant practise, however, he was later able to develop a clearness in speaking, and a straightforwardness of expression, which, in itself, approximated to the gifts of eloquence, so that at Berlin he was considered one of the best of university lecturers. His delivery was never of the demonstrative sort, which held an audience spellbound by its bubbling vivacity, its ravishing fire of words, or through a kaleidoscopic blending of current witticism with scientific truth. He never went rambling in a lecture, either in thought or in person. His de-

livery was usually cold and calculating; and yet in some moments he could arouse, through his own deep earnestness, the highest enthusiasm among his students for the subject whereof he spoke—an enthusiasm, the fruits of which have been well shown by the works of the many students, afterwards famous, who received their first impetus from contact with Müller during his periods at Bonn and at Berlin.

In this regard, it is almost needless to say that Müller's position in Berlin resulted in a powerful influence over the younger natural scientists, especially in the northern part of Germany. His personality, as we have seen it, was one to attract students and to hold them when once they knew him well. He planned for them, and often accompanied them on many student trips throughout Germany and even into Norway and Sweden for the purpose of extending various phases of their biological study. In spite of his apparent coldness and constraint, he was, as DuBois Reymond has said, always a ready "comerade," and his views, his books, his apparatus of all kinds, were ever willingly shared with all who desired them.

To the same degree in which Müller was independent in his thought and work, he desired this quality in his students. In his relations with them, notwithstanding his thorough friendliness, it appears that in the laboratories Müller would seldom enter into an ordinary conversation. Regarding this point, DuBois Reymond says in his "*Gedächtnissrede*," "The greatest reward for us students was when Müller relaxed and spoke in common conversation along the lines of highest pleasantry." Even before his fame as a leader in the field of natural science had gone abroad, and while dependent upon his worth as a teacher alone, he had constantly at his side a circle of eager students who clung to him with enthusiasm. Gathered about him in the earlier days at the University of Bonn, before he went to Berlin, one finds such men as Claparède, Haeckel, Lachmann, Lieberkuhn, Anton Schneider and Max Schultze. Upon his departure to Berlin in 1833, many of his students of the Bonn period followed him, and one need only mention the names of Haeckel, Ludwig, Bischoff, Schultze, Volkmann, Brücke, Helmholtz, Virchow and DuBois Reymond, to indicate the immeasurable significance which, as a teacher and leader of the young investigators of that time, Müller must have exercised. The lines of work which he established, his disciples and followers have carried out, and to what extent, we all realize—not as royal inheritors of that vast sovereign power of their master, but, we may say, as governors over the smaller territories into which, like the empire of Alexander, the field of natural science became divided after the death of its last great ruler. Of this famous group of students, now Haeckel alone remains, DuBois Reymond having died in 1896. Yet all these men, at some period of their lives, have rendered grateful

testimony to that common source of their first stimulus and earliest enthusiasm, Johannes Müller.

Look as we will through the history of natural science, we do not find an instance where a single individual, gathering about himself a body of select disciples, has by the infusion of his spirit of work sent abroad influences that have ruled so large a part of the territory of natural science. No such influence emanated from Haller, busily engaged in his collections and accumulation of the facts and theories of a century of physiological activity. Nor could it come from Cuvier, excluding from his circle of labor, as he did, the whole field of physiology and embryology, and preoccupied with his foibles of nobility. Nor was such influence from Darwin, secreted in the recesses of his study, modestly content to think, but not to speak. Nor from the combative Huxley, ever at the cannon's mouth with his evolutionary arguments. Nor yet from our more familiar Agassiz, with his noble retinue of followers, and a leader in our own popular thought of natural history though he was. These men have, it is true, been pillars in the development of the biological structure of the present time; yet their fields of labor have been most limited. But it was the nature of the case that it must be so, for no human individual, coming after Müller, could have the same grasp on the ever-extending realm of biological knowledge. Since his time there are few who have become masters of even a single territory.

In these days, when the scientific spirit is throwing its ever-increasing impetus into all lines of human activity, man has little opportunity to look back "to the mountains whence cometh his strength." The source of his to-day's blessings is either wholly overlooked, or, upon special occasions and anniversaries, is (with that feeling which Macaulay has called the "furor biographicus") made to glow in the colors of the sunset. Having avoided, as it is hoped, both of these extremes, we may quickly summarize what, for Johannes Müller, must ever stand as the criterion of greatness: With an all-including glance he was a master of the whole realm of natural science, which he widened until it became too great for its own government. With the certain power of genius, he studied the field of physiology, cleared away the rubbish, breathed into the earth his own spirit, and, in the end, left in the hands of his followers the thrifty seedling of modern comparative physiology, nurtured in the soil of an exact natural scientific method for the investigation of all life phenomena.

THE BEHAVIOR OF THE LARVAL AND ADOLESCENT STAGES OF THE AMERICAN LOBSTER
(HOMARUS AMERICANUS).

BY PHILIP B. HADLEY.

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THE BEHAVIOR OF THE LARVAL AND ADOLESCENT STAGES OF THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*).¹

BY

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(From the Biological Laboratory of Brown University and the Experiment Station of the Rhode Island Commission of Inland Fisheries.)

WITH TWENTY-TWO FIGURES.

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¹ The present paper is the last of the series of four in which the author has attempted to analyze the behavior of the larval and early adolescent stages of the lobster. The papers already published are the following, references to which may be found in the bibliography at the end of the present work: (1) The relation of optical stimuli to rheotaxis in the American lobster; (2) Galvanotaxis in larvæ of the American lobster; (3) The reaction of blinded lobsters to light.

I. INTRODUCTION AND HISTORICAL SUMMARY.

Every year is bringing new and valuable additions to our knowledge of the behavior of the Crustacea. Most of the investigations dealing with this subject are concerned, however, with the Entomostraca, while the behavior of the higher forms has been less studied. It is apparent, moreover, that the experimental work done has been chiefly upon adults, while little attention has been given to the behavior of the larval forms of those Crustacea, as the macrurous decapods, which undergo an extensive metamorphosis. It is the aim of the present paper to demonstrate certain phases in the reactions of larval and early adolescent stages of the American lobster (*Homarus americanus*) to light, and to analyze these reactions, so far as possible, into their constituent factors.

In the study of reactions to light it is apparent that the lack of a satisfactory terminology has led to considerable confusion. This is manifest when we attempt to apply the definition of positive or negative phototaxis, as given by LOEB, to the types of behavior which we find, for instance, in the lobster and in the shrimp, *Palemonetes* (LYON 1907). LOEB (1905, p. 29) states that "positively heliotropic animals are compelled to turn their oral pole toward the source of light and move in the direction of the rays to its source." In the larval lobsters, however, there may be a difference between the signs of body-orientation and what may be called progressive orientation. In body-orientation the animal in question *turns* with reference to the source of light; in progressive orientation it moves toward or from the source of light. Employing these terms, we may say that the body-orientation of the larval lobster under stimulation by light is invariably negative, whereas the progressive orientation may be either positive or negative, as the conditions of the case determine.

Secondly, what do we mean by intensity and by direction of light? Are we justified in assuming that a stimulus such as light can be effective in causing either kind of orientation through its directive quality? The answer to these questions depends largely upon arbitrary definitions. YERKES' (1903) exposition of what constitutes a phototactic reaction as differentiated from a photopathic reaction indicates very nearly the meaning that will be given to these terms in the present paper. Attention may be

called to one difference, however. It is inferred by YERKES that the sign of the phototactic response is dependent upon the previously assumed body-orientation of the organism. This is by no means necessarily true, for in the case of the larval lobster, it is clear that the orientation of the body has absolutely nothing to do with the sign of the consequent progressive orientation. For our present purposes we may, therefore, slightly modify the definition of YERKES by describing a *phototactic reaction as one in which the organism tends to place the longitudinal axis of the body parallel to the direction of the rays and to approach or recede from the source of those rays.*

If we so limit the meaning of a phototactic response, what shall we say regarding the nature of the so-called photopathic response? It is entirely possible (and indeed in the case of the larval lobsters, most probable) that again the view of YERKES (1903), that a photopathic reaction is one in which an organism "selects" a particular intensity of light, and confines its movements to the region illuminated by that intensity, is correct. But it is not so certain that the photopathic responses of the lobster larvæ are brought about by means of slight phototactic reactions, as YERKES (1903, p. 1) suggests for *Daphnia*. Therefore, for present needs, we may conclude that a *photopathic reaction is one in which an organism, without previous assumption of a body-orientation, "selects" regions of optimal light-intensity.* In the following account of experiments and observations, we shall see to what extent the behavior of the lobster larvæ conforms to these definitions of phototactic and photopathic reactions.

The movements of Entomostraca toward or from a source of light, and their reactions to rays of different wave lengths have been made the subject of investigation by many naturalists. In the earlier investigations it was commonly concluded that the intensity of light was the most important factor, and that organisms "chose" an optimal intensity. LUBBOCK (1881) and GRABER (1884) found that *Daphnia* gather in areas of greater light intensity. SCHOUTEDEN (1902) found that older individuals are negatively phototropic. These experiments, as repeated by DAVENPORT and CANNON (1897), YERKES (1899, 1903), and PARKER (1902), showed that *Daphnia* also manifests phototactic reaction. It was assumed, therefore, that some organisms may react either phototactically or photopathically. Later work of American in-

investigators has demonstrated that the Crustacea are more influenced by the directive factor of the light rays than by the intensity, and, more recently still, KEEBLE and GAMBLE (1904), in their excellent work on the color physiology of the higher Crustacea, have shown that the nature of the background may be an important factor in determining the reaction of many species.

The Malacostraca have received less attention than have the Entomostraca, and it is only for a comparatively short time that anything has been known concerning the reactions of either the larvæ or the adults of decapod Crustacea. With the adult forms of the decapods results have been readily obtained. HOLMES (1901) found that several species of terrestrial amphipods manifest a strong positive phototactic reaction, while all aquatic species are negatively phototactic. We know further from KEEBLE and GAMBLE (1904) that the adult form of *Palemon* is negatively phototropic and that *Hippolyte* is positively phototropic. *Hippolyte*, according to KEEBLE and GAMBLE, not only moves toward the light, but also "prefers" a white to a black background. *Macromysis inermis* reacts positively or negatively in accordance with the character of the background or the nature of the physical environment. It is positively phototropic on a white background, and negatively phototropic on a black background. Furthermore, when a choice of background is made possible, *Macromysis* "selects" the black. In the case of *Hippolyte*, the larvæ respond positively to light, as do the adults. BELL (1906) states that the adult crayfish is "somewhat negatively phototactic" and that difference in the intensity of light made but slight difference in the reactions. Other investigators have shown that the adults of several species of Crustacea react either positively or negatively to light. Very few investigators, however, have studied systematically the reactions of Crustacea in the larval stages. Among the first, LOEB (1893) reported the reactions to light of *Limulus* in the "trilobite stage." These larvæ, he said, are at first positive, and later, negative. PEARL (1904), by repeating LOEB'S experiments, ascertained that this larval stage of *Limulus* manifests at first a negative reaction, and that later, a relatively small number of individuals gives a positive reaction. It was learned by KEEBLE and GAMBLE (loc. cit.) that the response of the larvæ of *Palemon* is the direct opposite of the reaction of the adults. BOHN (1905) discovered that the larvæ of the European lobster (*Homarus vul-*

garis), although at first positive in their reaction to light, may later undergo certain changes. HERRICK (1896) states that larvæ of the American lobster react positively to light. BOHN (1905) learned that the reaction of *Artemia salina* was similar to that of *Homarus vulgaris*; and the writer has ascertained that the larvæ of the green crab, *Carcinus granulatus*, react sometimes positively and sometimes negatively, and behave very much like the larvæ of the lobster. The writer can verify the conclusions published by LYON (1906) that the larvæ of *Palemon* may react either positively or negatively to light.

The results of the small number of investigations which have been made upon the reactions of Crustacea in the larval stages, indicate the desirability of further systematic study of these reactions. PEARL (1904) has well pointed out the value of studying the "ontogeny of reaction," and of applying the knowledge thereby gained to the investigation of the more complex forms of response exhibited by adult individuals. Although the writer has not yet had an opportunity to study the behavior of the adult lobster, the present work shows that in the larval stages there are found diverse types of reaction, differing from one moment to another, and depending upon conditions which, even in the nicest experiments, are by no means readily discoverable; and, furthermore, that it is only by a systematic study of the reactions *through the developmental stages*, that many contradictory points can be cleared up, and the more complex behavior of the older animals explained.

II. BIOLOGY OF THE LOBSTER.

A brief résumé of the biology of the lobster will facilitate the understanding of later considerations. The life of the lobster consists of a series of stages or stage-periods, each of which represents the span of life between two successive moults, or castings of its shell. Of these stage-periods, the first four are passed through very rapidly, since the young creature usually moults four times in the first twenty days of its existence. These first few quickly passed stages (called the larval stages because they denote the successive emergence of one from another) include the most important changes in form, color, and manner of behavior, that the lobster undergoes. In each successive stage the animal is larger than before. The larvæ grow at the time of

moulting, but never between moults. From the fourth stage on, each successive stage-period is of longer duration and the changes which the adolescent lobster thenceforth undergoes are correspondingly less significant, being characterized chiefly by alterations in internal morphology as the adult functional type is gradually approximated. The first three stages of the lobster are free-swimming stages, and the activities are without apparent

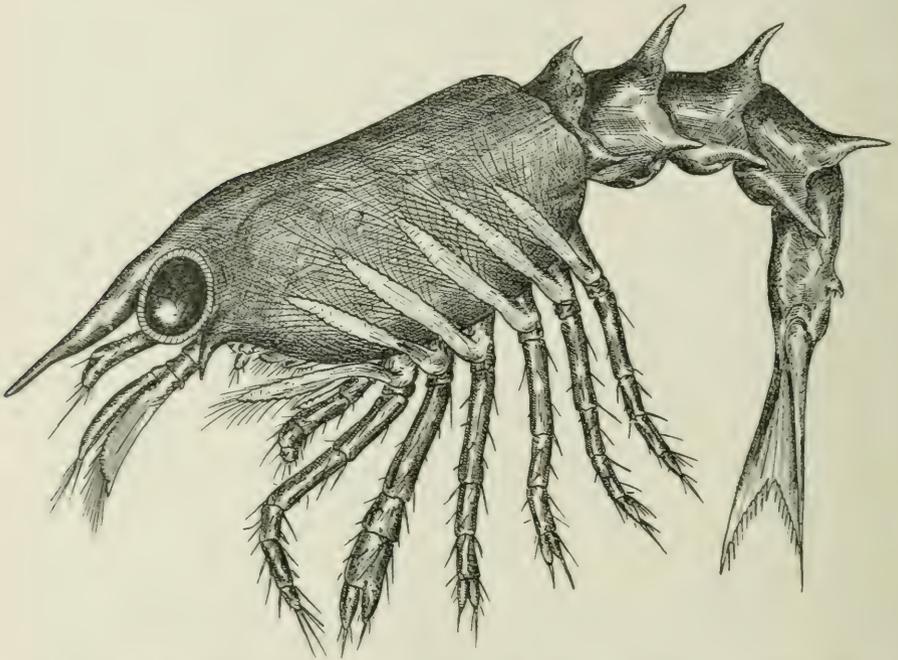


FIG. 1. Showing a young first-stage larval lobster about two days old. The eyes are large and prominent. The exopodites of the thoracic appendages are represented at the beginning of the downward stroke. This figure shows the typical swimming position of larvæ in the first three stages, the plane of the cephalo-thorax bent down at an angle of about 30° from horizontal.

coördination or aim. The larvæ are swept here and there by the tide and possess no power to evade the attacks of numerous enemies.

The swimming of the lobsters of the first three stages is accomplished by means of the feathered exopodites, or outer branches of the thoracic appendages (Fig. 1). These exopodites beat the water with short vibratory strokes, which tend to carry the larva back-

ward or forward or upward as the case may be,² and allowing it to sink toward the bottom when their motion ceases. The progressive movement and the body-orientation of the lobster in the first three stages are almost wholly dependent upon the activity of these organs. Occasionally, darting backward movements, caused by the sudden contraction of the abdomen, appear, but these are of slight importance in the reaction to light.

When the lobster moults to the fourth stage, the exopodites are lost. Consequently the forward swimming during and after the fourth stage is dependent upon the action of swimming appendages which after the second stage make their appearance on the under sides of the second, third, fourth and fifth abdominal segments. The fourth-stage lobsters swim with directness and precision, usually near the surface of the water. This surface-swimming may be due to stimulation by light, but, as the writer has suggested elsewhere (1906b), it is not improbable that this form of behavior is due in part to the food-seeking impulse. During the latter part of the fourth stage, contact-irritability begins to play an important rôle in determining the behavior of the young lobster. Now, as in the fifth and later stages, the creature no longer swims at the surface of the water, but seeks the bottom and attempts to burrow in the sand or beneath any object that presents itself. After the fifth stage, the adolescent lobster shows the same type of behavior as during the fifth stage, but with a gradual increase in the tendency to avoid light. Its reactions have now become fixed in every way.

III. APPARATUS AND METHOD OF PROCEDURE.

The manipulation of the various pieces of apparatus here described will be spoken of when the particular experiments in which they are used are mentioned. The room in which the experiments were conducted contained on two of the opposite walls windows 2 feet high and 8 feet long, before which extended work benches or tables. The two windows, which opened respectively to the east and west, were the only source of daylight, and, as occasion required, were heavily screened with black paper or cloth. At appropriate places in these screens were cut openings which could be readily closed. On the table before one of the windows was

² For details on method of swimming, see p. 258.

placed a box 2 feet high, 3 feet wide, and 2 feet deep, lined on the inside with black cloth, and containing, on the window side, slits or openings to correspond with the openings in the screen outside the box. On the room side, the box was fitted with a movable black curtain, which permitted the operator to move the jars or other apparatus contained within the box. This arrangement served to control the light falling upon the larvæ, which were put in suitable containers and placed inside the box.

Other pieces of apparatus may be described as follows: *Glass box A.* Of glass boxes two types were used for studying the photopathic and phototactic reactions of the larvæ. One was a rectangular wooden box having glass "windows" in each end and in the bottom. This box, which was 12 inches long, 6 inches wide, and 3 inches deep, was painted dull black on the inside and fitted with a light-tight cover. It was used in experiments which required illumination from the end, from below, or both.

Glass box B—This box was similar in most respects to box *A* (see Fig. 7). It was 12 inches long, 6 inches wide, and 5 inches deep. It had "windows" on each end and along one side. Like box *A*, it was painted black on the inside and was fitted with a light-tight cover. This cover contained three slits so arranged that diaphragms of wood or glass might, in an instant, be slid into place to divide the box transversely into four chambers of equal extent. Then the cover of the box might be removed if desired, leaving the partitions in place. The object of this arrangement was to make it possible to imprison the young lobsters wherever they chanced to be at any given time and so to ascertain, by count, in what manner and in what relative numbers they had responded to certain stimuli.

Of these two boxes, the former, while oftener placed in a level position on a laboratory table, was sometimes used in another way to study the photopathic reaction alone, or the photopathic and the phototactic reactions together. In these cases the box was placed over a light-shaft, which was merely a rectangular tube lined with black cloth, with a height of 18 inches and with a cross section of the same size as the bottom of the box. Over the upper end of this tube or shaft, the glass bottom of box *A* exactly fitted. At the bottom of the shaft was either a sheet of white paper or a mirror which was so placed as to reflect the rays of light coming from the window up through the shaft to the glass bottom of the

over-lying box. The rays that thus passed through the black-lined shaft and entered the box were practically parallel and at right angles to the plane of the bottom of the box. It is clear that, when the water in the box was very shallow, the rays of light passing up the shaft and striking the larvæ could have no directive influence, and that, when they passed through the graded light screens or through plates of colored glass, placed just beneath the glass bottom of the box, they could be effective only through difference in intensity.

Besides these boxes, use was made of certain glass jars, known as museum or brain jars, which were for the most part cylindrical in shape and varied in diameter from 20 to 25 centimeters. For certain experiments these were covered wholly or partially about their circumference with black paper, and the light was made to come from the top, bottom, or through a "window" in the side, as the case might require.

In addition to the apparatus mentioned above, several kinds of glass tubes were employed. Some were ordinary 15 centimeter laboratory test tubes, while others had a length of 40 centimeters and a diameter of 4 centimeters. These tubes were made with rounded ends so that there would be no obstruction to the light striking the tubes even at a slight angle, and the lobsters were introduced through an opening in the top. Another type of tube employed was the Y-tube, constructed of glass tubing, 4 centimeters in diameter as shown in Fig. 5. These proved exceedingly useful in testing the reactions of young lobsters, both to the intensity and the directive influence of the light rays, since the arms of the Y-tube could be readily covered with colored glass plates or fitted with black or white backgrounds, thus producing different conditions of light in each arm of the Y.

In many of the experiments it was desirable to use graded light screens. These were made by adding india ink to a solution of gelatine and allowing this to harden in the form of a wedge. The wedge-shaped screen permitted light to pass through in diminishing amount, from the thin edge to the thick edge, which was quite opaque. Graded light screens of red and blue were also made by adding to the gelatine a solution of eosin or methylene blue. It was by means of these, together with the colored glass plates that differences in the intensity of light were secured.

Since a particular response to light is often interpretable only

when the conditions previous to the hour of experimentation are taken into account, it was found desirable to secure such conditions for experiment that all influences which might be instrumental in determining the final reaction of the larvæ either before or during the time of actual experimentation should be clearly recognized. Accordingly, the data to be presented show not only the nature of the reaction of the larval lobsters at a few chosen periods in their life history, but they also make it possible to trace modifications in reaction as the young animals pass on from stage to stage and gradually approach the adult type. Numerical results were usually obtained by counting the larvæ which had been imprisoned in different compartments of the box by the sliding partitions. In other cases a large number of larvæ were put into a glass jar and the reaction of the majority was observed. The separation and selection of larvæ which gave either a positive or a negative reaction to the same stimulus was thus possible, but conclusions have been drawn only after a careful study of the exact accounts of many groups of larvæ. The exact intensity of light used in the experiments was not known, but the experiments were performed on such days and at such times as would make the conditions uniform. Before entering upon a detailed consideration of the experiments as a whole, it will be appropriate to state some ground for assuming that lobster larvæ react both to the intensity and to the directive influence of light. The preliminary experiments which led to this view may be presented as follows:

IV. PRELIMINARY EXPERIMENTS.

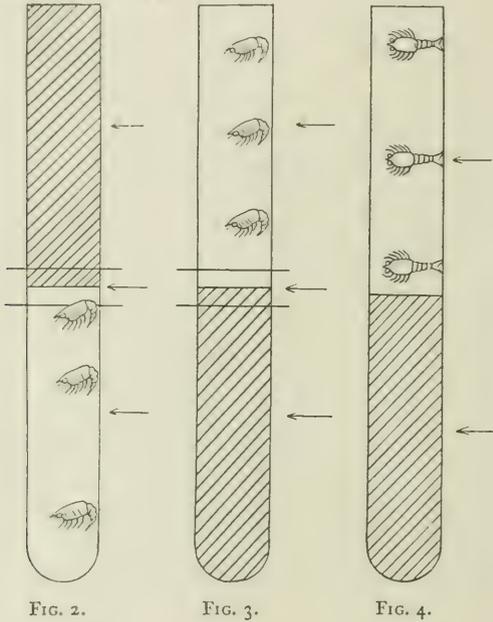
Experiment I—Glass tubes 15 centimeters long and 2 centimeters in diameter were filled with salt water and in each were placed six first-stage lobsters two days old. When the tubes were held vertically, there was no tendency shown for the larvæ to gather in any particular region of the tubes. When, however, a strip of black paper was wound in such a manner as to cover the upper half of a tube (Fig. 2) and records were taken every minute, the larvæ became distributed as follows:

NUMBER OF LARVAE PRESENT AFTER	UNSHADED AREA.	AREA WHERE LIGHT AND DARK MEET.	SHADED AREA.
1 minute.....	5	1	0
2 minutes.....	6	0	0
3 minutes.....	6	0	0
4 minutes.....	6	0	0
5 minutes.....	5	1	0
Total.....	28	2	0

It will be seen that the larvæ "seek" the light area. Next the paper was so arranged that the shaded part was below, as shown in Fig. 3. In this case the larvæ were always found uniformly in the unshaded area. In all cases the body-orientation of the larvæ was determined by the direction of the rays of light, which struck the tube at right angles; but at no time, it would seem, could this directive influence alone have been instrumental in causing the larvæ to remain in the region of greater light-intensity. The same general results were obtained when the tubes were laid horizontally on the table (Fig. 4) but still at right angles to the direction of the incident light rays which came from the side. These tests of the reaction of larvæ in glass tubes appeared at first sight to demonstrate that larvæ of a certain age and stage show a tendency to group themselves in regions of greater illumination, irrespective of the directive influence of light or of reaction to gravity. This, however, is not the only possible conclusion to be drawn from these facts.

To take, for instance, the case of the horizontally lying tube (Fig. 4), in which the larvæ gathered in the illuminated ends (the region of greatest light-intensity), and there oriented to the directive influence of the light. In the darkened area of the tube the larvæ did not undergo body-orientation, but swam about in many directions. When occasionally, they entered the more brightly illuminated end of the tube, they at once oriented to the directive influence of the rays and took the position shown in Fig. 4. Furthermore, the larvæ usually manifested a tendency to retain their body-orientation and thus to remain in the illuminated region when once they had entered it. Here, then, we have a case where the apparent reaction to the intensity of light is, in reality, determined, and maintained, partly at least, by the orienting response to the directive influence of light. In other words, the larvæ did

not, in this instance, "select" the region of greater light-intensity because of the intensity *per se*, but because they became imprisoned in it through orientation as a result of the directive stimulus. It is only through rays which strike the larvæ directly from above or from below that an approximately non-directive influence can be obtained.



FIGS. 2 and 3 show the orientation of the larvæ in tubes standing in the vertical position; Fig. 4, in the horizontal. The arrows represent the direction of the light rays striking the tubes from the side. The cross hatching represents the parts of the tubes covered with black paper.

Experiment 2. Reaction to intensity of light—In this experiment use was made of the glass-bottomed box *A* with the light-shaft, and the colored-glass plates or graded light screens. First the glass plates were arranged over the top of the light-shaft in the order blue, green, orange, red. The box was filled with salt water to a depth of 15 mm., and ten first-stage larvæ were placed therein. The light-tight cover was then put in place and the larvæ were allowed five or more minutes to become acquainted with their new environment. The result was as follows:

TIME.	BLUE.	GREEN.	ORANGE.	RED.
After 5 minutes.....	10	0	0	0
After 10 minutes.....	10	0	0	0
After 14 minutes.....	9	1	0	0
After 17 minutes.....	9	0	0	1
After 19 minutes.....	9	0	1	0
Totals.....	47	1	1	1

The results of these tests and others in which the order of the glass plates was changed, demonstrate the tendency of the larvæ to group themselves in the blue, which was the more brightly illuminated region. Similar experiments were performed with graded light-screens (strips of paper of different thickness or a gelatine wedge) substituted for the glass plates. The results in every case indicated that here also the larvæ reacted to difference in intensity. These experiments were performed with a belief that it is the refrangible rays of the spectrum alone that are active in determining the phototropic reactions of animals and plants. MIN-KIEWICZ (1906), however, has found that, although positively heliotropic animals usually react positively to the rays of shortest wave-length (violet or blue), and negatively heliotropic animals usually react to the rays of greatest wave-length (red or yellow), these phenomena of positive phototropism and positive chromotropism are not necessarily found together in the same organism. It is uncertain whether or not the larvæ of *Homarus* manifest chromotaxis. At the present time it can be said that the observed reactions of the larvæ to colored lights agree so well with the reactions to lights of varying intensity as determined by light screens, that they may fairly be considered responses to difference in intensity of light.

Experiment 3. Reaction to the directive influence of the rays—To demonstrate the response of the larvæ to the directive influence of the light rays the description of a single experiment will suffice. Similar experiments will be recorded later, in another connection. The conditions of this experiment are like those described in Experiment 2, i. e., box *A* was mounted over the light-shaft on the colored glass plates arranged in the order blue, green, orange, red. The ten first-stage larvæ contained in the box were more or less constantly oriented in the region of greatest light intensity, that is over the blue glass. Next, the small window situated at

the red extremity of the box was opened to the diffuse light of the room. The result was that the larvæ immediately oriented to the new rays, left the region of greatest light-intensity, the blue area, and moved backward in the direction of the incident light rays toward the source of the weaker light and, at the same time, into a region of lesser light-intensity at the red end of the box.³ The distribution at the end of 19 minutes was as follows: blue, 4 individuals; green, 1; orange, 1; red, 24. Here it appears that the larvæ, which at the beginning of the experiment were grouped in the area of greatest illumination under the influence of non-directive rays, were forced by the directive influence of the new rays to move from a region of greater into one of diminished light-intensity. As will be observed later, this experiment was tried under a great variety of conditions, and with larvæ of different stages and ages, with uniform results. Whenever the larvæ had an opportunity to move in the direction of the rays, they would do so, notwithstanding the fact that they thus passed from a region of greater to one of less illumination.

In the paragraphs immediately preceding, the purpose has been merely to indicate that in the behavior of the lobster larvæ we may observe reactions both to the intensity of light and to the directive influence of the light rays. The latter depends, first, upon the unequal stimulation of the two eyes, and second, upon the degree of illumination which affects both eyes. The conclusions which have been drawn from these few experiments receive further support from other experiments. But first, it is necessary to know whether there is any form of reaction common to all larval lobsters. To answer this question, which is of primary importance, it will be necessary to report in detail a series of tests, which were made upon many groups of lobsters during different periods of their metamorphosis and under different conditions of stimulation by light.

Experiment 4. Case I—In several instances larvæ which had been hatched from one-half hour to one hour were put in a glass jar, which was in turn placed in the dark box and submitted to illumination on one side from a narrow window. In every case

³ If this experiment appears uncritical because of the lack of information regarding the exact intensities of light at the opposite ends of the box, it may be answered that the intensity of light was measured by the only method available. Sensitized paper was placed inside the box, one strip over the end window, the other over the bottom at the blue end. The results showed that the light entering the blue end through the bottom of the box was much stronger than that entering the end window from the room.

the young larvæ at once swam backwards toward the source of light and grouped themselves closely together at the window side of the glass jar. So perfect was this orientation on the part of the newly hatched larvæ that, out of 100 individuals, not one showed a negative reaction.

Case 2—When the same larvæ were put in one of the long 40-centimeter glass tubes so placed in the dark box that the tube was parallel to the direction of the incident rays, the young lobsters in every case swam rapidly to the end of the tube nearest the window and remained there until the tube was reversed, when they again swam toward the window. These reversals might be continued for hours.

Case 3—When the same individuals, or other larvæ of the same group, were placed in box *B*, and this was turned with one end toward the window, the reaction of Case 2 occurred. They swam backward toward the window.

Case 4—Another group of fifty first-stage larvæ three days old was placed in a glass jar in the dark box and illuminated from the small window. All were definitely positive. Next, the circumference of the jar, except a vertical strip three inches wide on the light side, was covered with black paper, and the jar was so placed that direct sunlight had access to the open side. The larvæ immediately gathered on the darker side of the jar and remained there for one and a half minutes, after which they again returned to the sunlit side and remained there in bright sunlight as long as they were observed.

Experiment 6.—July 19, 3:30 p.m. Fifty first-stage larvæ, two days old, were put in a glass jar and this was placed in the dark box. Though the light was not bright at this time in the afternoon all the larvæ gave a positive reaction. The jar now was placed on a black background in the bright sunlight on the west table. Every lobster moved to the room side of the dish away from the light. Within two minutes, many began to go back to the window side, and this continued until all were again gathered there. After four minutes, however, they again returned to the room side and remained there for ten minutes, at the expiration of which time they were about equally divided between the room side and the window side of the jar. They were now put back in the dark box, and with the slight intensity of light at 7 o'clock in the evening, all were reacting positively. By 8:30 the box was fairly dark and the

orientation of the larvæ was indefinite. Suddenly the rays of a powerful acetylene light were thrown upon the jar. Immediately a negative reaction took place and continued for two minutes, when some of the larvæ began to return to the light. At the expiration of four minutes all the larvæ were reacting positively, and this reaction continued for several hours.

Experiment 7—July 22, 9:30 a.m. Forty-four second-stage lobsters, six days old, were placed in the glass jar, in the dark box. Eleven came at once to the room side of the jar. The jar now was moved nearer the small (three by three inch) window. As a result seventeen out of forty-four individuals gathered on the room side, but the definiteness of the positive reaction on the part of the window-side lobsters was lessened by desultory swimming. The jar was next placed on the west table, the room side and top of the jar being shielded by black paper. All the larvæ came to the room side of the jar. When replaced in the dark box (in light of much lesser intensity), the reaction again became uniformly positive.

Experiment 8—July 23, 9 a.m. Forty second-stage larvæ, seven days old, were placed in the glass jar on the east table, and exposed to strong light. All the larvæ at once oriented on the room (darker) side of the jar. These lobsters were next placed on the west table where the negative reaction continued throughout the afternoon. From 6 to 8 o'clock in the evening the light faded gradually. At 7:35 the body-orientation was nearly lost, but the orientation on the room side of the jar with diminishing definiteness remained in effect until 7:50, when the light had faded quite away and the lobsters were scattered throughout the jar.

Experiment 9—July 28, 9:30 a.m. Twenty third-stage lobsters, twelve days old, were placed in the glass jar in the dark box on a white background and submitted to light of slight intensity coming through the small window. All showed a strong positive reaction, and gathered on the window side of the jar. The next day in the afternoon, about fifty third-stage larvæ of the same group, now thirteen days old, were placed in the glass jar in the dark box on white background and submitted to light of medium intensity. Nearly all of the larvæ oriented on the room side of the jar, thus demonstrating a definite negative reaction.

Experiment 10. Case 1—June 26, 9 a.m. Ten fourth-stage lobsters, fifteen days old, were placed in the glass jar in the dark box

and submitted to light of medium intensity from the small window. There was no appreciable tendency to undergo either body or progressive orientation. The lobsters were much engaged in eating one another.

Case 2—The fourth-stage lobsters mentioned in the preceding paragraph were fed on chopped clam meat and placed in box *A* with the black interior. Light was admitted through the end window. Records of four tests made at two-minute intervals show that while nine were neutral in reaction, six were positive, and twenty-five were negative. The box was next lined with white paper and the same fourth-stage lobsters were submitted to the same external light conditions. The results show twenty-six positive, twelve neutral, and twelve negative individuals.

Case 3—August 7, 2:30 p.m. When twenty fifth-stage lobsters, twenty-five days old, were put in box *A* and illuminated through the end window, all, without exception, oriented in the dark end of the box.

Conclusions concerning the permanence of these reactions through the stages—In explanation of the ten experiments recorded above, it should be stated that the writer had at his command large numbers of larval lobsters of approximately the same age and stage which had been subjected throughout the whole of their early life to the same conditions of environment. Therefore it was possible to make a detailed systematic study, not of a few isolated individuals alone, but of whole groups. The result of this study is expressed in these experiments.

Whatever else the foregoing facts may demonstrate, the answer to our first question is evident. *There is no constant form of reaction on the part of the larval lobsters to the directive influence of the light rays.* For this reason one has no warrant for saying, without reservation, that the larval lobster is either positively or negatively phototactic. If it had been necessary to depend for material upon a few individuals of uncertain age, and to draw conclusions regarding the general behavior of all the larvæ after observing the behavior of these few individuals, the outcome would of course be far less satisfactory than in the present instance. It is to be regretted, perhaps, that no means were at hand to make a critical determination of the exact intensities of light to which the larval lobsters gave their recorded reactions, but it is apparent that such a refinement of method would not change the general conclusions reached.

With the foregoing facts in mind, it is clear that the problem before us becomes, not, what reactions do the larval lobsters in general give to light, but *how do the lobster larvæ of a certain age react to light under certain known conditions?* To this rather more complex question attention will now be given.

V. SYSTEMATIC ACCOUNT OF THE REACTIONS TO LIGHT OF
LOBSTERS IN THE LARVAL STAGES.

What is the nature of the reactions to light through the successive developmental stages, and by what conditions is it determined? Regarding the first of these points, it should be borne in mind that the subject matter concerned cannot be treated concretely, but that it is necessarily scattered through the long series of observations which follows, and that it is only from a consideration of the series *as a whole* that a clear idea of the gradual modifications in the reactions from the first to the sixth stage of the lobster's life can be obtained. As to the second point of inquiry, it is at once perceived that the conditions or factors which we seek to discover are of two sorts:

1. *Conditions which are peculiar to a certain definite age or stage in the development of the larva, and which may be designated as physiological conditions.*

2. *All outside influences, including the intensity and multiplicity of stimuli brought to bear upon the animals.*

In the following discussion it will be found of advantage to consider these two kinds of modifying conditions together; for they are found to be very much inter-related when a consideration of their mutual importance in bringing about any orientation of the young lobsters is involved.

It may be appropriate to mention at this point the method of securing the data here presented. The futility of taking young larvæ at random from the hatching bags without knowledge of their age or previous history was recognized early in the course of the investigation. It was considered advisable to work only with those lobsters whose previous history was definitely known. To this end the exact time of hatching of certain groups of larvæ was noted. In the large canvas hatching bags, used at the Wickford Station, hundreds of larvæ hatch in a single hour, and observations were made, as a rule, twice each day (morning and afternoon), upon

individuals taken from these groups, whose age was accurately known. During the course of the study, the history and the daily reactions of three groups of larvæ were followed and recorded. For the following account of the reactions of the first-stage larvæ, for instance, the records of these three groups for the first day, the second day, the third day, etc., were used. Only the reactions which appeared to be the most constant and typical have been introduced here. Therefore, although many variations in reactions were found to occur, the following section describes the typical daily reactions of the larval lobsters from the time of hatching through the fifth stage of their existence.

1. *First Larval Stage.*

As has been shown by preliminary observations and the experiments already mentioned, the lobsters of the first larval stage are usually strongly positive both in their photopathic and in their phototactic reactions. These reactions are manifested strongly in the few hours directly after hatching, when, as we shall presently see, the young lobsters react definitely, and to very slight differences in the intensity of illumination. When half-hour old lobsters were placed in the glass jar, and submitted to any kind or intensity of light (daylight, artificial, or colored), they responded well (especially when the intensity was increased by a white background) to slight differences in illumination; and reacted uniformly and invariably by moving, tail foremost, toward the source of light. In case of two sources of light, on opposite sides of the jar, the larvæ would respond to the rays which were the more intense. If the rays from two sources of light were introduced at right angles to each other, the resultant reaction, as has been shown for other organisms by many investigators, was determined according to the law of the parallelogram of forces.

It would appear that, in the behavior of the first-stage larvæ, we have the most delicate reactions to slight differences in light intensity that occur throughout the life of the lobster. During the early hours of the first larval stage, no individuals reacted negatively to the directive stimulus of the light, while in the later stages, although a majority of the larvæ manifested definitely one reaction or another, there were usually a few individuals which gave responses that were either indefinite or opposite to the rule.

Experiment 11. Case 1—Ten first-stage larvæ, five hours old, were placed in a glass tube 40 cm. long, and this was laid on the table at right angles to the plane of the window and parallel to the light rays entering through a narrow slit in the screen. All of the larvæ at once oriented themselves at the window end of the tube. Next, blue, green, and yellow glass plates were placed successively over the end of the tube next the window, leaving the opposite end clear, but none of these changed the definiteness of the positive reaction. When, however, an orange glass was used, the larvæ paused midway in the tube, at the border line of the orange light, and in their final orientation were scattered between this region and the orange end of the tube. When a red glass was superimposed, all the larvæ took a position at the border line of the red and the clear glass, this region representing the junction of the areas of strong and weak illumination.

Experiment 12. Case 1—In this experiment the glass bottomed box *A* was set up over the light-shaft with the colored glass plates arranged in the order, red, orange, green, blue, as described on p. 207. The box was filled to a depth of one inch with water and first-stage larvæ, twenty-four hours old, were introduced. Five minutes was allowed for the larvæ to become acquainted with the new environment. Records of four tests then made showed that while thirty-eight larvæ gathered in the blue area, only one was found in the red, one in the orange, and none in the green. Changing the order of the glasses in no way changed the results. This apparently demonstrates that there is a definite tendency on the part of these larvæ to orient themselves over the glass plates which admit the brightest light; and that the precise order of the plates makes no difference in orientation.

Case 2—In this instance the order of the glass plates was red, orange, green, blue. The same larvæ used in the above tests were employed, but the conditions of the experiment were changed. The window in the end of the box corresponding to the red glass was uncovered and the diffuse light from the room was allowed to stream through the box longitudinally. The object of this was to discover whether the larvæ which had previously given so definitely the positive photopathic reaction, could be induced to enter the region of diminished light intensity (at the red end of the box). In other words, whether the phototactic reaction could be made to overcome the photopathic. Between each of the successive

tests mentioned below, the light from the room and the light through the shaft were cut off in order that a scattering of the larvæ through the box might occur. In other cases the position of the box was reversed; and in still others both the position of the box and the order of glass slides, changed. The results of four tests are as follows (the arrow represents the direction of the light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		→ Red.	Orange.	Green.	Blue.
1	45 minutes	8	0	0	2
2	9 minutes	8	0	0	2
3	14 minutes	8	1	0	1
4	18 minutes	9	0	1	0
Totals		33	1	1	5

Case 3—In this instance the red and orange glass plates were removed and black paper substituted. The photopathic reaction was found to be definitely positive, the young larvæ grouping in the blue area. Now, as before, the window at the end of the box corresponding to that overlying the black paper was opened to the subdued light of the room, while brilliant daylight entered the blue end of the box. As will be observed, the conditions of this experiment are similar to those of Experiment II, save that, in this instance, a greater difference between the intensity of light at opposite ends of the box existed. Between tests the light from both sources was cut off and the larvæ were allowed to scatter. The results, which may receive the same interpretation as those of Experiment II, are tabulated below (the arrow indicates the direction of light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVAE.		
		→ Black.	Green.	Blue.
1	5 minutes	10	0	0
2	7 minutes	7	3	0
3	10 minutes	10	0	0
Totals.....		27	3	0

Conclusions from Experiments 11 and 12: In the results of the foregoing experiments, we have further evidence to support the conclusions drawn from Experiment 3. In Experiment 12 the larvæ passed from a region of greater (blue) to one of lesser (the red, or in Case 3, the black) light-intensity in moving toward the source of light in the direction of the incident rays. It must be assumed that in Case 3, there was a much greater difference in the intensity of light at the two ends of the box (overlying the blue glass and the black paper respectively) than in Case 2, or in Experiment 3. These experiments were performed many times, under several different conditions of light, and with larvæ of ages varying from a few hours to two days. The same results were obtained in every case, except that in the older first-stage larvæ the reactions were not so definite (more individual variations) and a stronger light was required to bring about the same responses as were manifested by larvæ under four hours old. In these cases, as also in Experiment 3, rays of lesser intensity (but in a horizontal plane) which struck the larvæ in such a way as to cause a body-orientation in which a normal swimming position was still maintained, were more influential in determining a progressive orientation than were the more intense rays which struck both eyes equally, but which came from below, and had a tendency (as will be shown in detail later) to throw the larvæ out of their normal swimming position. As the writer has shown elsewhere (1907a), galvanotactic reactions in the young lobsters occurred only when the tail or the back was turned wholly or partly toward the anode. Although at first sight it appears that the causes for this condition of reaction can have nothing in common with the causes which determine a progressive orientation to the directive influence of light rays only when the swimming position is favorable, it may not be inappropriate to suggest that here also the direction of the impact of light with reference to the axis of the body of the larva, may have some influence on the reaction.

Experiment 13. Case 1—Ten larvæ, twelve days old, were placed in box *A*, mounted over the light-shaft. When the glass plates were arranged in the order designated below, the photopathic reaction was as follows:

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		Red.	Orange.	Green.	Blue.
1	5 minutes	0	1	2	7
2	10 minutes	1	1	1	7
3	15 minutes	1	1	2	6
4	20 minutes	2	0	0	8
5	25 minutes	0	1	0	9
Totals.....		4	4	5	37

Case 2—When the order of the glass plates was changed to red, blue, orange, green, the following results were obtained: Red, 3; blue, 31; orange, 3; green, 3.

Case 3—After redistribution of the larvæ had taken place, the small window opening at the green end of the box was uncovered to the diffuse light of the room. The resulting reactions were as follows:

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		Red.	Blue.	Orange.	Green.
4	2 minutes	0	3	3	4
2	4 minutes	1	3	3	3
3	7 minutes	1	3	1	5
4	10 minutes	1	2	3	4
Totals		3	11	10	16

Case 4—Once more the order of the glass plates was changed to blue, green, orange, red, and the window at the red end was uncovered to the light of the room. The results of the three sets of tests were: Blue, 9; green, 5; orange, 3; red, 13.

Experiment 14—The following observations deal with cases of larvæ suddenly submitted to a light of great intensity, as for instance when they are brought from subdued daylight into full sunlight, or when the brilliant rays from an acetylene lamp fall upon larvæ which had been for sometime in darkness.

Case 1—July 18, 4 p.m. Fifty first-stage larvæ, about thirty hours old, which had been reacting positively in lights of low or medium intensity, were placed (in a glass jar) in the bright sunlight of the west table. Every larva at once moved to the room side of the jar. Within a few minutes, however, all returned to the window side of the jar. Ten minutes later they were divided

about equally on each side. Next they were returned to the dark box and submitted to the weak light from the small window. Here they manifested a definite positive reaction which continued until evening. At 8:30 these fifty larvæ were suddenly submitted to the intense rays of an acetylene light. The result was a universal negative reaction. Within two or three minutes, however, a few larvæ began to return toward the light, and within four minutes all had become positive in their reaction.

Case 2—A group of fourth-day first-stage larvæ in the glass jar was subjected to light of low intensity and found to manifest a positive reaction; when subjected to a much stronger light the same larvæ were still universally positive. This reaction, once established, endured through the period of gradually diminishing intensity of light accompanying the coming of night. The next morning these (now fifth-day) larvæ were found to be negative in reaction. It was feared, however, that the manner of reaction might have been changed because of the long period of confinement which they had undergone. For this reason a fresh lot of twenty-five larvæ from the same group (fifth-day, of the first and second stages), was secured. It was observed at this time that about a third of the number of those in the hatching bag had moulted into the second stage, and that the others were very near the moulting-period. When these larvæ were put in the glass jar, placed in the dark box and submitted to subdued light from the small window, six tests showed fifty-five to be negative, and ninety-five positive. When these same larvæ (now thirteen first-stage and twelve second-stage), under the conditions of stimulation stated above, were subjected to light of still greater intensity by placing the jar nearer the small window of the dark box the results showed that fifty-nine were negative and forty-one were positive.

At 3:30 p.m. these same larvæ were removed from the dark box and placed (in the glass jar) on the west table, where they were suddenly subjected to the bright afternoon sunlight. Every larva came to the room side of the jar and remained there so long as observed.

Case 3—The larvæ mentioned above were liberated and another lot of twenty-five (of the same group, but all in the second stage) was secured at 8 o'clock in the evening. The intense rays of the acetylene light were suddenly directed upon one side of the jar.

This resulted in a sudden and universal positive reaction which, however, soon became indefinite. The larvæ gradually returned to the darker side of the jar and, as in the case mentioned above, remained there so long as observed.

Case 4—When, on the other hand, another group of larvæ which was reacting positively to a light of low intensity, was brought by slow degrees into a light of great intensity, there resulted no sudden, temporary change of reaction such as that observed above. The reaction usually remained unmodified, but if it was reversed it remained permanently so. The same statement holds for larvæ which had been reacting negatively to light of low intensity. When they were brought by slow degrees into light of great intensity, seldom did a sudden temporary change in reaction result.

Conclusions from Experiment 14: The stimulation brought about by suddenly submitting larvæ to intense light may cause at least two kinds of response: first, in the case of early first-stage lobsters (about thirty hours old, and manifesting previously a positive reaction), a definite and universal, though temporary, negative response; second, in the case of early second-stage larvæ (about five days old, and giving previously a negative reaction), a definite and universal, though temporary, positive response. From Case 4 it appears that a gradual change of intensity (extending over an equal or even a greater range of intensities) may not bring about a similar result, although a permanent reversion in the reaction may sometimes ensue.

Larvæ which have recently moulted are most susceptible to slight differences in light-intensity; and the reaction of such larvæ is frequently negative, while the reaction of larvæ which are approaching the moulting-period is more often indefinite or positive.

Experiment 15. Case 1—The following experiment involved the use of the Y-tubes described on p. 207. Ten positively reacting lobsters, five hours old, were placed in the tube at the end designated *a* (Fig. 5, *B*). The Y-tube was then placed in position in the dark. Over one arm was laid a red glass, over the other arm an orange glass, and then the screen was drawn from the window to allow the light rays to strike the tube in the direction shown in Fig. *B*. Tests were made about five minutes apart. After each, the return of the lobsters to the (*a*) end of the tube was induced merely by reversing the tube so that the end (*a*) was

toward the window; the position of the red and orange glass was also reversed. The distribution at the end of each test was as follows:

TEST.	RED ARM.	STEM.	ORANGE ARM.
1.....	o	o	10
2.....	o	1	9
3.....	o	1	9
4.....	o	2	8
Totals.....	o	4	36

Case 2—Next, green and blue glass plates were substituted for the red and orange, the method of the experiment otherwise remaining the same, and the green and the blue glasses were reversed in position at the end of each test. A series of four tests showed the following results: Green arm, 11; stem, 2; blue arm, 27.

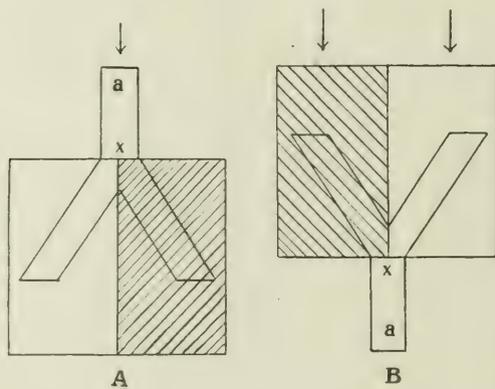


FIG. 5. Showing the Y-tubes as set up for experiment. The arrows indicate the direction of the light rays. The cross-hatched areas represent the glass plates of the darker color laid over the arms of the tubes. The ends designated *a*, represent the starting point for the negatively reacting (A), or the positively reacting (B), larvæ.

Case 3—One more test of the reaction of this group of positive larvæ was made at this time, which was far more delicate than either of the preceding, for the difference in the intensity of the glass plates used was less. In making a selection of glass slides two were chosen which had been purchased for “red glass.” On close inspection, however, and by test with sensitized paper, it was observed that one slide was somewhat lighter in color tone than

the other. These glasses were used in the next experiment. The darker of them may be designated as red, the lighter as ruby. The results of four tests were as follows: Ruby arm, 21; stem, 10; red arm, 9. In the last experiment, with this group of larvæ, it was found that a great intensity of light, striking the red slides, was required to bring about reaction; and that, even then, several larvæ would remain in the region designated x (Fig. 5, *B*), near the junction of light and dark. These experiments were repeated with both black and white backgrounds for the arms of the Y-tube. The results agreed with great uniformity, differing only in the length of time required for the reaction. From these last experiments we may conclude that the first-stage lobsters, at the age of five hours or less, are extremely sensitive to slight differences in the intensity of light, more so in fact than older lobsters of the first and later stages; for it was seldom with these older lobsters that the delicate reaction to the ruby and the red glasses observed in Experiment 15, Case 3, could be induced.

Experiment 16. Twenty first-stage larvæ, slightly over two days old (for which to light of nearly all intensities reactions on the first and second day had been positive), were put in the glass jar, and this in turn was placed in the dark box. They were submitted to light from a small window one inch wide and two inches high, before which the colored glass plates could be placed so as to illuminate one side of the jar with red, blue, green, or orange rays, as the case might be. The reaction in each of these lights was as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red.....	20	0
Orange.....	20	0
Green.....	19	1
Blue.....	18	2
White*.....	15	5
Day.....	3	17

* Subdued daylight passing through one or two thicknesses of white paper.

Here it is shown that the negative reaction to lights of great intensity, which was first discovered in larvæ thirty hours old (Experiment 14, Case 1), and which, as we shall see, persists for a variable length of time, has become accentuated and remains for the time permanent. The next series of observations were made upon lobster larvæ on the fourth day after hatching. Many of them

were nearing the moulting-period and preparing to pass into the second stage.

Experiment 17—July 17, 8:30 a.m. About one hundred fourth-day, first-stage lobsters (Group A) were taken from one of the hatching bags and placed in the glass jar in the dark box. The majority reacted positively to daylight through the small window. At 1 o'clock, when examined again, about one-half of them were reacting negatively. The jar was then removed and placed in the light of the west window where the intensity was greater. At once every larva became negative in reaction.

In order to determine whether this mode of reaction was a natural incident in the life of the larvæ of this age, or whether the response had been induced as a result of their having been so long subjected to experimentation, twenty-five first-stage larvæ (Group B) were removed from the same group as that from which the larvæ mentioned above were taken. When these twenty-five were put in a glass jar and placed in the west window beside the group mentioned above, they gave a positive reaction. After five minutes, half were positive and half negative. At 5:30 the sun was low and the light weak, but all the larvæ gave a negative reaction, which persisted, as did the negative response in Group A mentioned above, until far into the twilight.

It may be further noted in this connection, that five of the larvæ which reacted negatively in the afternoon were placed in absolute darkness for four and a half hours. It was believed that the positive reaction might be renewed; but this was not the case when they were again brought into daylight of several intensities.

Experiment 18. Case 1—July 20, 4 p.m. A number of fourth-day; first-stage larvæ were removed from the hatching bag and put in the glass jar. This was placed in the dark box and the larvæ submitted to red light through the three by three inch window. The resulting reaction was positive and remained so even when the intensity was still further diminished by inserting numerous sheets of paper behind the red glass. Finally, a point was reached where the positive orientation was lost and a homogeneous scattering occurred. When the intensity of the light was again increased, the positive orientation returned; but, with a still greater increase in intensity, this response became again less definite, and finally, in the more intense blue and white light, the negative reaction again appeared.

Case 2—In the evening, when other observations were made upon the same group under the influence of the acetylene light, burning dimly, the reaction in the glass jar was positive under all the colored glass plates. When the intensity was increased by substituting a lamp which burned more brightly, the group divided, half going to the positive and half to the negative side. When the intensity was increased still further (reinforced by a brilliant oil burner and reflector) a greater number gave a negative reaction. As it afterward transpired, the larvæ used in these last tests did not moult to the second stage until on or after the fifth day.

Case 3—July 23, 1:20 p.m. Fifty fourth-day, first-stage larvæ were put in the glass jar and placed in the dark box. In the red light the reaction was definitely positive. The reaction under the different intensities obtained by colored glass plates may be tabulated as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	50	0
Orange.....	47	3
Green.....	43	7
Blue.....	36	14
White.....	23	27

Case 4—July 31, 10 a.m. Twenty-eight first-stage and second stage larvæ of the fifth day (all nearly ready to moult to the second stage) were put in the glass jar and placed in the dark box. Under lights of different intensities the results were as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red.....	28	0
Orange.....	22	6
Green.....	18	10
Blue.....	12	16
White.....	14	14
Daylight.....	0	28

In this particular case it was observed that under the orange light the negative larvæ were of the second stage, while those which retained for the longest time the positive reaction (in the case of the blue and white glasses), were the lobsters which were nearest to the moulting-period. When fresh, clean larvæ, which had moulted into the second stage within a very few hours, were selected and submitted to several different intensities of light, they invariably gave the negative reaction.

Case 5—July 23, 1 p.m. Twenty fifth-day, second-stage larvæ were taken from one of the hatching bags and put in the glass jar. This was placed in the dark box and the larvæ were submitted to illumination from the red light. There was some random swimming, but the general reaction was positive, except in white light, in which three were positive and seventeen negative. Next, the jar was removed from the dark box and placed on the west table in subdued sunlight. Here the reaction was definitely negative. At 4:30 when the jar was returned to the box (at this time in the afternoon the light was much less intense than earlier) a positive reaction was obtained in red, orange and green light.

Conclusions from Experiments 16, 17, 18: From the result of the last three experiments the following tentative conclusions may be drawn. The general negative reaction to light of great intensity, begins on about the third day of the first stage, continues for the most part uninterruptedly until the moulting-period is near; just before the moult the reaction becomes indefinite or, more often, positive; directly after the moult into the second stage (which occurs on the fourth or fifth day of the first-stage-period), the reaction to lights of nearly all intensities again becomes definitely negative.

2. *Second Larval Stage.*

Experiment 19. Case 1—July 19, 8:30 a.m. Observation of a group of sixth-day, recently moulted second-stage larvæ demonstrated that a negative reaction took place when the larvæ were put in the glass jar and placed in the dark box. This was true for daylight coming through the three by three inch window, and in both blue and green light. In the case of orange and yellow light, however, the reaction was similar to that in either yellow or orange, but perhaps less definite. It may be here recorded that a group of first-stage larvæ, about one and a half days old, subjected at the same time to these conditions, gave a positive reaction, not only in orange, but also in blue, and even to white light. These reactions took place on both black and white backgrounds, but they were more definite on white. But when the stimulus of the orange rays was continued for ten minutes or more, in this case also, the negative reaction began to appear again and many larvæ came to the room side of the jar.

Case 2—July 23, 5 p.m. The larvæ used in this case were of the seventh-day group of the second stage, having been taken from the hatching bag at 9 a.m. At 5 p.m. under red, orange, green, blue and white lights, entering through the three by three inch window, all were definitely negative. They had also shown a negative reaction in several intensities of light in the morning. At 7 p.m. further observations were made on the same group of larvæ. The following quotation is from the daily note book.

“July 23, 7 p.m. One of the best demonstrations of the persistency of the negative reaction of these seventh-day larvæ was exhibited this evening. Larvæ taken from the hatching bags at 9 a.m. have reacted negatively at every observation during the day. At 7 p.m. it was observed that this group, which still remained in the glass jar near the west window, continued to present a definite negative reaction. This negative response continued until 7:55 p.m., when the light became too faint to determine either a body or a progressive orientation. Here it is to be observed that the negative reaction on the part of these second-stage larvæ was continued through a long series of gradually diminishing intensities of light. After all signs of body-orientation or progressive orientation had vanished in the case of the group of larvæ mentioned above, the intense light from the acetylene lantern was suddenly thrown open one side of the glass jar. A most definite negative reaction resulted. This response, it will be observed, is different from that recorded in Experiment 14, Case 3, for in the latter case the sudden illumination determined a definite positive reaction.”

Experiment 20. Case 1—July 24, 9 a.m. Thirty eight-day, second-stage larvæ were taken from one of the large bags and put in the glass jar in the dark box. The time of moulting into the third stage was near at hand, and many of the individuals were already “fuzzy” and sluggish in their movements. Illumination through the three by three inch window, by the colored lights, gave these reactions:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	30	0
Orange.....	27	3
Green.....	17	13
Blue.....	13	17
Day.....	13	17

Before we state the next case, one consideration must be noted. In the previous pages, use has been made of such terms as "third-day," "seventh-day," and "eighth-day" larvæ, to distinguish the age, and roughly the stage, of certain groups of lobsters. Because of the use of these terms, it must not be supposed that there is always a constant relation between the age and the stage of the larvæ. Among the larvæ of a single group which have been hatched and have developed under similar conditions, a fairly constant relation between the age and stage is invariably maintained. But for different groups of larvæ, this correlation does not necessarily exist, for it is entirely possible, and indeed it very frequently happens, that a group of seventh-day larvæ may be in the third stage, while a lot of eight-day individuals are in the second stage. The differences in rate of development are due to such factors as water density, temperature, food-supply, and conditions of light and darkness, which, as the writer has shown (HADLEY '06b), may act either directly upon the body processes, or indirectly by favoring or preventing the growth of various body parasites such as diatoms, protozoa, and algæ that naturally develop in profusion on the bodies of the young larvæ. This explanation will perhaps make clear why, in the following case, we apparently retrace our steps to consider the case of seventh-day larvæ. In point of fact, these larvæ were, at the time of experimentation, somewhat further developed than were the eighth-day larvæ mentioned in Case 1.

Case 2—July 20, 9 a.m. Twenty seventh-day larvæ (eight second-stage, twelve third-stage) were removed from the hatching bag, put in the glass jar, placed in the dark box and illuminated by the light through the three by one inch window. After a half hour, observation showed that the larvæ were equally divided between the window side and the room side of the jar. After five minutes' exposure to red light, thirteen larvæ were positive and seven were negative. When, however, the amount of light was increased by opening the large three by three inch window, only three larvæ remained positive while seventeen became negative. This proportionate reaction endured for several hours, or until observation ceased.

Case 3—July 20, 8 p.m. Twenty seventh-day, early third-stage larvæ were taken from one of the hatching bags, placed in the glass jar, and illuminated by an acetylene light. A more or

less scattering negative reaction at first resulted. When the amount of light was increased by supplementing the acetylene with a brilliant oil burner the response was more definitely negative.

Case 4—July 21, 9 a.m. Twenty-two eighth-day, early third-stage larvæ were taken from one of the hatching bags and put in the glass jar in the dark box. When subjected to subdued daylight through the three by one inch window, sixteen out of twenty-two gave the negative reaction. In orange light the reaction was seventeen negative, five positive; in red light eighteen negative, four positive. Here attention may be called to the fact that these third-stage larvæ gave a negative reaction to practically the same intensity of light as determined a positive response for larvæ in the late second stage.

Case 5—August 3, 2 p.m. Twenty eighth-day, early third-stage larvæ were taken from the hatching bags and put in the glass jar in the dark box. They were submitted to the colored lights, with results as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	8	12
Orange.....	6	14
Green.....	3	17
Blue.....	2	18
White	6	14
Day.....	0	20

Conclusions from Experiments 19 and 20: The conclusions which we draw from the two foregoing experiments support further those formulated for Experiments 16, 17 and 18, on p. 228. In Experiment 20, Case 1, was observed the definite positive response which was manifested toward the end of the second larval stage when the moulting-period was near. In Case 2, where a group of larvæ which included individuals of both the second and third stages was used, it was observed that the reaction was either positive or negative; and that those larvæ which gave the negative reaction most definitely or gave it first were usually the larvæ of the early third stage. In Cases 4 and 5, in which only third-stage larvæ were employed, it was observed that, in general, the reactions to lights of nearly all intensities were negative. As in the case of the first-stage larvæ, it was found that the reaction of second-stage larvæ, just before the moulting-period, usually changed from negative to positive, and again became negative at the beginning of the third larval state.

3. *Third Larval Stage.*

By the ninth day it is only in exceptional cases that the larvæ have not entered the third stage; and it frequently happens that they are nearly ready to enter the fourth. The swimming of the third-stage larvæ is much like that of the earlier stages except that in the third stage there is greater difficulty in using the swimmerets of the thoracic appendages, especially during the last part of the stage. One reason for this is the fact that, as the larvæ grow older and larger, they more often play the host to multitudes of diatoms, algæ and protozoa which gather in such quantities as seriously to interfere with the processes of swimming and eating. In the preparation for the moult from the third to the fourth stage, moreover, occur the most important changes that the young lobster undergoes in the course of its life. These changes appertain not alone to modifications in the external form of the body and to the form and functions of many of the body appendages, but also to points of internal structure. Among the changes during this period of metamorphosis we may enumerate the following as important in connection with our study of behavior: (1) The loss, in the moult from the third stage, of all functional swimming attachments of the thoracic appendages; (2) the great development of both the first and second pairs of antennæ and of the chelipeds; (3) the accession of functioning swimmerets on the under side of the second to sixth abdominal segments; (4) a great change in the form of the body, and a consequent modification of the manner of swimming.

In view of these important changes, which are taking place in the anatomy of the lobsters as they pass from the third into the fourth stage, it does not appear unjustifiable to believe that these processes have an influence on the behavior of the larvæ even before they emerge in approximately the adult structural type, endowed with a new body form, new functional apparatus and new reactions. We shall now undertake a study of the behavior of the third-stage larvæ as they approach and finally pass this most critical period of their life history.

Experiment 21. Case 1—July 22, 9:30 a.m. Thirty ninth-day, third-stage larvæ were removed from the hatching bag, put in the glass jar and placed in the dark box. Under stimulation by the red rays, although there was no definite positive reaction, most of

the larvæ swam about at random on the window side of the jar. When orange glass was substituted for red, half of them came to the room side of the jar. In the case of green glass, a few more reacted negatively, and when blue glass was substituted for green, all but five larvæ gave a negative response. These five did not manifest a definite positive reaction, but swam at random on the window side of the jar. When the colored glasses were removed and the larvæ were submitted to the influence of diffuse daylight through the small window, all reacted negatively.

Case 2—August 4, 9 a.m. Twenty ninth-day, third-stage larvæ were taken from one of the hatching bags and placed in the dark box. Stimulation by the colored light resulted as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	6	14
Orange.....	3	17
Green.....	2	18
Blue.....	2	18
White.....	0	20
Daylight.....	0	20

Case 3—In the present case it was attempted to learn whether the sign of the photopathic reaction in the larvæ of this stage corresponds to the sign of their phototactic reaction. To this end, ten ninth-day, third-stage larvæ, fresh from the hatching bag, were placed in the glass-bottomed box *B*, which was set over the light-shaft and mounted upon colored glass plates. After each observation either a period of five minutes was allowed for a uniform distribution of the larvæ to take place, or the box itself was reversed, leaving the glass plates in the same order. In other instances the order of the glass plates was changed. During this experiment the water in the box was eighteen to twenty mm. deep. The results are presented below:

RED.	ORANGE.	GREEN.	BLUE.
4	0	1	5
1	0	2	7
RED.	ORANGE.	BLUE.	GREEN.
2	1	3	4
1	1	4	4
RED.	BLUE.	GREEN.	ORANGE.
1	5	3	1
2	2	3	3
BLUE.	RED.	GREEN.	ORANGE.
6	0	3	1
5	1	2	2

The larvæ which were used as stated above, and which presented a positive photopathic reaction in every instance, were next transferred to the glass jar and placed in the dark box. Here, and in tubes, the assumed phototactic reaction was uniformly and definitely negative; and this was true in the case of lights which were both of greater and of lesser intensity than in the tests above mentioned.

Case 4—To confirm the results obtained in Case 3, similar tests were made with another group of ninth-day, third-stage larvæ, fresh from the hatching bag. Notwithstanding the fact that this series of observations was not started until 5 o'clock in the afternoon when the light was fading, the results were similar to those obtained in Case 3. That is to say, the photopathic reaction was definitely positive, but the phototactic reaction, as shown when the larvæ were transferred to the glass jar in the dark box, was as definitely negative.

Experiment 22—The following experiment and observations concern the tenth-day, third-stage larvæ. Most of these lobsters were well along in the third stage, and many were covered with body parasites.

Case 1—July 23, 9 a.m. Thirty tenth-day, third-stage larvæ were transferred from one of the hatching bags to the glass jar and placed in the dark box. After having been submitted for one-half hour to light coming through the red glass (three by one inch window), the reaction was uniformly negative. In the case of orange, yellow, green, blue and white light the results were the same. In all of these reactions, however, one fact was noticeable, the body-orientation of these larvæ was much less definite than in any previous case of the same or earlier stages.

Case 2—July 26, 9 a.m. A mixed lot of thirty third-stage larvæ, most of which were ten days old, although some were older and some younger, were transferred from the hatching bag to the glass jar. When submitted to the colored lights in the dark box, the following results were obtained:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	3	27
Orange.....	13	17
Green.....	8	22
Blue.....	13	17
White.....	0	20

In consideration of the apparent fluctuations in the sign of reaction manifested by the above-mentioned larvæ, it may be noted that these lobsters represented a group in which some were "early," others "advanced," third-stage larvæ. Indeed many were approaching the third moulting-period; the significance of this for the behavior of the larvæ we shall consider in the next few cases.

Case 3—July 27, 2 p.m. Thirty eleventh-day, third-stage larvæ were transferred to the glass jar and placed in the dark box. Under colored lights, although the general reaction was negative, many were positive. Experiments made upon the larvæ in the glass-bottomed box *B* to determine the photopathic reaction at this time, showed that the larvæ gave neither a definitely positive nor a definitely negative reaction. Other tests indicated a definitely positive reaction. When, however, light was admitted to the box through the end window (as well as through the bottom), first from the red end, then from the blue end, of the box, there resulted a definite negative phototactic response. The arrows show the direction in which the light entered the box.

→ RED.	BLUE.	ORANGE.	GREEN.
1	2	1	6
1	1	0	9
0	0	0	10
→ RED.	ORANGE.	GREEN.	BLUE.
0	0	0	10
0	0	1	9
RED.	ORANGE.	GREEN.	BLUE. ←
5	1	2	2
6	0	2	2
9	1	0	0

The foregoing cases demonstrate that these larvæ manifested a definitely negative phototactic reaction under the conditions of illumination described; and that, by those rays which had a directive influence, they could be driven into a region of either greater or lesser light intensity, as represented by the blue and by the red ends of the box, respectively. It might be argued that, so long as the eyes of the larvæ are homolaterally stimulated, variations in intensity can not cause or change the orientation, and that orientation results only from a heterolateral stimulation. But this is by no means true, for it has been noted in the foregoing pages, and it will be further demonstrated, that slight differences in intensity,

when coincident with a homolateral stimulation, may even reverse the index of progressive orientation.

Case 4—July 24, 9 a.m. Thirty-five eleventh-day, third-stage larvæ were transferred from the hatching bag to the glass jar and placed in the dark box. The reactions to the colored lights were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	15	20
Orange.....	16	19
Green.....	8	27
Blue.....	8	27
White.....	7	28

Next, the jar was placed in full daylight, on the table before the west window. All larvæ came to the room side. In this case there were seven larvæ which became the special object of observation, since they invariably manifested a positive reaction until they encountered daylight. This group was set aside, and before night four of the seven had moulted into the fourth stage; consequently their exceptional behavior was due to the fact that they were in a different physiological condition than the majority of the group used in Case 4.

Experiment 23. Case 1—In this experiment is continued the examination of the reactions of other twelfth-day larvæ which were approaching the third moulting-period. Twenty-three larvæ were placed in the glass jar and observed under the influence of the colored lights in the dark box. The results were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	6	17
Orange.....	15	8
Green.....	6	17
Blue.....	4	19
White.....	3	20

Case 2—At 3:30 p.m. Ten larvæ from the above groups were transferred to the glass-bottomed box *B*, which was set up over the light-shaft upon the colored glass plates. The results were as follows: Blue, 19; green, 3; orange, 4; red, 4. During the course of the day, many of these ten larvæ moulted to the fourth-stage.

Case 3—July 29, 9 a.m. By this date there were very few third-stage larvæ left in any of the groups whose actual age was known. Indeed there are few cases in which the development is so slow that the third-stage larvæ endures to the thirteenth or

fourteenth day. In this particular instance, twenty larvæ were transferred to the glass jar and placed in the dark box. The resulting reactions to the colored lights were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	16	4
Orange.....	16	4
Green.....		
Blue.....	13	7
White.....	9	11
Day.....	0	20

It may be observed in the account of the last three experiments how the general reaction of the third-stage larvæ has gradually changed from negative to positive; and how it requires an increasingly greater intensity of light to determine a negative response in the larvæ which are approaching the fourth stage. In the next case the culmination of this gradual change is reached, since the third-stage larvæ almost uniformly manifest a positive reaction which is as definite as that of the newly-hatched larvæ.

Case 4—July 30, 2 p.m. Thirty fourteenth-day, third-stage larvæ secured from a group in which nearly all had entered the fourth stage, were transferred from the hatching bag to the glass jar and placed in the dark box under the influence of colored lights:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	30	0
Orange.....	30	0
Green.....	30	0
Blue.....	30	0
White.....	28	2
Day.....	23	7

It is here observed that, when as indicated above, the jar was removed from the dark box and placed on the west table in daylight, only seven larvæ became negative. All the others remained positive, even in this light of great intensity. This case represents the strongest and most definite maintenance of the positive reaction in late third-stage larvæ ever observed by the writer. These larvæ moulted into the fourth stage very soon after the above observations were made.

Case 5—In the following test other members of the group of larvæ used in the previous case were employed. The aim was to learn whether or not the photopathic reaction* in these larvæ was in agreement with the phototactic reaction described in Case

0. The larvæ were placed in the glass-bottomed box over the light-shaft; fifteen minutes was allowed for the first orientation, and five minutes was given for each of the others:

AFTER	BLUE.	GREEN.	ORANGE.	RED.
15 minutes.....	6	2	2	0
20 minutes.....	6	1	1	2
25 minutes.....	4	1	5	0
30 minutes.....	4	5	0	1
35 minutes.....	3	7	0	0
40 minutes.....	2	7	0	1
Totals.....	25	23	8	4

It thus appears that the photopathic reaction of the larvæ was definitely positive. After this series of observations the larvæ were returned to the glass jar and placed on the west table. In the faint daylight which remained, the positive reaction was manifested and continued as long as the light lasted.

Conclusions from Experiments 20, 21, 22 and 23: As has been noted, these experiments deal with the reaction of larvæ as they pass through the third and enter the fourth stage. In Experiment 20 (Cases 2, 3, 4 and 5) it was shown that, in general, the majority of early third-stage larvæ reacted negatively, frequently to light of weak intensity, and invariably to light of greater intensity. In Experiment 21 it appears (1) that this negative response was fairly characteristic of the early third-stage larvæ; (2) that, notwithstanding this negative phototactic reaction, the photopathic response might be definitely positive (Experiment 21, Case 3) thus appearing to indicate that, at least at a certain period in the life of the third-stage larvæ, a positive photopathic reaction and a negative phototactic response may be given by the same individual. Experiment 22 demonstrates (1) that, as the third-stage advanced, the positive reaction, was more frequently and more easily determined by light of all intensities (Case 2), and that an increasingly strong illumination was required to bring about a negative reaction (Case 4); (2) that the photopathic response, if anything, remains throughout the stage, positive (Case 3), while the sign of the phototactic response may change with the intensity of the light (Cases 2 and 4).

In Experiment 23 it is observed that the negative reaction to strong light was still prominent in the behavior of the twelfth-day

larvæ (Case 1), while on the thirteenth and fourteenth days, as the moulting-period to the fourth stage approached, the negative reaction was less easily determined (Cases 3 and 4). It was observed furthermore, that these larvæ continued to manifest a very definite positive photopathic response (Case 5), and that this was maintained until the end of the stage-period.

General conclusions on the behavior of larvæ of the first three stages—As the larvæ, after the very definite positive photopathic and phototactic reactions characteristic of the first part of the first larval stage, pass on through the first stage-period, lights of low intensity (red, orange, twilight, etc.), gradually lose their efficiency in bringing about a positive phototactic reaction, while, on the other hand, lights of a greater intensity (green, blue, daylight, etc.) determine, more and more easily, a negative response. This negative phototactic response, which may enter on the third day of the first stage-period, changes again to positive as the first-stage larvæ draw near the first moulting-period. At this time, the lights of low intensity are again effective in bringing about a positive reaction, which is maintained until the larvæ have moulted into the second stage.

While the photopathic reaction of newly moulted second-stage larvæ remains positive, the phototactic response is more often negative, and this negative response is commonly maintained until toward the end of the second stage-period. At this time, as was observed in the first stage-period, a positive reaction again becomes manifest as the larvæ approach the period of moulting into the third stage.

While the positive photopathic reaction still obtains, the newly moulted third-stage larvæ commonly manifest a negative phototactic reaction, and this, as was the case with the second-stage larvæ, is retained until the moulting-period into the fourth stage approaches. At this time the reaction again becomes positive, and continues so until the larvæ have entered the fourth stage. These general points in the behavior may be illustrated by the following diagram (Fig. 6).

The foregoing facts serve to emphasize further the statement made on an earlier page, that we can not justly say that the larvæ of *Homarus* are positive to light or negative to light, or that they react in this way to intensity, and in that way to the directive influence of the light rays. But these observations do show that

the larval lobsters manifest a type of behavior which includes widely varying kinds of reaction, even to the same stimulus. The point has been, not to learn what reaction the lobster larvæ give to light, but to ascertain the conditions which so play upon the mechanism of these organisms as to produce the wide range of responses observed. The causes of the daily and the hourly variations in the kinds of reactions manifested by organisms is a field which is, even at the present day, largely given up to speculation, and all sorts of explanations have been brought forward from the view of the rhythmical succession of certain movements resulting from purely internal stimuli, to the view of cycles of change in certain metabolic products under the influence of external stimulation, and their consequent reaction upon the nervous processes of the organism. The fact of variations in the reactions of larvæ of the European lobster (*Homarus vulgaris*) has been noted by

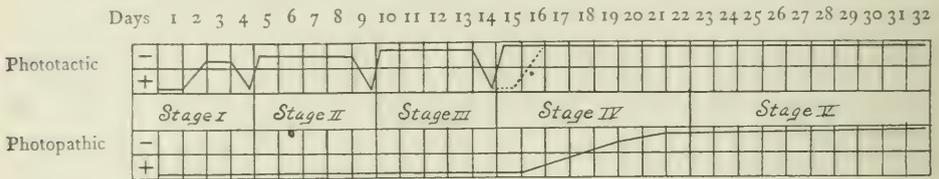


FIG. 6. Diagram recapitulating the nature of the phototactic and photopathic reactions of lobsters in the first five stages. The dotted line in the upper series indicates that the early fourth-stage lobster may give a positive phototactic reaction to light of very great intensity. For further explanation, see General Conclusions on p. 239.

BOHN (1905, p. 10). After having made several observations upon recently hatched larvæ, he comes to the following conclusion. "De ces diverses observations, il semble résulter que *le sens de déplacement des larves de homard subit des variations occellantes de signe*, qui, bien que influencées par l'éclaircissement actuel sont en relation avec les heures de la journée."

Although certain phases of behavior in some marine animals may be explainable on the ground of rhythmically recurring reactions which bear a certain relation to the hours of the day, the present writer's experience with larvæ of all ages and stages of the American lobster makes it quite impossible to attribute the variations in the reaction of lobster larvæ to such causes. The hours of the day, except as they are accompanied by corresponding differences in the intensity of light, have nothing to do with

the form of reaction displayed by the lobster larvæ. This is readily shown, first, by the fact that, at any corresponding time on two successive days (and especially when a moult has intervened), the reactions of the same larvæ may be quite dissimilar. Here the reactions are explainable on the grounds of (1) the stage of the larvæ and their age in the stage-period; and (2) the intensity of the light and of other stimuli which are brought to bear. This conclusion is shown furthermore by the fact that larvæ at corresponding times in the different stage-periods usually manifest similar types of reaction. Thus does it appear that, although the diverse forms of reaction are partly due to the differences of intensity in actual illumination, the underlying cause is some physiological change which the larvæ undergo as they gradually approach and pass the crises of their moulting-periods.

4. *Fourth Stage.*

We come now to a consideration of the reactions to light of the fourth-stage lobsters. It has been observed in previous pages that the most striking change, not only in body-form but also in life-habits, which takes place in the life of the lobster, occurs during the transition from the third to the fourth stage. It is the aim of the present section to analyze the reactions of the fourth-stage larvæ and to exhibit the conditions which determine or modify these reactions.

In the previous pages the lobsters under consideration have been referred to as the "second-day" or the "fifth-day" larvæ, etc., as the case might be, and this terminology was of advantage, because the first three stage-periods are so brief that changes may occur even in two consecutive days. The fourth stage-period, however, is much longer (usually eight to twelve days) and the differences in reaction on two consecutive days may be slight or inappreciable. For this reason, then, in the following consideration we shall divide the fourth stage-period into three parts, viz: the early, the mid, and the late fourth stage-period.

Experiment 24. Reactions of early fourth-stage lobsters. Case 1. Photopathic reactions—July 28, 10 a.m. Ten early fourth-stage larvæ were put in the glass-bottomed box *B* and this was placed over the light-shaft. The arrangement of the colored plates and the resulting orientations were as follows. The results

indicate that the early fourth-stage lobsters show a slight tendency to remain in the more brightly illuminated areas.

RED.	ORANGE.	GREEN.	BLUE.
1	1	2	6
2	2	1	5
2	3	2	3
—	—	—	—
5	6	5	14
RED.	ORANGE.	BLUE.	GREEN.
4	1	2	3
2	2	2	4
0	2	5	3
0	1	4	5
—	—	—	—
6	6	13	15
GREEN.	BLUE.	ORANGE.	RED.
2	4	1	3
1	4	2	3
3	3	2	2
—	—	—	—
6	11	5	8
<i>Totals.</i>			
BLUE.	GREEN.	ORANGE.	RED.
38	26	17	19

Case 2. Phototactic reaction—August 7, 5:30 p.m. Ten early fourth-stage larvæ were placed in box *B* and the end window of the box was opened to the diffuse light of the west window. As has been explained, this box was so constructed that in a moment glass plates could be slid through the cover, and into such position that they would divide the floor area of the box between the ends into four equal parts. Beginning with the end toward the light these may be numbered 1, 2, 3, 4, respectively, and the results showing the imprisonment of the larvæ in two instances, may be recorded as follows:

1.	2.	3.	4.	1.	2.	3.	4.
2	2	0	6	2	1	2	5
7	0	0	3	0	1	2	7
2	0	2	6	0	0	1	9
0	0	2	8	0	0	3	7
—	—	—	—	—	—	—	—
11	2	4	23	2	2	8	28

In the second of these instances an acetylene light was used, the intensity being diminished by inserting a red glass between the burner and the window in the end of the box toward the light.

Case 3. Phototactic reaction—August 9, 3:40 p.m. Ten early fourth-stage lobsters were transferred from the confining bag to box *B*, and this was placed with the end toward the west light. In this case, colored glass plates were placed at intervals in front of the end window to modify the intensity of the light entering the box. A five-minute intermission was allowed between observations. The results, which clearly establish a negative phototactic reaction, are presented in the following table:

COLOR.	1.	2.	3.	4.
	2	1	2	5
	1	1	2	6
	2	1	3	4
	0	0	2	8
Orange	5	3	9	23
	0	1	2	7
	0	1	4	5
	1	3	2	4
	0	1	1	8
Red.....	1	6	9	34
	1	0	1	8
	0	0	0	10
	1	1	0	8
	1	2	2	5
Green.....	3	3	3	31
Totals.....	9	12	21	78

Case 4. Phototactic reaction—In the following case, in which the same lobsters were used the source of illumination was the acetylene light and the intensity of the light which entered the end window of box *B* was modified in two ways: (1) by the colored glass plates placed between the light and the window in the end of the box; (2) by the distance of the light from the box. The results, which demonstrate a definite negative phototaxis, were as follows (in all cases the figure 1 indicates the division of the box nearest the light; 4 the division farthest from the light):

COLOR.	DISTANCE.	1.	2.	3.	4.
Red.....	2 inches.....	3	1	2	4
		1	0	1	8
		1	2	3	4
		1	1	1	5
		Totals.....	6	4	9
Red.....	6 inches.....	2	1	1	6
		1	3	2	4
		3	0	1	6
		1	2	2	5
		Totals.....	7	6	6
Red.....	12 inches.....	3	1	2	3
		4	2	1	3
		1	3	2	4
		2	4	4	2
		Totals.....	10	8	9
Blue	12 inches.....	0	1	4	5
		1	1	3	5
		3	2	0	5
		2	2	0	6
		Totals.....	6	6	7
Blue.....	2 inches.....	2	0	1	7
		1	1	2	6
		2	1	2	5
		2	1	3	4
		Totals.....	7	3	8
Totals.....					
Totals.....		36	27	39	97

Case 5—One observation on the behavior of the early fourth-stage lobsters is difficult to harmonize with the reactions mentioned in the previous cases. When at night the rays from an acetylene light were brought to bear upon very early fourth-stage lobsters, swimming in the confinement bags, they would sometimes swim directly toward the light. This reaction was often so strongly manifested that the natural rheotactic response to the influence of the water current circulating in the bags was quite obscured in the areas of greatest illumination, because the young lobsters followed—so to speak—the course of the rays from the acetylene lantern. If this reaction represents a true phototactic response, then it must be said that very early fourth-stage lobsters may, under appropriate conditions of stimulation, respond positively to the directive influence of light, not, as do the earlier stages or the late fourth-stage by turning from the light, but by “heading”

into it. In an earlier paper (HADLEY 1906b), the writer has assumed this to be a true phototactic response. One other instance which appears to support this view may be recorded as follows.

Case 6—Ten sixteenth-day, fourth-stage lobsters were placed in a large slender dish, which was set in the dark box. The larvæ manifested no tendency to undergo either body-orientation or progressive orientation. Next, the same lobsters were placed in the glass-bottomed box, now lined with white paper, which greatly intensified the light within. This box was put with the end window toward the bright sunlight, and the records of five trials (ten larvæ in each) indicated that, when the light was sufficiently intense, the early fourth-stage lobsters might give a positive phototactic reaction. In this instance twenty-six larvæ were positive, twelve negative, and twelve neutral.

When the white paper was removed, and four more tests were made, the results showed that twenty-five larvæ were negative, six positive, and nine neutral.

Experiment 25. Reaction of mid-fourth-stage lobsters, Case 1. Phototactic reaction—August 10, 3:30 p.m. Ten mid-fourth-stage lobsters were transferred from the hatching bags to box B, and the experiment was continued in daylight as in Experiment 24, Case 2. The results show a definite negative phototactic reaction, and may be tabulated as follows (similar results were obtained when a white lining in the box was used, though in this case, they showed a less definitely negative reaction):

COLOR.	1.	2.	3.	4.
Orange.....	1	1	1	7
	0	1	2	7
	0	0	1	9
	1	1	2	6
Totals.....	2	3	6	29
Blue.....	0	1	2	7
	1	0	1	8
	1	1	2	6
	1	1	1	7
Totals.....	3	3	6	28
Ruby.....	0	0	1	9
	0	2	1	7
	1	1	4	4
	1	0	3	5
Totals.....	2	3	9	25
Grand Totals.....	7	9	21	82

Case 2. Photopathic reaction—August 9, 3:30 p.m. Ten fourth-stage lobsters were removed from one of the confinement bags and placed in 16 mm. of water in the glass-bottomed box. The glass plates were arranged in the order given below, and tests were made at five-minute intervals. The results, which showed a diminished tendency to remain in the areas of greatest illumination, are represented in the following table:

RED.	ORANGE.	GREEN.	BLUE.
3	2	1	4
4	0	3	3
1	2	1	6
2	2	4	2
2	4	2	2
—	—	—	—
12	10	11	17

When, some hours later, the same lobsters were tested again the results of five trials were as follows: Blue, 13; green, 9; orange, 7; red, 21; apparently in this instance it can not be said that the mid-fourth-stage lobsters were either positively or negatively photopathic. Yet the last instance shows a tendency toward a negative reaction.

Experiment 26. Reaction of late fourth-stage lobsters. Case 1. Photopathic reaction—August 12, 2 p.m. Ten late fourth-stage lobsters were transferred from one of the confinement bags (where the majority had already entered the fifth stage) to the glass-bottomed box which was placed over the light-shaft in order to test the photopathic reaction. In this case nine consecutive tests were made, three minutes being allowed for each orientation. The results, which are characteristic of all other tests, and which show a tendency on the part of the lobsters to avoid the light, may be recorded as follows:

No.	BLUE.	GREEN.	ORANGE.	RED.
1.....	1	2	1	6
2.....	1	0	3	6
3.....	3	0	2	5
4.....	3	4	1	2
5.....	1	2	1	6
6.....	3	1	0	6
7.....	5	3	0	2
8.....	1	1	1	7
9.....	4	2	2	2
Totals.....	22	15	11	42

Case 2. Phototactic reaction—August 10, 3:30 p.m. Ten late fourth-stage lobsters were taken from one of the hatching bags and put in box *B*, which was placed in the dark box so that the end window faced the light, the intensity of light being modified in each case by interposing colored glass plates between the end window and the light. The tests, which were made at three-minute intervals, and which showed a very definite negative reaction, were as follows (in the fourth tests of the first and last sets respectively, one lobster was accidentally killed, thus making the totals incomplete):

COLOR.	1.	2.	3.	4.
	1	1	1	7
	0	1	2	7
	0	0	1	9
	1	0	2	6
Orange.....	2	2	6	29
	0	1	2	7
	1	0	1	8
	1	1	2	6
	1	1	1	7
Blue.....	3	3	6	28
	0	0	1	9
	0	2	1	7
	1	1	4	4
	1	0	3	5
Red.....	2	3	9	25
Totals.....	2	8	21	82

Conclusions on the reaction of fourth-stage lobsters—The observations thus far made upon the behavior of fourth-stage lobsters appear to demonstrate the following points: (1) Throughout the entire fourth stage-period (with the exceptions noted under Experiment 24, Cases 5 and 6), the lobsters manifest a negative phototactic reaction, which is accentuated in the latter part of this stage. This behavior is quite different from the positive reaction which supersedes the negative in the case of second and third-stage larvæ just previous to their moult into the third and fourth stages respectively; (2) This type of reaction after the first part of the fourth stage-period, cannot be reversed or modified, as was

the case in earlier stages, by using different intensities of light (3). The photopathic reaction, which in the early fourth-stage lobsters is definitely positive, changes by the latter part of the stage to negative in the majority of individuals. Thus it can be observed that, just as the third-stage larvæ might at the same time (or successively) manifest both a negative phototactic and a positive photopathic reaction, so may the lobsters of the fourth stage. Other points regarding the behavior of fourth-stage lobsters will receive consideration in connection with the subject of contact-irritability.

5. *Fifth Stage.*

The body-form of the fifth-stage lobster is similar to that in the fourth-stage, and we might therefore expect to find similar types of reaction. It will be seen, however, that there are many points of difference in behavior which are of such a nature that they can not be attributed, either wholly or in part, to changes in body-form or in the swimming appendages. The changes are doubtless the consequence of modifications which have taken place in the body-processes or in the physiological states of the lobsters themselves, and which have resulted from the cumulative stimulation during the earlier life of the lobsters. Generally speaking, it may be said that the reactions of the fifth-stage lobsters are fairly typical for the adult form, and are especially characterized by the light-shunning tendency. This form of behavior could be observed readily by watching the lobsters in their confinement cars; but, for the sake of certainty, the same experiments, to which the larvæ of earlier stages had been subjected, were repeated with the fifth-stage lobsters. Since the reactions did not appear to undergo any noticeable modification as the lobsters passed through the fifth stage, there is no need for considering the early, mid and late fifth stage-periods separately, as was done for fourth-stage lobsters. The type of reaction presented in the early fifth stage-period differs in no way from the behavior of lobsters in the late fifth stage-period; and both are characteristic of the behavior in all later stages.

Experiment 27. Case 1. Photopathic reaction—In the first instance, ten fifth-stage lobsters were transferred from one of the confinement bags to the glass-bottomed box and this was placed over the light-shaft. The method used was the same as in pre-

vious experiments. In the second instance the blue glass was removed, and the space where it had lain was left clear, thus permitting the reflected daylight to enter this area of the bottom of the box. The results of both tests show a negative reaction which was more definite in the second instance.

BLUE.	GREEN.	ORANGE.	RED.
2	1	2	6
2	1	2	5
3	1	1	5
2	3	2	3
—	—	—	—
8	6	7	19
DAYLIGHT.	GREEN.	ORANGE.	RED.
0	2	2	6
0	3	2	5
1	2	2	5
0	2	2	6
1	1	3	5
0	2	4	4
—	—	—	—
2	12	15	30

Case 2. Phototactic reaction—Further demonstration of the definitely negative phototactic response of fifth-stage lobsters was given by the experiments on contact-irritability (Exp. 29, p. 256). Here is clearly shown the extreme manifestation of this negative phototactic response, which frequently would have culminated in fatal results by driving the lobsters from deep to shallow water and leaving them stranded where they would certainly have died had they not been returned to the water at the end of the experiments. Here, as has been found in the case of many animals, the total behavior is completely dominated by the light influence. It may be said further that in the case of the fifth-stage lobsters light of different intensities does not cause a change of reaction from positive to negative, or from negative to positive, as was the case in the earlier stages; nor do we ever find the individuals "heading" into the light, as may be the case in the fourth-stage larvæ. For the fifth-stage lobsters any intensity of light which influences their behavior in any degree, determines, under experimental conditions, both a negative body-orientation and a negative progressive orientation.

In the foregoing pages it has been shown that larvæ which were positively photopathic could be made to pass from regions of greater to regions of lesser light intensity by submitting them to

the directive influence of light of sufficient strength. In these cases, it was observed that the photopathic reaction was invariably subservient to the phototactic, although the latter was also very dependent upon a certain optimal intensity for bringing about a positive or negative response. In the following instance we shall observe that, although the directive influence of the light rays is capable of modifying the orientations which relative intensities of light have determined, still the directive influence can not quite obliterate the evidence of a photopathic reaction, as was possible in the younger larvæ. In other words *the tendency of the fifth-stage lobster to "select" the darker regions has become almost as firmly fixed as has the tendency to react negatively to the directive influence of the light rays.* In the first larval stages the photopathic response invariably gives way to the phototactic. In the fifth the two tendencies clash; and the resulting orientation of the lobster is determined, not by one, but by both of these factors.

(A.) *Case 3. Photopathy versus phototaxis*—Ten fifth-stage lobsters were put in box B. This was mounted upon the colored glass plates over the light-shaft as in previous experiments. The preliminary observation showed that there was a definite tendency for the lobsters to congregate at the red end of the series of glass plates, thus demonstrating a negative photopathic reaction. Now the window at the red end was opened to diffuse light. After a period of ten minutes, observations of the position of the lobsters were begun, and continued at five-minute intervals. The following results show that, although the negative phototactic response is still manifested, it has been greatly modified by the tendency on the part of the lobsters to avoid the brightly illumined area at the end of the box:

DAYLIGHT.	GREEN.	ORANGE.	RED.
1	4	2	3
1	3	3	3
2	3	3	2
1	3	4	2
1	2	4	3
2	3	3	2
<hr/>	<hr/>	<hr/>	<hr/>
8	18	19	15

In the next case, the end of the glass plate series, which in the previous instance admitted reflected daylight, was covered with a blue glass and the illumination of this area thus rendered less

intense, while the end window of the box (at the red end) remained open, as in the last experiment. The results, which demonstrate that the phototactic reaction had still further overcome the photopathic, were as follows:

BLUE.	GREEN.	ORANGE.	RED.
2	2	4	2
1	3	2	4
3	2	3	2
3	2	2	3
4	3	2	1
2	3	2	3
—	—	—	—
15	15	15	15

In the last two instances it becomes apparent that the fifth-stage lobsters, unlike the early-stage larvæ, could not be forced, by the directive influence of the light rays, into an area of greater light-intensity. In other words, the tendency to manifest a negative phototactic reaction was not sufficiently strong to overcome the tendency to give a negative photopathic response.

(B.) *Experiment 28. Phototaxis leading to fatal results*—Before bringing to a close this consideration of the reactions to light in lobsters of the fourth and fifth stages, it may be appropriate to introduce the results of some experiments whose aim was to show the extreme nature of some phototactic reactions. In other words, attempt was made to determine whether or not the strong directive influence of the light rays could compel the larvæ so to act that they would do injury to themselves as in the familiar case of the moth that flies into the flame, or of *Ranatra*, mentioned by HOLMES (1906). The reactions of the fourth-stage and fifth-stage lobsters will be considered together.

Case 1. Fourth-stage lobsters—For this series of experiments box *B* was set up as represented in Fig. 7, being supported at one end so that the bottom of the box made an angle of about fifteen degrees with the table. The box was filled with water so that when it was slanted, the water-line did not quite reach the angle made by the bottom and upper end, *B*. In this way there was created an inclined plane, slanting from the window end, *A*, of the box to the higher end, *B*. The water consequently diminished in depth as the end, *B*, was approached. At this end there was an inch or more of the bottom of the box not covered by water. The light from the window, *L*, was reflected into the box by the mirror,

M, for the purpose of discovering whether the larvæ in presenting their negative phototactic reaction, would allow themselves to be driven into the shallow water. By means of a hole in the bottom of the box, the water could be withdrawn very gradually (a few drops a minute), so that if the larvæ persisted in remaining in the

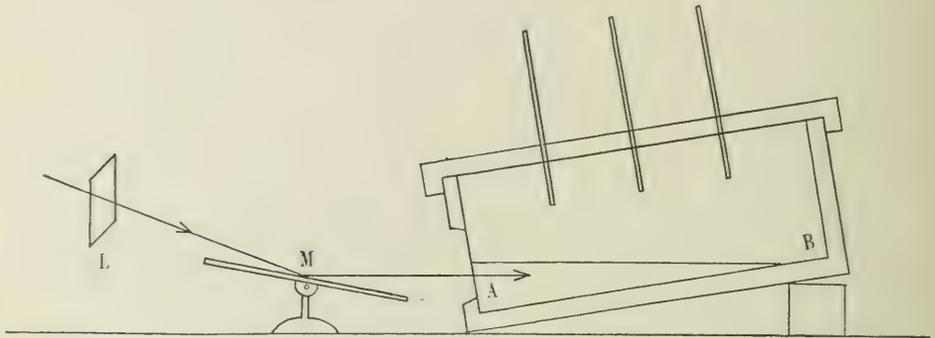


FIG. 7. Diagram of apparatus as set up to test the extreme phototactic reactions, leading, in the case of fourth and fifth-stage lobsters, to fatal results. *L*, source of light; *M*, reflecting mirror; *A*, end of box adjacent to "window;" *B*, end of box not covered with water, where the lobsters were stranded. In the cover of the box are shown the sliding partitions.

shallow area, they would, in the course of a few minutes, be stranded on the dry bottom. Ten fourth-stage lobsters were first used for experiment and the results, ascertained by counts made as in all other cases, were as follows: (The arrow shows the direction of the light coming through the end window of the box, while the numbers at the top of the columns represent the division areas of the box):

TEST.	→ 1.	2.	3.	4.	NUMBER STRANDED.	TIME (after).
1	1	1	3	5	4	5 minutes
2	1	2	1	6	3	10 minutes
3	0	1	1	8	6	20 minutes
4	1	1	3	5	5	50 minutes
Totals.....	3	5	8	24	18	

The results of this experiment and of several others similar to it, show, that out of a total of twenty-four larvæ which gathered

in the area farthest from the light, eighteen allowed themselves to be stranded rather than to retrace their course into deeper water, and in so doing to approach the light.⁴

Case 2. Fifth-stage lobsters—When the same experiment involved the fifth-stage lobsters, the results were similar. The only difference that could be observed was that the intensity of the reaction was greater for the fifth-stage than for the fourth. The result of twelve tests, each with ten lobsters showed the distribution to be as follows: Area 1, nine; area 2, ten; area 3, twenty-one; area 4, eighty, of which seventy were "stranded." These last would have perished, had they not been returned to the water at the end of each successive test.

(C.) *Conclusions concerning the reactions to light of fifth-stage lobsters*—The results of the foregoing experiments on the reactions of fifth-stage lobsters, demonstrate the following points: (1) Like the fourth-stage lobsters, the fifth-stage lobsters are negatively phototactic from the beginning of the stage to the end of it, and this holds good for all intensities of light which cause any reaction whatever. (2) Unlike the early fourth-stage but much like the late fourth-stage lobsters, the fifth-stage lobsters are negatively photopathic from the beginning of the stage to the end. (3) This negative photopathic reaction, unlike the photopathic reactions of the earlier stages (in which case the photopathic reaction was entirely subservient to the phototactic), has itself become a well grounded tendency, and, although it can be modified, it can not be entirely obliterated (so far as its value in causing a certain orientation is concerned) by the tendency to react to the directive influence of the light rays. (4) The intensity and energy with which the late fourth-stage, but especially the fifth-stage, lobsters manifest a negative phototactic reaction may lead to results fatal to the lobsters themselves.

(D.) *Contact-irritability versus reaction to light*—In the preceding section the phototactic and the photopathic reactions, together with some points of their inter-relation, have been considered. We shall now examine that response of lobsters to solid portions of their immediate physical environment which may be ascribed to contact-irritability or thigmotaxis.

It frequently happens that single types of reaction (phototaxis, chemotaxis, geotaxis, and the like) may be studied to best advan-

⁴It should be noted, however, that the water in no case receded more than 5 to 10 mm. as measured horizontally on the bottom of the box.

rage only when another stimulus of known effect is present and operative. For instance, if the two conditions of stimulation which respectively bring about a photopathic and a phototactic reaction are so arranged as to oppose one another (i. e., by determining opposite reactions in the larvæ), and if the constant effect of one set of conditions is known, then it is possible to form an estimate of the persistency of the reaction determined by the opposed set of conditions. For example, if light rays of low intensity coming through the end of box *B*, resulted in driving the enclosed larvæ, which had just previously given a negative photopathic reaction, to the opposite end of the box, and at the same time forced them from a region of low into a region of high intensity, we should say that the negative photopathic reaction of these larvæ was of slight importance as compared with the phototactic. If, on the other hand, it was learned by experiment that the rays entering the end window of box *B* would not force the negatively photopathic larvæ from the dark into the brightly illuminated end of the box, but resulted in their gathering in the middle of the box (for instance, in the green or orange area) then it might be inferred that the negative photopathic reaction had a greater influence in determining the final reaction of the larvæ, although it was in this case directly and strongly opposed by the tendency to manifest a phototactic reaction. In the following experiments, made to discover the value of contact-irritability in determining the reaction of the larvæ, the principle mentioned above was made use of, and in this instance a combination was made between experimental conditions which would allow the demonstration of contact-irritability, and those which would insure the manifestation of negative phototaxis if no other modifying conditions (such as contact-irritability) were present. But before going farther with the description of the technique of the experiments, a few observations on the behavior of the lobster larvæ under natural circumstances may be considered. This may form a better basis for the consideration of experiments dealing with contact-irritability versus reaction to light under the especially devised conditions to be described.

It might reasonably be imagined that the loss of the swimming branches (exopodites) of the thoracic appendages, which takes place with the entrance to the fourth stage, would at once determine a very radical change in the habits of lobster larvæ. We should surmise that the larvæ would immediately abandon their

pelagic manner of existence and enter upon a more sedentary life among the rocks and weeds of the sea bottom. But this is by no means the case, for never in the life history of the lobster do we find surface swimming more strongly manifested than in the fourth stage, and just after the loss of those accessories without which swimming would have been impossible in any of the earlier stages. The energetic surface-swimming of the fourth-stage lobsters was evident from many observations, made under both natural and experimental conditions. It was observable not only in the large hatching bags but also in the quiet water surrounding the bags and hatching apparatus. One case is especially noteworthy. In July a steam launch, of which the captain lost control, rammed one of the floats which suspended six large hatching bags containing lobsters in various stages. As a result many fourth-stage lobsters were suddenly liberated in the water about the hatchery. When order had been restored, an attempt was made to recover the lost lobsters, and over five hundred of the fourth-stage which were swimming actively at the surface of the water were picked up with scrim nets. A far different phenomenon obtains in the behavior of fifth-stage lobsters under natural conditions. This is illustrated by an interesting sequence of changes in the swimming habits. When the majority of the lobsters in the bags were in the fourth-stage, they usually swam near the surface. As the larvæ moulted into the fifth stage, fewer lobsters were to be seen. The reason for this was ascertainable if one poked with a stick about the mass of weeds and algæ adhering to the sides and bottom of the bag. Here could be found, carefully hidden, a large number of fifth-stage lobsters. By the time all the individuals in the bag had passed to the fifth-stage, scarcely one could be discovered swimming freely. Whenever a number of fifth-stage larvæ were liberated in the open water, it was an interesting sight to observe them swim for a moment, then turning head down, disappear for good in the deeper water—a great contrast to the behavior of the fourth-stage lobsters under similar conditions.

Another set of observations refers to the burrowing instinct of the young animals. When early fourth-stage lobsters were transferred to glass dishes, on the bottom of which was a layer of sand, gravel and a few broken shells, they at first paid no heed to these conditions, but for several days continued to swim as persistently as ever. Finally, however (usually within two or three days after

having been placed in the dish), the lobsters began to plough through the sand of the bottom, especially near the rim of the container, and to construct burrows beneath shells, stones or other objects in the sand. Yet, even after these burrows were completed, the fourth-stage lobsters seldom remained in them, but came out and crawled rapidly over the bottom or swam more or less actively near the surface of the water. When, on the other hand, fifth-stage lobsters were introduced into the dishes containing sand, gravel, and shells they commenced burrowing at once and when the burrows were completed they showed a much greater tendency to remain therein than did the late fourth-stage larvæ. Although the fifth-stage lobsters came out for food, free swimming was seldom indulged in during such sorties. The question now arises as to what conditions or factors cause the energetic surface-swimming of the early fourth-stage lobsters and the bottom-seeking and burrowing habit of the late fourth and the fifth stage. Are these reactions to be explained as phototropic, geotropic, or thigmotropic reactions? Or do all three of these, and perhaps still other factors, unite in determining the final result? While we are not yet prepared to venture an answer to these queries, the records of a few simple experiments which were undertaken to ascertain the value of the part played by contact-irritability in determining the orientation of the fourth and fifth stage lobsters, under certain known conditions, will be presented.

Experiment 29. Fourth-stage lobsters—The technique employed in the present experiment was as follows: One-half of the bottom of box *B*, was sprinkled with sand to the depth of five mm., the box was filled with salt water to a depth of 3 cm., ten early fourth-stage lobsters were introduced, and the box covered. The aim was to learn whether, in the total absence of light, the larvæ would “choose” either the sanded or the clear area. The result of a typical test is presented below. The readings were taken every five minutes, and after each reading the lobsters were caused to distribute themselves about the box:

SANDED AREA.		CLEAR AREA.	
1.	2.	3.	4.
4	3	2	1
2	2	3	3
3	2	2	3
1	1	4	4
—	—	—	—
10	8	11	11
18		22	

These and other tests were made, but in no case was it apparent that the early fourth-stage lobsters showed any preference for the sanded area. When, in another series of four trials involving ten lobsters each, the window at the sanded end of the box, was opened so as to allow the rays to stream through, every lobster but one was driven to the compartment farthest from the light. When this experiment was tried with late fourth-stage lobsters, it appeared that a greater number remained on the sanded area, even in the presence of the light conditions mentioned above. The results of a typical experiment of this sort involving five trials of ten lobsters showed that, while thirty were driven to the clear space, ten remained on the sanded area.

Experiment 30. Case 1. Fifth-stage lobsters—In this instance ten fifth-stage lobsters were placed in box *B* as arranged for the previous experiment, no light being admitted at the end of the box. The record of seven trials separated by a period of from five to ten minutes, showed a decided preference for the sanded areas; while forty remained on the sanded region, only twenty gathered on the clear area.

Case 2—In the next instance the end window at the sanded end of the box was opened to the light, but with a red glass so interposed that the intensity of light in this region was not great. A period of from ten to forty-five minutes was allowed for each orientation. Although the influence of the light tended to drive the lobsters off the sanded area the results of six trials (ten lobsters each) showed that thirty-seven fifth-stage lobsters remained in contact with the sand, while twenty-three moved to the clear area.

Case 3—In the next series of six trials (ten lobsters each) the intensity of light was modified by substituting an orange glass before the end window. The results showed twenty-five on the sanded area, thirty-five on the clear.

Case 4—In the last series of six trials (ten lobsters in each) the conditions were still further modified by removing the orange glass and thereby greatly increasing the intensity of the light which entered the end window of the box. This demonstrated that a light of great intensity would drive the fifth-stage lobsters off the sanded area. At the end of the experiment only thirteen lobsters remained on the sanded area, while forty-seven remained in the clear region. Finally, the sand was removed from the box, and the reaction of these lobsters was tested with unobstructed light

entering the end window. The resulting reaction was invariably and definitely negative; and this with light of all the intensities used in the previous cases.

Conclusions from experiments on contact-irritability versus reaction to light—Although these experiments can hardly be called critical, they demonstrate that the presence of the sanded area in the box did modify the reactions of the fifth-stage lobster. That there was manifested a tendency to remain in contact with the sand, to burrow in it, and not to be dislodged by such intensities of light as would normally rout the entire group of lobsters and send them to the end of the box farthest from the light. These facts, moreover, cannot be said to hold true for the fourth-stage lobsters that were used in the foregoing experiments, and which showed no well defined preference for the sanded area, at least in the early part of the stage-period.

VI. MECHANICS OF ORIENTATION.

The aim of the present section is to report the results of a series of observations which were made in order to answer the following question: By what movements of the lobster larvæ are the reactions to light accomplished? In our effort to answer this question we shall, for the present, attempt to avoid so far as possible considerations which deal directly with the ultimate causes of orientation; in other words, we shall limit ourselves to the observation of the actual movement of the body, or of certain parts of the body, of individual larvæ; and attempt to show what relation exists between these movements and the external factors which appear to determine them. First, however, it is necessary to establish some points regarding the natural behavior of the larvæ when the influence of external stimuli is at the minimum.

1. *The normal behavior of the larvæ*—In view of the fact that swimming constitutes the chief activity of the larval lobsters, our question resolves itself into the following: What is the nature of the normal swimming? When one first observes the behavior of individual larvæ amidst the thousands contained in the large hatching bags no difference is evident in the swimming of the first three stages. In all instances the back of the larva is, for the most part, uppermost, the abdomen bent under and downward at an angle of about 60° from the longitudinal axis of the cephalo-

thorax, which in turn is inclined about 30° from the horizontal plane. In daylight this position may be maintained without modification for several minutes, but the equilibrium is often interrupted by other body-movements which, upon superficial examination, appear to be of a most diverse and ill-ordered nature. There are leanings, turnings, fallings, somersaults, revolutions and rotations which follow each other in no apparently definite sequence, and which disturb the general equilibrium greatly or slightly as the case may be.

Whether the balanced equilibrium, the devious rotations or other activities are present, the exopodites or swimming attachments of the thoracic appendages beat the water more or less constantly with short vibratory strokes, sometimes lifting the larvæ high toward the surface, and again allowing them to sink to the bottom, where they frequently lie for some moments almost motionless, only again to resume their varied activity. Now they swim forward, now backward, now lurch to the side, now to the rear, always maintaining more or less energetically these apparently aimless movements. Such is the nature of the swimming in daylight or other brilliant illumination; but for our purpose it cannot be called the normal swimming of the lobster larvæ. It is only under special conditions that the latter may be observed; and, in view of the fact that it is the conditions of light which influence more strongly than any other factors the behavior of the larvæ, it is only when they are under certain light-conditions that we may expect to find manifested what we may call the characteristic or normal swimming.

The twilight or nocturnal swimming of the larval lobsters invariably gives us the fairest example of natural behavior. At such times alone (or when the larvæ are submitted to artificially produced twilight) variations in temperature and the multiplicity of conflicting cross-light influences are eliminated. Frequently when the twilight was so dim that observation was rendered difficult, the swimming was delicate and regular, and the young larvæ would mount up, bird-like, to the surface of the water, hover many seconds in a single position, or swim backward or forward with equal ease. In such a case, when a lighted match was brought near the side of the jar in which the larvæ were confined, the same restless and uncertain swimming, characteristic of the diurnal activities, was again manifested, together with the accompanying leanings and

rotations. From these facts it may be assumed that the twilight swimming of the larvæ probably represents the natural behavior or at least the behavior that arises purely from the internal states themselves; and that the peculiar antics characteristic of the daylight swimming represent a type of behavior chiefly due to the action of external stimuli.

The question now naturally arises—Do the various turnings, rotations, leanings, and fallings which constitute the apparently haphazard behavior of the larval lobsters when swimming in daylight or other brilliant illumination, give any indication of method? Observations have given a suggestion as to the means whereby we may attempt to ascertain the value of certain light-conditions in determining these peculiar forms of behavior.⁵

If larval lobsters of any of the first three stages are subjected to the influence of light which comes from one direction only, as from the side, the first fact observable is that the larvæ undergo a certain body-orientation; they turn away from the light and place the long axis of the body parallel to the direction of the rays. The second fact which may be noticed is that the larvæ move in the direction of the light rays either toward or from the source of illumination. A third fact, which is of prime importance and which involves those stated above, is that no matter whether the progressive movement of the larvæ be toward or away from the source of light, the orientation of the body (head away from the source of light) remains unchanged. To state the matter briefly we may say that, whatever the nature of the progressive orientation of the larvæ, *the body-orientation is at all times, and under all conditions, negative.* BOHN (1905, p. 8) has clearly pointed out this fact for the larvæ of the European lobster. In this regard he says: • “En général, les larves de homard se placent dans le sens négatif; même, dans les premières heures après l’éclosion, alors qu’elles se groupent vis-à-vis des lamps, leur tête se tourne du côté opposé, et les larves s’approchent de la lumière en regardant l’obscurité, c’est-à-dire en reculant. Ainsi, après l’éclosion, l’orientation a lieu dans le sens négatif, mais le déplacement se fait dans le sens positif. Dans le suite, si le sens de l’orientation

⁵ Many of the observations which follow were made previous to the writer’s knowledge of the excellent work of GEORGES BOHN (1905) along similar lines, upon the larvæ of the European lobster, *Homarus vulgaris*. The writer would acknowledge, however, his great indebtedness to this investigator, whose work has proved suggestive in the highest degree, and whose observations on the mechanics of behavior the writer has been able, in the majority of instances, to verify as well as supplement.

reste le même, le sens du déplacement peut changer." LYON (1906) has recorded a similar observation for several larval stages of *Palemon*. This condition of affairs is rather at variance with the majority of observations on the phototactic reactions of animals and it is contrary to the condition of body-orientation which we find in the fourth stage of the lobster itself, for in this stage (at least in some of the assumed phototactic reactions) the body-orientation brings the head toward the source of illumination instead of away from it as is invariably the case in the first three stages.

The question has already arisen as to what we may mean by a positive phototactic reaction, for in this case it is clear that we may very frequently have a negative body-orientation coupled with a positive progressive orientation. Until we know more regarding the differences between body-orientation and progressive orientation, it may be considered safe to say that the *direction of the progressive movement*, with respect to the source of illumination, may be held as the surest criterion of the sign of the phototactic response of animals. On the other hand the point has been made clear by some writers, that in the body-orientation of organisms the definite relation of the body-axis to the lines of active force is the primary consideration for all problems of progressive orientation. However this may be, we have before us at least one instance wherein, although the relation of the body-axis to the lines of force is an important consideration, the body-orientation *per se* has little or nothing to do with the question of the positive or negative progressive orientation of the organism; for as we have already observed, conditions which invariably determine a negative body-orientation may determine either a positive or a negative progressive orientation, as other circumstances demand. We may, therefore, first concern ourselves with the *mechanics of progressive orientation* and then turn with better understanding to the *mechanics of body-orientation*, for these two reactions apparently depend upon quite different circumstances.

2. *The mechanics of progressive orientation*—The only means of locomotion possessed by the larvæ of the first three stages are the exopodites of the thoracic appendages and the strong, flexible abdomen with its broad terminal fan (Fig. 1). It is but seldom, however, that the latter is used, and never when it is a question of progressive orientation to light. We are then confronted with the problem: How, by the motion of the thoracic exopodites

alone, is the larval lobster able to execute those movements which determine his progress either toward the source of illumination or away from it?

If the larval lobsters in any of the first three stages be put in a glass jar which is surrounded by black paper and placed in subdued daylight, the short vibratory strokes of the exopodites can be readily observed. At one time, certain individuals may be seen to swim rapidly backward, and again forward, with no apparent change in the position of the body or in the direction of the stroke of the exopodites. If, however, the thoracic appendages themselves be carefully watched, one can observe that, from time to time, these limbs undergo either a forward shifting (extension) as shown in Fig. 8, or a backward shifting (contraction) as shown in Fig. 9. This change from the "anterior" position to the "pos-

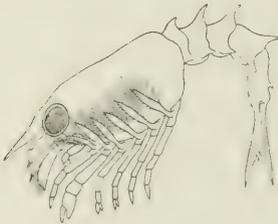


FIG. 8.

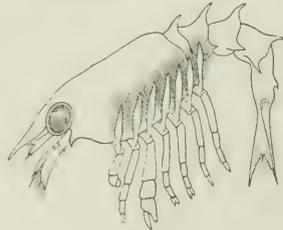


FIG. 9.

FIG. 8 shows a larval lobster with the thoracic appendages in the extended or "anterior" position; the resulting movement is forward and upward.

FIG. 9 represents the appendages in the contracted or "posterior" position; the resulting movement is backward and upward.

terior" position may occur at short intervals, each position may persist for some seconds, or there may be a successive alteration with periods of longer duration in either one position or the other. It may be observed further, that when the thoracic appendages take the "anterior" position, the direction of the strokes of the exopodites becomes somewhat forward as well as downward, and the *resulting motion of the larvæ becomes backward and upward*. When, on the other hand, the thoracic appendages assume the "posterior" position, the stroke of the exopodites becomes backward and downward; and *the resulting motion of the larvæ becomes forward and upward*. During a great part of the time, the upward movement of the larvæ, as a result of the outward and downward stroke of the exopodites, does little more than compensate for the natural tendency to sink toward the bottom. For this reason the

progress of the larvæ may often be directly forward or directly backward with but slight deviation from the horizontal plane; while at other times, when the stroke of the exopodites is directly outward and downward (exclusive of either the "forward" or "backward" factor), the larvæ may mount to the surface in nearly vertical lines.

It thus becomes evident that the progression of the larvæ, backward or forward, upward or downward, is largely determined by the position (state of extension or contraction) of the thoracic appendages. In other words, if for the greater part of the time these appendages are in the "anterior" position the phototactic reaction of the larva is positive; but on the contrary, if the thoracic appendages are more frequently in the "posterior" position, then the consequent reaction of the larvæ is negative. Naturally the next important question which arises is: What conditions determine the "anterior" or the "posterior" position of the thoracic appendages? It cannot be questioned that these changes are directly due to certain variations in the intensity of the illumination and are modified by the "physiological state" of the larvæ themselves; and that, furthermore, the state of extension or contraction of the thoracic appendages, and the stroke of the exopodites, are regulated to a great degree through the mediation of the eyes and the nervous system of the larvæ. But further consideration of this subject must be postponed until later. In the meantime we may turn our attention to the mechanics of body-orientation.

3. *The mechanics of body-orientation*—Under the present heading we shall consider the nature of those peculiar movements which the lobster larvæ undergo when they are under diverse and changing conditions of stimulation, in order to explain the cause of these actions and to show their relation to certain definite laws which may be said to regulate to a great degree the body-orientation of the larvæ. As we have observed, it is the influence of light which is most active in determining the behavior of the larvæ; furthermore, it is in the absence of such influences as diverse and changing conditions of illumination afford that the most realistic picture of the normal behavior of the larvæ is obtained. It will then prove the most practical method of approaching this problem, first, to obtain conditions of light which allow natural behavior (normal swimming); and then, by gradually modifying these conditions, to observe the effects upon the behavior of the larvæ.

A. THE EFFECTS OF DIRECT LIGHTING AND SHADING. *Technique and Methods of Observation*—This section deals more especially with the directive influence of light rays so introduced as to strike the larvæ from different directions; from before, from behind, from the side, from above, from below, or obliquely to the body-axis. These conditions were obtained, for the most part, in two ways. The larvæ were placed either in a cylindrical glass jar, or in an especially constructed rectangular glass box (similar, perhaps, to the *révélateur* used by BOHN), three inches wide, six inches long, and two and a half inches deep, all sides and the bottom being of glass. Either of these receptacles might be placed in the dark box already described. To regulate the intensity, slides of colored glass were used as in the earlier experiments,

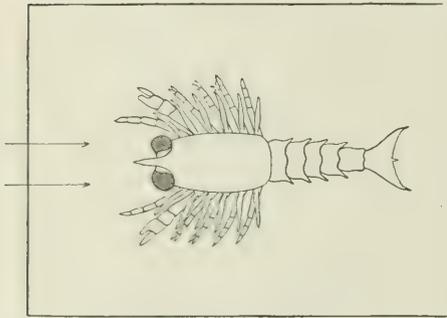


FIG. 10.

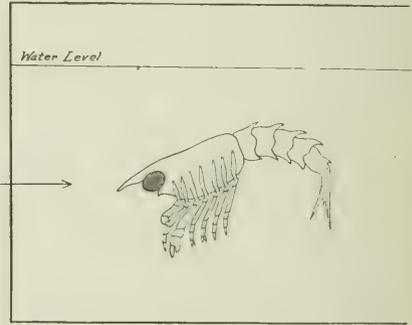


FIG. 11.

FIG. 10 represents a dorsal view, Fig. 11 a lateral view, of a larval lobster in the glass container. For description, see Case 1, p. 265.

while to change the direction of the rays a series of mirrors was employed. In certain instances, when light from the bottom was required, the receptacle containing the larvæ was placed upon a glass plate raised a certain distance above the bottom of the box, and the mirror was placed below. In still other instances the direction or the intensity of the light was modified by the use of light-absorbing (black) or light-scattering (white) backgrounds. These were used more frequently when the observations were made in diffuse daylight, and the subdued light came to the glass containers from several different directions. From the experiments it appears very probable that in determining the orientation of the organisms, the backgrounds were instrumental only in regulat-

ing the amount and the general direction of the light which they reflected or absorbed. First, however, we shall consider the effects of suddenly throwing the light from a certain direction upon larvæ oriented in various positions.

Case 1. Illumination from before—In the first instance the behavior of a single larva was studied (the stage does not matter). It was oriented in the rectangular container, in the dark box with its head toward the three by one inch window, which was closed (Fig. 10), but in such relation to the glass box that its longitudinal axis was parallel to the direction of the rays of light coming from this window when it was opened. While the larva was so oriented, the screen was drawn aside and light from the small window was allowed to strike the larva "head-on." Under these conditions, one of two reactions resulted. The larva underwent either a forward or a backward somersault, or rotation, which brought the back below with the head directed away from the source of illumination. Whether the rotation was backward or forward made no difference in the resulting orientation and which one occurred depended upon the direction of the rays of light which struck the eyes of the larva. In normal swimming the body of the larva in any of the first three stages is bent about 30° from the horizontal. Now if the rays of light had the direction of *A* or *B* (Fig. 12) the rotation was usually forward, while if the light came from below, direction *C*, the rotation often was backward. After this first orientation the larva (position *B'*) frequently performed a rotation on its long axis, either to the left or right, which brought the back again uppermost, and it then progressed in the direction of the rays, either toward or away from the source of illumination.

Corollary 1—If the rays striking the eyes of the larva had the slightly oblique direction shown in Fig. 13, *a* or *c*, but were in direction or plane *B* (Fig. 12), then the larva pivoted at the middle of its own longitudinal axis and swung to one side or the other, always keeping the back uppermost.

If the rays of light took the direction designated $a^1 - a^4$ or $c^1 - c^4$, the result was the same; the larva swung until the longitudinal body-axis was parallel with the incident rays, and the head was directed away from the source of illumination.

Corollary 2—If the rays striking the eyes of the larva had the oblique direction, $a^1 - a^4$ or $c^1 - c^4$ (Fig. 13) in plane *A* of Fig. 12, then the resulting movement was a combination of the forward

rotation and the side swing (Cor. 1). In other words, the larva performed a side-somersault, and ended with the back directed below and to the side. Whether it turned to the left or to the right depended upon the direction of the rays in either the *a* or the *c* series. At the end of this reaction the larva usually became righted again with the back above and the head away from the light, and continued its progressive orientation in one direction or the other according as the reaction was positive or negative.

Corollary 3—If the rays striking the eyes of the larva had the oblique direction $a^1 - a^4$ or $c^1 - c^4$, and were in plane *C* of Fig. 12, the resulting reaction was a combination of the backward rota-

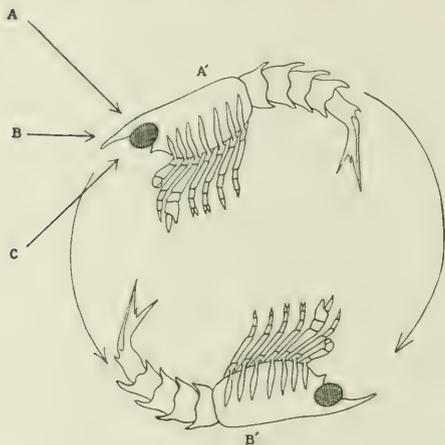


FIG. 12. For description, see Case 1, Cor. 1.

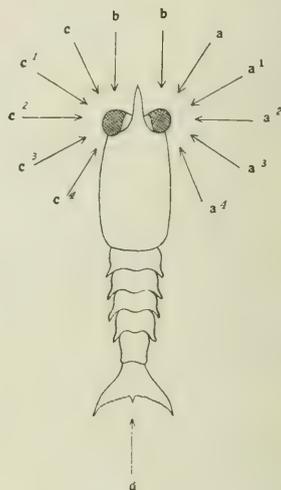


FIG. 13. For description see Case 1, Cor. 2.

tion and the side swing (Cor. 1). That is to say, the larva performed a backward side-somersault, became oriented as in Corollary 1 and 2, again turned the back uppermost, with the eyes directed away from the source of light, and continued its progressive orientation, in one sense or the other.

Case 2. Larva lying with back downward; head toward light—In these instances, the larva was oriented head toward the (closed) window, and back downward. The rays were introduced from before, as in Case 1. It may be said that this orientation was difficult to obtain. Often it was necessary to wait fifteen minutes

or more before it occurred, then at the proper moment the light was admitted and the consequent reaction observed. On the other hand, it was common to find the larvæ on their backs and oriented obliquely to the rays of light. When the larva was oriented in this manner and the light was admitted, there usually occurred either a forward or a backward rotation (Fig. 14), but the forward rotation was most common. Whichever one occurred, however, the final orientation was the same: the back of the larva was again brought uppermost, and the head was directed away from the source of light.

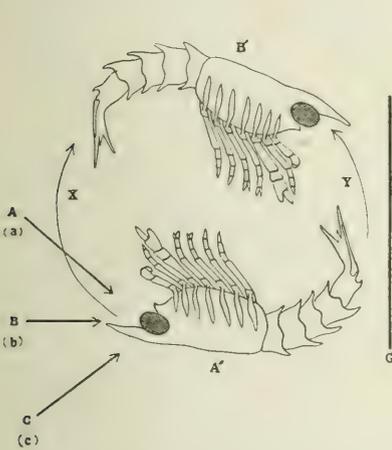


FIG. 14. For description, see Case 2.

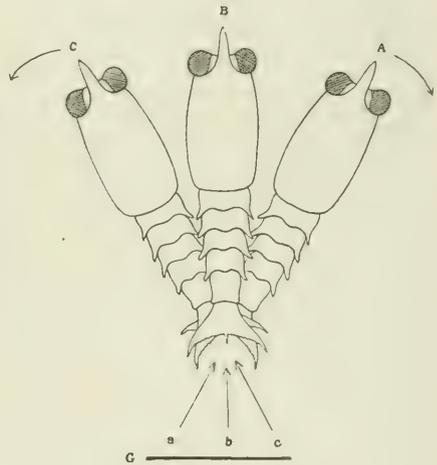


FIG. 15. For description, see Case 4.

Corollary 1—If the larva was oriented with the back below, the head toward the closed window, and the body-axis oblique to the direction of the incident rays, the resulting orientation was a combination of the upward and forward rotation and a swing of the body, pivoted on the middle of its long axis, away from the incident rays (this last reaction was similar to Case 1, Cor. 1, except that in the former instance the larva oriented back below). The final orientation was as in Case 2 (Fig. 14, *B'*). Whether the incident rays were in plane *A*, *B*, or *C* did not appear to make as much difference in the manner of orientation when the lobster was lying back below. It was observed that rays coming from above (plane *A*) more frequently determined the backward rota-

tion; and that rays coming from below (plane *C*) more often determined a forward rotation.

Case 3. Larva lying with the side downward; head toward light—In this case, the larva was oriented with one side uppermost and the head turned toward the source of light. The conditions may be represented by Fig. 14, if it be imagined that for the present case the larvæ are lying in a horizontal plane rather than in the vertical as originally intended in this figure. The arrows *A*, *B* and *C* represent rays in the same vertical plane, while (*a*), (*b*) and (*c*) represent them in a horizontal plane. When the light was admitted to a larva so oriented, the reaction was similar to that described under Case 2. In the present instance, however, when the rays had the direction (*a*), the backward rotation was more likely to occur than when the rays had the direction *A* as in Case 2. Rays in the direction (*b*) or (*c*) almost invariably determined a forward rotation, in which, if the larva was fatigued, it would merely turn through 180° in the same plane, and become oriented, still lying on the side, but with its head away from the source of light. If, however, the larva was fresh and active at the end of the rotation of 180° in the arc of a circle (*A'*), it would rotate through 90° on its longitudinal axis and come into the normal swimming position with the back uppermost and the head directed away from the source of light.

Case 4. Larva oriented with back above; head directed away from the source of light—When the larva was thus oriented and the light was so introduced that the rays streamed in a direction parallel to the longitudinal axis of the larva, no change in the body-orientation took place. The progressive orientation, however, might continue as either positive or negative. In case, however, the light came from the sides *a* or *c* (Fig. 15) the larva reacted by swinging (pivoted on the middle or end of its longitudinal axis) to either one side or the other, and it might then undergo positive or negative progressive orientation. If the direction of the rays changed through the series, *a*, *b*, *c*, the larva could likewise be made to swing as regularly as a pendulum and for long periods of time, according as the light came from one side or the other. Indeed the animal was quite at the mercy of the influence of light.

In case the light came somewhat from above as shown in Fig. 16, *A*, the larva would incline itself farther forward, the number of degrees of rotation depending upon the degree of the angle

formed by *A* with the horizontal. When the angle was slight the forward rotation of the larva was but a few degrees, and it continued to swim in this body-position, and might undergo a positive or negative progressive orientation, as ordinarily. When, however, the angle between *A* and the horizontal was greater, the degree of rotation of the larva was proportionately greater, and in certain cases it might undergo a rotation of 180° and fall to the bottom.

When, on the other hand, the incident rays struck the larva in the direction of *C* (Fig. 16), then the larva underwent a backward rotation whose degree was dependent upon the breadth of the

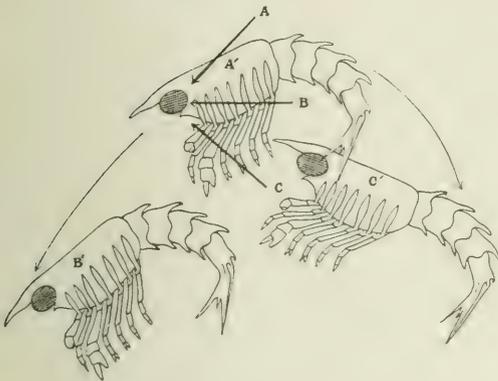


FIG. 16. For description, see Case 4.

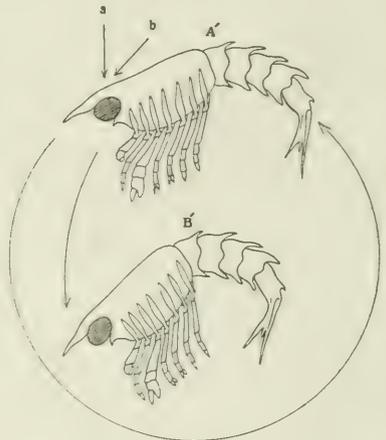


FIG. 17. For description, see Case 6.

angle between *C* and the horizontal. If the angle thus formed was slight, the backward rotation of the larva was correspondingly slight, and it would continue to swim in the position designated *C* (Fig. 16), undergoing positive or negative progressive orientation as other conditions of light might determine. If the angle formed between *C* and the horizontal was great, the degree of backward rotation of the larva was proportionately greater, and a fall to the bottom, tail downward, might result.

Corollary I—When the direction of the rays was determined by compounding the vertical series of light factors (*A*, *B*, *C*, Fig. 12) with the horizontal series (*a*, *b*, *c*, Fig. 15), the resulting reaction was a combination of the two types of behavior described above.

Case 5. Larva oriented with back above and longitudinal body-axis at right angles to direction of light rays—When the larva was oriented as above and the rays were introduced at right angles to the longitudinal axis (Fig. 13, a^2 , c^2) the behavior was similar to some phases of Case 1, Cor. 1. The larva swung directly away from the source of light until its longitudinal axis was parallel to the light rays, with the head directed away from the source of light. Obviously the swing might cover from 1° to 90° and either positive or negative progressive orientation might follow.

If the larva was lying with the back below, but otherwise oriented as in the previous instance to the directive influence of the rays, the reaction was the same; namely, a swing to one side. This resulted in placing the longitudinal axis parallel to the rays of light. Frequently, in such case, the larva would undergo a rotation on its own axis, so that it assumed a position with the back uppermost and the head directed away from the source of light. Whether or not this "righting reaction" occurred, appeared to depend largely upon the degree of freshness. Individuals which had undergone fatigue more frequently refused to rise from the bottom. It was at no time possible, however, to fatigue the larvæ to such an extent that they would not give the "swinging-reaction" into line with the light rays. By alternately changing through an arc of 30° the direction of the light which struck the larvæ from behind (Fig. 15, a , b , c), they could be made to swing, pivoted on the middle or end of their longitudinal axis, in an arc of equal degree. This pendulum-like activity in answer to the change in direction of the light-stimulus was extremely constant and in no case was it observable that the reaction was diminished by fatigue in spite of long periods of such alternate directive stimulation. It may be added here that prolonged direct stimulation from behind never produced a change in the body-orientation of the larva. The progressive orientation, however, might take place in either the positive or the negative sense.

Case 6. Larva oriented with back above; light enters from above—Under the conditions mentioned above, the larva was forced to give one or two reactions, depending upon the degree of intensity and the suddenness of introduction of the light:

(1) In some instances (especially when the light had the direction, b , Fig. 17), the larva first rotated through an arc of greater or less curvature and finally assumed a new swimming position

with the longitudinal axis of the body bent at a greater angle from the horizontal plane (Fig. 17, *B'*). This new swimming position was usually maintained so long as the conditions of light remained the same, but was sometimes replaced by the second form of reaction, which usually occurred when the light had the direction *a*, and which was merely an exaggerated form of the first.

(2) In this second type of reaction the rotation of the larvæ was not limited to an arc of a few degrees, but was extended into a forward "somersault." This in turn took place in one of two ways: (*a*) the larva might accomplish a rotation of 360° and return to its original position with the back above, but since the stimulation from above remained the same, it would not rest in this position, but would continue for a time to perform complete rotations without pause, after which it would come to rest as shown in Fig. 17, *B'*. This new swimming position was sometimes maintained as long as the conditions of light remained unchanged, though it might give place to further rotations; (*b*) the larva might, as a result of the forward rotation, come to rest with the back directed below, but this orientation was only momentary, because the influence of the light from above immediately determined a backward rotation. This last reaction might culminate when the larva had gained the new position shown in Fig. 9, *B'*, or it might be continued into one or more backward rotations through 360° and culminate after a greater or less number of such rotations, by coming into the new swimming position mentioned above. This orientation would be maintained as long as the same conditions of light were in effect; or it might be interrupted from time to time by rotations in arcs of varying degrees, and in either of the directions mentioned above.

Corollary 1—If, when the larva was oriented as in Case 6, the light was introduced from both sides and above, the resulting reaction was a combination of the forward rotation and the side swing. If the light came from above and behind (Fig. 17, *b*), then the direct assumption of the new swimming position *B'* more frequently resulted without the variable number of rotations through 180° or 360° .

Case 7. Larva oriented with back below; light enters from above—Under the above conditions of orientation (Fig. 18) there was usually one constant form of reaction. The larva would undergo a backward rotation through about 120° , and come into a new

swimming position with the axis of the body bent downward several degrees from the normal swimming position (perhaps 45° from the horizontal), the exact amount appearing to be dependent upon the intensity of the light. This new swimming position was usually maintained as long as the conditions of light remained unchanged. It might sometimes be interrupted by backward rotations through 360° . These rotations invariably culminated in the assumption of the new swimming position (Fig. 18, *B*). In case the direction of the rays was both from the side and from above the resultant reaction was a combination of the reaction described above and the direct side swing.

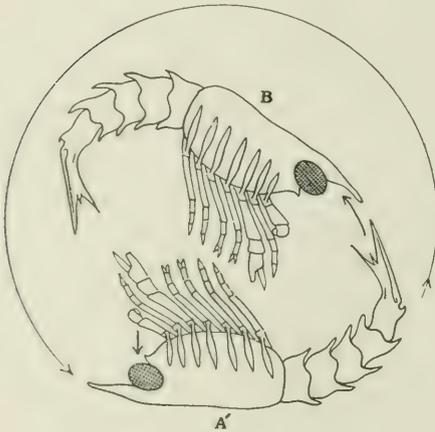


FIG. 18. For description, see Case 7.

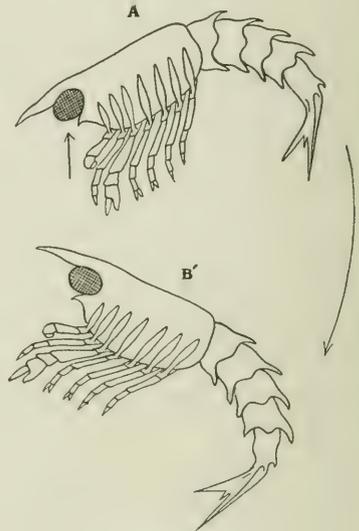


FIG. 19. For description, see Case 8.

Case 8. Larva oriented with back above; light enters from below—Under these conditions of orientation, the nature of the reaction was similar to that described in Case 6. Usually there resulted a direct backward rotation through a few degrees, which produced a new swimming position, Fig. 19, *B'*. This was usually constant while the conditions of light remained the same, but it was sometimes interrupted by backward rotations through an arc of greater extent, or even by a variable number of complete backward rotations through 360° . At the end of these, however, the new swimming position *B'* was invariably assumed. Combinations of the

directions of the light (as both from the side and from above) produced modification in the reaction, but these could at any time be predicted if the individual constituents of the light were known.

Case 9. Larva oriented with back below; light enters from below—Under the conditions of orientation stated above the resulting reaction was similar to that described under Cases 6 and 8, but reversed. As in these instances, one of two results usually occurred: (1) The larva would undergo a forward rotation through a variable number of degrees, and assume directly a new "swimming-position" as shown in Fig. 20, *B'*. It was readily observed that the head was directed upward and away from the

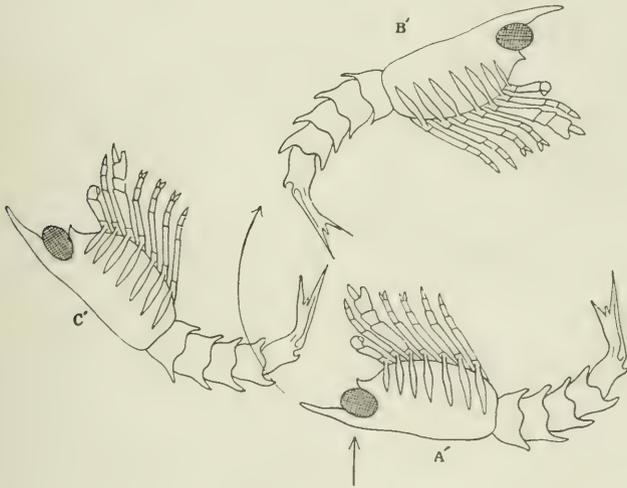


FIG. 20. For description, see Case 9.

light, not downward at an angle of about 30° from the horizontal, as in the normal swimming position; (2) it might happen, however, that instead of assuming this orientation the larva would merely come to an orientation with the back below and with the head directed upward as a slight angle as shown in Fig. 20, *C'*. It might, again, undergo one or more complete rotations forward, through 360° and then assume the new position shown in Fig. 20, *B'*, which position might be retained as long as the light conditions remained unchanged. The definiteness in these two reactions could be modified, as a result of changing slightly the direction of the light.

In addition to the facts regarding the effect of direct lighting upon body-orientation, which have been presented in the form of these nine cases, several other conditions might be mentioned:

1. If the longitudinal axis of the larva was parallel to the direction of the incident light rays, and the head away from the light, then the introduction of light produced no change in the body-orientation, but it might cause a positive or a negative progressive orientation.

2. In order that the unmodified forward or backward rotation might occur, it was learned that the light rays must strike both eyes with equal intensity, and consequently in a direction exactly perpendicular to any transverse body-axis of the larva.

3. In case the incident rays came from a direction that was not exactly perpendicular to the transverse axis of the larva, be the angle of difference ever so slight, the perfect backward and forward rotation would not occur, but would be greatly modified by swingings of, and revolutions on, the longitudinal axis of the body.

4. This type of behavior could not be observed unless the conditions of light were reduced to a single directive influence, and this factor handled with very great precision.

The effect of blocking the illumination—In the previous section we have examined the reactions which were brought about by suddenly introducing rays of light in directions which maintained a certain definite and specified relation to the longitudinal or transverse axis of the larval lobsters. In the present instance, however, we are to consider the nature of the reactions which are produced as a result of suddenly excluding or blocking the principal source of light by which the larvæ have just previously been stimulated. The "cut-off" was made by closing the window through which the light came, and thus leaving the larvæ in the subdued and diffuse light which entered the dark box from the room. Since the body-orientation of the larvæ to the directive influence of the light is always the same, obviously there could not be many different varieties of orientation caused by the change in the conditions of light. Such as were possible, however, may be described as follows:

Case 10. Larva oriented with the back above and the longitudinal body-axis exactly parallel to the incident rays—In case the larva was oriented as described above, when the light was shut off

there usually resulted a forward rotation through 180° . This reaction caused the larva to become oriented (often on the bottom) with the back below and the head toward the previously existing source of light. This position was not maintained, but was succeeded by a "righting reaction," usually a revolution on the longitudinal axis, which brought the back again uppermost. After this response the larva might swim in diverse directions.

Case 11. Larva oriented with the back above and the head away from the light, which comes slightly from the side—If, when the larva was oriented as described above, the light was suddenly cut off, there resulted a swing of the long body-axis so that the larva was brought more or less nearly to face in the opposite direction; i. e., in the direction from which the light had previously come. This orientation, however, was not permanent, but other consequent reactions occurred and the larva might swim in one of several directions.

Case 12. Larva oriented as in Fig. 17, B'—If the direction of the light was from above, and the orientation of the larvæ as in Fig. 17, B', when the light was cut off, the head of the larvæ would swing upward to face the direction from which the rays had previously come. Consequently, however, the orientation became that of the normal swimming position.

Case 13. Larva oriented as in Fig. 20, B'—When, as the result of light stimulation from below (as in Case 9), the larva was oriented with the head directed upward, and the illumination was suddenly cut off, the head of the larva would swing downward to face the direction from which the light had previously come; sometimes the larva would perform a rotation in an arc of greater or less extent and fall to the bottom. The body-orientation with head downward was not maintained, however, but was at once superseded by the normal swimming position.

It thus appears from these cases that there was usually an excessive movement to produce the new body-orientation; but that these movements invariably ended in the assumption of the normal swimming position.

Résumé of experiments on the effects of direct lighting and shading—(A) The effect of suddenly submitting the larval lobsters to a light which has a directive influence is to cause the larvæ to orient themselves in such a manner that the longitudinal axis of the body finally assumes a definite relation to the direction of the

light rays. This orientation is a position with the long axis of the body parallel to the light rays, and with the head turned away from the source of light. (B) The effect of suddenly blocking the light to which the larvæ are reacting phototactically is to cause a new body-orientation by which the head is usually brought to face the direction from which the light had previously come. In either of the cases mentioned above the body-orientation is brought about by a single motor reflex or by a longer or shorter series of motor reflexes, some of which are "over-produced" movements.

These movements include the following types:

1. *Forward or backward rotations,⁶ or somersaults*—These were rotations in an arc, of a few degrees, which directly determined a new swimming position with the head raised or lowered, depending upon the direction from which the light or shadow had been introduced. In other cases these rotations took the form of a variable number of complete rotations through 360° , either backward or forward, in which the body of the larva formed a constant part of the circumference.

2. *Revolutions on the longitudinal axis of the body or rollings*—The revolutions or rollings took place either to the right or left, but usually in such direction that the back of the larva became directed more or less toward the light. They might be through a few degrees, or they might exceed 90° , in which case the larva fell to the bottom. In the case of larvæ one of whose eyes had been injured this revolution took place very rapidly, often at the rate of one hundred and fifty per minute, and always in a determined direction, the normal eye over, the injured eye under (HADLEY 1907b).

3. *Swingings of the longitudinal axis of the body*—These reactions were swingings in such a direction that the head was brought by the shortest path to face the dark, and the tail to point toward the light.

⁶Three similar types of movement are described by BOHN (1905, p. 4) as follows:

1° *Mouvement de manège*—l'animal décrit un cercle de plus ou moins grand rayon, l'axe du corps, courbé en arc, faisant partie constamment de la circonférence; la rotation se fait tantôt dans le sens des aiguilles d'une montre, tantôt dans le sens inverse. Parfois, au lieu de décrire un mouvement de manège pur, l'animal décrit des courbes de rayon variable qui constituent une sorte de spirale.

2° *Mouvement de rotation en rayon de roue*—l'axe du corps ne dévie pas; il est une des parties d'un des rayons du cercle décrit, et non une partie de la circonférence du cercle: la tête peut se trouver à la circonférence ou au centre.

3° *Mouvement de rotation sur l'axe, ou roulement*: l'animal tourne autour d'un axe longitudinal qui traverserait le corps dans sa longueur; la rotation commence par une inclinaison de l'animal d'un côté, et le sens de la rotation se trouve ainsi déterminé. Le roulement peut s'accompagner d'un mouvement de translation et devient un mouvement en pas de vis.

4. *Rotations in the radii of a circle*—In these the longitudinal axis of the larva formed a radius, and with either the head or the tail at the center the animal rotated about a fixed point. These reactions were uncommon and, as yet, unexplained.

These four types of movement seldom occurred separately, except under especially devised experimental conditions. Under natural conditions, they were usually combined to form a composite action. To the previously mentioned simple components, however, all the more complex movements of the larval lobsters could be reduced.

B. THE EFFECT OF SCREENS AND BACKGROUNDS—It is probable that the reactions which are brought about through the use of backgrounds, are, generally speaking, dependent upon the same factors and conditions of illumination which are effective when light-absorbing or light-scattering screens are used. The term "screening" has been employed by BOHN (1905) to designate his method of submitting organisms to the influence of surfaces of light and shade. This investigator made use of screens of black and white of such size that he could readily bring them close to the sides of the glass containers in which the organisms under observation were placed. He has made a special study of the reactions of Crustacea to the influence of such screens, and in several instances the observations of the writer upon the larvæ of *Homarus americanus* merely confirm certain points in BOHN's earlier work. In many instances, however, new facts have been added.

The influence of white screens—The lobster larvæ were confined in a cylindrical jar, crystallization dishes, or in a rectangular glass container. The latter was used most frequently. The larvæ were then placed in the dark box and this was illuminated in such a manner that a general twilight was produced and the directive influence of light was at a minimum. While making observations it was even found necessary that the writer should wear a black mask over his face and collar, and, often, darken his hands in order not to modify the uniform light. For white screens pieces of white cardboard were employed, and brought over, under, or beside the receptacle containing the larvæ, as the case might require. Sometimes the screen was brought gradually toward the container, sometimes abruptly; but in all cases the results were definite and agreed with great uniformity. In order to secure the best results with the white screen, it was found best to reduce the

intensity of light within the dark box below the degree used in the case of the black screens. The results of the series of experiments with white screens may be summarized as follows:

Case 14—When the larva was oriented with back above and the screen, held vertically, was so introduced from before that its plane was at right angles to the longitudinal axis, and parallel to any transverse axis of the larva, there resulted a rotation through 180° with, perhaps, a fall to the bottom. After this, and as a result of a revolution on the body-axis, a “righting reaction” usually occurred and the back would again be brought above. Now, with the head directed away from the white screen, the larva might either approach or depart from it, according as the progressive orientation was positive or negative. Sometimes, instead of producing a rotation through an arc of 180° , the larva underwent a series of rotations, its body forming a constant part of the circumference. The final orientation mentioned above would, however, invariably succeed. In case the screen was not held squarely before the larva, but somewhat at an angle to any transverse axis, the consequent reaction was a direct side swing away from the screen in order to place the longitudinal body-axis perpendicular to, and the head away from, the screen. In other cases there resulted a combination of the side swing and the forward rotation, so that the larva performed a sort of “half-somersault,” and eventually assumed the normal swimming position, with the head directed away from the screen, as pointed out above.

Case 15—When the larva was oriented with the back above and the screen, held vertically, was made to approach the posterior end of the larva, no change in the body-orientation resulted. There might occur, however, either a positive or a negative progressive orientation.

Case 16—In this case the larvæ were swimming promiscuously about the container. When the screen was made to approach larvæ which held a position with the back above and one side turned toward the screen, these larvæ experienced a swing of their longitudinal axis so that the head came to be directed away from the screen and the longitudinal body-axis at right angles to the plane of the screen.

Case 17 When the screen, held horizontally, was made to approach, from below, a larva which held the normal swimming position, one of two reactions (which probably represent different

degrees of the same reaction) resulted: (1) The larva would swing the head upward as shown in Fig. 20, *B'*, and maintain this swimming position so long as the light condition remained unchanged, or (2) it might, on the other hand, experience this same reaction in an exaggerated form, i. e., there might result a backward rotation through 180° , which reaction would cause the larva to fall to the bottom and to assume a position with the back below and with the head directed upward at a slight angle as shown in Fig. 20, *C'*. Usually, however, this form of orientation resulted only when the light was of greater intensity, such as that secured in cases of direct illumination.

Case 18—When the larva was oriented in the normal swimming position and the white screen was made to approach from above, the reaction was similar to that described for Case 6, p. 270. The one difference was that while the direct lighting often caused a number of complete rotations through 360° before the final body-orientation was assumed, the white screen, on the other hand, usually acted by changing the swimming position directly to that of Fig. 17, *B'*. This difference in response was probably due to the difference in the intensity of light (direct or reflected) coming from above.

The black screen—The method of conducting the experiments with the black screen was almost the same as that for the white screen. There was one point of difference. It was found that, in order that the black screen should determine any reaction of the larvæ, it was necessary to have a slightly greater illumination within the dark box. The following report of cases shows the result of making the screen to approach, from various directions, the larvæ diversely oriented.

Case 19—When the larva was in the normal swimming position and the back screen was presented opposite the head, and at right angles to the longitudinal axis, the orientation was not changed, but was retained constantly so long as the screen remained in position.

Case 20—When the larva was in the normal swimming position and the screen was made to approach from behind, so that its plane was parallel to a vertical plane passing through both eyes of the larva, there usually resulted a forward rotation of 180° in the arc of a circle. This reaction brought the back of the larva below, and the head toward the black screen. This position was

at once further modified by a revolution of 160° on the long body-axis, either to the left or right (determined by the nature of the lateral or secondary illumination), and the larva again assumed the normal swimming position, but with the head directed toward the black screen. In case the plane of the screen was not exactly parallel with the vertical plane passing through the eyes of the larva, the reaction was not represented by the simple forward rotation, but was modified by side movements.

Case 21—When the larva was in the normal swimming position and the black screen approached from the side, several reactions might occur. Most commonly the larva underwent a swing of its longitudinal axis so that the head was brought to face the screen. Another reaction sometimes observed was a rolling, or revolution, on the long body-axis, in such a manner that the back moved away from the screen. At the same time there occurred a swing of the longitudinal axis which caused the head to be directed toward the screen. These two reactions might occur simultaneously, and the resulting reaction be a blending of the two components mentioned above. The rolling on the longitudinal body-axis was seldom over 90° from normal (back above), usually less. Yet in cases where the illumination in the dark box was greater, or when the screen was introduced suddenly, the rolling motion might exceed 90° , and the larva fall to the bottom of the container.

Case 22—In this instance the larva oriented in the normal swimming position and the screen was made to approach from above. This combination produced several forms of reaction. In cases where the general illumination in the container was not great, the larva merely experienced a slight change in the direction of the longitudinal body-axis; the head assumed a superior position, so that the long axis of the body was nearly horizontal, or even directed upward at a small angle, rather than bent downward at an angle of 30° from horizontal, as in the normal swimming position. On the other hand, if the illumination was greater, the larva might undergo a rotation on its own longitudinal axis through 180° and fall, back downward, to the bottom. Whatever reaction occurred, it could be explained as an effort of the larva to turn the head toward the black screen, and the degree to which this was attained depended very much upon the intensity of illumination throughout the container. The type of reaction mentioned above was demonstrated to better advantage

in the following experiment. A large tube containing a number of larvæ was placed in an upright position on the laboratory table, and the upper half covered with a roll of black paper. The larvæ gathered in the more brightly illumined end of the tube, which was below. So long as they swam in the lower part of the illuminated area, they assumed the normal swimming position, but whenever they came into the upper regions, and approached the edge of the black paper, the direction of the longitudinal body-axis was changed from 30° below horizontal to 30° or even more above the horizontal plane.

Case 23—In the following case the larva was oriented in the normal swimming position and the screen was made to approach from below. As a result the larva usually reacted by a slight forward rotation, the head passing through an arc of a few degrees, and producing a still greater angle between the longitudinal axis and the horizontal plane. This new swimming position was seldom subject to further modifications so long as the light conditions remained unchanged. Regarding the reactions of the larvæ of *Homarus vulgaris* under similar experimental conditions, BOHN (1905, p. 11) remarks: "Si la larve nage le dos dirigé le haut, il y a roulement de 90° ou de 180° , la par suite la larve dévie lateralement ou tombe."

Such a result as the above was not observed by the writer. On the other hand, it was observed that, whatever the body-orientation of a group of larvæ might be previous to the approach of the black screen from below, its presence usually determined a rise of the larvæ from the bottom of the container to the upper waters, where normal swimming was manifested so long as the screen beneath remained in place. When it was removed, however, or replaced by a white screen, the consequent reaction was, as we have already seen, characterized by rotations and revolutions through 90° or 180° . These reactions in turn resulted in bringing the larvæ again toward the bottom, and in determining a consequent absence of larvæ in the regions near the surface of the water.

Case 24—In this instance the larvæ were oriented with back below, and the black screen was made to approach from behind in such a manner that the plane of the screen was parallel with a vertical plane passing through both eyes of the larva. Under these conditions (see Fig. 14, *A'*) the reactions were as follows. When the black screen, *G*, was introduced, the larva, *A'*, under-

went a forward rotation through an arc of 180° , and assumed the normal swimming position, B' , with the back uppermost and the head facing the screen. This orientation was maintained with a greater or less degree of constancy so long as the conditions of light remained the same. If, on the other hand, the screen was so placed, or the larva had such a position, that the plane of the screen was not exactly parallel to the vertical plane passing through the two eyes of the larva, a different reaction was experienced. In this instance the first response was a revolution on the longitudinal axis, usually through 180° . This resulted in bringing the back of the larva uppermost, and was usually followed by a swinging of the longitudinal axis, which brought the head to face the screen. The direction of this side swing (to the left or the right) was determined by the angle which the longitudinal axis of the larva made with the screen. For instance in Fig. 15, the larva designated A' would swing to the right, while the larva designated C' would swing to the left, each in the direction indicated by the arrows. In other words we may say that the larva would swing in that direction which brought the head, by the shortest course, to face the screen. But the two reactions mentioned above might, as in previous cases, be blended to form a composite reaction, which differed from either of its simple components.

Case 25—In the present instance the larva was oriented lying on its back and the screen was introduced from before. Under these conditions, as in Case 19, there was no modification in the body-position. In certain instances the larva underwent a revolution through 180° on its longitudinal axis and assumed a position with back above and head still directed toward the black screen; but in the great number of cases the orientation remained unchanged.

Case 26—In case the larva was oriented with the back below and the screen was made to approach from the side the reactions were as follows. The larva experienced a rolling or revolution on its longitudinal axis, in consequence of which the back moved away from the screen through an angle of 90° , occasionally more. At the same time there was a swinging of the longitudinal axis, itself, so that the larva came face to face with the screen, eventually with the back uppermost. During this reaction the larva often departed from the screen. As in Case 21, mentioned

above, these two reactions might occur at the same time, and then the resulting reaction was a composite.

Case 27—In the present case the larva was oriented with back below and the black screen was introduced from above. Under these conditions it usually underwent a slight forward rotation with a consequent rise from the bottom, and came into a new swimming position with the longitudinal axis directed somewhat upward as shown in Fig. 20, *B'*.

Case 28—In this instance the larva was oriented with back below and the black screen was introduced from beneath. The reactions were usually as follows. The larvæ underwent a revolution of about 180° on its longitudinal axis, and assumed practically the normal swimming position, with the back uppermost and the head bent downward at an angle of about 30° . In other cases, however, this new position was brought about by a different sort of reaction; namely, a backward rotation through an arc of 180° . This resulted in throwing the larva again into the normal swimming position.

Generally speaking, we may say that, when black or white screens were made to approach larvæ of any one of the first three stages, diversely oriented, the larvæ manifested two forms of response. First, a motor reflex, which tended to place the longitudinal axis in a certain relation to the plane of the screen; secondly, and subsequent to the first response, a progressive orientation, toward or away from the screen, as the luminosity of the screen, the physiological state of the larvæ, and other conditions of the case, determined. When the white screen was used, the larvæ commonly became oriented with the head directed away from the screen. In the case of black screens, on the contrary, the head was directed toward the screen and the back more or less away. These reactions occurred whether the screens were made to approach from above, below, behind, or the side. After body-orientation had taken place, the larvæ might approach or recede from the black or the white screen, according as they were reacting positively or negatively.

The mechanics of reaction upon which orientation to the screens was found to depend, agree, for the greater part, with the types of reaction to black screens reported by BOHN (1905), who has made a careful study of the effects of causing a black screen to approach the larvæ of *Homarus vulgaris*, diversely oriented. There are,

however, certain disagreements. First, it is certainly true that bringing the black screen parallel to the longitudinal axis of the larva frequently determined a rolling of the larva on its own longitudinal axis, whatever the original orientation may have been. But in Case 21, certain orientations of the larva were noted in which these rollings did not occur. It is true, moreover, that the progressive orientation often took place in that direction in which the back was directed. But several instances were observed wherein the orientation to the black screen resulted merely from a swinging of the longitudinal axis of the larvæ so that the head was directed toward the screen and where consequent progressive orientation was either a movement backward or forward, head foremost or tail foremost, as in positive or negative phototaxis.

We have now examined somewhat in detail the effects of sudden illumination and of sudden shading, the effects of white screens and of black. If we now compare the detailed results of these studies, we note that the effects produced by introducing a white screen are comparable with those obtained by suddenly admitting illumination, while the results brought about by black screens are comparable to those determined by suddenly cutting off the light. In other words, the larvæ appear to respond to the influence of screens of black and white by reactions which are dependent upon the same simple forms of response observed under the conditions of direct lighting and shading.

In view of this correspondence in the nature of reaction to direct lighting and to screens of black and white, it may be considered probable that the screens and backgrounds are instrumental in determining the behavior of the larvæ, only in so far as they are themselves the source of (reflected) illumination. Thus, when the black background causes a swing of the larva, as a result of which it comes to face the screen, we cannot say that the primary factor is the blackness of the screen; but rather that the small amount of light reflected from the screen permits rays of light from other directions to become effective. The larva "heads" to the black screen because his eyes encounter no light rays coming from this direction; and he turns away from the white screen because his eyes encounter stronger reflected light from this than from any other direction.

The effect of backgrounds—The question of the influence of backgrounds in determining the orientation of crustacean larvæ

has been brought forward by KEEBLE and GAMBLE (1904). Aside from the effects of screening, the more general problem of backgrounds did not receive especial attention in the course of the present investigation, but, as we shall see, the question of screening which we have discussed in the preceding section is probably only a single phase of the problem of backgrounds. The following experiments which were performed more or less at random in connection with other experiments, but which deal with the question of backgrounds, may, however, be presented.

By the term background, as it is used in the present case, is meant the permanent color-tone of the surrounding walls (as a whole or in part) which confined the young larvæ. This condition was somewhat different from that determined by the use of screens which were movable and could be placed at any angle with reference to the body-axis of the larvæ. Backgrounds were employed in several different ways. They were sometimes represented by the black or white lining of the reaction boxes; again, by the ground upon which the glass dishes or tubes rested, and in still other cases by the outer covering of these dishes, or tubes. The subject may be considered under two heads: (1) the effect of backgrounds in connection with the purely photopathic response; (2) their effect in determining the "choice" of a particular region of light-intensity when phototaxis also is operative. In view of the fact that the investigation of the first phase of this problem was not undertaken in the present work, we may pass directly to the consideration of the second point stated above.

The effects of backgrounds in connection with both the phototactic and the photopathic response—Under this head we may consider those conditions of experiment, which, although they be chiefly productive of reactions to the directive influence of the light, nevertheless were modified by response to the intensity of the light. These conditions were secured by the use of Y-tubes. The following experiments serve to show why, in the case of the larval lobsters, the tendency to gather in the brighter areas (assumed positive photopathy) is often associated with positive phototaxis; and why a tendency to gather in the darker areas (assumed negative photopathy) may be associated with negative phototaxis. In the diagrams of Fig. 21 are represented the Y-tubes as set up for experiment. Those whose arms are above were arranged for experiment with larvæ having positive phototactic reaction; those

whose arms are at the bottom, for larvæ having a negative phototactic reaction. In tubes *A* and *B* one side of one arm was fitted with a band of black paper which extended half over the circumference of the arm and a very short distance down each stem. In tubes *C* and *D* the same arrangement existed, save that white instead of black paper was used. In every case the light rays came from the window in the direction of the arrows. In all cases of larvæ manifesting a negative reaction, the start was made at the end of the tube (lying horizontally on the table) nearer the window. In the case of positively reacting larvæ, the start was made from the end of the tube farthest from the window. The end marked *a* in every instance was the end *from which* the larvæ moved, the purpose of the test being to determine in which arm of the tube the larvæ would eventually gather.

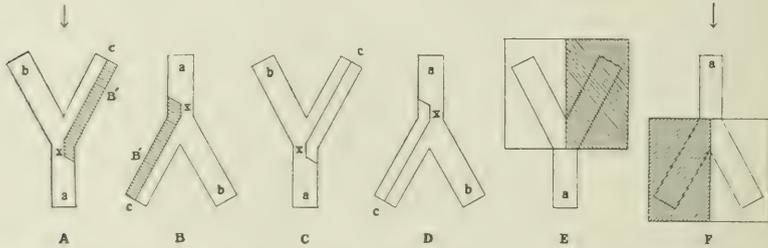


FIG. 21. Showing the Y-tubes set up for experiment. In every case the light came from above in the direction of the arrows. The tubes whose arms are above were set up for positively reacting lobsters; those whose stems are above, for negatively reacting lobsters. In tubes *A* and *B* the cross-hatched areas represent the part covered with black paper. In tubes *C* and *D* the clear area was covered with white paper. Tubes *E* and *F* are shown equipped with the glass plates placed over the arm. In every instance the larvæ were started from the end of the tube designated *a*. For further explanation, see *Cases 29-33 inc.*, pp. 286-289.

Case 29—The tube was arranged as in Fig. 21, *A*. Ten positively-reacting, first-stage larvæ were placed in the Y-tube, and, by certain manipulations of the light and by virtue of their positive reaction, they were made to congregate in the stem end. Then suddenly, the direction of the light was changed so as to come in the direction of the arrows. Immediately the larvæ oriented with their heads toward the end *a*, and passed through the tube toward the light. As soon as they approached the region marked *x* they came under the influence of the dark background bounding the side of the tube. Immediately, as we have seen to be the case in previous instances, the longitudinal body-axis swung so that the

head came to face, more or less obliquely, the dark background, *B'*. The directive influence of the rays, however, continued to draw the larvæ on, but since they must travel in the direction in which the tail pointed, they entered the arm *b*, and passing close to the inside continued until further progress was prevented by the end of the arm. Space will not be taken to show the numerical results of this and similar experiments. Suffice it to state that nearly all of the positively reacting larvæ, of whatever stage or age, when submitted to these conditions of experiment, reacted as has been described above. This experiment was modified by placing the Y-tube so that the uncovered arm of the tube rested upon a piece of black paper. The results were invariably the same; the majority of the larvæ progressed to the arm of the tube not overlying the black ground.

Case 30—In this case the conditions of the experiments were further modified by reversing the Y-tube so that the arms pointed away from the window. In this instance larvæ which were manifesting a negative reaction were employed, and were first placed in the end (*a*), nearer the window. When the light was admitted the larvæ at once oriented with their heads directed away from the light and began to move away from the window. When they had reached the point designated *x*, they immediately underwent a swing of the longitudinal axis, as in previous cases, so that the head was directed toward the black ground, bounding the outer surface of the arm *c*. Thus they would continue, passing close to the inner wall of the tube until the majority had gathered in this arm. In this instance, however, the larvæ would usually rest between *x* and *c*, instead of moving to the end of the arm.

Case 31—Here the black background bounding the outer side of one arm was exchanged for a white ground of the same size and having the position shown in Fig. 21 *C*. Third-stage larvæ giving a positive reaction were employed for the experiment. They were started in the end *a*. When the light was admitted, the usual body-orientation resulted, and the larvæ began their progression through the tube toward the window. When they had arrived at *x* they came under the influence of the white ground and turned their heads away from this side. Progressive orientation then continued and the larvæ eventually became grouped in arm *c*. Similar results were obtained when half of this arm of the tube was laid over a sheet of white paper.

Case 32—The previous experiment was further modified by reversing the Y-tube so that the arms were directed away from the window (Fig. 21, *D*). Larvæ which were giving a negative reaction were employed. They were placed in the end *a*, and the light was admitted. After the usual body-orientation had taken place, the progression away from the window began. When the larvæ reached the point *x*, and had come under the influence of the white ground bounding one side of the tube they would swing their heads toward the right and continue their progress until all were gathered in arm *c*. This was somewhat unexpected. It eventually transpired, however, that the white ground bordering the outer surface of the tube did not act as a reflector or intensifier of the light rays, but as an opaque shield, cutting off the rays which would otherwise have entered the arm *c*. Thus, as in *Case 30*, the negatively reacting larvæ had merely grouped themselves in the arm where the light was least bright. When the Y-tube was so placed that half of arm *c* rested upon a sheet of white paper the result was different. The larvæ congregated in arm *b*, which was, under these conditions, the region of least light intensity.

Case 33—The four cases mentioned above were supplemented by other experiments involving the use of colored glass plates. As described in Experiment 15, these plates were so placed over the arms of the Y-tube that a difference in the intensity of light striking one arm was caused by interposing a red, orange or yellow glass plate between that arm and the source of illumination. In these cases the positively reacting larvæ gathered in the arm where the light-intensity was the greater, while the negatively reacting larvæ grouped themselves in the arm where the light was least bright. As a rule, the larvæ of earlier stages seemed to be more susceptible than the others to slight differences in the intensity of light at the entrance to the arms.

Thus is explained the tendency for positively reacting larvæ to gather in regions of greater light-intensity, and on the other hand, the tendency of negatively reacting larvæ to congregate in regions of lesser light-intensity. This condition of affairs has, no doubt, given many investigators reason to believe that such reactions are but manifestations of a positive photopathy; and that photopathy and phototaxis are fundamentally the same. We now know, however, that the reaction just described in *Case 5* is due to the combined effects of two tendencies; the one to turn the head

toward the dark areas (areas of non-stimulation); the other to move in the direction of the longitudinal axis of the body either toward or from the source of light. Were we dependent upon such experiments as these for our belief in the existence of a separate response to light-intensity, regardless of directive influence of light, we might well say that the photopathic and phototactic responses are, in the end, one and the same. But the writer has adduced in the previous section other data which separate more clearly these two types of reaction.

VII. ANALYSIS.

It has for some time been the custom to state that certain organisms are positively phototactic or positively photopathic, and that other organisms are negatively so. The index of reaction for several crustaceans has been so recorded, but the observations are usually incomplete, often uncritical, and sometimes of questionable significance. It is true that, in a very general way, organisms react positively or negatively to light. For instance, it may be said that the lobster shuns the light, that *Palemonetes* is attracted by the light, and that the larvæ of *Limulus* avoid the light. The definite statement, however, that the larvæ of *Limulus* are negatively heliotropic, or that *Palemonetes* and larvæ of *Homarus* are positively phototactic, is as inadequate as would be a biography written on the basis of a single day's association with a human individual. It may be true that by the time the adult stage is reached, the reactions of many animals have become more or less stereotyped, so that reactions like those of the moth to the flame, are easily predictable. In the larval and adolescent stages, on the other hand, the reactions are frequently more variable. To say that the lobster of the second larval stage is positively phototactic or positively photopathic is, as has been demonstrated, by no means a correct interpretation of the facts of the case, for slight changes in the conditions of stimulation may be sufficient to reverse the index of reaction. This variability doubtless occurs in many arthropods. It thus becomes evident that, although the young lobsters may be regarded as machines upon which many different external forces act and cause certain reactions, still (except for the definite body-orientations which are invariably determined by the directive influence of the light rays) they are

machines the nature of whose operations can seldom be predicted unless the age, the stage, the kind and degree of the stimulus, are accurately known. These conditions of reaction indicate the extent to which the behavior of young lobsters is determined by their physiological states; and the foregoing experiments show in what way these physiological states change, not only from one stage-period to another, but even during the same stage-period, through the influences of metabolism, development, and perhaps still other factors. The extent to which the natural behavior of animals in their natural environment can be explained on the basis of the results of laboratory experiments depends largely upon the animal and the kind of reactions involved. It is quite probable that some of the characteristics of reaction, which have been described in the present paper, determine in a large measure, the daily behavior of the larval and early adolescent lobsters when they are in their natural environment. Unfortunately, however, we know too little regarding the behavior of lobsters under natural conditions, to attach great importance to far-reaching explanations of their daily activities on the basis of laboratory experiments. A few points, however, may be noted. The reports of biological surveys make it clear that, at the surface of the ocean or of bays in which lobsters are known to live and breed, the stage most often taken in the tow-nets is the fourth; the larval stages are much less frequently found, the fifth stage seldom, and later stages never. Observations which were made on lobsters of different stages taken from the Wickford hatchery and liberated in the surrounding waters of Narragansett Bay yield similar evidence regarding the immediate natural distribution. In these cases the lobsters of the larval stages were found to swim for a brief time, then gradually disappear from the surface; the fourth stage lobsters swam actively at the surface so long as they were observed; while the fifth and all later stages plunged at once into the deeper water and were immediately lost to sight.

As the writer has already suggested, it is impracticable to attempt to explain the natural behavior of larvæ of the first three stages, on the basis of the reactions which have been discussed at some length in the present paper. The light (depending upon its intensity and directive influence; and upon the age, stage, and previous condition of the larvæ) may determine at one time a positive, at another a negative, response, so that the general reaction

of groups of lobster larvæ can in no way be readily predicted. One exception to this may be stated. The first-stage larvæ, directly after hatching, would be strongly drawn to the surface of the water by virtue of both their photopathic and of their phototactic response. After the first day or two, however, begins that modification and variation in the phototactic action which, for groups of uncertain age and condition, makes any accurate prediction of their movements quite impossible.

In the case of the fourth-stage lobsters there is a better basis for the correlation of the natural and experimental types of behavior. We know that, under experimental conditions, hungry fourth-stage larvæ, when submitted to food stimuli, will rise immediately to the surface of the water and swim about excitedly for some moments; we know also that the early fourth-stage larvæ, under certain experimental conditions will leave a region of low light intensity and remain in regions of greater light intensity. We have learned, moreover, that the same fourth-stage larvæ, under different experimental conditions, will usually shun the light when it has a single directive influence, and travel in the direction of the rays away from their source. Finally, we have observed that the fourth-stage lobsters, except in the latter part of the stage-period, show a definite tendency to remain at the surface of the water.

The question now arises: What is the cause of this surface-swimming? Is it a response to the intensity of light, to the directive influence of light, to hunger, or to gravity? Although we know something of the effects of several of these factors when they act separately, it is difficult to ascertain their individual influence when they work in combination. If, however, we can discover any parallel between a certain type of reaction under experimental conditions and a certain mode of behavior under natural conditions, and find that as one is modified or lost the other is also, then, and then only, are we justified in believing that we know the determining cause of the particular type of natural behavior in question. We have such a parallel between the photopathic (and occasionally the phototactic) reactions and the surface-swimming tendency of the fourth-stage lobsters. As the former becomes modified and is eventually replaced by the negative reaction, so the latter is changed and finally gives way to the bottom-seeking tendency as the lobsters pass on through the fourth stage-period. With

such a parallel before us, it cannot be doubted that there exists a certain causal relation between the positive photopathic reaction and the surface-swimming tendency on the one hand, and the negative photopathic reaction and the bottom-seeking tendency on the other. But the photopathic reaction may not alone be responsible for the surface-swimming tendency on the part of the fourth-stage lobsters. The presence of food particles in the water excites them strongly, and causes them, when in the glass jars, to swim excitedly at the surface of the water. It therefore appears quite within the bounds of possibility that chemotropism may also play a part in determining the surface-swimming of the fourth-stage lobsters.

The explanation of the behavior of the fifth and all later stages, in the light of the foregoing experiments, rests upon a more certain basis. We have observed that the fifth-stage lobsters invariably manifest both a negative phototactic and a negative photopathic reaction. In general this may be said to explain the fact that lobsters in the fifth and all later stages shun the light at all times. Little work was done on the behavior of the older lobsters, and it is hoped that future investigations may continue along this line.

In connection with the mechanics of orientation, the writer has shown that the reaction of larval lobsters to light is made up of two components—body-orientation and progressive orientation; and that the former is primary while the latter is secondary. In the earlier pages of this paper it was demonstrated that the *progressive orientation* is dependent upon a great number of conditions, and that the orientation responses are relatively complex reactions which are dependent in great measure upon the obscure, changing, internal conditions which are embraced under the general term, "physiological states." In later pages, on the other hand, attention has been directed to those conditions of light which determine the *body-orientation* alone; and the results recorded have made it clear that the movements producing the body-orientations are types of action which simulate more closely pure reflexes, direct, constant, and invariable.

As BOHN (1905a) has well said, it is impossible to take definite account of the complicated series of phenomena which take place in the nervous system of animals even as low as the arthropods, for these are dependent not alone upon complicated connections between neurons, but also upon their variable states. Yet it is

apparent that this difficulty applies rather (at least in the reactions of the larval lobsters) to those movements which determine the *progressive orientation* to light, than to those which determine *body-orientation*. Even in the latter somewhat less complicated and more easily explained phenomena, however, we are still far from recognizing the underlying causes.

It is true that we can understand in a way why the "posterior position" of the thoracic appendages determines a negative response, while the "anterior position" determines a positive response. We can, moreover, understand why a more intense illumination of the eye on one side causes a greater activity of the swimmerets on that side, and a consequent swing of the larva away from that side. This phenomenon was well shown by experi-

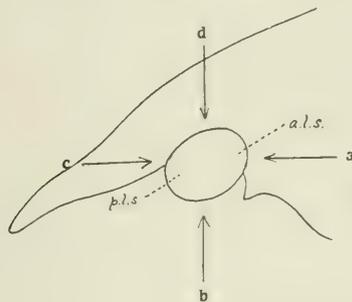


FIG. 22. Diagram showing the rostrum and one eye of a larval lobster; *a, b, c, d* represent direction of light striking the eye from behind, below, in front and above; *a.l.s.* represents posterior lateral surface; *p.l.s.* represents anterior lateral surface. For further explanation, see p. 297.

ments which the writer performed upon larvæ with blinded eyes (HADLEY 1908). These experiments demonstrated that, when the right eye was blinded, the direction of forward swimming was invariably to the right; in other words, the exopodites beat more vigorously upon that side of the body whose eye was most stimulated, and the larva was, in consequence, "pulled around" like a boat. These reactions are explainable on the grounds of a heterolateral stimulation and a consequent unequal action of the muscles on the two sides of the body. But we do not understand as clearly how or why the action of the light striking with equal intensity the corresponding areas of the posterior surface of the eyes (Fig. 22), for instance, brings about these "anterior" or "posterior" positions of the thoracic appendages, and the con-

sequent positive or negative reactions. Nor do we understand why, when the larva is in one "physiological state," a certain intensity of light (striking equally the posterior lateral surface of the two eyes) causes a positive reaction, while if the same larva is in another "physiological state," the same light (striking with the same intensity the same parts of the eye-surfaces) causes the opposite reaction; or again, why when the larva is in the *same* "physiological state," one intensity of light causes a positive reaction, while light of slightly less intensity determines a negative reaction. No more do we know why the illumination of the upper surface of the eyes (Fig. 22, *d*) causes a forward rotation; or the illumination of the lower surfaces (*b*), a backward rotation; or the illumination of the anterior surface (*c*), a forward or a backward rotation. These as yet unexplainable conditions of reaction may well convince us that, however simple and mechanical some of these reactions appear to be, many of them are extremely complex, and indicate a very complex relation between the different regions of the eyes and the nervous centers. Yet, as has been stated, to such a degree as any of these reactions can be explained, those which are concerned in the processes of body-orientation are more easily interpretable on the "simple-reflex" hypothesis. In view of this fact the writer would differ from the conclusion reached by BOHN (*loc. cit.*, p. 41): "Tous ces phénomènes (the reactions of larvæ of *Homarus vulgaris*) sont en relation avec des états physiologiques particuliers. Sous l'influence de l'éclairement, l'état physiologique des larves de homard ne tarde pas à changer, et les tropismes aussi." The present writer would limit the application of this theory to those reactions of the larval lobsters which are concerned with progressive orientation, excluding body-orientation.

Regarding the relation of the type of reaction found in the larval lobsters to the tropism theories, inference has already been made in the preceding paragraphs. First, to what extent does the behavior found in the larval lobsters agree with the local action theory of tropism? The primary demand of this theory is that the body of the organism should become so oriented with respect to the source of illumination that the anterior end is made to point either toward or from the source. Under these conditions the index of reaction is said to be positive or negative, according as the organism moves toward or from the light. "This

orientation is produced, according to this tropism theory, by the direct action of the stimulating agent on the motor organs of that side of the body on which it impinges. A stimulus striking one side of the body causes the motor organs of that side to contract or extend or to move more or less strongly. This, of course, turns the body till the stimulus affects both sides equally; then there is no occasion for further turning and the animal is oriented" (JENNINGS 1906a, p. 266). This is also brought out by HOLT and LEE (1901, p. 479), "The light operates, naturally, on the part of the animal which it reaches." Thus, this tropism theory requires that, in order to determine the direction of movement, the stimulus must act more strongly on one side of the body than on the other. It is needless to say also that in the majority of cases the same conditions of stimulus which cause an animal to direct the head away from the source of the stimulus, also determine a movement in the same direction. Therefore, if we separate, as has been done in this paper, *body-orientation* from *progressive orientation*, we can say that, in most organisms, the index of body-orientation agrees with that of progressive orientation; the conditions of stimulation which cause the one likewise determine the other. Let us now see to what extent the behavior of the larval lobsters agrees with these requirements of the local action theory of the tropisms. In order to treat the matter concretely we must consider it under two heads. First, body-orientation; then, progressive orientation.

It has been shown in the previous pages that, whatever the sign of progressive orientation may be, the *body-orientation is invariably negative*; and that this body-position is produced as a result of diverse reactions which are attributable to the relative intensities of light which strikes the eyes of the larvæ. This body-orientation, moreover, is constant; it is not dependent upon the age, stage, previous stimulation, hunger, "physiological state," or upon any modifications of the external stimulus, such as changes in intensity, duration of stimulation, etc. The orienting reaction always comes about in the same way, so that we here have a case where the "same-stimulus-same-reaction" principle invariably holds. In other words, the reactions by which the larval lobsters secure the characteristic body-orientation are typical and invariable motor-reflexes.

Beyond producing the body-orientation, the direct motor-reflex

ceases to influence the behavior of the larval lobsters. From this moment on, a multitude of conditions appear to be brought to bear to determine the consequent *progressive orientation* of the young animals in one sense or the other. No longer can we say, "same stimulus, same reaction" (SPAULDING 1904), for there is now no constant form of reaction even to the same stimulus. The reactions appear to be no longer so dependent upon the nature of the *external stimulus*, but are more largely regulated by the "physiological states." This we might consider as the cumulative result of a long series of previously acting stimuli, to which others are constantly being added with two effects; first, of bringing about a definite reaction determined by the nature of the stimulus and by the present physiological state; second, of further modifying the physiological state itself, so that even the reapplication of the same stimulus might provoke a quite different reaction. It can not be doubted that the series of changes, which occur in the behavior of the lobster larvæ as they pass through the successive stages, is largely due to this gradual modification of the physiological condition—the cumulative effect of a long series of antecedent stimuli.

We may sum up the preceding paragraphs by saying; (1) The reactions by which the *body-orientation* of larval lobsters is produced are invariable motor reflexes, and the method of such orientation is, therefore, quite in accord with the requirements of the local action theory of tropisms. (2) The reactions by which the *progressive orientation* is produced, although appearing to be simple reflexes, are not invariable but are dependent upon many conditions of stimulation, and especially upon the physiological states.

In view of these facts, it appears that, while the body-orientation of the larval lobsters is not of primary importance in determining the index of the progressive response to the directive influence of the light rays (since the body-orientation and the progressive orientation are dependent upon quite different factors), still it is of primary importance in determining the general line along which the movement shall take place, either toward or from the source of light. It is shown by these points that this type of response is not in agreement with JENNING'S theory (1906b), in which the process of orientation is of secondary importance, for neither the immediate nor the final body-orientation of lobster larvæ to light

can be characterized as a "selection from among the conditions produced by varied movements" (JENNINGS 1906b, p. 452). Indeed there are no "varied movements" in the reactions by which the body-orientation to light is brought about. The only way in which the term "random movements" can be applied to the orientation of the larval lobsters is in its relation to the variable extent of the revolutions or rotations. It cannot be denied that this *degree* may be dependent upon the physiological states of the larvæ (for instance, fatigue or freshness), but, after all, this point is irrelevant to the present discussion, since it is the direction of the immediate turning and not the extent of it, which is the important consideration.

The foregoing experiments throw but little light upon the question of intensity of light versus direction of light. Indeed it is probable that the latter phase of the problem is not of great importance except in cases where the light rays are effective by passing through the body as in the case of the electric current, which, as the writer has shown elsewhere (HADLEY 1907a) causes reaction only when the direction of the current holds a certain relation to the longitudinal axis of the larvæ. It is clear, however, that the direction of the light rays does modify the reactions of the larval in two ways: (1) By determining *which of the two eyes shall be most stimulated*, thus causing a body-orientation in which the longitudinal body-axis is thrown into line with the direction of the light rays, so that the eyes shall be equally stimulated; (2) by determining *what parts of the surfaces of the two eyes shall be stimulated equally*, and thus producing a body-orientation in which the posterior lateral surface (Fig. 22, *a.l.s.*) of the eyes receives the strongest stimulation, and the anterior lateral surface (*p.l.s.*) the least. These reactions, and the consequent progressive orientations of the larvæ, the writer has called reactions to the directive influence of the light. That there may be, in addition to these responses, reactions to the intensity of light as HOLMES (1901) and others have considered possible, it is still permissible to believe, and in the earlier pages of this paper the writer has pointed out some reactions of larval lobsters, which, although not perfectly understood, may be included under the head of photopathic response.

The foregoing experiments were carried on at the Experiment Station of the Rhode Island Commission of Inland Fisheries at

Wickford, Rhode Island, where exceptional facilities were found for obtaining material of all ages and stages. The writer's thanks are especially due to Prof. A. D. MEAD of Brown University for making possible an opportunity for this line of inquiry and for material assistance; to Dr. R. M. YERKES of Harvard University, and to Dr. H. E. WALTER of Brown University for friendly criticism during the preparation of the paper; also to Mr. E. W. BARNES, Superintendent of the Wickford hatchery, for many kindnesses.

VIII. SUMMARY.

1. Larval and early adolescent lobsters present both phototactic and photopathic reactions as these responses are defined on p. 201.

2. There is no constant type of response for all larval lobsters, but a modification of reaction occurs through the metamorphosis of the larvæ.

a. First-stage larvæ, directly after hatching, give definitely positive phototactic and photopathic reactions which endure for about two days, after which the phototactic reactions change to negative, becoming positive again shortly before moulting into the second stage.

b. Both early second-stage and early third-stage larvæ manifest a negative phototactic reaction, which usually becomes positive shortly before moulting into the third and fourth stages, respectively.

c. The photopathic reaction of the first three larval stages is commonly positive from the beginning to the end of the stage.

d. The phototactic reaction of the fourth-stage lobsters is usually (*i. e.*, except in cases where intense light is used in connection with early fourth-stage lobsters) negative throughout the stage-period, and the photopathic reaction, positive during the early fourth stage-period, eventually becomes negative.

e. During the fifth stage-period, and in all later stages, both the phototactic and the photopathic reactions are strongly negative.

3. While the photopathic reaction of the larval lobsters remains constant, the phototactic reactions are subject to modification as a result of changes in the intensity or in the direction of light.

a. During the early first stage-period no intensity of light used changes the index of the phototactic or of the photopathic response, but later an intense light may reverse the index of the phototactic reaction.

b. Throughout the second and third stage-periods, the index of the photopathic reaction is not reversible, but during the early part of these periods the negative phototactic reaction, and during the latter part the positive phototactic response, may be reversed temporarily by using light of great intensity (suddenly introduced).

c. During the fourth stage-period the negative phototactic response can not be reversed (except in such instances as are noted in Exp. 24, Cases 5 and 6), but the positive photopathic reaction of the early fourth stage-period may be reversed temporarily by using light of very great intensity.

d. None of the negative responses of the fifth-stage lobsters can be reversed by using light of any intensity whatsoever.

e. Submitting larvæ to darkness for periods of 2 to 12 hours does not change the index of reaction.

4. The reactions to light can be modified by other factors; contact-irritability is first manifested in the middle or later part of the fourth stage-period, and henceforth determines (about equally with light) the behavior of early adolescent lobsters.

5. Laboratory experiments explain some of the aspects of the behavior of the young lobsters under natural conditions of environment: (1) The positive photopathic reaction, and the positive phototactic reaction (to lights of very great intensity) together with the response to food stimuli may unite in determining the surface-swimming of the early fourth-stage lobsters. (2) The negative photopathic reaction, the negative phototactic reaction together with the response to contact-stimuli may unite in causing the late fourth, fifth and all later-stage lobsters to leave the surface water, and to burrow at the bottom of the sea.

6. The reaction of larval lobsters to light depends upon two factors; body-orientation and progressive orientation.

7. The body-orientation is invariably negative and is due to the difference in illumination of the two eyes of the larva. It is brought about by invariable reflex movements which tend to bring the longitudinal axis of the body parallel to the rays of light, with the head away from their source.

8. The progressive orientation may be either positive or nega-

tive, and is due to the position (extension or contraction) of the thoracic appendages. If these have the "anterior position," the reaction is positive; if they have the "posterior position," the reaction is negative. These positions appear to depend upon the intensity of light which strikes the posterior lateral surface of the eyes equally.

9. The larvæ orient to screens and backgrounds of black and of white by reflex movements identical with those by which they react to direct illumination and shading.

10. The reactions by which the body-orientation to light is produced, are invariable motor-reflexes, quite in accord with the local action theory of tropisms. The reactions by which the progressive orientation to light is produced, although appearing to be simple reflexes, are not invariable or constant, but dependent upon "physiological states."

11. In all the reactions to light (except the photopathic) the body-orientation is of primary importance, since progressive orientation cannot occur until the body-orientation has been established.

12. None of the reactions to light can be interpreted as "a selection from among the conditions produced by varied movements." They are not trial (and error) reactions, in the sense in which this expression is used by JENNINGS and HOLMES.

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A VACUUM STOPCOCK.
BY FREDERICK G. KEYES.
Science, N. S. XXVIII, 1908, p. 735.

A VACUUM STOPCOCK

DURING the winter of 1908 work was undertaken on the gas production of *Bacillus coli* in synthetic culture media. The method of work consisted of growing the organism in high vacuum. In the course of this work considerable difficulty was experienced in maintaining absolutely tight stopcocks and as a result a stopcock was devised that appears to satisfy the conditions for a gas-tight stopcock.

The ordinary stopcocks had to be reground with jeweler's rouge, and while this precaution rendered the stopcock gas-tight under constant temperature conditions, it was found that the changes in temperature from room

plane as the oblique drilling, a drilling is made as far as the level of the lead X. From this point it continues at a right angle as indicated in the diagram. The operation of the stopcock is as follows. The stopcock being in the position indicated in Fig. 1, the plug is turned through 180°, thus bringing it into the position indicated in Fig. 2. The stopcock is then connected with the pump and the small bulb exhausted. Turning the plug through another 180° will open the passage from X to Y and then it may be opened and closed at will without the small bulb A ever coming into communication with the passage.

In the above arrangement the atmosphere is exerting its pressure to hold the plug in place, thus overcoming the resilience of the

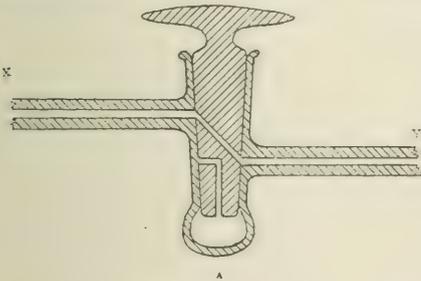


FIG. 1

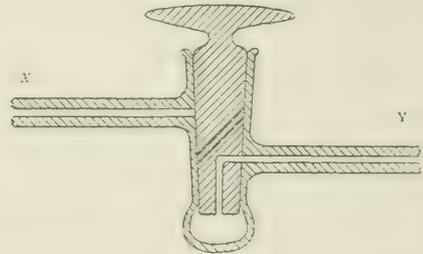


FIG. 2

to incubator caused the two ground surfaces, assisted by the resilience of the lubricant, to separate and thus make the stopcock leak. To overcome these difficulties the stopcock had to be tied into place and mercury placed in the exposed lead.

The stopcock devised to overcome these difficulties is explained by the two diagrams. The passage from X to Y leads through an obliquely drilled plug as in the ordinary improved vacuum stopcock. At A a small bulb takes the place of the ordinary open end. Into the center of the plug, and in the same

lubricant and pressing the two ground surfaces together constantly, in spite of the temperature changes that tend to let one surface expand away from the other. The lubricant is composed of gutta-percha, hard paraffin wax and a heavy mineral oil; and answers admirably. Many similar lubricants are described in the literature.

The above stopcocks were very neatly constructed by Eimer and Amend.

FREDERICK G. KEYES

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SIMPLE SYNTHETIC MEDIA FOR THE GROWTH
OF *B. COLI* AND FOR ITS ISOLATION
FROM WATER.

BY MAURICE L. DOLT.

Journal of Infectious Diseases, V, 1908, p. 616.

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MAURICE L. DOLT

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CHICAGO

SIMPLE SYNTHETIC MEDIA FOR THE GROWTH OF *B. COLI* AND FOR ITS ISOLATION FROM WATER.*

MAURICE L. DOLT.

(From the Bacteriological Laboratory of Brown University.)

THE purpose of this research was first, to prepare a simple synthetic culture medium for the growth of *B. coli*, and second, to find a simple synthetic medium to be used in water analysis, which would favor the growth of *B. coli* and would inhibit the growth of the other organisms commonly present in water.

The advantages of a synthetic medium are plain. As its chemical composition is exactly known it can be easily and quickly prepared, and can always be duplicated. Results obtained by its use are always uniform and comparable. By the use of such a medium some light may be thrown on bacterial metabolism.

I. SIMPLE SYNTHETIC MEDIA FOR THE GROWTH OF *B. coli*.

Some experimental work has been done already with synthetic culture media for the growth of *B. coli*. Galimard and Lacomme[†] give the chemical composition of several media on which *B. coli* and certain other organisms grow well. They worked with amido acids as the bases of their media. One of their media had the following composition:

Leucin.....	7.5 gr.
Alanin.....	2.0 gr.
Tyrosin.....	traces
Glycerin.....	15 gr.
Sodium chloride.....	0.5 gr.
Magnesium sulphate.....	0.05 gr.
Calcium glycerophosphate.....	0.2 gr.
Sodium carbonate.....	to neutralize
Distilled water.....	1,000 c.c.

The following organisms were found to grow on this medium:

- B. pyocyaneus*
- B. prodigiosus*
- B. coli* R²
- Pneumobacillus* of Friedlander
- B. tetragenus*
- Staphylococcus aureus*
- Sarcina superba*

* Received for publication October 29, 1908.

[†] *Jour. de physiol. et path. générale*, 1907, 9, p. 481.

B. coli was also grown on several other media similar to the above but containing other amido acids such as glycocoll, aspartic acid, etc.

MacConkey¹ showed that *B. coli* and other intestinal bacteria grow well on an agar medium containing 0.5 per cent of sodium taurocholate, while the common bacteria are to a great extent inhibited.

Jackson² states that the bile salts, when added to a Standard agar medium, exert a strong restraining action on most species of bacteria which grow at blood heat. This restraining action is selective, it favors the growth of *B. coli*, retards the growth of certain streptococci, and actually kills off the majority of species which grow at 37° C. Jackson says that the effect must be due to the cholic acid radical which is common to both salts.

Both MacConkey's and Jackson's media have a very complex chemical composition and a variable one. Galimard and Lacomme's medium has the advantage of having a fixed chemical composition but is still too complex to be of practical value in water analysis. If their medium could be simplified and if the inhibitive property of Jackson's medium could be given to it we would have a medium of practical value.

As *B. coli* was known to grow on several synthetic media containing amido compounds the following was tried:³

Sodium chloride.....	0.5 gr.
Disodium phosphate.....	0.2 gr.
Ammonium lactate.....	0.6 gr.
Asparagin.....	0.4 gr.
Distilled water.....	100 c.c.
Sodium carbonate.....	to neutralize

B. coli freshly isolated from feces grew very well on this medium. After 12 hours at 37° C. there was a strong turbidity in the inoculated tubes; after 24 hours there was a heavy sediment at the bottom of the tubes and a pellicle at the surface.

Ammonium lactate was then omitted from the medium and the following tried:

¹ *Thompson Yates Laboratories Rep.*, 1900, 3, p. 41; 1901, 3, p. 151; MacConkey, A., and Hill, Chas. *ibid.*, 1901, 4, p. 151.

² *Biological Studies by the Pupils of William Thompson Sedgwick*, Boston, 1906, p. 292.

³ In all cases throughout this work C. P. chemicals and water distilled in glass were used.

Sodium chloride.....	0.5 gr.
Disodium phosphate.....	0.2 gr.
Asparagin.....	1 gr.
Distilled water.....	100 c.c.
Sodium carbonate.....	to neutralize

B. coli also grew well on this medium. This medium contains but one organic compound, the other substances are all inorganic salts.

The next experiment was to determine whether *B. coli* can grow on amido compounds alone. The results are given in Table 1.

TABLE 1.

NUMBER OF MEDIUM	COMPOSITION OF MEDIUM	GROWTH OF <i>B. coli</i> AT 37° C.	
		In 24 Hours	In 48 Hours
1.....	Glycocoll 1 gr. Distilled water 100 c.c.	None	None
2.....	Glycocoll 1 gr. Sodium chloride 0.2 gr. Distilled water 100 c.c.	None	None
3.....	Glycocoll 1 gr. Potassium chloride 0.2 gr. Distilled water 100 c.c.	None	None
4.....	Asparagin 1 gr. Distilled water 100 c.c.	None	None
5.....	Urea 1 gr. Distilled water 100 c.c.	None	None

All made neutral to phenolphthalein with NaOH.

Under the above conditions *B. coli* does not grow on glycocoll, asparagin, or urea alone. These experiments are controls on the purity of our salts and of our distilled water and their freedom from the salts which we shall find later are required for the growth of *B. coli*.

The next experiments were tried to show what inorganic salts *B. coli* requires in addition to asparagin. The latter was selected as the organic base of the media not only because it was less expensive than the others but also because further experiments showed it to be the most favorable. The more common soluble inorganic salts were tried. The results are given in Table 2.

The experiments in Table 2 show that *B. coli* grows on a combination of asparagin with either sodium or ammonium nitrate or sodium or ammonium phosphate but grows much better on the phosphates than on the nitrates.

TABLE 2.

NUMBER OF MEDIUM	COMPOSITION OF MEDIUM		GROWTH OF <i>B. coli</i> AT 37° C.	
			In 24 Hours	In 48 Hours
6.....	Asparagin	1 gr.	None	None
	NaCl	0.2 gr.		
	Distilled water	100 c.c.		
7.....	Asparagin	1 gr.	None	None
	KCl	0.2 gr.		
	Distilled water	100 c.c.		
8.....	Asparagin	1 gr.	None	None
	NH ₄ Cl	0.2 gr.		
	Distilled water	100 c.c.		
9.....	Asparagin	1 gr.	None	None
	CaCl ₂	0.2 gr.		
	Distilled water	100 c.c.		
10.....	Asparagin	1 gr.	None	None
	MgCl ₂	0.2 gr.		
	Distilled water	100 c.c.		
11.....	Asparagin	1 gr.	None	None
	Na ₂ SO ₄	0.2 gr.		
	Distilled water	100 c.c.		
12.....	Asparagin	1 gr.	None	None
	K ₂ SO ₄	0.2 gr.		
	Distilled water	100 c.c.		
13.....	Asparagin	1 gr.	None	None
	(NH ₄) ₂ SO ₄	0.2 gr.		
	Distilled water	100 c.c.		
14.....	Asparagin	1 gr.	Slight	Slight
	NaNO ₃	0.2 gr.		
	Distilled water	100 c.c.		
15.....	Asparagin	1 gr.	None	None
	KNO ₃	0.2 gr.		
	Distilled water	100 c.c.		
16.....	Asparagin	1 gr.	Very slight	Slight
	NH ₄ NO ₃	0.2 gr.		
	Distilled water	100 c.c.		
17.....	Asparagin	1 gr.	Good	Very good
	Na ₂ HPO ₄	0.2 gr.		
	Distilled water	100 c.c.		
18.....	Asparagin	1 gr.	None	None
	K ₂ HPO ₄	0.2 gr.		
	Distilled water	100 c.c.		
19.....	Asparagin	1 gr.	Good	Very good
	(NH ₄) ₂ HPO ₄	0.2 gr.		
	Distilled water	100 c.c.		

All made neutral to phenolphthalein with NaOH.

The next step was to determine whether the concentration of these salts has any influence on the growth and whether the combination of two salts would be an improvement.

The following table (Table 3) gives the results there enumerated. As far as could be noticed the increase in the concentration of the salts or the combination of two salts does not improve the growth.

TABLE 3.

NUMBER OF MEDIUM	COMPOSITION OF MEDIUM	GROWTH OF <i>B. coli</i> AT 37° C.	
		In 24 Hours	In 48 Hours
20.....	Asparagin 1 gr. NaNO ₃ 0.2 gr. Distilled water 100 c.c.	Very slight	Slight
21.....	Asparagin 1 gr. NaNO ₃ 0.4 gr. Distilled water 100 c.c.	None	No better than on 20
22.....	Asparagin 1 gr. NH ₄ NO ₃ 0.2 gr. Distilled water 100 c.c.	None	Very slight
23.....	Asparagin 1 gr. NH ₄ NO ₃ 0.4 gr. Distilled water 100 c.c.	None	No better than on 22
24.....	Asparagin 1 gr. Na ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Very good
25.....	Asparagin 1 gr. Na ₂ HPO ₄ 0.4 gr. Distilled water 100 c.c.	Good; same as on 24	Very good; same as on 24
26.....	Asparagin 1 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Very good
27.....	Asparagin 1 gr. (NH ₄) ₂ HPO ₄ 0.4 gr. Distilled water 100 c.c.	Good; same as on 26	Very good; same as on 26
28.....	Asparagin 1 gr. NaNO ₃ 0.2 gr. Na ₂ HPO ₄ 0.2 gr.	Good; same as on 24	Very good; same as on 24
29.....	Asparagin 1 gr. NH ₄ NO ₃ 0.2 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good; same as on 26	Very good; same as on 26
30.....	Asparagin 1 gr. NaNO ₃ 0.2 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Good
31.....	Asparagin 1 gr. NaNO ₃ 0.2 gr. NH ₄ NO ₃ 0.2 gr. Distilled water 100 c.c.	Slight	Good
32.....	Asparagin 1 gr. Na ₂ HPO ₄ 0.2 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Good

All made neutral to phenolphthalein with NaOH.

We may decide then that either one of the two following media may be considered favorable for the growth of *B. coli* at 37° C. A good growth is obtained even in the first 24 hours.

MEDIUM 1

Asparagin..... 1 gr.
Na₂HPO₄..... 0.2 gr.
Distilled water..... 100 c.c.

MEDIUM 2

Asparagin..... 1 gr.
(NH₄)₂HPO₄..... 0.2 gr.
Distilled water..... 100 c.c.

Made neutral to phenolphthalein with NaOH.

2. THE USE OF THE ABOVE MEDIA FOR THE ISOLATION OF *B. coli* FROM WATER.

A. *Lactose-asparagin agar*.—Inasmuch as in the routine of water analysis a solid medium is required we next directed our attention to the combination of the simple media described, with agar, for the purpose of isolating the colon bacillus by the plate method.

The agar was purified by cutting it into small pieces and soaking in distilled water for 24 hours, and the following medium which may be called lactose-asparagin agar was prepared:

Purified agar (3 per cent solution).....	250	c.c.
Asparagin	2.5 gr.	}
Na ₂ HPO ₄	0.5 gr.	
Distilled water	250	

Made neutral to phenolphthalein with NaOH and 1 per cent lactose added.

Plates were made using this lactose-asparagin agar and 1 per cent azolitmin¹ solution in the usual manner. Several samples of water slightly polluted with *B. coli* were plated with the azolitmin-lactose-asparagin agar. Numerous colonies developed in each plate after 24 hours at 37° C. Several red colonies were isolated and proved to be *B. coli*.

The above medium, judging from repeated trials, appears to be just as effective as the Standard litmus-lactose agar for the isolation of *B. coli* and besides it has the advantage of having a fixed and simple chemical composition.

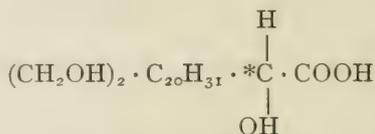
B. *The addition of certain substances to the above medium for the purpose of inhibiting the growth of the bacteria in water other than B. coli*.—Jackson has proved by experiments that the bile salts (sodium taurocholate and glycocholate) favor the growth of *B. coli* and restrain the growth of other forms of water bacteria. He proved that this restrictive action was due to the cholic group of the bile salts.

Sodium glycocholate and taurocholate could be added to the above medium to restrain the growth of other bacteria. But pure bile salts are too expensive to be used on a large scale. The use of

¹ There are several kinds of azolitmin on the market. Kahlbaum's C. P. azolitmin was used exclusively in these experiments. One gram was dissolved in 100 c.c. of distilled water and the solution boiled for 15 minutes. The solution which at first is slightly red turns to a blue after boiling. Prepared in this way the azolitmin solution does not need to be treated with an alkali to bring it to the right reaction. It may be used directly with any culture medium which is neutral to phenolphthalein. Other samples of azolitmin do not act in this way.

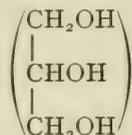
bile itself would defeat the object of these experiments as its composition is so complex and variable.

It was thought that very probably simpler and cheaper substances could be found which would have the same selective action. A consideration of the chemical structure of cholic acid led to the following: Cholic acid is



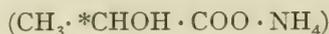
It has two primary alcohol groups (CH_2OH), and one a symmetrical carbon atom indicated by a star (*). Many substances could be selected having either an asymmetrical carbon atom, or the (CHOH) group, or the (CH_2OH) group, or all of them combined. The following substances were tried:

Glycerin



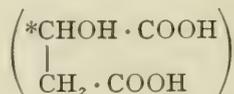
which has two primary alcohol groups and one secondary alcohol group.

Ammonium lactate



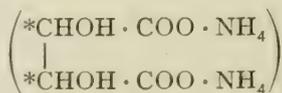
which has the secondary alcohol group and an asymmetrical carbon atom.

Malic acid



which has the secondary alcohol group and an asymmetrical carbon atom.

Ammonium tartrate



which has two secondary alcohol groups and two asymmetrical carbon atoms.

Experiments were then begun to determine whether these various substances could be substituted for the asparagin with the idea that if this is possible they might serve both as a food for *B. coli* and as inhibitory agents for the other organisms.

The results are given in the following table (Table 4):

TABLE 4.

NUMBER OF MEDIUM	COMPOSITION OF MEDIUM	GROWTH OF <i>B. coli</i> AT 37° C.		
		In 24 Hours	In 48 Hours	In 72 Hours
33.....	Glycerin 1 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Very good	Very good
34.....	Ammonium lactate 1 gr. Na ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Good	Very good	Very good
35.....	Malic acid 1 gr. (NH ₄) ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	Slight	Slight	Slight
36.....	Ammonium tartrate 1 gr. Na ₂ HPO ₄ 0.2 gr. Distilled water 100 c.c.	None	None	None

All made neutral to phenolphthalein with NaOH.

These experiments were repeated several times with the same results; a good growth always occurred on media 33 and 34; a visible growth on 35, and no growth at all on 36.

Solid culture media were then made with the above solutions in the same way that the lactose-asparagin agar was prepared. A series of comparative tests was then conducted in the Laboratory of the Rhode Island State Board of Health. Samples of water known to be slightly polluted were plated on the ordinary Standard litmus-lactose agar and at the same time on azolitmin-lactose-asparagin agar, azolitmin-lactose-glycerin agar, azolitmin-lactose-ammonium lactate agar, and azolitmin-lactose-malic acid agar. The results appear in the following table (Table 5).

As will be seen from this table the results were very satisfactory. The red colonies were well developed and characteristic of *B. coli* on the four synthetic media. There were fewer red colonies on the synthetic media than on the Standard medium but the numbers

TABLE 5

Plate No.....		Standard Agar			Asparagin Agar			Glycerin Agar			Ammonium Lactate Agar			Malic Acid Agar		
		I	2	3	I	2	3	I	2	3	I	2	3	I	2	3
Pawtuxet River	Red colonies	5	2	2	5	0	2	0	1	0	0	2	0	0	0	1
Feb. 26, 1908	Total "	20	18	14	12	8	2	0	2	0	0	4	2	0	0	1
Pawtuxet River	Red "	18	16	15	3	0	0	1	3	0	1	1	2	0	0	0
Mar. 11, 1908	Total "	24	22	20	10	9	13	1	3	0	4	3	6	0	0	0
Pawtuxet River	Red "	10	6	7	3	2	3	2	4	4	1	2	2	2	0	1
Mar. 25, 1908	Total "	14	10	14	5	4	4	2	4	5	1	2	2	2	0	1
Pawtuxet River	Red "	10	15	13	2	3	2	3	3	3	3	3	3	2	0	1
April 8, 1908	Total "	25	24	18	2	4	4	4	14	9	5	8	4	2	0	1
Ten Mile River	Red "	2	2	1	1	1	0	2	1	0	0	2	1	0	0	0
Mar. 2, 1908	Total "	16	18	14	14	21	16	12	14	24	8	20	4	3	0	0
Ten Mile River	Red "	4	3	4	1	2	0	2	1	1	3	0	1	0	0	2
Mar. 18, 1908	Total "	20	14	20	4	4	1	3	3	2	3	1	3	0	0	4

were always fairly proportional. Very few colonies other than red ones appeared on the glycerin, ammonium lactate, and malic acid plates. On the asparagin agar plates there were more colonies other than red ones than on the other synthetic media. On the malic acid agar there were never any other colonies than the red ones, and the red ones were themselves in smaller number. In this connection it is suggested that it might be possible in the case of slightly polluted water to use malic acid agar to plate a larger amount than 1 c.c. of the water to be tested. Experiments were not carried on along this line. No spreading colonies ever appeared on the four synthetic media while there were many on the Standard agar plates. Some of the red colonies on the Standard agar were not at all characteristic of *B. coli* while the red colonies on the four synthetic media were all of the *B. coli* type.

It was then thought advisable to prove whether all the red colonies on the four synthetic media were *B. coli*. All the red colonies were carefully fished from the plates made April 8, 1908, from the Pawtuxet River water. There were 38 red colonies fished from the three Standard agar plates as controls, seven from the three asparagin agar plates, nine from the three glycerin agar plates, nine from the three ammonium lactate agar plates and three from the three malic acid agar plates. Each one was run through the following tests for *B. coli*: (1) morphology; (2) agar slant; (3) gelatin stab; (4) fermentation of dextrose; (5) coagulation of milk; (6) reduction of nitrates.

The results are as follows:

TABLE 6.

Origin of the Colonies	No. of Red Colonies	No. of <i>B. coli</i> Colonies	Percentage of <i>B. coli</i>
Standard litmus-lactose agar.....	38	18	48
Litmus-lactose-asparagin agar.....	7	7	100
Litmus-lactose-glycerin agar.....	9	9	100
Litmus-lactose-ammonium lactate agar.....	9	9	100
Litmus-lactose-malic acid agar.....	3	3	100

The above table shows that of all the red colonies which developed on the Standard litmus-lactose agar only about half of them were *B. coli*, while all the red colonies which developed on the four synthetic culture media were true *B. coli*. The above table also shows that there were more *B. coli* per c.c. of water developing on the ordinary agar than on the synthetic media.

SUMMARY.

1. *B. coli* does not grow on dilute (1 per cent) solutions of asparagin, glycoll, or urea.
2. It grows very well on a 1 per cent solution of asparagin if 0.2 per cent of sodium phosphate is added.
3. Of all the soluble inorganic salts sodium and ammonium nitrate and sodium and ammonium phosphate are the only ones which can be used with asparagin for the growth of *B. coli*.
4. Substances having an asymmetric carbon atom in their molecule and a CHOH group, such as glycerin, ammonium lactate, malic acid, can be used instead of asparagin for the growth of *B. coli*.
5. These substances seem to favor the growth of *B. coli* and inhibit the growth of water organisms.
6. Very simple synthetic culture media can be used in place of the ordinary litmus-lactose agar or the various bile media and they have several advantages in the routine work of detecting *B. coli* in water.
7. Of the four synthetic media suggested two are especially recommended. Their composition is as follows:

I

- | | |
|---|----------|
| Purified agar (3 per cent solution) | 500 c.c. |
| Glycerin 5 gr. } | 500 c.c. |
| Ammonium phosphate 1 gr. } | |
| Distilled water 500 c.c. } | |
- Sodium hydroxide solution is used to neutralize and 1 per cent lactose is added just before sterilization.

II

Purified agar (3 per cent solution).....	500 c.c.
Ammonium lactate 5 gr. }	500 c.c.
Disodium phosphate 1 gr. }	
Distilled water 500 c.c. }	

Sodium hydroxide solution is used to neutralize and 1 per cent lactose is added as before.

Both of the above media are to be used with 1 per cent azolitmin solution in the usual way.

S. These media have thus far given extremely satisfactory results for the isolation of *B. coli* in practical water analysis.

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(Anatomical) Laboratory of
Brown University

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