is, at its greatest development, nothing more than a highly complicated, self-supporting *pod.*

The sporophyte, then, may be considered in its widest sense as *a result of vegetative reproduction applied to the fertilized egg.* As the thallus of Marchantia is cut into gemmæ, so the egg of Marchantia may be cut into the cells of the sporophyte. The strict analogy of sporophytes is, I suppose, not questioned. The question as to their homology must be studied from the physiological point of view, as well as through the researches of anatomists and embryologists. Without either dissenting from or endorsing the view of Bowers, the writer has tried only to show that emphasis may be laid upon conditions surrounding the sexual act as a help to a clearer comprehension of the phenomena of alternation.

A COMMENSAL ANNELID.

BY E. A. ANDREWS, PH.D.

CASES in which Annelids are believed to live more or less directly dependent upon other Annelids, upon Crustacea, Gasteropods, Echinoderms, and even upon Cœlenterates, are not unknown, but yet form by far the exception rather than the rule in the economy of this group. Of the reported cases some must be regarded as mere temporary refuge of Annelids in cavities offered by the shells or bodies of other creatures; some are such mechanical associations as are presented in the complicated assemblage of various Annelid tubes in sponges or molluscan shells, etc.; while yet others—and these are few—are illustrations of true commensalism, which may pass over into parasitism, as in the Oliognathus living in Bonellia, the Hæmatocleptes living within another Annelid, or the well-known Alciope living inside Ctenophores.

In 1885 Dr. Brooks called my attention to a very interesting case of commensalism involving an Annelid found at Beaufort, N. C., and which is complicated by the fact that three diverse animals—Annelid, Crustacean, and Hydroid—are here concerned, forming, as it were, a triple alliance, in which each is, moreover, dependent upon the shell of a fourth, a Gastropod.

Over the immense sand-flats of " Bird Shoal " the interdependence of various creatures is especially well illustrated, and this seems in part due to the fact that the entire absence of stones and rocks leads to the burdening of the more securely fixed animals and plants by those less able to resist the changing tides, waves, and moving sand. Thus we find the stout tubes of the Annelid, Diopatra, which project several inches from the sand, seized upon by Algæ, Hydroids, Molluscs, Annelids, and especially by large Ascidians, as the only available, somewhat stable foundation to build upon. Here also occurs in great abundance the small hermit crab (*Eupagurus longicarpus*), inhabiting the empty shells of various small Molluscs, especially the most accessible one,—that of the Gasteropod, *Ilyanassa obsoleta.* Quite a large proportion of the shells so inhabited are covered over almost completely by colonies of the interesting Hydroid, Hydractinia, though the constant moving about of the crab keeps a small circular area of the shell free from this growth, owing to the friction of the shell against the sand as it is dragged along. Undoubtedly the Hydractinian is benefited by this association, since it may obtain some of the food not used by the crab, and since it is upon a surface kept by the crab above the bottom, and protected from the constant danger of permanent burial in the sand. If, on the other hand, the crab, as seems probable enough, is protected by the presence of so well-armed a creature as the Hydroid, we would have here a cause of " mutualism." With this combination of Hydroid and crab is also associated a commensal,—a small Annelid of the family Spionidæ and genus Polydora. Of several hundred shells examined, fifty per cent. were inhabited by this Polydora, in addition to the crab. In those without Hydroids the Annelid is less abundant, but such shells are often very old or broken, or else but temporarily used by the crab. Occasionally an empty shall contains an Annelid; but here we may assume that a crab has recently occupied it and only been out for a short time, since the majority of available shells are either taken possession of by the hermit or else became buried or washed away. In no case could an Annelid be found in a shell containing the original proprietor,—the Ilyanassa.

A somewhat similar case of an Annelid occurring in the dwelling of a hermit crab was long ago noticed by Quatrefages, but there the Annelid, a Nereis, may possibly have taken up only temporary quarters within the shell. This, however, seems not to be the case with the Nereis described by Wirén in 1888, which, it would appear, has been modified by its well-acquired habit of living inside such shells. The Polydora, however, does not merely live within the pre-formed cavity of the Gasteropod shell, as the Nereis would, but, by boring a tunnel in the columella, and by partly filling up some of the spiral cavity of the shell with a calcareous tube of its own manufacture, reconstructs the shell to fit its own needs.

The general character of the dwelling made by the Annelid within the Gasteropod shell may be inferred from a view of the shell cut lengthwise into halves, as in Fig. 1. The external opening of the tunnel is seen on the inner lip of the mouth of the shell as a conspicuous rounded hole, which leads by a long passage inside the columella up to the spiral part of the shell. Here the tunnel opens out again into the apical chamber of the shell by the round hole seen in the figure. The inner opening, however, is continuous with a calcareous tube built into the chamber of the shell in such a way as to completely block it and prevent the posterior end of the crab, or any other object, from pressing up into the smallest terminal spirals. This tube is bent or coiled in various ways, but may present, as in the figure, a cross-section suggesting that of a Mammalian cochlea. Made of a calcareous, cement-like mass, it may be the debris of the bored-out tunnel, but is more probably a special calcareous secretion of the Annelid such as some of its relatives are known to make.

This description applies only to certain cases, since many irregularities are observed both in the calcareous tube and in the tunnel, and some shells present external openings near the apex and apparently communicating with the Annelid's dwelling.

Only one adult Annelid is found in each shell, and this may be seen, in part, even without destroying the shell, since, when the crab is not too active, the anterior part of the Polydora may protrude from the external opening in the columella, reach about in the water, and presumably find and swallow food in the sand or currents of water. Yet it is very easily disturbed, and then to be found only within the columella, or even in the upper calcareous tube, where it may be variously coiled about, since the dwelling is everywhere wide enough for the Annelid to bend back and forth upon itself. The part of the old shell utilized by the Annelid is thus intermediate between that the crab occupies and that covered over by the Hydroid. The former, in drawing in and out of the shell, tends to limit the excursions of the Annelid by dragging its claws over the columella and orifice of the Annelid's tunnel; the latter extends up to the very edge of the Annelid's place of exit. Sometimes the Annelid's tunnel appears to have been cut through into the chamber occupied by the hermit, but then covered in again by a calcareous layer protecting the Annelid from contact with the crab.

Considering how impossible it would be for the Annelid to keep the shell free from sand and prevent its burial, it is obvious that this Polydora, if it lives, as it appears to, only in such a commensal state, is dependent upon the habit of the hermit crab, and thus exists in what is a somewhat recently acquired environment. As, however, other species of Polydora are known to make tunnels into various Gasteropod and Lamellibranch shells, dead or alive, it is evident that this particular species has not departed so widely from the habit of its kind.

Before describing the interesting breeding habits of this commensal Annelid, we will give an account of its structure and of certain organs especially illustrated in the figures.

The body (Fig. 2) is about a millimeter wide, about twenty-five long, and rather flat, with little color except the bright red of the blood in the conspicuous dorsal vessel and in the branchiæ. These reach half way across the back, and each contains a vascular loop that passes from the dorsal vessel to the tip of the branchia, then back again into the body. The limb of this loop nearer the middle line or to the dorsal surface may possibly act as a heart, since it contains peculiar branching, nucleated protoplasmic processes suggesting the cells of an embryonic vertebrate heart, and to be interpreted as part of a mesenchyme, formed, like the blood, outside the cœlom. The ventral side of each branchia, that next the animal's back, bears along it a band of large ciliated cells, each with a large tuft of fine cilia. A similar row of such cells is found extending transversely across the back of each somite, and corresponding nearly to the lines of attachment of the internal septa. The branchia begin upon the sixth somite (Fig. 7), and are present, though very small, at the posterior end of the body (Fig. 8).

The setæ in the dorsal bundles are attenuated, lance-like, and straight (Fig. 3), while in the ventral bundles they present bifid tips, provided with a delicate scroll or enveloping hood (Fig. 4), except anteriorly, where they are entirely replaced by simple, lance-shaped, bent ones (Fig. 5), each with a delicate flange on its convex side. The setæ of the large fifth somite (Fig. 6) are especially modified as a set of about six very stout, golden-colored hooks, each with a prominent flange projecting from its side near the tip. In the figure some of these hooks are still young, and growing up into place beside the perfected ones. In addition to these large spines, there are a few delicate, lance-shaped ones, as seen in the same figure.

The shape of the animal's head is not easily made out, as it is drawn back into the first somite upon the slightest disturbance, and generally remains there in preserved specimens. In Fig. 7 its general form, as made out from living specimens, is represented somewhat imperfectly.

The cephalic lobe or head is slightly emarginate anteriorly, and bears two delicate antennæ that stand just dorsal to the mouth, as a part of the upper lip, and are richly supplied with sensory hairs. In the head are also two pairs of black eyes that on section appear to have only a simple larval structure. Each consists of a minute mass of large, dark-brown pigment granules, forming a sort of cup about fifteen microns in diameter, and partly surrounding a homogeneous spherical mass of equal size, that stains darkly. All this lies some distance from the surface, and may be said to be in the dorsal part of the brain, since the brain is not separated from the epidermis, but lies with its dorsal ganglion cells intermixed with the epithelial cells, in part at least.

As far as the sections go, the appearance of the eye is so simple as to suggest that it may be interpreted as merely one or two epidermal cells, with clear, refracting outer ends, and pigment in the middle part. The inner tips of such cells may be supposed to connect with the brain. It is to be noted, also, that the same sort of pigment granules occur here and there in neighboring epidermal cells in small collections or isolated.

Posterior to the head are the two great tentacles, with a ciliated groove on the under side; while below, on each side of the mouth, is a very prominent, glandular, lateral projection of considerable size. The pharynx is ciliated, and may be everted with definite ridges and grooves between the above two lateral lobes.

At the posterior end of the body (Fig. 8) there is a peculiar series of about fourteen papillæ, placed about an elliptical area, within which the digestive tract terminates in a longitudinal slit.

In the internal anatomy of this Annelid there is one fact of considerable interest,—that is the dorsal opening of the excretory tubes, the nephridia. From the ciliated internal opening of each nephridium (Fig. 9) a somewhat coiled tube proceeds dorsally to make its way between the dorsal longitudinal muscle and the adjacent epidermis, and then, passing towards the middle of the back, opens finally by a small ciliated orifice not far from the median line and about mid-way from one end of the somite to the other. This is shown in a very diagrammatic way in the figure as made out in several sections of preserved specimens.

This dorsal position of the external nephridial openings is very unusual among Annelids, but is not confined to this species nor to those closely related to it. Thus, though the statement of Ehlers concerning numerous dorsal openings in Polynoe seem to have been negatived by the observations of Haswell, Bourne, and Kaltenbach, and those described by Cosmovici in Sthenelais and Hermione may also need investigation, yet other cases seem surely established. Such are the single dorsal openings, anteriorly, in certain Hermellidæ and Serpulacea, the dorsal openings in some of the Capitellidæ, as well as those somewhat dorsal ones in Chætopterus, according to both older observations and the recent account of Joyeux Laffuie. In the Spionidæ, finally, we find dorsal openings recorded by Jacobi in 1883 for two species of Polydora.

That these openings have secondarily moved up from a ventral through a more lateral position to the dorsal one seems to be at present a more probable assumption, considering such lateral openings as those found in Polyophthalmus and the various positions present in different somites of Chætopterus, than that the dorsal lateral and ventral nephridial openings refer back to some ancestral condition where numerous nephridial tubes were present as in certain earthworms.

In the above diagram (Fig. 9) the nerve cord is also shown as two separate strands, each retaining its primitive position within the epidermis; anteriorly, however, the two cords come close together on the ventral mid-line.

A few facts regarding the breeding habits and development of this commensal Annelid also came under observation during July and August, and might be observed, presumably, through a larger part of the summer.

The eggs are laid in peculiar transparent cases within the part of the shell occupied by the Annelid, either in the tunnel or in the manufactured tube, or in both. These cases consist of elongated series of sacs, firmly united into cylindrical masses fastened to the walls of the tube in which they are built. As shown in Fig. 10, each sac or chamber of the case contains a very large number of eggs, of a yellowish color, and often has an irregular stalk on one side that evidently represents the place of final closure when the secreted sac was finished. The entire structure reminds one forcibly of similar egg-cases in certain Molluscs; moreover, as in those animals, we find here also irregularities at the end of the series of sacs. Thus the terminal sacs (Fig. 11) are smaller, contain few eggs, are often quite defective in shape, and may be so aborted as to contain no eggs at all. The eggs also, full of yellow yolk and presenting large irregular cleavage cells, add to this resemblance.

The cleavage of the eggs is complete but unequal, and results in a few large cells full of yolk becoming covered over apparently by smaller cells containing less yolk. The resulting larvæ remain for a long time within the egg-sacs, closely crowded together. At an early stage these larvæ are probably about the same as the pear-shaped larva of Leucodora figured by Meczniknow in 1865, and may be regarded as trochospheres much distended by food-yolk. Such a stage is represented from a ventral view in Fig. 12, where the large triangular mouth lies at the bottom of a ciliated depression of the small anterior end, while the main rounded mass is filled with food-yolk showing imperfectly the outlines of a few large entoderm cells. A ventral ciliated band is present, as well as an imperfect post-oral ring, or rather two lateral ciliated areas, since, as in some other Annelid larvæ, the cilia are absent in the median area, both dorsally and ventrally.

Sections of this larva (Fig. 13) show that there is an outer ectodermal layer surrounding the entodermal yolk,—in which latter, however, the cell outlines do not appear,—that there is a paired mesoblast, and that the œsophagus ends blindly in the yolk mass. Moreover, sections to one side of the median plane show peculiar, large, ciliated cells, about the mouth, of which there is an especially large pair just posterior to the mouth. One of these is seen in the figure.

These larvæ are about .02 mm. long, and pass gradually into a stage with three pairs of setæ bundles and a length of .35 mm. These latter have four eye spots, an additional band of cilia anterior to the anus, but still a large mass of yolk in the thick walls of the digestive tract, surrounded by the body-cavity.

This stage with three pairs of setæ bundles is found for a long time, though much growth in the size of the body takes place, and conspicuous pigment areas appear when the late larval form such as shown in Fig. 14 results. The occurrence of this phase of larval growth, in which three somites are functional for some time, has been observed in several Annelid larvæ, and is suggestive from its resemblance to the Nauplius condition of certain Arthropods.

These older larvæ are found inside the Annelid's dwelling, sometimes in company with younger larvæ and even eggs, though it is probable that they escape out into the water about this stage. In swimming about the provisional setæ are brought into play as organs of defense, apparently, being thrown out at right angles to the body when the animal is disturbed, and trailed a ng close to its sides when it swims quietly by means of the cIlia. These setæ are noticably barbed, excessively long, and unlike the adult setæ ; forming a good illustration of the *provisional* Annelid seta.

This larva is conspicuous from the metamerically placed dorsal pigment blotches, which, it will be noticed, precede the external appearance of the somites, and are, moreover, represented upon the heart by a pair of small black areas near the eyes.

The digestive tract now presents three well-marked divisions —a mouth and short, ciliated œsophagus leading abruptly into a capacious intestine, with some yolk in its walls yet, and opening posteriorly into a short rectum that ends at the anus. Here there are two papillæ with long sensory hairs, such as also occur in a tuft upon the median part of the head.

In sectioning the adult Polydora, eggs in various stages of formation are found within the body-cavity. The ovary, in fact, appears as a mere mass of modified peritoneal cells, attached to and covering over the vascular loops near the nephridia (Fig. 9). The youngest ova do not differ perceptibly from the ordinary peritoneal cells over the blood-vessels, but they soon enlarge and become more and more filled up by accumulating yolk globules. In this way there is formed a large botryoidal mass of large and small cells (ova), projecting freely into the body-cavity, and not covered by any membrane. Thus attached to blood-vessels, the ova attain a diameter of .06 mm., and then break loose into and float freely in the body cavity (Fig. 9.) Here they continue to grow till, when apparently ripe, they have a diameter of .09 mm. In the ovum there is a large nucleus, nearly .02 mm. thick, and a very conspicuous nucleolus five microns in diameter. This nucleolus is peculiar in having one or more rounded elevations or lateral protuberances upon it, which may be half as thick as the main body of the nucleolus.

The striking parts of the nucleolus are, I presume, described by Vejdovsky in Sternaspis as "bückelchen," but declared by Giard, in his remarkable observations upon Spio, to be the result of fusion of certain extra nuclear "cells" with the proper nucleolus. The body of the ovum is full of large yolk-spheres, staining dark with osmic acid, and having an average diameter of perhaps 2 microns. Presumably the eggs pass from the body-cavity by the nephridia, but no observations were made upon this point.

Since the eggs, when laid, are concealed within a tortuous passage removed from the external water, and as all the large Annelids examined are females living solitary, one in each shell, there seems a need for some special means of insuring the fertilization of these eggs. In fact, some shells contain, besides the large female, a minute individual about 4 mm. long, which it was thought might be a male. The only one preserved and sectioned, however, does not suffice to decide this question. In its body-cavity there are, however, numerous cells and cilia that strongly suggest spermatozoa in process of formation; and if this be the case, we would have here an interesting case of dimorphism, at least of great discrepancy in size, between the two sexes. Moreover, these small Annelids may occur in many more cases than actually observed, no special attention being given to their detection at that time. If males, living thus in the dwelling of the female, they would furnish a ready solution of the above difficulty in regard to the fertilization of the eggs.

I have not succeeded in finding this commensal Annelid in the shells inhabited by the same hermit crab upon the New England coast, and believe that it, like many other of our southern forms, is an undescribed species, and would suggest the name *commensalis* asdescriptive of its peculiar habits. Its chief characters would be asfollows:

Polydora commensalis, sp. n.

The female (Figs. 2–8). Cephalic lobe usually retracted, slightly emarginate, bearing minute sensory antennæ anteriorily and four black eyes dorsally, the posterior pair nearer together. Tentacles in contraction, as long as the body is wide. Body flattened, of about 100 somites; length, 25 mm.; width, 1 mm.; colorless, translucent posteriorly, intestine dark, blood-vessels conspicuous.

Branchiæ begin on the sixth somite, increase rapidly to equal half width of body, and diminish rapidly near posterior end of body; each has a line of large ciliated cells, as also does the dorsal surface of each somite. Anus surrounded by about 14 papillæ on each side,—a short posterior one, a much longer one, four shorter anterior, and then one still shorter. Dorsal setæ long, acuminate (Fig. 3); ventral setæ curved and with a flange (Fig. 5) till the twelfth somite is reached, then gradually replaced by an increasing number of forked setæ (Fig. 4); setæ of fifth somite six yellow hooks, each with a sharp flange on side near tip, and also a cluster of delicate hair-setæ. Found at Beaufort, N. C., living as a commensal in holes excavated in Gasteropod shells inhabited by *Eupagurus pollicaris* and overgrown by Hydractinia. Eggs laid in series of cases inside these dwellings; larvæ as in Figs. 12–14. Male thought to be much smaller than the above female form, and to live in the same shell.

EXPLANATION OF FIGURES.

FIG. 1.—Shell of Ilyanassa, cut open to show the openings into the columella and the built-up passage in the cavity of the shell on the left, all made by Polydora. × eight diameters.

FIG. 2.—General appearance of *P. commensalis*, dorsal view, preserved specimens. (Camera, Zeiss. 4 A).

FIG. 3.—Ends of dorsal setæ. (Camera, Zeiss. 4 F.)

FIG. 4.—Forked ventral setæ, with flange. (Camera, Zeiss. 4 F.)

FIG. 5.—Pointed, anterior, ventral setæ. (Camera, Zeiss. 4 F.)

FIG. 6.—Setæ of left side in fourth segment. (Camera, Zeiss. 2 D.)

FIG. 7.—Anterior region of the body. (Camera, Zeiss. 2 A.)

FIG. 8.—Posterior end of body. (Camera, Zeiss. 2 A.)

FIG. 9.—Diagram of cross-sections of body, showing dorsal openings ot nephridia, separate nerve-cords, ovary and free ova, digestive tract and blood-vessels, parapodia, muscles, and branchia. (Camera, Zeiss. 2 A.)

FIG. 10.—Part of an egg-case, showing eggs in several chambers. (Camera, Zeiss. 2 A.)

FIG. 11.—End of such a case, showing aborted chambers and cleaving eggs. (Camera, Zeiss. 2 D.)

FIG. 12.—Larva, ventral view. (Camera, Zeiss. 4 G.)

FIG. 13.—Vertical, longitudinal, but not median section of Fig. 12. (Camera, Zeiss. 2 F.)

FIG. 14.—Advanced larva, showing provisional setæ and metamerically arranged pigment blotches. (Camera, Zeiss. 4 G.)

PLATE I.

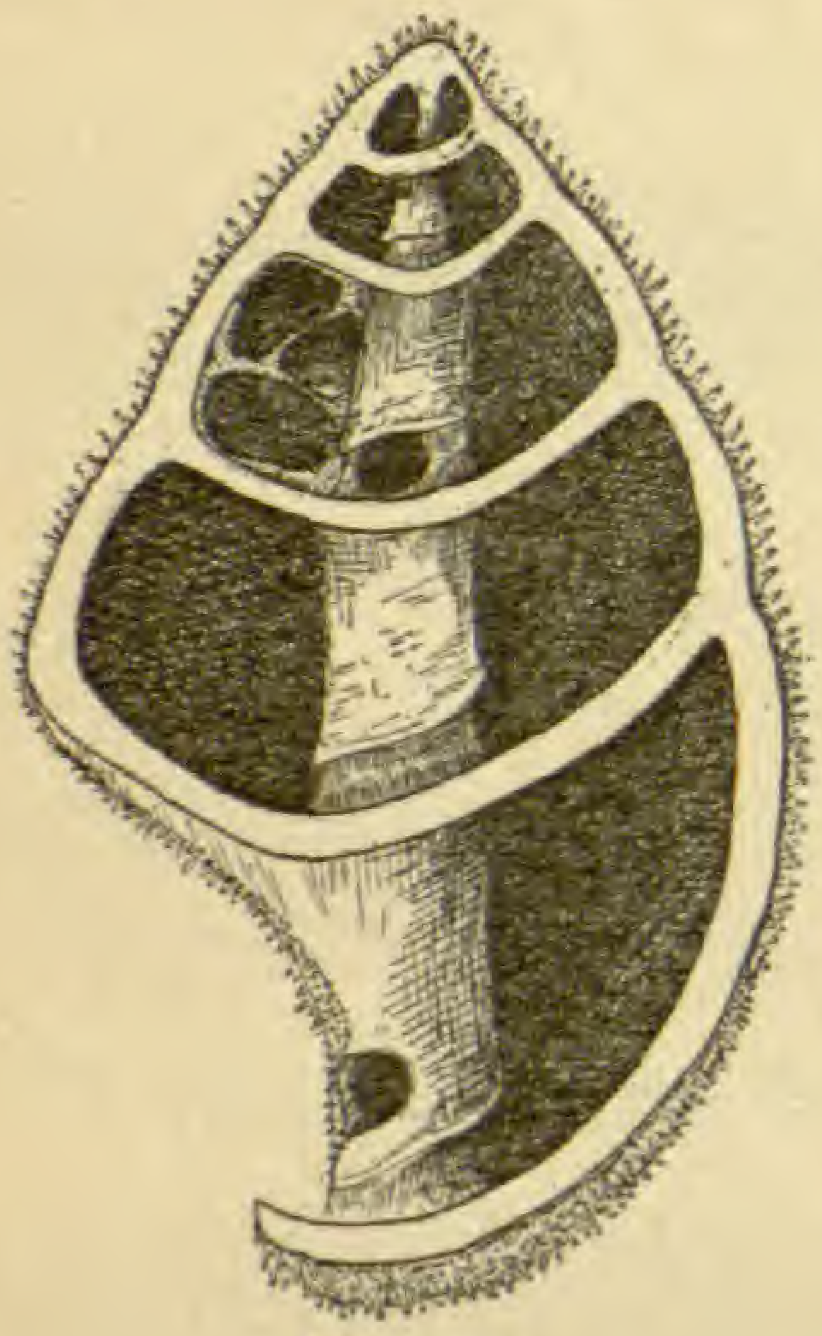


FIG. 1.


FIG. 2.


FIG. 3.


FIG. 4.


FIG. 5.


FIG. 6.

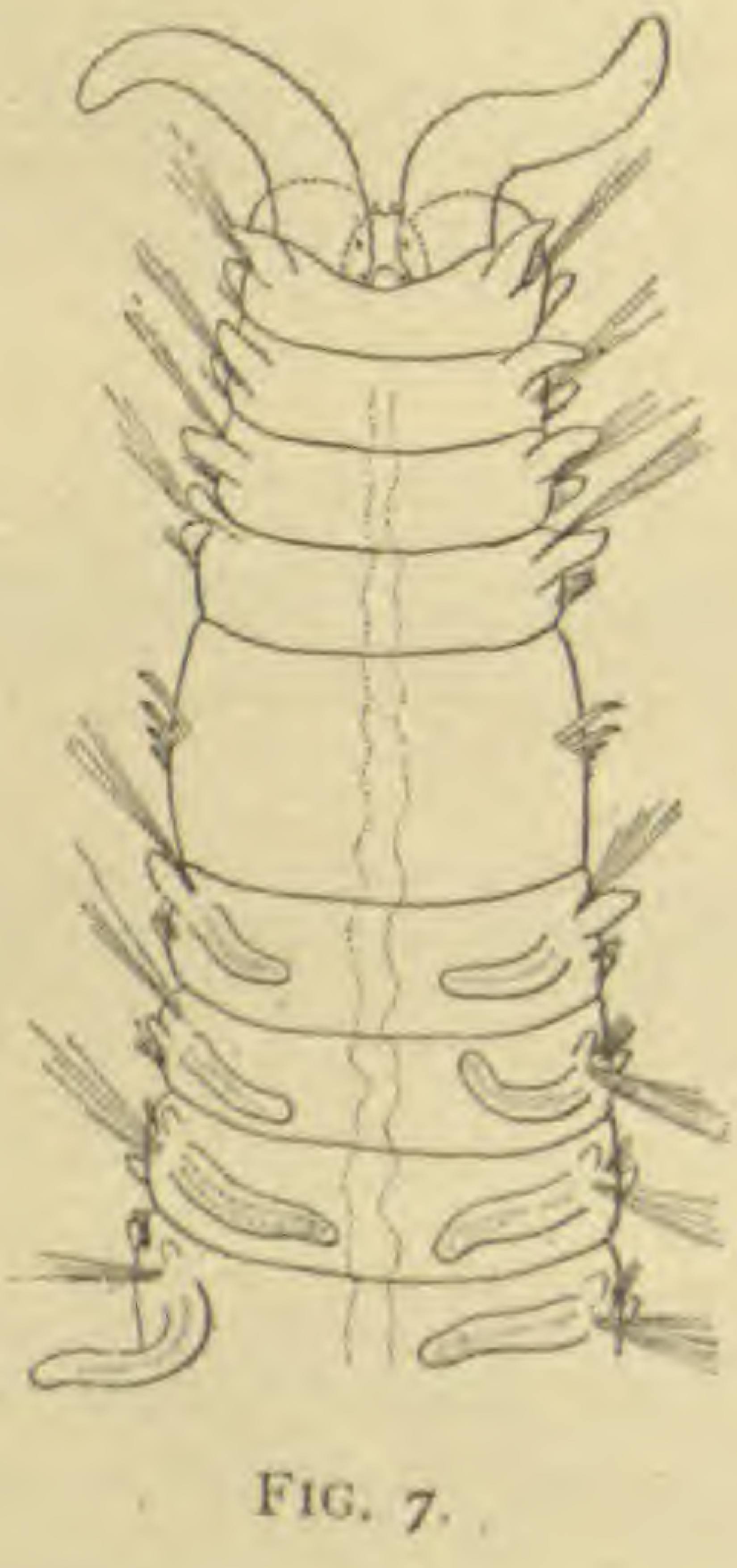
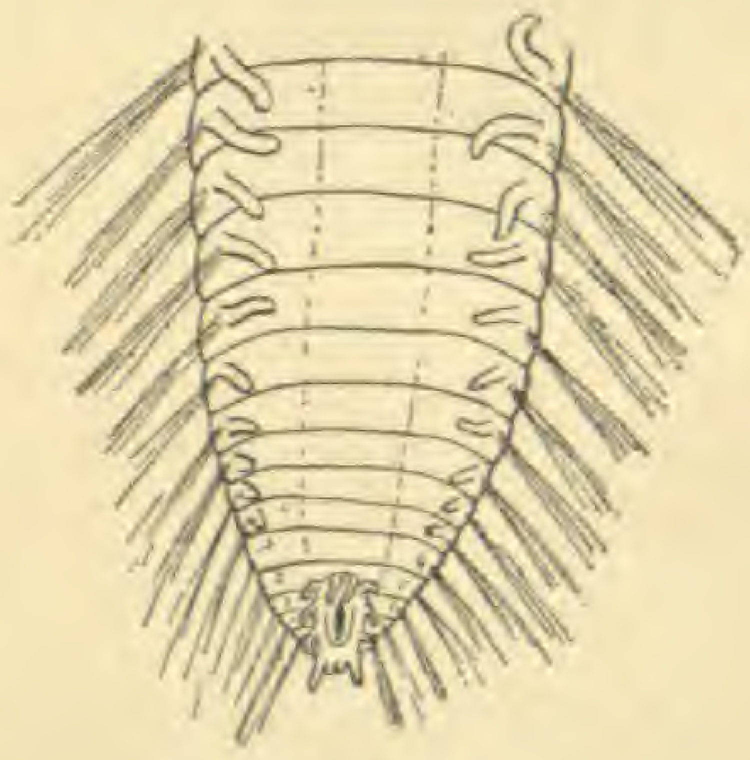


FIG. 7.

Polydora commensalis.

PLATE II.



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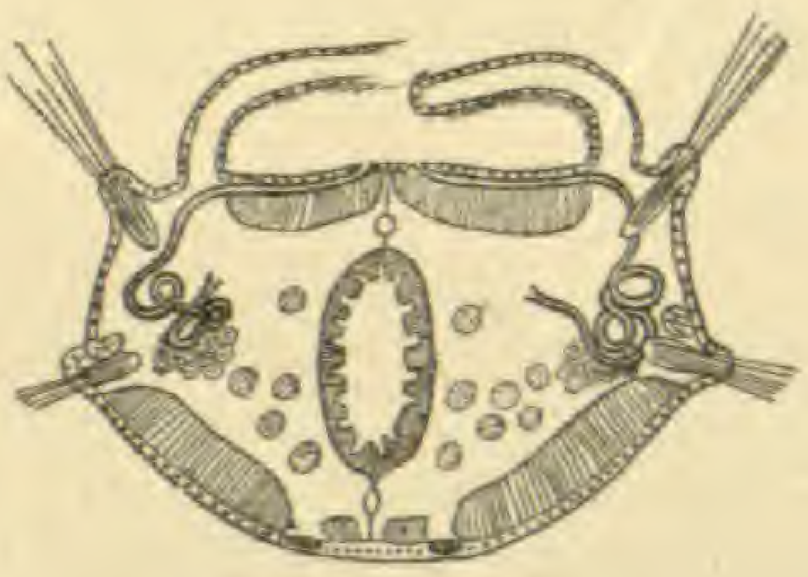

FIG. 9.

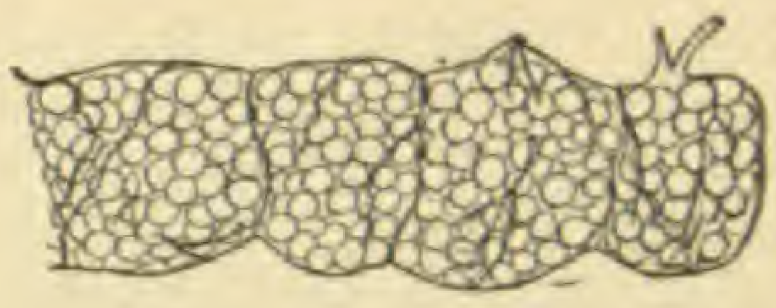

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

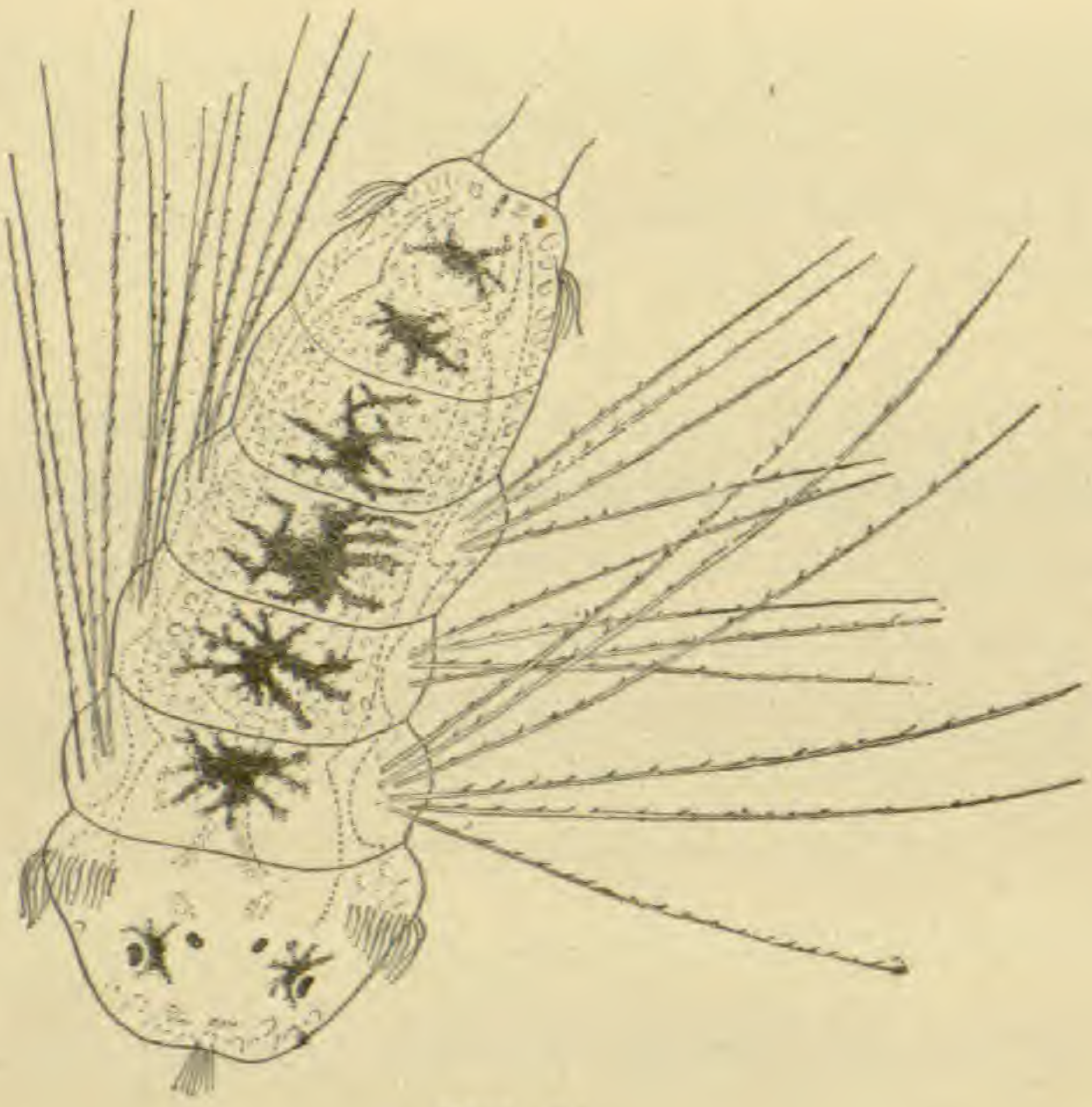

FIG. 14.

Polydora commensalis.

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THE AMERICAN NATURALIST

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ol. XXV. JANUARY, 1891. No. 289

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PHILADELPHIA:

FERRIS BROS., PUBLISHERS

SIXTH AND ARCH STREETS

ered at the Philadelphia Post-Office as second-class matter.