

THE DEVELOPMENT OF AN APODOUS HOLOTHURIAN (CHIRIDOTA ROTIFERA)

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SIX FIGURES

In the summer of 1897, while enjoying the privileges of the Johns Hopkins Biological Laboratory at Port Antonio, Jamaica, I collected a number of specimens of a small holothurian (*Chiridota rotifera*) on the reef at Titchfield Point, where it lived in the sand beneath the broken pieces of coral rock. This species is of more than usual interest because like its near relative, *Synaptula hydriformis* [= *Synapta vivipara* (Oerst.)], the eggs undergo their development in the body-cavity of the mother and the young are born at an advanced stage. Among the specimens which I collected, were half a dozen, which contained young in the body-cavity, and it was my hope that I might be able to study the development of *Chiridota* in the same way and to the same extent as I had already done with *Synaptula*. The material collected in 1897 was not sufficient, however, to make such a study possible, and it was accordingly put aside until another opportunity should present itself for collecting *Chiridota*. In April, 1899, I made a brief visit to Bermuda and there I found the desired holothurian quite common. Not having facilities for laboratory work, I simply gathered all the adult *Chiridotas* I could find and preserved them in alcohol. In November, 1902, and again in March, 1909, it was my good fortune to be able to revisit Jamaica, but on neither occasion did I find *Chiridota* at all common, and only a few small specimens were obtained.

Dr. Brooks was greatly interested in the discovery of *Chiridota* at Port Antonio in 1897, and desired me to complete my study of

the development if possible. In later years, he expressed the hope that I would publish such results as I had obtained. When, therefore, it was suggested that his former students publish a volume of zoölogical papers as a tribute to his memory, it seemed to me especially appropriate that I should prepare an account of the development of *Chiridota*, so far as the material at hand would permit. Fortunately the Bermudan material has proved to contain some much-desired stages, in an excellent state of preservation, and has thus supplemented that from Jamaica quite satisfactorily. The recent papers by Östergren ('07), Becher ('07, '08, '10) and Edwards ('09) have been a further stimulus to my work, arousing, as they have, renewed interest in the phylogeny of holothurians. The present paper consists of two parts, one devoted to the account of *Chiridota rotifera* and its development, the other to the bearing of the facts there set forth, on the phylogeny of the class.

PART I. THE NATURAL HISTORY AND DEVELOPMENT OF
CHIRIDOTA ROTIFERA

Few species of *Chiridota* are better characterized than *rotifera*, the only member of the genus known to occur in the West Indian region. It was first described by Pourtales in 1851 from Florida specimens and is easily recognized by its small size, distinctive color, numerous wheel-papillae, and the minute rods in the skin. Although large individuals when fully extended are nearly 100 mm. long, the great majority of specimens are less than 60, even when living; preserved specimens are usually 30-50 mm. in length. The color in life is pale flesh-red, with either a pink or a yellow tinge, but this ground color is obscured by the convex, white spots, known as "wheel-papillae," formed by the clusters of calcareous wheels in the skin. These wheel-papillae are numerous, often crowded, and occur all over the body; in young individuals, however, they may be few and scattered on the ventral side. The twelve tentacles are white or cream-colored and have 8-14 digits. In alcoholic specimens the colors are usually deepened and are fairly persistent, but after some months they

are apt to fade and the specimens may become entirely bleached. The calcareous deposits in the skin are of two kinds; the six-spoked wheels, usually about .12 mm. in diameter, characteristic of the genus, which are collected in the wheel-papillae, referred to above; and small, somewhat flattened, curved rods with enlarged and often slightly branched ends, which are about .05 mm. long and are scattered all through the interambulacra.

The habitat of this little holothurian, so far as my experience goes, is always coral sand, in shallow water, just inside a reef exposed to surf. Here, under a slab of rock or some similar shelter, it finds a congenial home and often (especially in Bermuda) a number of specimens will be found occupying the limited area beneath a single rock. In Jamaica, the companions of *Chiridota*, in such a spot, are the two little echini, *Brissus unicolor* and *Echinoneus semilunaris*, and occasionally a small synaptid; but in Bermuda, the usual companion is *Leptosynapta roseola*. *Chiridota* is not hardy, and specimens brought into the laboratory at Port Antonio lived but a few hours and were never very active. Curiously enough the pentactula larvae were much more hardy than the adults, for they lived more than twenty-four hours after removal from the body of the mother, and showed no effect from solutions of magnesium sulphate which completely narcotized the adults.

Owing to their sensitiveness to changed conditions, observations on the *Chiridotas* in the laboratory yielded no facts of interest. We can only assume that fertilization of the eggs and the birth of the young take place as in *Synaptula*; the study of preserved material has thrown no light on these points. Specimens collected in Bermuda in April, and in Jamaica in July and August, contain young in various stages of development, but whether breeding occurs all the year, as seems to be the case in *Synaptula hydriformis*, is not proven. In every specimen examined which contained young, these were all of approximately the same stage of development, indicating their origin from a single ripening of ova. No evidence of two or more overlapping broods, such as occur in full-grown *synaptulas*, has been found. The number of young is commonly much greater than in *Synaptula*, for while small *Chiridotas* may contain only a few larvae, the full grown

specimens often contain many score. One Bermudan specimen, less than 50 mm. long (after preservation), contained no less than 522 young, three times as many as I ever found in a *Synaptula*. As no larvae over 3 mm. long were found, and none with more than eight tentacles, it is very possible that the young are born in the eight-tentacled stage, which would be much earlier than birth occurs in *Synaptula*. Further study of living material is necessary to settle some of these interesting points.

The mature eggs of *Chiridota* were not seen, nor were any of the segmentation stages observed; but to judge from the youngest embryos found, the eggs, blastulae and gastrulae, must be very similar in size and appearance to those of *Synaptula hydriformis*. A few specimens of the earliest developmental stage which has been observed were found in a small adult at Port Antonio in 1897 and one of them is shown in fig. 1. It is a uniformly ciliated embryo, within which the hydro-enterocoel has separated from the primitive gut and already shows the constriction by which the hydrocoel is to be formed. This embryo corresponds in all essentials with the similar stage in *Synaptula*.

In the next stage observed, which was also found in a Port Antonio *Chiridota*, the body is a little more elongated and there are indications of bands of cilia longer and more vigorous than those which still cover the embryo. The hydrocoel is well-formed and is connected with the outside by the pore-canal. The enterocoel has already divided and the two parts lie, one on each side of the primitive gut. There is no indication of a mouth. This embryo corresponds closely in all the details of its inner anatomy to the similar stage of *Synaptula* but is noticeably different externally in the absence of a mouth and in the presence of ciliated bands. With the very small amount of material available, I have not been able to determine positively, the arrangement of these bands, but they are very similar to those figured by Semon ('88) for the corresponding auricularia larva of *Labidoplax digitata*.

The next oldest larva of *Chiridota* was found in one of the Bermudan adults and was not seen alive. It is shown in fig 2. The ciliated bands are quite prominent, especially at the larger ante-

rior end; at the narrowed posterior end, they are less distinct but seem to be confined to the sides and ventral surface; their general arrangement is like that found in the auricularia of *Labidoplax*. The uniform covering of cilia seems to have disappeared with the development of these bands. There is still no mouth but the blastopore remains open. The hydrocoel clearly shows the beginnings of the five primary tentacles and less distinctly the first rudiments of the "secondary outgrowths." On the pore-canal, the thin-walled swelling, regarded as the remains of an "anterior coelom" is very conspicuous. Near the blastopore are several minute, discoidal calcareous bodies. At this stage, the larva of *Chiridota* is rather strikingly intermediate between the corresponding stage of *Labidoplax* (Semon, '88, pl. 6, fig. 3) and that of *Synaptula* (Clark, '98, pl. 11, fig. 15). While the external form is unlike either, the ciliated bands and calcareous particles resemble those of *Labidoplax*, and the general appearance and arrangement of the inner organs correspond to what is seen in *Synaptula*. In the absence of a mouth at this stage, *Chiridota* is quite unique.

A very few larvae, a little beyond the stage just described, were found in a small adult at Port Antonio in 1897. The hydrocoel was beginning to encircle the foregut, the primary tentacles were very conspicuous and the secondary outgrowths were correspondingly large. These larvae are peculiar because, in spite of this development of the hydrocoel, the uniform ciliation of the body still persists and ciliated bands cannot be distinguished.

A large proportion of the larvae found, both at Port Antonio and in Bermuda, were well beyond this stage and have the appearance shown in fig. 3. Four ciliated bands are commonly present, though the most anterior is hard to make out and may be wanting; the other three are not of uniform width or density at all points, but seem to be best developed ventrally. The hydrocoel has completed its growth around the foregut and the primary tentacles are very conspicuous, completely over-shadowing the secondary outgrowths which have developed very little. The polian vessel is very evident in the left ventral interradius. The "anterior coelom" on the pore-canal has reached its maximum development. The right and left coelomic vesicles have coalesced and the result-

ing body-cavity is very distinct. The blastopore has closed and the larval gut has bent forward and then backward again. There is still no mouth, nor did I find any evidence of a differentiated nervous system. The calcareous particles at the posterior end of the larva have undergone marked development. The discoidal plates (fig. 5 *a*) have outgrowths on the margin (5 *b*) which grow out rapidly as projecting rays (5 *c*). The plate is no longer flat but somewhat convex at the center, and the rays, instead of lying in the same plane with it, curve upward and outward towards the surface of the body (5 *d*). The tips of the rays extend laterally (5 *e*) until they finally coalesce into a solid rim, and thus a fully developed wheel is formed (5 *f*). These wheels are about one-twenty-fifth of a millimeter in diameter and have about a dozen spokes, though the number varies from ten to fourteen; one was found with only nine. These wheels are never very numerous and they are never aggregated into papillae but are scattered irregularly in the skin. The remarkable point about them, however, is that while there is no known species of Chiridota in which the adult has wheels with more than six spokes (normally), in the genus *Trochoderma* the wheels have 10-16 spokes and their development is exactly like those of the larval Chiridota. (Compare Theél '77, pl. 2, or Clark '08, pl. 7, figs. 9-12, with fig. 5). Ludwig ('92) has pointed out that the wheels of the Myriotrochiniæ (to which *Trochoderma* belongs) differ from those of the Chiridotinae in having a simple, solid hub. The wheels of the larval Chiridota have the hub simple and solid. In view of these interesting facts, it is quite correct to say that so far as the calcareous deposits are concerned, Chiridota passes through a *Trochoderma* stage. Semon ('88, pl. II, figs. 5 *a-c*) has figured the wheels found in the auricularia, which he considers to be that of *Labidoplax digitata*; they differ only a little from those found in the larval Chiridota rotifera, chiefly in having 16 spokes. It is certainly most remarkable if the larva of one of the Synaptinae really develops wheels as its first calcareous deposits. The occurrence of wheels with many spokes in the larva of Chiridota rotifera has raised the question in my mind whether the larva which Semon supposed to be the auricularia of *Labidoplax digitata* was cor-

rectly identified. These auricularias were not raised from the eggs nor was their development carried beyond the pentactula stage; they were collected in the tow at Naples and no evidence is offered to show that they are really the young of *Labidoplax*. It is true that no *Chiridota* is known from the Mediterranean Sea, but Semon himself discovered at Naples the interesting *Trochodota venusta*, which has wheel-shaped deposits like those of *Chiridota*. I venture to suggest, therefore, that the question as to what auricularia Semon studied is still open, and until further evidence is offered, I must decline to believe that young synaptids ever develop wheel-shaped deposits. This position is strengthened by the fact that in *Synaptula hydriformis* the first calcareous particles to appear are simple, straight rods, from which (except in the tentacles of course) the plates and anchors rapidly develop.

Pentactula larvae of *Chiridota* were found in many adults, both at Port Antonio and in the Bermudan material, and one of them is shown in fig. 4. No young were found between the stage shown in fig. 3 and the fully developed pentactula, but it is not difficult, in the light of what we know about the development of *Synaptula*, to see how the greater complexity has been brought about. The most important changes are at the anterior end, where an invagination has apparently taken place, giving rise to an atrium, in the center of the floor of which the mouth has arisen by further invagination. The growth of the tentacles upward around the mouth leaves the wall of the atrium, for a time, as a conspicuous collar surrounding the five tentacles. The latter are square-tipped and provided with a greatly thickened glandular and sensory epithelium at their free ends, particularly on the outer side. The alimentary canal has pushed backward to the extreme end of the body, where the permanent anus has formed. The "anterior coelom" on the pore-canal is scarcely visible, but the polian vessel, positional organs and radial nerves are all conspicuous. The beginnings of the calcareous ring are also plainly visible. Traces of the ciliated bands may still be seen on the body. Except for these, the atrial collar, the shape of the tip of the tentacles, and the wheel-shaped deposits in the body-wall, the pentactula of *Chiridota* agrees in all particulars with that of *Synaptula*. There

are no traces of radial water vessels and the development of the water-vascular, nervous, sensory, muscular and alimentary systems is, so far as I can see, identical in the two genera. In *Synaptula* the mouth is formed much earlier and the atrium develops on the ventral side instead of at the anterior end, but these differences cannot be regarded as of any particular importance. They are doubtless due to the accelerated development of *Synaptula*.

The living pentactula of *Chiridota* is most interesting to watch, for the tentacles, which serve as sensory, locomotor and feeding organs, are in constant motion, while the surrounding collar seems to be equally active. Possibly its movements may be respiratory, but I am rather inclined to think they are merely the result of the activity of the tentacles. In the older pentactulas, the tentacles are vertically notched at the tip; the depth of this notch increases with the growth of the tentacle, and thus the pair of terminal digits is formed.

None of the *Chiridotas* collected in Jamaica contained young beyond the pentactula stage, but several Bermudan specimens provided older material. The principal changes which occur in the course of growth are the complete disappearance of the ciliated bands and the atrial collar, the marked development of the two terminal digits on the tentacles, and the appearance of groups of the characteristic six-spoked wheels. The calcareous ring is more noticeable and calcareous rods appear in the tentacles. Neither at this stage, nor in the pentactula, are there any "glandular organs" or "contractile rosettes" present in the skin, such as are found in *Synaptula hydriformis* and *Leptosynapta minuta*. At the close of the pentactula stage, the secondary outgrowths of the hydrocoel, which have remained quiescent beneath the radial nerves, begin to show signs of activity. Their subsequent development is exactly as in *Synaptula*, except that they do not grow simultaneously. The first to develop are those under the latero-ventral nerves; these push out dorsal to the nerves and thus give rise at the same time to the sixth and seventh tentacles. This seven-tentacled larva (fig. 6) was first observed by Ludwig ('81) in *Chiridota rotifera*, and subsequently ('98) by the same eminent zoölogist in *Taeniogyrus contortus*. It appears to be a well-

marked stage of development, but the succeeding tentacles are visible before the sixth and seventh are nearly as large as the original five. In the material of *Chiridota* at hand, I have found only three specimens in which the eighth tentacle can be seen. In each of these, the new tentacle is formed by the "secondary outgrowth" beneath the *right* dorsal nerve pushing out dorsal to that nerve. Our eight-tentacled larva, therefore, has two tentacles in each of the dorsal interradii, while the two ventral interradii have only the primary tentacle in each, a noticeably symmetrical arrangement superficially, but one which leaves the left dorsal and mid-ventral secondary outgrowths of the hydrocoel entirely undeveloped. Whether the ninth and tenth tentacles arise, as in *Synaptula*, from the latero-ventral "secondary outgrowths," I have been unable to determine, as no specimens were found with even the rudiments of these two tentacles. Becher ('07) has found an eight-tentacled stage in *Rhabdomolgus*, like that of *Chiridota*, while the adult retains permanently the ten-tentacled stage, like that of *Synaptula*. It is fair to presume, therefore, that *Chiridota* passes through such a stage.

The calcareous particles in the eight-tentacled *Chiridota* larva deserve a word. The rods in the tentacles are fairly numerous and lie parallel to the long axis. The Trochoderma-like wheels are still to be found, scattered chiefly on the posterior part of the body. There are four or five heaps of *Chiridota*-like wheels in the interradii, two or three near each end of the body. While most of these wheels have six spokes, as they should have, some have seven, and a few have eight. It is noticeable that such variations from the normal are much more frequent than in adult *Chiridotas*, where a wheel with more than six spokes is really very rare.

SUMMARY

1. The development of *Chiridota rotifera* is essentially like that already fully described for *Synaptula hydriformis* (= *Synapta vivipara*, Clark, '98).

2. The early larval stages of *Chiridota* (succeeding the gastrula) differ from those of *Synaptula* in the ovoid form, the

presence of ciliated bands and wheel-shaped deposits, and in the absence of a mouth.

3. The pentactula larva of *Chiridota* differs from that of *Synaptula* in the presence of traces of ciliated bands, an atrial collar, wheel-shaped calcareous deposits, and square-tipped or slightly bifid tentacles.

4. The calcareous wheels developed in the larvae of *Chiridota* resemble in their development, in the number of spokes, and in certain details of structure, those which are found in adults of *Trochoderma*, and are essentially different from the true *Chiridota*-wheels, which appear after the pentactula stage. Whether the auricularia larva, with similar *Trochoderma*-like wheels, found at Naples by Semon and considered by him to be the young of *Labidoplax digitata*, really belongs to that species, must be considered still an open question.

5. The development of *Chiridota*, though accelerated by its viviparous habit, is apparently not so rapid as that of *Synaptula*. This is indicated by the later formation and anterior position of the atrium, the much later formation of the mouth, and the more deliberate formation of the second quintet of tentacles.

6. The viviparous habit appears to have been acquired by *Chiridota* much more recently than by *Synaptula*. This is indicated by the much larger number of young in a brood, by their all being of a single age, by their slower development, by their apparently earlier birth, by the retention of the ciliated bands of a free-swimming auricularia stage, by the unequal development of the secondary tentacles, producing seven- and eight-tentacled larval stages, by the more conspicuous and persistent "anterior coelom," and by the absence of larval "glandular organs."

PART II. THE PHYLOGENY OF THE HOLOTHURIANS

In any discussion of the phylogeny of a class of animals, we ought to distinguish so far as possible between the interrelationships of the groups which make up the class, and the relationships of the class as a whole with other classes. Among Echinoderms this can easily be done, for not only is the phylum a remarkably

distinct one, markedly separate from all other animal types, but each of its component classes is equally distinct, truly annectant living forms being practically unknown. The facts from which the phylogeny of holothurians is to be deduced can be set forth more clearly and the hypotheses which their study has led me to adopt can be made more comprehensible if we first consider the interrelationships of the orders of holothurians, and then discuss the relationship of the class to other echinoderms.

The relationship of the orders of Holothurioidea to each other

Östergren, in a recent paper ('07) has set forth quite fully his views on holothurian interrelationships, and as they differ in some important particulars from those held by Ludwig and others, they will serve admirably as a basis for this discussion. He recognizes five orders of holothurians (Dendrochirota, Aspidochirota, Molpadonia, Elasipoda, Apoda) and I shall, for convenience, here use his names and accept these orders without further discussions other than to say that I am not sure the names are in all cases tenable. Östergren bases his classification on his own extensive morphological and physiological studies (though of course giving due weight to the work of other investigators), and he lays particular emphasis on the functions of organs and their relation to the habits of the animal. He describes his ancestral form (Stammholothurie) as having a soft body-wall strengthened by scattered calcareous plates; creeping about by the contractions of the body musculature; and feeding on the organic matter in mud ("ernährte sich von Schlamm"). It had "twenty (or ten?)" short tentacles, without ampullae, five radial canals and a number of scattered pedicels. The posterior part of the gut (cloaca) served as a respiratory organ, but there were probably no "waterlungs" developed. From such an ancestor, Östergren derives his five classes of holothurians, finding its nearest living representatives among the Elasipoda; such genera as *Capheira*, for example, differing only a little from this "hypothetische Stammform."

It is not necessary to criticize this theory in detail here, but there are three general criticisms which seem to me to seriously affect

its value. In the first place, Östergren apparently considers simplicity of structure as implying a primitive condition; he scarcely refers (except as regards the absence of feet in Apoda) to the secondary simplicity often produced by changed habits, and which is sometimes called "degeneration;" he certainly has failed to give due weight to the existence of this factor. In the second place, he assumes that the ancestral holothurians were mud-loving and mud-eating forms; if these ancestors were worm-like in habit and structure this view is tenable, but if they were allied to the regular echini, as many zoölogists consider probable, it is hard to maintain; certainly in the Echinoidea, it is only among the highly specialized forms, the spatangoids, that we find mud-loving and mud-eating species. Moreover, there is little doubt that the early Metazoa were all plankton-feeders and many Dendrochirota retain that habit still. It is hard to believe that the class Holothurioidea had not arisen before the competition for food on the floor of the sea led to the use of organic mud as food. In the third place, to find the most primitive and ancestral form of holothurians in the exclusively deep-water group of elasipods is to run counter to one of the principles, which modern oceanographic work has established; namely, that the inhabitants of the abyssal regions are more or less highly specialized forms, the simpler and less modified forms occurring in water of little or moderate depth.

If Östergren's paper errs on the side of overlooking secondary simplicity and of definitely asserting his deductions, no such criticisms can lie against Becher's ('07) exhaustive study of *Rhabdomolgus*. It is difficult to find a theoretical conclusion definitely asserted in Becher's work, and it is almost as hard to find what characters of *Rhabdomolgus*, if any, are to be considered primitive. The evidence for and against the view that a given character is ancestral is carefully set forth and only occasionally is it possible to decide what Becher's own opinion is.¹ The general conclusion

¹These statements do not apply at all to Becher's later paper ('08) in which his discussion of questions of holothurian phylogeny is very clear and satisfactory. While his conclusions are not wholly in accord with my own it is not necessary to discuss them here.

appears to be that while *Rhabdomolgus* is primitive in some particulars, it is not to be considered as very near the ancestral holothurian. From the point of view of holothurian phylogeny, the most important facts set forth in Becher's paper are the presence of rudiments of radial canals in the adult *Rhabdomolgus*, accompanied by zigzag rows of "tastpapillen," which very possibly represent the remains of pedicels; the interradial position of the five primary tentacles; and the points of origin of the five secondary tentacles. These facts are all in accord with the conditions which I have found in *Synaptula* and *Chiridota*. They show clearly the close relationship of *Rhabdomolgus* to the other Synaptidae and their common descent from a pedate ancestor with five primary interradial tentacles. There is also indicated the possibility of an eight-tentacled and asymmetrical ancestral form.

The existence of ancestral asymmetry is questioned by Edwards ('09) who suggests that, since he found in *Holothuria floridana* a different origin for tentacles 1-5, from that found by Ludwig ('91) in *Cucumaria planci*, it will not do to assume an identical development for all pedate holothurians even in the early stages. Edward's discovery that the five primary tentacles of *Holothuria* do not arise from the same radial canals as in *Cucumaria* is of great importance, but it is even more interesting to note that tentacles 6-10 arise in *Holothuria* from the same radial vessels and in the same order that they do in *Cucumaria*, *Synaptula*, *Chiridota* and *Rhabdomolgus*. In other words, while tentacles 1-5 are not homologous in the three families concerned, the radial canals and tentacles 6-10 are.² It is further of interest to note as bearing on a possible asymmetrical holothurian ancestor, that in all these genera, whose development has been studied, the mid-ventral radius is precocious and develops its organs earlier than the others.

² On p. 222 of his paper, Edwards says: "While Clark does not suggest the homology, it is possible to regard these 'secondary outgrowths' as the last vestiges in the degeneration of the protoholothuroid radial canals." I beg to call attention to the following passages from my memoir: "the second series corresponds to those which in *S. digitata* give rise to the radial water-canals" (p. 63); "the secondary outgrowths of the hydrocoel ring in Synaptidae are homologous with the five outgrowths of the hydrocoel ring in the true holothurians" (p. 69). Further emphasis on the same point will be found at the bottom of p. 81. It is hardly fair, therefore, to say that I did not "suggest the homology."

From our present knowledge of holothurian development, certain facts seem to be definitely determined. Of these the most important is that the five primary outgrowths of the hydrocoel in the Synaptidae, which give rise to the five primary tentacles, apparently have no homologs in the pedate holothurians. Associated with this is the fact that the secondary outgrowths of the hydrocoel in the Synaptidae are homologous with the radial canals of the pedate holothurians. These outgrowths (= radial canals), moreover, give rise to tentacles 6-10, in the same order and from the same radii, in all holothurians. Furthermore, in *Synaptula*, tentacles 11-13 also arise from these secondary outgrowths, and it seems to me probable that in synaptids with 15 or more tentacles, the additional ones arise from the same outgrowths too. As a corollary to these facts we are forced to conclude that the first five tentacles of *Cucumaria* and *Holothuria* have no homologs in the synaptids. It is, of course, possible to imagine that through some kind of inexplicable shifting, the primary interradial tentacles of the synaptids have been moved laterally and then outwardly on to the radial canals in the pedate holothurians, and thus to maintain that the primary tentacles are homologous in the two groups. There is no evidence, however, of such movement and it seems hardly probable; but it is clearly not impossible.

Some recent writers (Perrier, MacBride, Östergren) have seemed to minimize the essential difference between the Synaptidae and the other holothurians as revealed by their development, but in my judgment this difference far outweighs any of the morphological resemblances between the two groups. The unique character of the five primary tentacles of the synaptids is so remarkable that Ludwig's classification, by which the *Holothurioidea* are divided into the two subclasses *Actinopoda* and *Paractinopoda*, ought to be accepted. Since it is the first five outgrowths of the hydrocoel which give rise to the primary tentacles of the synaptids, while the secondary outgrowths (= radial canals) only appear subsequently, it seems to me we must suppose that interradial outgrowths (tentacles?) preceded radial canals in the development of the water-vascular system and that we must regard the *Paractinopoda* as the older group. The persistence of

primary tentacles and the complete degeneration of the radial canals in the adult, in addition to the entire loss of pedicels, seems to me to confirm this view. In 1898, I pointed out that there were three possible views regarding the relationship of the synaptids to the other holothurians: (1) that the synaptids are the primitive stock of the class; (2) that the synaptids represent a more primitive branch of echinoderms than that of the pedate holothurians; (3) that the synaptids are degenerate pedate holothurians. At that time I held to the third view. The works of Becher and Edwards, taken in connection with my study of *Chiridota*, lead me to believe now that the second view, which was first proposed by Cuénot ('91), is quite as near the truth. While I do not think it can be questioned that the synaptids are degenerate, pedate holothurians, I am satisfied that the pedate form from which they arose (the "Urholothurie" of Ludwig, "Stammholothurie" of Östergren) differed in certain very important points from any known form. I picture it as a short, thick-bodied creature with five stout, simple, interradial tentacles, much like a pentactula in form and moving like it, chiefly by means of the tentacles. Unlike the pentactula, however, it had well-developed radial water-canals with each of which was associated a double series of pedicels. From such an ancestor the Paractinopoda have arisen, losing the pedicels and radial canals, while the Actinopoda have developed with the loss (or extraordinary shifting) of the five primary tentacles. Before the separation of the two sub-classes certain pedicels close to the circular water-canal became modified into tentacles, and in the Actinopoda, five of these (one in each interradius) seem to have replaced the primary tentacles. If Edwards' and Ludwig's observations are both correct, the same radial canals did not supply these five "pedicel-tentacles" in the two groups, *Aspidochirota* and *Dendrochirota*, and this would seem to indicate the separation of these two groups while this character was still unfixated. The origin of tentacles 6-10, curiously enough, appears to have been fixed for all three groups at an earlier period. At what point the *Elasipoda* began their divergence it is hard to say, but it may have been about the same time as the separation of the *Aspidochirota* and *Dendrochirota*. There can be little doubt that the *Molpadonia* were

derived from the *Dendrochirota* at a comparatively recent date and there is good reason for thinking *Eupyrgus* has had a different origin from the rest of the order and has simply converged into the group.

The relationship of the Holothurioidea to other Echinoderms

If the proposition made above, that the five interradial tentacles of the synaptid pentactula are characteristic organs of the ancestral holothurian, be accepted, the first question which naturally arises, when we consider what relation the holothurians bear to other Echinoderms, is this: What interradial outgrowths of the hydrocoel are there in other Echinoderms with which these tentacles can be homologized? At first approach the problem seems a very difficult one, for so far as our knowledge of echinoderm embryology goes, the only direct outgrowths of the hydrocoel in the other classes are the radial canals, pore-canal and polian vessels, all of which are also present in our hypothetical holothurian ancestor. A careful study of recent work of Grave ('02) and MacBride ('03) on the development of echini, has led me to the rather surprising conclusion that *the primary tentacles of synaptids are homologous with the dental sacs of the echini*. This idea at first seems preposterous because the dental sacs of echini have no connection whatever with the hydrocoel. More careful consideration shows, however, that this objection is far from conclusive. Both Grave and MacBride show that the dental-sacs of echini arise as five interradial outgrowths of the left coelomic pouch, which lies below (or on the inner side of) the hydrocoel and from which the hydrocoel itself arose. These outgrowths push out between the budding radial canals, and thus these two series of outgrowths come to occupy the same position with relation to each other which the primary and secondary outgrowths of the hydrocoel occupy in the pentactula. There is, of course, this important difference that in the young echinoid, the lumens of the dental sacs have no connection with the water-vascular system, while in the pentactula the homologous lumens are continuous with that of the circular water-canal. If, however, the essential identity of the left hydrocoel and the left posterior coelom

in the echinoid larva be admitted the importance of this difference is somewhat diminished, since the lumens of the dental sacs are for sometime continuous with that of the left posterior coelom. There is, moreover, another feature in the development of the young echinoid, which is strikingly like one shown in the development of the pentactula. This is the invagination of an ectodermal plate, forming the so-called "amniotic cavity," from the floor of which the oral disc of the sea-urchin arises. In all essentials this process is similar to the formation of the "atrium" in the development of the pentactula, and the relation of the radial canals and dental sacs to the floor of the amniotic cavity is identical with that of the primary and secondary outgrowths of the hydrocoel to the floor of the atrium.

If the homology of parts, between the young echinoid and the pentactula, here suggested, be accepted, we have new proof of the close relationship of holothurians and echini. The presence of jaws (and hence of dental-sacs) as a fundamental character of echini has recently received remarkable confirmation by Mr. Agassiz's announcement ('09) that in the very young *Echinoneus* (a simply organized spatangoid) a complete set of jaws is developed only to be rapidly resorbed. The presence of five conspicuous interambulacral tentacles as a fundamental character of para-actinopod holothurians is confirmed by the observations on *Chiridota*, published herewith. The assumption that these two sets of structures are homologous is purely hypothetical but seems to me justified by the facts already known.

Granting this hypothesis, it follows naturally that in the probable ancestor of both echini and holothurians, the separation of the hydrocoel from the left coelomic pouch did not take place until the outgrowths for the radial water-vessels and, alternating with them, the rudiments of five primary tentacles, had been formed. In other words, the water-vascular system was not a closed system but was a part of the body cavity, and the lumens of both radial vessels and tentacles were continuous with the body cavity. In echini, however, owing to the formation of heavy calcareous deposits (teeth) in these primary tentacles, their development has been greatly retarded, and the hydrocoel forms and separates from the rest of the coelom before they arise. In

paractinopod holothurians, on the other hand, the development of the primary tentacles has been accelerated by their usefulness as tactile and locomotor organs, and, therefore, they have come to surpass the radial water vessels, not only in size but in their earlier and more rapid development.

It would be easy to draw a picture of the hypothetical echino-holothurian ancestor in accordance with the theory here proposed, but it could hardly be worth while. Suffice it to point out that the five primary interradial tentacles of such an ancestor doubtless assisted in the pushing of food into the mouth, and because of this use two very different lines of development opened up. Along one line, the tactile function was specialized and the organs became delicate, sensory tentacles, while along the other line, the mechanical function of scraping food, from the surface on which the animal crept, was specialized and the organs became hard, non-sensory teeth, accompanied by the necessary muscles and calcareous supports. The loss of a hard dermal skeleton in the one case, and its perfected development in the other, were naturally correlated accompaniments. In accordance with this theory, it may be possible to homologize the perignathic girdle of echini and the calcareous ring of holothurians. I am inclined to think, however, that such a homology does not exist. But it does seem to me probable that there is a true homology between the radially placed sphaeridia of echini and the paired positional organs, accompanying the radial nerves of synaptids. At present, however, I have no evidence to offer bearing on the point.

SUMMARY

1. Östergren's view that the ancestral holothurian was a mud-loving Clasipod-like form is rejected for three reasons: (1) Too little weight is given to the difference between primary and secondary simplicity of structure; (2) The ancestral holothurian was probably not a mud-loving but a plankton-feeding³ form; (3)

³ By "plankton-feeding form," is meant an animal that lives on micro-organisms which it takes from the water about it. In this case, I would include also the gathering of micro-organisms from the rocks or hard bottom on which the ancestral form lived.

Deep-sea animals, such as the *Elasipoda*, are, as a rule, highly specialized forms.

2. Becher's work has shown that *Rhabdomolgus* is essentially a synaptid in structure and development.

3. Edwards' work has shown that tentacles 1-5 in *Holothuria* are not homologous with tentacles 1-5 *Cucumaria*, but that tentacles 6-10 are homologous in *Holothuria*, *Cucumaria* and the *Synaptidae*.

4. Ludwig's division of the *Holothurioidea* into two sub-classes, *Actinopoda* and *Paractinopoda*, is accepted, since tentacles 1-5 of the *Synaptidae* are interradial outgrowths of the hydrocoel, and have no homologs in the other holothurians, while tentacles 1-5 of the pedate holothurians have no homologs in the *Synaptidae*.

5. Since the primary outgrowths of the hydrocoel in synaptids develop into organs lacking in the *Actinopoda*, while the secondary outgrowths correspond to the actinopod's primary hydrocoel outgrowths, it would seem that the *Synaptidae* are an older and more primitive stock.

6. The ancestral holothurian is pictured as a pentactula-like animal, but provided with radial water-vessels, accompanied by double series of pedicels.

7. The *Paractinopoda* have arisen from such a form with retention of the primary tentacles and loss of radial water-vessels and pedicels. The *Actinopoda* have developed the radial water-system and lost the primary tentacles.

8. The five primary tentacles of the *Synaptidae* are possibly homologous with the dental-sacs of echini.

9. The "atrium" of the pentactula is possibly homologous with the "amniotic cavity" of echini.

10. In synaptids the tactile function of the tentacles has been specialized to a high degree, while in echini, the homologous organs have, through the mechanical function of scraping, been developed into teeth.⁴

⁴ I trust this statement will not be taken at its face value, as pure Lamarekianism. I personally feel no doubt that natural selection, acting on slight variations, has been the real agent at work.

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PLATE 1

EXPLANATION OF FIGURES

1 Old gastrula of Chiridota. $\times 70$. *ar* = archenteron; *bl* = blastopore; *hy-en* = hydro-enterocoel.

2 Young larva of Chiridota. $\times 70$. *ac* = anterior coelom; *ar* = archenteron; *bl* = blastopore; *cb* = ciliated bands; *cp* = calcareous particles; *hy* = hydrocoel; *len* = left enterocoel; *ren* = right enterocoel; *wp* = water-pore. The hydrocoel already shows the five primary outgrowths and even the secondary ones are indicated.

3 Very young pentactula of Chiridota. $\times 70$. *ac* = anterior coelom; *al* = alimentary canal; *bc* = coelom, *cb* = ciliated bands; *cp* = calcareous particles; *ht* = primary tentacles; *pv* = polian vessel; *wp* = water-pore.

4 Pentactula of Chiridota. $\times 70$. *a* = anus; *ac* = anterior coelom; *atc* = atrial collar; *cb* = ciliated bands; *cp* = calcareous particles; *cr* = calcareous ring; *i* = intestine; *pt* = primary tentacles; *pv* = polian vessel; *rn* = radial nerve; *so* = sense-organ; *st* = stomach.

5 Figures showing the development of the trochoderma-like wheels (*f*) from the simple discs (*a*). $\times 310$.

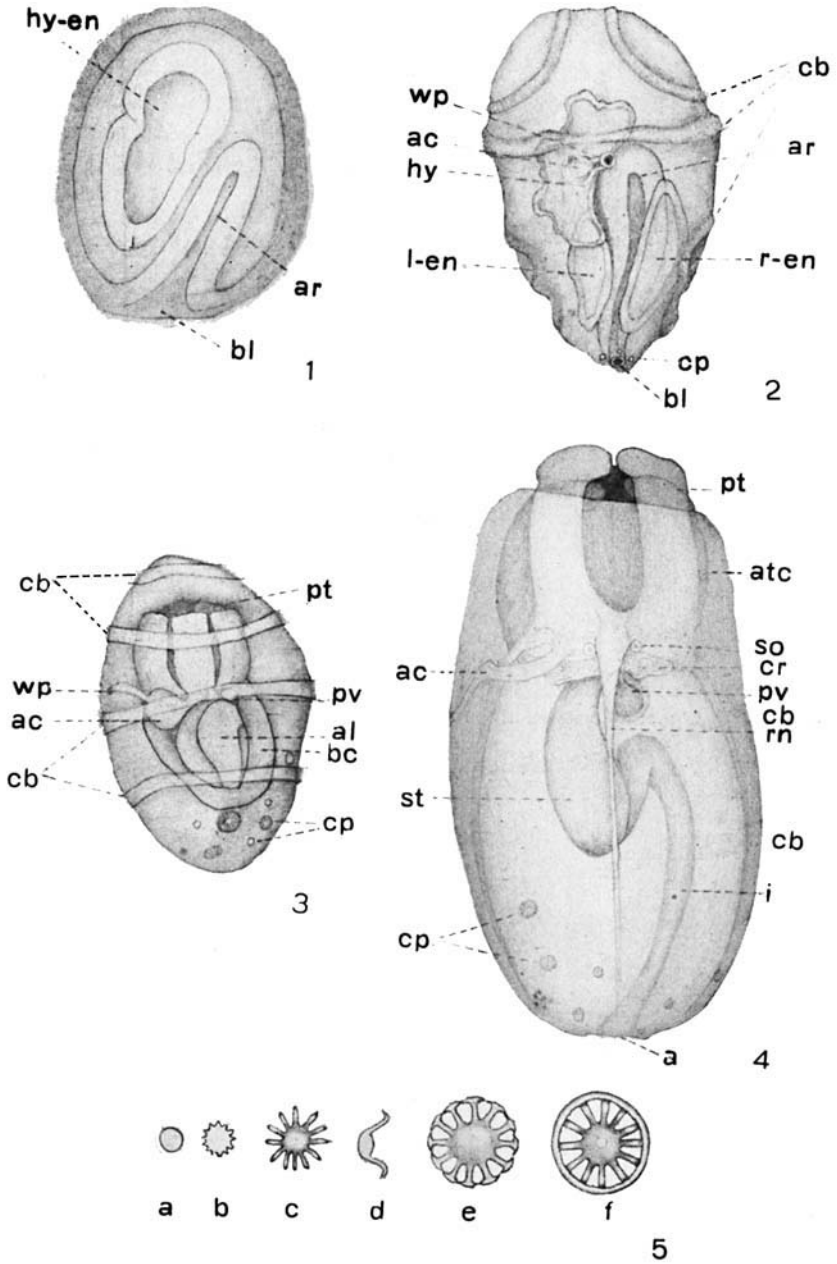
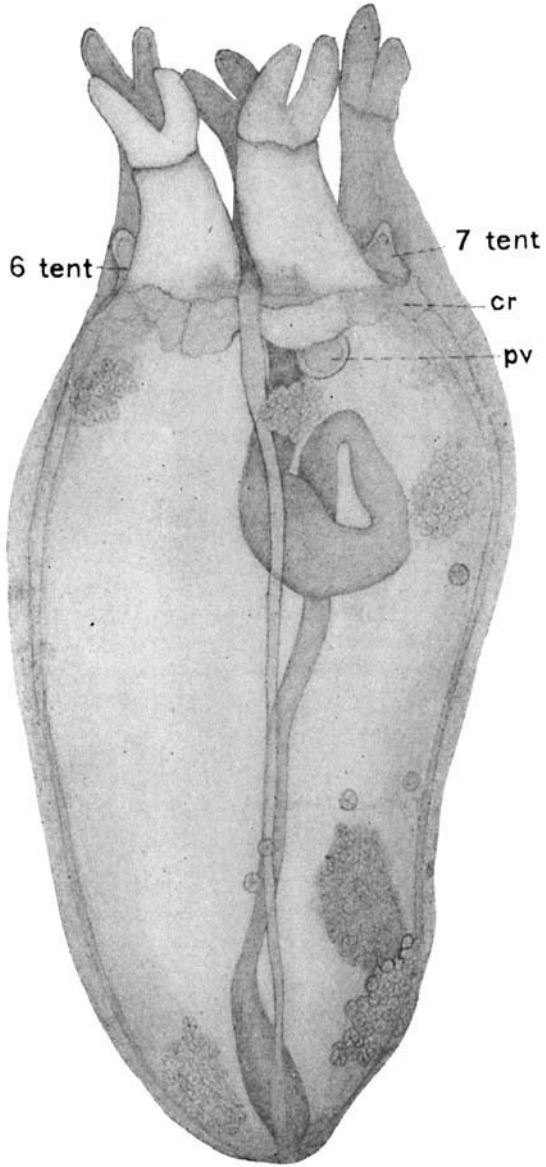


PLATE 2

EXPLANATION OF FIGURE

6 Seven-tentacled young of *Chiridota*, seen from the ventral side. $\times 70$. *cr* = calcareous ring; *pv* = polian vessel. The beginnings of the sixth and seventh tentacles are shown, and the heaps of six-spoked wheels are conspicuous. The wheels with numerous spokes are still common, however.



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