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DEVELOPMENT, NATURAL HISTORY AND INTERSTITIAL HABITS OF THE APODOUS HOLOTHURIAN *CHIRIDOTA ROTIFERA* (POURTALES, 1851) (ECHINODERMATA: HOLOTHUROIDEA)

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ABSTRACT

The apodous caribbean holothurian *Chiridota rotifera* (Pourtales, 1851) broods its young in the coelom. Development is thus viviparous and all the young from an adult are apparently released simultaneously. Reproduction occurs year-round and upon release young *Chiridota rotifera* burrow in soft sediments and find sand. The tentacles (oral tube feet) used in burrowing and feeding develop at a very uniform rate within cohorts. The young of *Chiridota rotifera* are remarkably similar in morphology and behavior to specimens described as a new genus and species *Psammothuria ganatii* by Rao (1968).

Previous work on synaptid holothurians reveals a propensity in the group for viviparity, possession of unique many-spoked wheel spicules by the embryos and young, and the existence of interstitial forms. In his review of brooding holothurians Vaney listed four viviparous synaptids, *Synaptula hidriformis* (Oersted, 1849), *Leptosynapta minuta* Becher, 1906, *Taeniogyrus contortus* Ludwig, 1898, and *Chiridota rotifera,* and sice then two more viviparous species have been discovered, *Trochodota dunedinensis* John, 1939 and *Leptosynata clarki,* Heding, 1928, studied by Everingham (1961). Many-spoked wheels have not been found in adults of any holothurian, but have been reported in the embryos or young of the synaptids *Leptosynata minuta* and *L. inhaerens* (Müller, 1848) by Becher 1906, *Synapta digitata* (plate II, figs, 5A, b & c in Semon, 1888) and in the giant larva *Auricularia nudibranchiata* Chun, 1896 by Inaba (1934) and Pawson (1970). Two members of the family which are known to have interstitial habits during at least part of their life histories are *Leptosynapta minuta* studied by Becher (1906) and *Psammothuria ganatii* Rao, 1968). *Chiridota rotifera* possesses all three of these traits.

The larvae of synaptids show an incredible diversity, ranging from the largest, most elaborate of all freeliving holothurian larvae, *Auricularia nudibranchiata,* and the

only known commensal echinoderm, *Rynkatorpa pawsoni* Martin, 1969, which lives attached to angler-fishm to *C. rotifera* which is brooded in the females coelom and assumes an interstitial existence upon its release.

Materials and Methods

Several small *Chiridota rotifera* were discovered on 4 March 1969 by Mrs. Anna Fenchel living interstitialy in sand and detritus through which she was systematically searching for marine rotifers. The sand was scooped from the upper centimeter of the bottom adjacent to the Crandon Park Marina at Key Biscayne, Florida in water which was about 20 cm deep at the time of collection during neap low tide.

The specimens were approximately 1.5 mm in length when first observed by the author on 7 March, 1969. Four individuals were placed in a 500 ml jar about one half full of sea water supplied with fine sediment. The jar was vibrated slightly atop an air-conditioner, and the temperature of the water was maintained at approximately 23° C. The animals were pipetted from the jar to a watch glass for observation and photographs. The sediment and water was changed daily. No food supplement was ever added, but the quantity of sediment provided was increased as the animals grew.

For histological study the specimens were fixed and decalcified in Bouin's solution for three weeks. Serial sections were prepared at eight microns and stained with Harris' hematoxylin and eosin. In addition to sectioned material, whole mounts were prepared of ten-tentacled young discovered in a museum specimen (UMML No. 43:50). These specimens were stained with borax carmine.

Additional specimens, both young and adults, from a variety of habitats were examined.

Result and Discussion

Clark (1910) characterizes the habitat of the adult *C. rotifera* as being in coral sand under rock fragments behind reefs at Jamaica and Bermuda. In Biscayne Bay, Florida *C. rotifera* is found in the sea grasses *Halodule wrightii* Ascherson and *Thalassia testudinum* (Koenig), though not frequently or in great abundance. Specimens were found in 16% of samples taken in *Thalassia* at Bear Cut Miami Florida with a mechanical sampler (O' Gower and Wacasey, 1967). Several small specimens of *C. rotifera* have been collected by Mr. Julio García using otter trawls, in lower Biscayne Bay, Florida, in areas dominated by *Thalassia* and the algae *Batophora orstedii* J. Agardh and *Laurencia* sp. Among the specimens from lower Biscayne Bay are one ten-tentacled specimen collected during July of 1969, one 2 mm long collected in October of 1968, and two specimens collected in August of 1969 -one 2 mm long and the other 5 mm long. All of these specimens were observed after

preservation in formalin. The author has collected specimens of 10 mm to 35 mm in length from the calcareous algae *Halimeda opuntia* (Linnaeus) at Harry Harris County Park on Key Largo, Florida. *C. rotifera* lives in a variety of habitats ranging from coral rubble behind reefs to shallow inshore grass communities in bays.

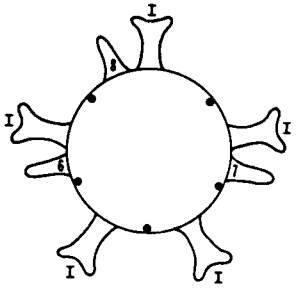
Collection of very small individuals in October 1968, and March, June and July 1969 confirms Clark's (1910) suggestion that reproduction occurs throughout the year.

The stage of development at which the young are released from the coelomic cavities of the female is quite variable. Clark (1910) stated that pentactula larvae dissected from adults survived in captivity better than adults. He found no young brooded beyond a stage with five primary tentacles and three rudimentary ones, nevertheless an adult 3.1 cm long and 0.9 cm in diameter collected in Largo Sound, Florida on 13 March, 1959 (UMML No. 43:50) contained 51 young, all of which had ten equal-sized tentacles with four digits each, while young with as few as five tentacles have been collected in the field. The time of release of young may correspond with some environmental condition rather than a particular developmental stage attained by the young.

H. L. Clark (1910) studied the early development of *C. rotifera* from larvae preserved in the coelomic cavities of adults collected in Jamaica (summer) and Bermuda (April). The earliest stages were uniformly ciliated gastrulae in which the hydroenterocoel had already separated from the primitive gut. The cilia segregate into distinct bands and eventually a doliolaria with four ciliated bands results. Unlike free-living doliolaria, the *C. rotifera* doliolaria lack a mouth. The hydrocoel has five prominent primary tentacles at this stage, and the midventral polian vesicle is well formed. Spicules are present, but rather than being like those of adult *Chiridota rotifera,* are many-spoked. In the pentactula stage, the five tentacles protrude extrernally and have square, highly-glandular sensory tips. The mouth is formed by invagination of the area between the tentacles. As the pentactulae develop, the many-spoked wheels become out-numbered by typical six-spoked wheels. The tentacles bifurcate resulting in five tentacles with two digits each. The original tentacles are interambulacral, and the earliest secondary tentacles arise in the interambulacra above the ventral lateral nerves. The seven-tentacled specimen figured by Clark measured 2.1 mm.

Clark (1910) found three specimens in which the eighth tentacle had began to grow from a position dorsad to the right dorsal nerve. This began growing while the sixth and seventh tentacles were still much smaller than the original five. The first eight tentacles are therefore arranged in pairs in each of the three dorsal interambulacra, and singly in each ventral interambulacrum (Fig. 1).

Since there is no metamorphosis in *C. rotifera,* growth and development are processes of enlargement and elaboration of the body and organ systems of the young.



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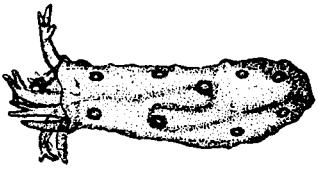

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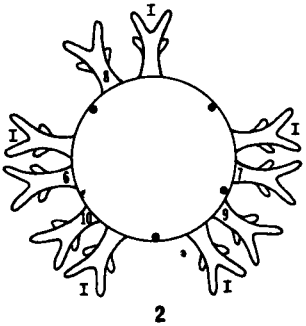

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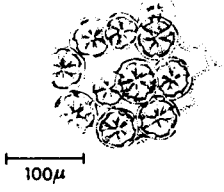

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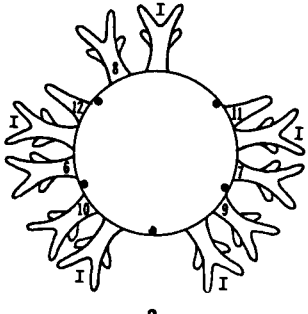

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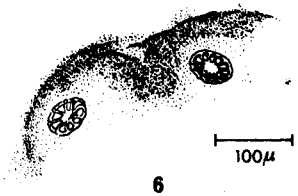

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Plate 1. Fig. 1. Diagram showing the positions of the five primary tentacles (I) and tentacles 6 through 8 relative to the ambulacra (the dark spots). Fig. 2. Same, ten tentacle stage. Fig. 3. Same, twelve tentacle stage. Fig. 4. Drawing taken from a photomicrograph of a living *Chiridota rotifera* with ten tentacles (5 mm long). Fig. 5. Wheel papilla drawn from photomicrograph showing six spoked wheels. Fig. 6. Typical solitary many-spoked wheels drawn from a photomicrograph.

Some of the major aspects of these processes as they were observed in laboratory specimens are related below.

4 March 1969: *C. rotifera* possessed five primary tentacles.

7 March 1969: The four specimens each had five primary tentacles and two or three inconspicuous secondary tentacles (Fig. 1). Each of the primary tentacles had two digits. Each specimen had five interambulacral rows of wheel papillae with three to four papillae per row. All specimens were approximately 1.5 mm long.

10 March: Each specimen had ten equal tentacles with four digits apiece. Tentacles nine and ten were also interambulacral, and arose dorsal to the primary ventral tentacles (Fig. 2). The result was an outwardly symmetrical arrangement of five pairs of interambulacral tentacles. The length of the animals had increased to 3 mm.

17 March: The specimens had grown to 4 mm but still had only three to four wheel papillae per row.

28 March: Little change was noticed except that the animals had grown to 6 mm. One specimen was relaxed in magnesium sulfate and preserved in Bouin's solution.

2 April: The animals maintained their steady growth until reaching 7 mm on this date. There were six to seven wheel papillae in each row.

5 April: Tentacles eleven and twelve began to appear as small bulges off the ring canal. One specimen had two bulges, while the other two specimens had the rudiments only of tentacle eleven.

6 April: All three specimens had rudiments of tentacles eleven and twelve, adult number of tentacles being reached approximately one month after the animals were collected. These tentacles arose in the dorso-lateral interambulacra dorsad to the primary tentacles (Fig. 3).

The process of tentacle formation was clearly visible through the nearly transparent body walls of the animals. The water vascular portion of the tentacles simply grew anteriorly until reaching the body wall surrounding the mouth. From this time on the integument was carried along as a covering over the water canal. The new tentacles were then formed like gloves being stretched over fingers. One specimen was preserved in Bouins solution. All were 7 mm long.

8 April: The water was cooled accidentally to approximately 12 degrees Centigrade.

14 April: While both specimens were still 7 mm long, tentacles eleven and twelve had grown to one half the length of the other ten. There was no indication of external bifurcation of tentacles eleven and twelve, but the internal water vascular portion had begun to divide at its tip.

15 April: The water was accidentally cooled again to 12 degrees Centigrade, this time for over twelve hours.

16 April: There was some evidence of external bifurcation on the tips of the new tentacles. The specimens had shrunk to 5 to 6 mm long.

21 April: Both specimens had four digits on each of the ten old tentacles and two digits on tentacles eleven and twelve. The specimens were 6 to 7 mm long. (Fig. 4).

23 April: The specimens measured 8 to 9 mm long.

9 May: In both specimens the new tentacles were equal in length to the other ten, but still had only two digits.

13 May: All twelve tentacles of both specimens had four digits. There were seven wheel papillae per row.

19 May: Both specimens measured 10 mm in length.

27 May: The specimens were found dead. Both were 10 mm long and still had but four digits on each of their twelve tentacles. They presumably starved after two days without a change of sediment.

Growth and development of four specimens of *C. rotifera* were observed for two and one half months. During this time, growth was primarily in length with only slight increases in diameter from approximately 1 mm initially to about 1.5 mm. The growth rates of the specimens were remarkably uniform. New tentacles appeared virtually simultaneously in all individuals, and the body lengths were almost equal throughout the period of observation. This uniformity was also observed in 51 young specimens preserved inside an adult (UMML Mus. No. 43:50), all of which were of approximately equal length and possessed ten tentacles.

All twelve tentacles of *C. rotifera* are interambulacral. Tentacles six and seven arise ventral to the primary tentacles in each of the dorso-lateral interambulacra, and the eighth arises on the right side of the dorsal primary tentacle. The two ventral interambulacra have but one tentacle each until tentacles nine and ten arise dorsad to the primary tentacles. In laboratory animals tentacles eleven and twelve arose about one month after numbers nine and ten had arisen. They arose almost simultaneously in each of the dorsolateral interambulacra in positions dorsad to the primary tentacles. The end result is an adult tentacular symmetry with two tentacles in each ventral interambulacrum, three in each dorsolateral interambulacrum, and two tentacles in the dorsal interambulacrum (Figs. 1, 2 & 3).

The very young *Chiridota rotifera* were almost completely transparent; the only color was due to a sparse number of very small acumulations of tiny red granules. These clumps of granules were concentrated in five longitudinal rows. After two

months, pigmentation was still not well developed, with the principal difference being that each accumulation of colored granules was somewhat larger, and they were more generally distributed over the body surface. The body wall became slightly thicker and therefore less transparent (Fig. 4).

The spicules of adult *C. rotifera* are of two kinds: supporting rods in the tentacles and six-spoked wheel spicules which are found in the body wall (Fig. 5). The wheels are formed in clusters which project from the body in characteristic wheel papillae. These papillae seem in part to serve the same functions for the apodous *C. rotifera* that tube feet do for aspidochirotes and dendrochirotes. They help the holothurians grip the substrate in locomotion or to hold fast to an object. These papillae are scattered over the surface of the adult *C. rotifera* but are in rows in the young, one row per interambulacrum. When the specimens, were 1.5 mm long each row was composed of only three to four papillae, while at 6 mm the rows had seven to eight papillae each; and this number was retained until the animals died at a length of 10 mm. The first spicules formed are many-spoked wheels (Fig. 6) characteristic of larvae and young of synaptids (Clark, 1910). As the young develop, the six-spoked wheels gradually become predominant. In the ten-tentacled stage there still is a small number of many-spoked wheels in the integument though they are found only singly rather than clustered into wheel papillae. The sizes of the papillae increase as the animals grow, due to an increase in the number of wheels in each clump.

Histological sectioning showed that the digestive tract was initially simply a recurved tube of approximately equal diameter throughout its length. Later it differentiated into two distinct portions; an anterior, highly-thickened, glandular stomach and a posterior, thin-walled intestine. Ingested fine sediment was passed quickly through the glandular portion (approximately 15 to 30 minutes) but was compacted and passed slowly through the latter section (approximately two hours). Presumably enzymes were mixed with the sediment in the glandular portion and digestive products were slowly extracted from it in the posterior portion.

The longitudinal muscle bands and radial nerves are prominent internal bands which mark the ambulacra. The only changes in the muscular and nervous systems were increases in size commensurate to the increase in size of the animal.

Young *Chirodota rotifera* are very active both day and night. Feeding is accomplished as the animal burrows through the substrate of fine sand or mud, pushing most of the material back along the body and thrusting a small amount of it into the mouth. The tips of the tentacles are highly innervated and particles seem to be selected primarily on the basis of size, as small pieces of sediment and detritus adhere to the outer surface of the tentacles on the knobby surface of the digits. In feeding, the digitate portion of the tentacle is thrust into the open mouth. The mouth then constricts somewhat, and the tentacle is withdrawn. No particular order of tentacle use was observed. The remarkable feature about the tentacles is that they are adapted for burrowing through the substrate rather than being

primarily feeding structures. Feeding seems to be an incidental feature of burrowing, and the animals can burrow without feeding. The digits are on the outside rather than the inside surface of the tentacles. In burrowing a tentacle is pushed forward and out as the digits direct the substrate away from the mouth. The tentacle is then bent backwards along the body, and the bulk of the material handled is released there. The tentacle may then be thrust into the mouth or simply returned for another stroke.

The young *C. rotifera* stayed beneath the surface of the substrate and in addition covered the body with a layer of sediment. This coat of sediment could be washed off with the stream from a pipette, but provided very effective camouflage. The covering habit was acquired over a period of time with little or no covering being done in the first three weeks of observation. The habit of covering developed to such an extent that the holothurians were never visible except as clumps of detritus and sediment.

Clark (1910) observed, *"Chiridota* is not hardy, and specimens brought into the laboratory at Port Antonio (Jamaica) lived but a few hours and were never very active. Curiosuly 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 sulfate which completely narcotized the adults." The authors has kept adults in the laboratory for several weeks by transferring them each day to a fresh supply of mud which is deep enough to allow them to burrow. They starve and die in a matter of hours if their food supply is exhausted. The young are much more easily kept than adults, because they require less sediment and can survive longer periods of starvation. Young *C. rotifera* have great ranges of tolerance to adversities, withstanding foul water for several hours and temperatures as low as 12° C for over twelve hours. Being very active animals, they are quite sensitive to lack of food, but can survive for at least a day after having processed all the substrate available to them.

C. rotifera showed marked behavioral adaptions to the stress conditions mentioned. Reactions to starvation and foul water are the same. The animals shed their sediment coats, replace the sediment material in the gut with fluid, and move actively on the surface of the substrate. In this conditions they are nearly neutrally bouyant and probably easily transportated by tidal currents or even mild wave action. No active swimming was observed such as that described for the apodous holothurians *Leptosynapta inhaerens* by Costello (1946), *Leptosynapta albicans* by Glynn (1965), *Labidoplax dubia* by Hoshiai (1963), or for "young synaptids" by Clark (1907). Response to lowered temperature is similar except that the specimens virtually cease all movement and lie exposed on the substrate in a much contracted condition. Conceivably, migration of a meter or less could transplant the animal to a satisfactory microhabitat, because substantial small scale differences in water quality and temperature prevail in the shallow water habitat of the young animals, thus, these responses to stress are adaptive.

Young *C. rotifera* collected in fine sand grew well provided with fine mud which they ingested during the course of burrowing. The rates of development of four specimens reared were remarkably uniform. Like other synaptids they possess many spoked wheel spicules as embryos and these wheels resemble those of the giant auricularia larva *Auricularia nudibranchiata,* whose adult stage is still unkonwn.

Several lines of evidence suggest that the larvae of *C. rotifera* may be released in response to favorable environmental conditions rather than at a particular development stage. Clark (1910) found that pentacula larvae dissected free from their mothers could be maintained in the laboratory more easily than adults. Also, while Clark found no young with more than eight tentacles being brooded and the present study was prompted by the discovery of free-living young with only five tentacles, I found 51 ten-tentacled young being brooded in another individual. The behavioral responses of young *C. rotifera* to unfavorable conditions show the ability of this species to respond quickly and adaptively to stresses.

The study of *C. rotifera* casts doubt on the validity of an interstitial synaptid, *Psammothuria ganatii* described by Rao (1968) as a new genus and species. His designation is based primarily upon the species possession of eight bifurcated tentacles. This condition is reminiscent of the eight-tentacled stage of *C. rotifera,* and the interstitial habits of *C. rotifera* suggest that *Psammothuria ganatii* may be simply an interstitial stage in another synaptid's life history. *C. rotifera* with eight tentacles are comparable in size (2 mm long) to *P. ganatii* (2.5-4.0 mm long), and the gonads of *P. ganatii* are unconvincingly described as "two small unbranched massive structures with short gonoducts (which) are located on the anterior part of the coelom . . ." without histological confirmation that they truly are gonads.

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Resumen

Chiridota rotifera (Pourtales, 1851), es una holoturia o pepino de mar ápodo del Caribe cuyas crías se incuban en el celoma. Así, el desarrollo es vivíparo y todas las

crías de un mismo adulto son, aparentemente, liberadas de forma simultánea. La reproducción se lleva a cabo durante todo el año. Al ser liberadas, las crías de *C. rotifera* se establecen en los sedimentos blandos y arenas finas. Los tentáculos o pies orales tubulares, usados para establecer sus madrigueras y en la alimentación, se desarrollan a ritmos muy uniformes en las diversas cohortes de pepinos, Las crías de *C. rotifera* se asemejan, notablemente, tanto en su morfología como en comportamiento, a los ejemplares descritos como *Psammothuria ganatti* por Rao, quien propone ese nuevo género y especie en 1968.

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