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THE LARVAE OF A DISCINID (INARTICULATA, BRACHIOPODA)

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The first account of a discinid larva was given by Mueller (1860). This larva from the sea off Santa Catarina, Brazil, had a pair of thin, approximately circular valves with no hinge, a lophophore with a median tentacle and 4 pairs of cirri, a pair of eyespots, a pair of statocysts, a pedicle, 5 pairs of stout mantle setae and a large number of fine mantle setae. Further specimens (Mueller, 1861), also with 4 pairs of cirri, remained free-swimming for about 5 or 6 days before they became attached to the bottom and sides of glass vessels in the laboratory.

Simroth (1897) reported two inarticulate larvae, one with 3 pairs of cirri and two bunches of extremely fine setae and the other with 4 pairs of cirri and 3 widely separated stout mantle setae. The former, he believed (p. 4), would not develop any more cirri during its pelagic larval life. This belief, the morphological differences between the two larvae and the fact that one was obtained near the surface and the other from a depth of 1000 to 2000 meters, led him to the conclusion that one was adapted to planktonic life at the surface, and the other to life at great depth (p. 6). He further concluded (p. 5) that the larvae belonged to two different species of a single discinid genus.

Blochmann (1898) obtained 10 larvae from the Strait of Rhio in the Pacific identical with Mueller's larvae both in structure and in the stage of development. He considered them as larvae of *Pelagodiscus atlanticus* (King) since the adults of this worldwide species were reported from both the Atlantic and the Pacific. However, in his alum-carmine-stained specimens, he only found nephridia on either side of the stomach where Mueller (1860) had previously seen only statocysts.

Yatsu (1902) described a discinid larva off Japan with a pair of statocysts, 5 pairs of stout setae and a large number of fine mantle setae. He mentioned the possibility (p. 107) that the free-swimming discinid larvae at the stage of 4 pairs of cirri made their way towards the coast shortly before settlement.

Eichler (1911) obtained two large larvae from a depth of 3000 meters at 66 degrees S. Lat. and 90 degrees E. Long. These also had 4 pairs of very long cirri, a pair of statocysts, 4 pairs of stout setae and a great number of fine setae. He also

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attributed these to *Pelagodiscus atlanticus,* adding (p. 384) that they had given up pelagic life and were changing over to a sessile mode of life.

Ashworth (1915) found 6 larvae of *Pelagodiscus* from a depth of 40 fathoms in the Indian Ocean. These also had 4 pairs of cirri and led him to believe (p. 66) that the younger stages might live on the sea bottom and hence escaped capture.

In the present study a complete series of larvae was obtained. The smallest was even smaller than the smallest ever reported (Simroth, 1897) and the largest exceeded in size all the largest larvae ever reported, except for the two of Eichler (1911). Moreover, the larvae of medium size in the present series showed the transitional stages between the two larvae described by Simroth (1897), thus serving to provide evidence for the probable identity in species of the two larvae of Simroth. The nature of the organs lying on either side of the stomach was also studied, since these were differently interpreted by Mueller (1860) and Blochmann (1898). The morphological changes during the larval stage were described. The larvae were compared with those previously found and their similarities and differences discussed.

Materials and Methods

Thirty-three larvae of a discinid were obtained by surface plankton hauls carried out in the daytime in the shallow water of the Johore Strait off the north coast of Singapore Island. Two of them were caught on August 28, 1952 (Table I, nos. 15 and 17), one each on September 21, 1952 (not in Table), September 28, 1952 (Table I, no. 2) and June 12, 1953 (Table I, no. 1). The others, which were obtained on November 16, 1952, formed a continuous series of transitional developmental stages and are presumed to belong to the same species. Before the adults are discovered in the vicinity of Singapore, these larvae are provisionally identified as those of a discinid on the grounds of the resemblance of some of the stages in the present series to similar larvae reported by Mueller (1860), Simroth (1897) and others.

The shell and setae of each larva were measured with a calibrated ocular micrometer under a monocular microscope. Shell dimensions were taken with the larva lying on its dorsal or ventral valve. The shell length was the shortest distance between the anterior and posterior edges of the shell along the sagittal plane, when both edges were in the same plane of focus. Similarly, the width of the shell was the distance between the right edge and the left edge at the widest part of the shell when both edges were in focus.

The number and type of setae and the number of paired cirri in the larvae were recorded. The absence or presence of statocysts was noted.

All observations were carried out on live specimens in the Department of Zoology, University of Singapore.

Results

A moderately young discinid larva consisted of a dorsoventrally flattened body enclosed between two shell valves. These were slightly convex externally, not hinged but merely held together by muscles and other soft tissues. The visceral cavity occupied a small central part in the posterior half of the space between the

TABLE I

Shell dimension and the type, number and length of setae in discinid larvae with 4 pairs of cirri from the Johore Strait

Specimen no.	Shell valve				Length in μ of embryonic seta										Type and number of setae		
	Dorsal		Ventra		No. 1		No. 2		No. 3		No. 4		No. 5		Embryonic	Early larval	Late larval
	Length μ	Width μ	Length μ	Width μ	Left	Right	Left	Right	Left	Right	Left	Right	L.	R.	Left Right	Left Right	Left Right
1	462	500	349	455											0	1, 1	24, 24
2	401	479	337	434											0	1, 1	0
3	382	437	326	407											0	2, 2	0
4			347	429													
5			346	424													
6	311	364	291	364											0	4, 5	0
7	311	364	288	356											0	2, 2	0
8	308	358															
9	282	330	265	323		1213		1289							0, 2	3, 3	0
10	271	326	259	318	1198		1213	1243							2, 1	3, 3	0
11	253	302	245	297	1107		1228								2, 0	2, 2	0
12	242	284	239	276	1152	1198	1167	1213				917			2, 3	0	0
13	241	288	243	288	121	1137	1152	1122							0	3, 2	0
14	233	259	219	251											1, 2	2, 2	0
15	217	242	212	238		773		1228		819					3, 3	(1), (1)	0
16	216	251	208	245	1092	1092	1084	1084	819	834	857	834			4, 4	3, 3	0
17	216	236	197	232													
18	213	242	207	236	1152	1152		1289			857	857			2, 3	3, 3	0
19	207	239	199	228	1152	1122	1228	1198			925	917			3, 3	0	0
20	184	212	179	204					796	781	819	803			2, 2	3, 3	0
21	179	199	173	193		1167		1213							0, 2	0	0
22	179	196			1092	1107	1182	1137	788		758				4, 2	0	0
23	168	183	156	173	1175	1152	1175	1167		872					2, 3	0	0
24	161	183	160	184	1198	1213	1243	1228	773	773		766	99	83	4, 5	1, 2	0
25			157	169		1031				803	773	773			1, 3	0	0
26	158	173	147	161	1213	1182	1243	1243		788		773			2, 4	0	0
27	143	151	130	138	1122	1137	1228	1198	879	879	940,				4, 3	0	0
28	140	145	130	136					788		803	834			2, 1	0, 1	0
29	124	125	104	111		1137	1228	1228	819	849	849	819			3, 4	0	0
30	115	124	112	118		1084	1122	1152			948	955			2, 3	0	0
31	108	115	98	99			1243	1228	894	894	925				3, 2	0	0
32					1078	1078	1038		728		697				4, 1	0	0

shell valves and was almost filled with the stomach and the intestine (Fig. 1). A cone of tissue projected laterally from the lateral body wall at the level of the stomach. This setal cone contained the bases of the long straight, brittle setae, which will be referred to as the embryonic setae in the present study. This cone also housed the muscles to move these setae.

The rest of the space between the shell valves not occupied by the visceral cavity constituted the mantle cavity. In the front part of this was a contractile columnar projection of the anterior body wall. This column contained the oesophagus,

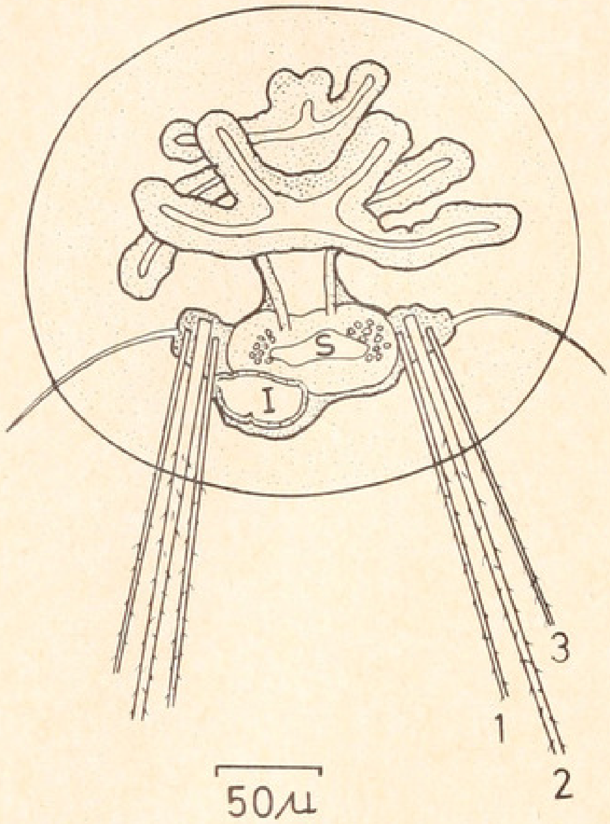

FIGURE 1. Ventral view of a young discinid larva (no. 15, Table) with embryonic setae (1–3) and a curved seta issuing from each setal cone. The stomach (S) and intestine (I) almost fill up the visceral cavity.

pharynx and muscles and continued anteriorly into the lophophore. Muscular movements of the column and lophophore brought about extension and expansion or retraction and contraction of both column and lophophore.

The larval lophophore consisted of a central disk roughly horizontal in position with the more or less centrally placed mouth on the ventral side. At the periphery of the disk 9 lophophoral processes radiated out. One of these, the tentacle, pointed anteriorly in the sagittal plane, and the others, the cirri, were more lateral in position. All the larvae in the present series had 4 pairs of cirri. Each cirrus on one side of the mouth usually corresponded in position and size with the one directly opposite on the other side, thus forming a pair.

A thin layer of mantle tissue lined the inner surface of the mantle cavity. In widely separated regions along the lateral border of the ventral mantle typically 4 stout curved setae appeared on each side of the medium-sized larvae. From each lateroposterior border of the dorsal mantle appeared another. These 5 curved setae will be referred to as the early larval setae.

In the oldest larvae yet another kind of setae appeared in the lateral border of the mantle. They were shorter and more flexible than the other two types and will be referred to as the late larval setae.

The lengths and widths of both the dorsal and the ventral shell valves were tabulated in Table I, in which the larvae were arranged in descending order of magnitude of the length of the dorsal shell valve wherever possible. Data on the different kinds of setae on the left and the right side of the body were also included.

Both shell valves were transversely oval in shape in the youngest larvae, although occasionally one valve or the other was circular, *e.g.*, the dorsal valve of no. 29 and the ventral valve of no. 31 in Table I. However, while the dorsal shell valve maintained approximately the same oval shape during the entire larval stage, the ventral one changed shape. The convex posterior edge of this in the youngest larvae gradually became less and less curved until it became almost a straight line when the larva attained about 219 μ in ventral valve length (no. 14). The posterior edge remained straight even at 243 μ ventral shell-valve length (no. 13), but with further growth it gradually developed a slight but noticeable bay near the median line, when the ventral-valve length reached 265 μ or so (no. 9). This bay became more prominent with further larval growth to 326 μ (no. 3) and deeper still in larger larvae.

This change in shape of the ventral shell valve was presumably caused by a slowing down of deposition of shell material at the posterior end. The deceleration was greatest near the sagittal plane, becoming less laterally.

With the exception of larvae nos. 13 and 24, in both of which the two shell valves were equal in both length and width, and of no. 6 in which the two shell valves were equal in width, all the larvae had unequal shell valves. In each of them the dorsal shell valve was slightly longer and wider than the opposing ventral one. This difference was slight throughout this series with the exception of the largest larvae (nos. 1 to 3), in which the difference was considerable.

The external surface of both shell valves was smooth. There was no observable growth line with the exception of larva no. 2. In this there was an oval area, 168 μ long and 183 μ wide, which appeared as a prominent growth line on the dorsal shell valve.

In the smallest larva (no. 31 in Table I) the alimentary canal consisted of the mouth, pharynx or oesophagus, stomach, intestine and the anus. In an older larva such as no. 15 the intestine was constricted near the distal end to form another chamber. The highly extensible oesophagus was long and slender when the lophophore was everted during swimming. When this was retracted the inner end of the oesophagus projected into the stomach in the form of a valve-like fold, almost completely closing the opening of the oesophagus into the stomach. The stomach was a large sac with its lateral diameter greater than its anteroposterior one. The high epithelium laterally indicated distinct regions of phagocytosis. The intestine was a thin-walled tube with a distinct constriction separating it from the stomach. It was directed to the right lateroposteriorly in young larvae but either laterally or anterolaterally in older specimens. The anus, not easily distinguishable except during defecation or after, was a slit about 2 to 2.5 μ in diameter.

Defecation was observed in larva no. 19. It was preceded by a flattening of the stomach in the anteroposterior direction. The stomach and the intestine then shrank visibly and progressively as particles from the hind part of the intestine escaped through the anus. Meanwhile the constriction between the stomach and the intestine also diminished in diameter. Presumably during defecation muscular contraction of the wall of both the stomach and the intestine was responsible for the expulsion of the faecal material.

Statocysts, absent in young larvae, occurred in the oldest larvae nos. 1 to 3. Each of these had a statocyst situated dorsally in the visceral cavity at each postero-lateral corner of the stomach. Each statocyst had a central cavity, in which danced 15 to 25 statoliths. The cilia on the inner epithelium of the statocysts were also observed to stir vigorously.

The pedicle occurred in larva no. 6 and in the larger larvae as an oval vesicle posterior to the stomach. It was absent in younger larvae.

The embryonic setae were the first to appear among the three different kinds of setae found during the larval stage in a discinid. They were observed in young larvae of dorsal shell length of 179 μ and under (nos. 21–32 in Table I) before another kind of setae were formed, with the exception of larvae nos. 24 and 28. They were equal in number on the two sides of the body, unless lost by accident or some other cause. The usual number appeared to be 4 per setal cone, although 5 had been observed in one larva (no. 24). In every setal cone the 4 or 5 setae were not of the same length and diameter, but were very regularly arranged in a definite order. The embryonic seta nearest the midline (no. 1 seta in Fig. 1 and Table I) was the second longest and second thickest among the four on each half of the body. The next one, occupying a more lateral position, was invariably the longest and the stoutest (no. 2 in Fig. 1 and Table I). The next one was the shortest and the thinnest (no. 3 in Fig. 1 and Table I). The outermost one (not shown in Fig. 1) was slightly longer and slightly thicker than the one medial to it. In larva no. 24 of Table I a fifth embryonic seta occurred outside the other four. This was the shortest and the finest in the larva.

Short spines were found on all the embryonic setae in approximately four irregular, longitudinal rows starting from a region about halfway between the base of the setae and the posterior edge of the shell (Fig. 1). Those on the coarser setae appeared to be stouter than those on the finer ones. They seemed to occur throughout the length of the setae.

The lengths of the different embryonic setae on both sides of the body were summarized in Table I. Due to the widely differing diameters of the first medial two, they could be distinguished from each other. The third and the fourth setae were, however, not easily distinguishable when removed from the larva. The diameter of each decreased very gradually from base to tip. The color was darker than that of other setae that appeared later. The embryonic setae were stiff and brittle. They broke off when they collided with hard objects on a slide. In older larvae they decreased in number and were absent in the oldest larvae.

The early larval setae appeared in an older larva during its early planktonic life. They occurred singly in widely separated regions along the mantle border. They were curved, stout setae, tapering rapidly in the last quarter or so to a sharp point. The stoutest among them was situated at each posterolateral region of the ventral shell valve and was equipped with stout spines. The maximum number of early larval setae seemed to be five on each side, although this was attained only on one side of larva no. 6. Of these, four issued from the ventral mantle, and one from the dorsal mantle. Many larvae had only 3 or fewer setae on each side. The stoutest seta was 300 to 350 μ long, the others, only half as long.

Larva no. 15 (Fig. 1) had a curved seta, morphologically indistinguishable from an early larval seta except in length, in diameter and in its point of origin. It was more slender and shorter. It issued not from the mantle border but from the setal cone. Whether it was produced during the embryonic or the larval stage is not known.

The late larval setae were the last to appear in the larva and were found only in the oldest larva (no. 1). In this there were about 24 of them evenly spaced in the lateral region of the mantle between the most anterior and the most posterior early larval setae. Finer and more flexible than these, they tapered gradually to a fine point.

Rotational movements of the dorsal shell valve were observed in a submerged larva lying with its ventral valve motionless at the bottom of a microscope slide. Protrusion and retraction of the lophophore, bending, extension and shortening of the individual cirri occurred now and again.

In swimming the anterior edges of the shell gaped open, the lophophore emerged from the shell and the tentacle and cirri spread out radially. The cilia on both the tentacle and cirri beat vigorously to drag the larva forward with the two bundles of primary setae trailing behind. On collision with another object the cilia immediately stopped beating and the larva sank. During forward progression the flat body regularly rotated about the anteroposterior axis and the two bundles of embryonic setae were sometimes parallel to each other and sometimes pointing outward from each other at an angle. On several occasions each bundle was simultaneously moved medially past each other to form a cross as the larva swam forward. The various positions of these setal bundles indicated a fine control by the muscles in the setal cone. While the animal was at rest, movements of individual embryonic setae in a bundle were also observed.

Movements of the early larval setae were also observed. These were capable of independent movements. The stoutest one on each posterolateral region was especially active and was seen to make intermittent lashing movements in the gape between the two shell valves. Whether these movements were an aid in swimming is not known. Movements of early larval setae increased in intensity and frequency when they collided with objects on the slide under observation in the microscope.

Discussion

The oldest larva in the present study resembled the discinid larvae described by Mueller (1860, 1861), Simroth (1897, Blochmann (1898) and Yatsu (1902). The youngest, however, though resembling the youngest discinid larva of Simroth in many ways, differed from it in the following respects. Firstly, Simroth's larva had 3 pairs of cirri instead of the 4 in the larvae of the present series. Simroth (1897, p. 4) believed that the larva with 3 pairs of cirri was in a stable state and that it would not develop additional cirri during its larval stage. Secondly, the innermost embryonic setae in Simroth's larva were bent. Thirdly, the longest embryonic seta in Simroth's larva no. 1 was the one next to the outermost, whereas in all the larvae examined in this study it was the one next to the innermost.

Presumably not realizing that the two discinid larvae he described could have been two different developmental stages in the ontogeny of a single species, Simroth (1897, p. 5) assigned them to two different species of discinids. However, the larvae in the present study consisted of a continuous series of growth stages, including those that are transitional stages between the two discinid larvae of Simroth. These stages included larvae that possessed both the embryonic and the early larval setae. The loss of the embryonic setae occurred in older larvae, thus transforming them into the more familiar so-called "Mueller's larvae." Obviously the larvae in the present study should be attributed to one single species of discinid. Their adults still remain to be discovered in the vicinity of Singapore. However, Blochmann (1898) relegated the 10 larvae from the Rhio Strait and those of Mueller (1860, 1861) to *Pelagodiscus atlanticus* (King).

The succession of three different types of setae in the brief span of discinid planktonic larval stage is a unique phenomenon unknown in brachiopod ontogeny. The present study showed the presence of two bunches of long embryonic setae on the lateral cones of the body wall in the youngest larvae in which the cirri were just mere short lobes of the lophophore. These lobes or short cirri of the lophophore were similar in appearance to those of the youngest planktonic larvae of *Lingula anatina* (Lamarck) the present author had observed and also to those of embryos of *Lingula* at the end of the embryonic period (Yatsu, 1902). Since the two bunches of embryonic setae were already present in the youngest larvae obtained, and also similar in length, width and appearance to those of older larvae, they were presumably embryonic structures elaborated from the substance stored in the fertilized ovum. The present work also showed the first appearance of the early larval setae in larvae of about 140 μ dorsal-valve length. These were obviously not normally present in younger larvae. These setae are called early larval setae, since they developed in early larval life. Another kind of setae, called late larval setae, appeared only in the oldest larva in the present study and in the larvae described by Mueller, Simroth, Blochmann, Yatsu, Eichler and Ashworth. These late larval setae, formed in late planktonic life of the larvae, prepared them for settlement to the sessile life of the postlarva. They reminded one of the setae that appeared near the end of the planktonic larval period of *Lingula* (Yatsu, 1902, Chuang, 1959). Simroth (1897, p. 15) regarded both the embryonic setae in his smaller larva and the early larval setae in his other larva as flotation aids. Presumably these two types of setae could also serve a protective function by making the larvae into less easily swallowed morsels. Moreover, they could be used in steering while afloat or drifting in a current. The rapid succession of three different types of setae is presumably an indication of their great necessity to these larvae. Mueller (1861) reported the resorption of the stoutest early larval setae and the loss of others in his discinid larvae that settled down to a sessile life in the laboratory. The present study (Table I) showed a gradual loss of not only the early larval setae in older larvae, thus confirming Mueller's observations, but also of the embryonic setae.

Simroth's larva no. 1 of 220 μ greatest diameter (1897, p. 3 and Tafel I, Fig. 1) was equivalent in size to no. 20 (Table I) of the present study, but in the development of setae it was in the same stage as larvae nos. 21 to 32 with the exception of nos. 24 and 28, which apparently had an earlier development of the early larval setae. His larva no. 2 of 420 μ diameter (p. 5 and Tafel I, Fig. 2) was equivalent in shell size to no. 5 but in setal development to no. 1 of the present study. Thus

Simroth's no. 1 was a discinid larva before the appearance of the early larval setae, while his no. 2 could well be an older larval stage of the same discinid species after the loss of the embryonic setae and the appearance of the next two types of larval setae, contrary to his (1897, p. 5) conclusion that the two larvae belonged to two different species of the same genus.

During the larval stage the shell valves changed in shape and proportion. In both shell valves there was a change from an almost circular plate of the youngest larvae to a pronounced oval with a greater transverse diameter. Next there was an ever-widening difference between the transverse and the longitudinal diameters of each shell valve during the last part of the larval life. Meanwhile the dorsal shell valve also increased in diameter much faster than the ventral. Finally there was a striking but gradual change in the posterior edge of the ventral shell valve from a convex to a concave one. This was presumably brought about by a finely adjusted modification of shell growth along the medial third of the posterior mantle edge. The formation of a bay at the posterior margin of the ventral shell valve, just as the formation of the pedicle, is a preparation for settlement to a sessile life. It is through this bay presumably that the pedicle is extruded for attachment to the substratum at the time of settlement.

Mueller (1860) reported the presence of a pair of statocysts in his discinid larvae. Although Blochmann (1898) denied their presence, they were observed by Yatsu (1902), Eichler (1911), Ashworth (1915) and the present writer.

A pair of eyespots, first reported by Mueller (1860), occurred only in the larvae found by Ashworth (1915). They were not observed by other writers.

If the sequence of appearance of organs during ontogeny can serve as an indication of their usefulness, then the pedicle, the statocysts and the late larval setae, which appeared towards the end of the larval stage, are presumably of little functional value to the larvae during the planktonic stage. They are presumably of use during settlement and the sessile life that follows.

In the ontogeny of *Glottidia* (Brooks, 1879) and *Lingula* (Yatsu, 1902; Chuang, 1959) shell size, as well as the number of pairs of cirri, increases during the planktonic larval life and either of them can be a fair index of the stage of larval development. In the ontogeny of a discinid, Table I showed that only shell size increased while the number of cirri remained constant at 4 pairs during the entire larval stage. Hence only shell size of a discinid larva could indicate the stage of development. Discinid larvae with 4 pairs of cirri need not necessarily be at the same stage of development, contrary to the belief of previous writers. In addition to shell size, the occurrence of organs or structures that develop at a definite stage during ontogeny may be a useful index of the age of the larvae. Such organs or structures include the different types of setae, the statocysts, the pedicle, the bay or notch on the ventral valve and the nephridia.

Mueller (1860), p. 79) rightly believed that his larvae were near the end of their larval life and on the way to adopting a sessile life. The absence of younger stages, he thought, was an indication that these had up till then remained in the shell of the adult. Ashworth (1915, p. 66), on the other hand, believed that the younger stages might live on the sea bottom and thus escaped capture. The occurrence of a series of developmental stages including the youngest larvae in the surface plankton of shallow water seems to indicate that the young stages can occur near the surface. The capture of these young and old stages near the shore also indicates the random movements of both young and old to or away from shore, contrary to the belief of Yatsu (1902, p. 107) that the larvae shortly before settlement made their way towards the coast.

Discinid larvae were obtained from February to April (Mueller, 1860, 1861) in the South Atlantic Ocean, from July to August or September (Yatsu, 1902), off Japan in the Northern Pacific and in October (Ashworth, 1915) in the northern part of the Indian Ocean. They were captured in the tropical West Pacific in July (Blochmann, 1898) and in June, August, September and November by the present author. This indicates the restriction of breeding to the summer and autumn. More intensive collection may possibly extend the breeding season in tropical waters.

Summary

1. Thirty-three discinid larvae were obtained one meter below the water surface in the daytime in the shallow part of the Johore Strait, north of Singapore.

2. The oldest among them, 462 μ in longitudinal diameter, resembled the "Mueller's larva" discovered by Mueller and referred to *Pelagodiscus atlanticus* (King) by many subsequent authors.

3. The youngest among them, 108 μ long and 115 μ wide in dorsal shell, resembled Simroth's smaller discinid larva of 220 μ diameter in many essential features.

4. The larvae in this study showed a gradual transition in many morphological characters, indicating that they were a series of developmental stages in the ontogeny of a single discinid species.

5. The two bunches of long embryonic setae were gradually replaced by the curved early larval setae in the medium-sized specimens. Towards the close of the larval stage the third kind of setae appeared from the mantle border.

6. The dorsal shell valve maintained its oval shape during the entire larval stage. The posterior edge of the ventral one, however, gradually changed from convex to concave, passing through a stage when it was almost a straight line.

7. The statocysts and the pedicle appeared in older larvae.

8. The number of cirri remained constant throughout the larval stage.

9. The larvae were compared with the discinid larvae previously recorded. Their developmental changes and the breeding season of discinids were discussed.

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