

RHIZOCEPHALA (CRUSTACEA: CIRRIPIEDIA) FROM THE DEEP SEA

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ABSTRACT

The Danish Galathea Expedition collected eight species of rhizocephalans. *Cyphosaccus jensi* n.sp. and *Sacculina abyssicola* were taken at depths between 3500 and 4000 m. *Lernaeodiscus triangularis* n.sp. and the highly aberrant *Pirusaccus socialis* n.gen., n.sp. derive from 2600 m. *Cyphosaccus cornutus*, *Boschmaia muniticola* and *Triangulus* sp., were collected from ca. 600 m depth, and *Tortugaster discoidalis* n.sp. in the sublittoral zone. Reexamination of additional deep-sea rhizocephalans has led

i.a., to the discovery of one more new species, *Galatheascus babai* n.sp. *Triangulus boschmai* Brinkmann, 1936 (family Lernaeodiscidae) is transferred to *Tortugaster* (family Peltogastridae). A list is presented of the twenty-three species and another few unidentified specimens of rhizocephalans that have been recorded from depths greater than 600 m; four of these species are truly abyssal forms. The available information on reproduction in rhizocephalans from the deep sea is reviewed.

INTRODUCTION

The Danish Galathea Expedition round the World collected eight species of rhizocephalans, four of which are new to science. One species represents a new genus. Two species were taken at depths between 3500 and 4000 m, and two other at 2600 m depth.

A few hitherto disregarded finds of rhizocephala-

lans from the deep sea have been examined when possible, and identifications suggested. The paper contains a list of all rhizocephalans recorded from depths greater than 600 m.

All specimens, including types, are deposited in the Zoological Museum, Copenhagen.

Family PELTOGASTRIDAE

Tortugaster discoidalis n.sp.

Fig. 1

Material:

"Galathea" St. 616, Milford Sound, New Zealand (44°37'S, 167°53'E), 290 m, 19 Jan. 1952. Mud, 11.5°C - 2 specimens.

Diagnosis: Internal cuticle without retinacula. Body twisted to form a flattened, almost circular disk, indented in left side.

Description: One large specimen (holotype) attached far back on the abdomen of a male *Munida subrugosa* (White), its stalk piercing the center of the 6th abdominal segment. A much smaller specimen (paratype) is present slightly to the right of the midline on the telson. On the boundary separating the 6th segment and the telson a circular mark indicates the position of a third specimen, now lost. The size of the mark suggests that the third specimen was intermediate in size between the other two.

The holotype has the mantle aperture directed backwards with reference to the host. The body is

broadest (10.5 mm) in its anterior half. From the region of the stalk, which is placed near the center of the dorsal side, the body diminishes in width (to ca. 6 mm) and is twisted towards the left side. In both dorsal and ventral views the entire body thereby acquires a more or less circular outline and resembles a disk, the dorsoventral thickness of which is 2.5-3.0 mm at most places. In dorsal view the whitish visceral mass occupies the central part of the disk and lies curved around and to the right of the very short stalk. Except for extremely fine wrinkles running along the morphological longitudinal axis of the body, the surface is quite smooth.

Examination of the internal cuticle at three different places on the body did not reveal any retinacula.

The second specimen is subtriangular in outline and 1.5 mm broad.

The holotype was cut into transversal sections (10 μ m) and stained with hematoxylin + eosin. The internal anatomy and the location of the receptacles, vasa deferentia and colleteric glands correspond closely to that of *T. fistulatus* as described by Reinhard (1948). As in *T. fistulatus* the vasa deferentia are highly convoluted, an exceptional situation among peltogastrids. In accordance with the more discoidal body shape in *T. discoidalis*, the visceral mass is very broad and ventrally flattened rather than rounded and sausage-shaped as in *T. fistulatus*.

Tortugaster Reinhard was erected to accommodate *T. fistulatus*, a parasite of *Munidopsis robusta* A. Milne Edwards, *M. spinifer* (A. Milne Edwards) and *M. bahamensis* Benedict from off Tortugas and St. Augustine, Florida, and the north coast of Cuba

(Reinhard 1948, 1958). *T. discoidalis* n.sp. is distinguished from the type-species by having a more flattened body and by the absence of retinacula. It seems to be a peculiarity of the genus that members of both species attach very far back on the host's abdomen, a most unusual position in rhizocephalans. This habit is shared with *Triangulus boschmai* Brinkmann, all examined specimens of which (19) were attached on the 6th abdominal segment (Brinkmann 1936). The general organization of *T. boschmai* is so clearly similar to that of *Tortugaster* (family Peltogastridae) and dissimilar from that of *Triangulus* (family Lernaediscidae), that the species is here transferred to *Tortugaster*. *Tortugaster boschmai* n. comb. is known from a few Scandinavian localities; it has been found parasitizing *Munida tenuimana*, *M. sarsi* and *M. rugosa* down to a depth of 670 m (Høeg & Lützen 1985).

Cyphosaccus norvegicus Boschma, 1962

Fig. 2

C. norvegicus Boschma, 1962, p. 50, figs 1 & 2.

Material:

"Valdivia" St. 262, near the coast of Somalia (4°40'N, 48°39'E), 1242 m. - Ca. 8 specimens.

Doflein & Balss (1913: 158) reported that a specimen of *Munidopsis tridentata* (Esmark) (identical with *M. serricornis* (Lovén)) had parasites attached to the abdomen. The specimen, borrowed from Zoolo-

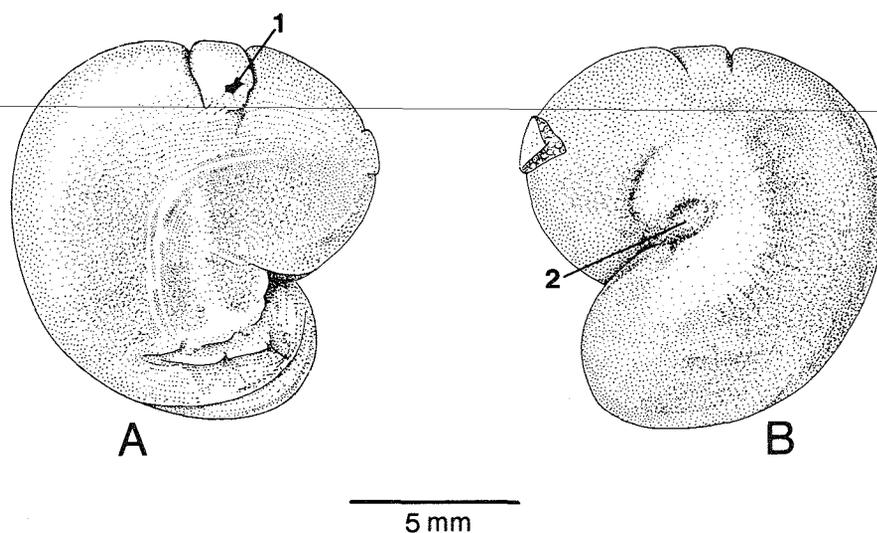


Fig. 1. *Tortugaster discoidalis* n.sp., holotype, seen in ventral (A) and dorsal (B) views. 1, mantle opening; 2, stalk region.

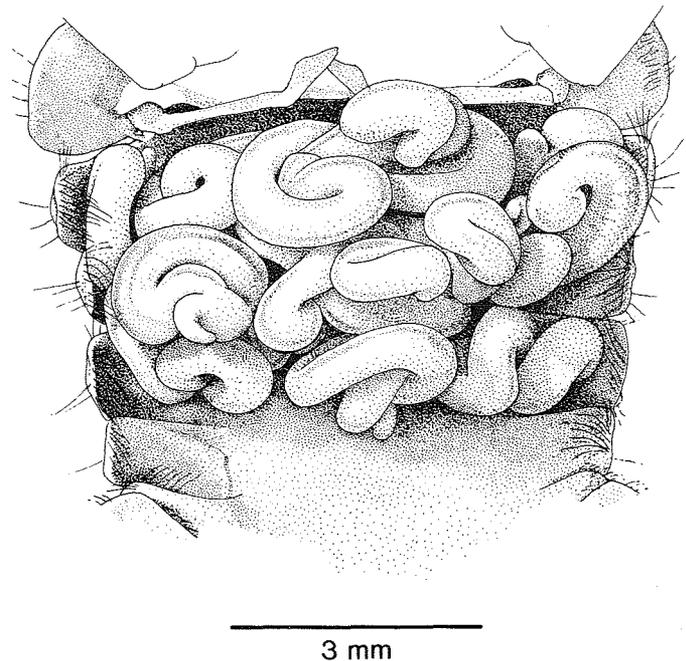


Fig. 2. *Cyphosaccus norvegicus* Boschma, attached to the abdomen of *Munidopsis serricornis* from the coast of Somalia (1242 m).

gische Staatssammlung in Munich, bears ca. 8 very well-preserved, whitish externae of *Cyphosaccus norvegicus* Boschma, all of the same size and apparently ovigerous. Until now this species has only been taken at a few localities along the Scandinavian coasts (Høeg & Lützen 1985). According to Dr. Jens Høeg, Institute of Comparative Anatomy, the species is quite common between 250 and 300 m depth in the Trondheim Fjord, W. Norway. The host in Scandinavian waters is also *Munidopsis serricornis* (Boschma 1962: as *M. tridentata*).

Cyphosaccus cornutus Reinhard, 1958

C. cornutus Reinhard, 1958, p. 299, fig. 2.

Material:

"Galathea" St. 202, off Natal (25°20'S, 35°17'E), 590 m, 21 Feb. 1951. Sand. - 9 specimens.

Description: Attached to segments 2-4 on the ventral side of the abdomen of a male *Munida militaris* Henderson.

All specimens are of the same size and measure ca. 10 mm in total length. The two arms are bent in the way characteristic of *C. cornutus*, but are distinctly more slender than in the single specimen illustrated by Reinhard. While the arms are widely separated in some specimens, they are approximated in others,

and the angle between them is consequently subject to much variation. Viewed through the transparent mantle wall, only one flask-shaped receptacle is visible (near the end of the posterior arm), which agrees with Reinhard's observation that in this species the two receptacles (Reinhard: testes) tend to fuse. Judging from the identical thickness of the mesentery and the appearance of the segmented eggs, reproduction was apparently synchronized in all nine specimens.

The earlier record is from *Munidopsis erinacea* (A. Milne Edwards) from Playa Baracoa, Cuba, 330 fathoms (604 m).

Cyphosaccus jensi n.sp.

Fig. 3; Pl. 14, Fig. 1

Material:

"Galathea" St. 726, Gulf of Panama (05°49'N, 78°52'W) 3670-3270 m, 13 May 1952. Clay, ca. 2.0°C. - 26 specimens, at least 1 and possibly 3 of which parasitized by a cryptoniscan epicaridean.

Diagnosis: Posterior arm almost twice as long as anterior arm, the two arms curved towards each other. Stalk long and distinctly set apart from rest of body.

Description: Attached to the ventral side of the abdomen of a female *Munidopsis antonii* (Filhol).

The material consists of 14 specimens that are still attached to the host, and 9 detached specimens found in the same jar. In addition, 3 specimens were separated from their host onboard and transferred to a tube, labelled "from a galatheid from St. 726". Dr. Keiji Baba, Kumamoto University, Japan, who identified the galatheids taken during the expedition, has kindly informed me that 3 species of *Munidopsis* were taken at St. 726, namely *M. antonii* (3 males, 1 non-ovigerous female), *M. vicina* Faxon (3 males, 10 females), and a member of the *M. subsquamosa* complex (a male). Since the 3 isolated parasites closely resemble the parasites from the female *M. antonii* in both shape and size, and since none of the other specimens of *Munidopsis* were apparently infected, it is almost certain that all 26 parasites came from the same host specimen.

The parasites still attached issue from a fairly small area consisting of a broad zone occupying the middle of abdominal segments 2-4. In the same region were a large number (25-35) of circular, closely packed marks resembling low cephalopod suckers. These could either represent 1) scars from in-

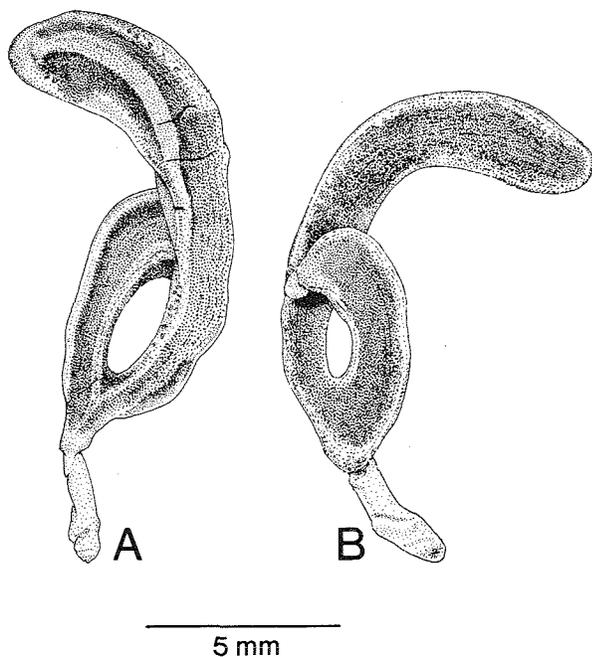


Fig. 3. *Cyphosaccus jensi* n.sp. Dorsal view of holotype (A) and ventral view of one of the paratypes (B).

dividuals of the same breed of parasites that had fallen off, e.g., during the dredging or handling the material, 2) scars from an earlier generation of parasites now replaced by those present, or 3) buds belonging to a future generation. As only one host specimen was available, the abdomen was not sectioned, a procedure which might otherwise have revealed the nature of these marks. From the area where the stalks issue the bodies of the parasites are directed backwards and to both sides of the host's abdomen and nearly touch the inner side of the segmental pleura (Pl. 14, Fig. 1).

One of the detached parasites, an ovigerous specimen, was selected as holotype (Fig. 3A). A non-ovigerous specimen, which was sectioned, proved to be parasitized by a cryptoniscan epicaridean; two other non-ovigerous specimens (not sectioned) were perhaps likewise parasitized.

The body is fundamentally V-shaped, but both arms are curved towards each other; the posterior arm is almost as long as the anterior one. Slender at the point of origin, both arms gradually become broader towards the tip. All specimens are of about the same size; the total length of most of them is 18-21 mm, the maximum width ca. 2.0 mm. In the parasitized specimen the visceral mass is greatly distended and broader (1.8-2.9 mm) than the others. The anterior arms of all specimens terminate in a

nipplelike protuberance, which in the parasitized specimens seems to be pierced by an extremely fine canal (birth pore). Such a pore seems absent in the other specimens, but this was not controlled by sectioning. The mesentery is narrow, extends along the entire length of the sac and is very distinct from outside. The stalk is prominent, slightly bulbous terminally and 3.0-5.0 mm long. The external surface of the ovigerous specimens is very finely longitudinally wrinkled, while in the parasitized ones it is distended and completely smooth.

Except for the parasitized specimen(s), all specimens were ovigerous. Close inspection of the offspring seen by transparency through the thin mantle (or incidental perforations of it) indicated that the embryos of all specimens were more or less in the same, and not very advanced, stage of development. The visceral sac of all ovigerous parasites was represented by an extremely narrow string of tissue. These facts suggest that all specimens had reached the same stage in their life cycle, which is in accordance with the possibility aired earlier that one generation of synchronously developing parasites may succeed another on the same host specimen.

The parasitized specimen was cut into 10 μ m thick serial sections and stained with hematoxylin + eosin. The sections showed that there are two receptacles included in the mesentery at the posteriormost tip of the body (one was sterile, the other filled with sperm cells). Colleteric glands, of which in this genus two occur near the base of the peduncle, could not be found, but they may have degenerated due to the specimen being parasitized. Neither was there any trace of an ovary.

The female cryptoniscan parasite with a few associated hermaphroditic larvae occupied the entire mantle cavity of the rhizocephalan host and penetrated even into the stalk region. The ovary contained numerous embryos, all in the same developmental stage.

Remarks: *J. jensi* n.sp. is distinguished from the other species by its far larger size, greater curvature of both arms and, particularly, its long stalk; the stalk is diminutive in *C. chacei*, *C. cornutus*, and *C. norvegicus*.

A characteristic feature of all described species of *Cyphosaccus* is the fact that they are always gregarious. Another peculiarity of this genus is the fact that the mantle aperture is a blind canal and that, according to Reinhard, a birth pore develops at its place when the progeny are ready to be emitted from the

mantle cavity. Whether the orifice thus formed remains a permanent structure serving the same purpose in subsequent clutches is not known. Even more puzzling is how the male cyprids, in the absence of a mantle aperture, gain access to the receptacles (the "testes" of Reinhard and Boschma) of the virginal parasite. These problems are presently being studied in *C. norvegicus* by my colleague, Dr. Jens Høeg, after whom I have the pleasure to name the new species.

Mayo (1974) and Wenner (1982) reported rhizocephalan specimens probably referable to *Cyphosaccus* on several Atlantic deep-sea galatheid-ean species down to a depth of ca. 5180 m (*Munida iris iris* A. Milne Edwards, *Munidopsis bermudezi* Chase, *Munidopsis crassa* Smith and *Munidopsis rostrata* A. Milne Edwards, see also Table 1). In addition, Dr. Baba has informed me that according to the late Professor H. Boschma, who examined them, but never published on the find, some rhizocephalans from galatheids which Dr. Baba collected off the east coast of New Zealand were referable to a species of *Cyphosaccus*.

Boschmaia munidicola Reinhard

Fig. 4

B. munidicola Reinhard, 1958, p. 301, fig. 3.

Material:

"Galathea" St. 626, Tasman Sea (42°10'S, 170°10'E), 610 m, 20 Jan. 1952. Globigerina ooze, ca. 7.6°C. - 4 specimens.

Description: Four specimens were attached ventrally on the middle of the abdomen of a large female *Munida gracilis* Henderson; the longitudinal axis of the parasites were at right angles to that of the host.

The body is V-shaped. The longer anterior arm (ca. 7.5 mm) is bent sharply backwards and the posterior arm (ca. 5.5 mm) curved so that the mesenterial side is concave. Both arms are broadest (ca. 2 and 1.5 mm respectively) near their middle; while the posterior arm tapers gently towards its tip, the anterior one is evenly rounded at the end. At the mesenterial side of the anterior summit there is a ring-shaped thickening of the cuticle; sections of one specimen showed that this area is pierced by a minute pore.

One specimen was embedded in paraplast and cut into 12 µm thick serial sections and stained with hematoxylin + eosin. This revealed that the two

small colleteric glands and the two receptacles are located as in *Boschmaia*, i.e. the glands near the anterior end of the visceral sac, the receptacles close to the stalk; in the allied *Cyphosaccus* the receptacles are situated near the posterior end and the colleteric glands in the vicinity of the stalk. It is a peculiar fact that in all four specimens the stalk arises on the left side of the externa, as is the case in *Cyphosaccus*, but contrary to the situation in *Boschmaia* where it is said to issue from the right side. But since the specimens resemble *B. munidicola* so closely I have provisionally referred them to this species, assuming that they represent a form that is laterally reversed to that described by Reinhard.

Previous records of *B. munidicola* are from *Munida irrasa* A. Milne Edwards from N. Carolina and Florida (14 and 179 m).

Galatheascus babai n.sp.

Fig. 5

Material:

"Soyo-Maru" St. 104, S. of Kyushu, Japan (31°12'N, 131°42,4'E), 1125 m. - 1 specimen.

Baba (1981) mentioned the occurrence of a rhizocephalan on a female *Uroptychus nigricapillis* Alcock (Galatheidea). He generously lent me his specimen, which represents a new species of the pelto-gastrid *Galatheascus*, and which I have the pleasure of naming *Galatheascus babai* n.sp. after its discoverer.

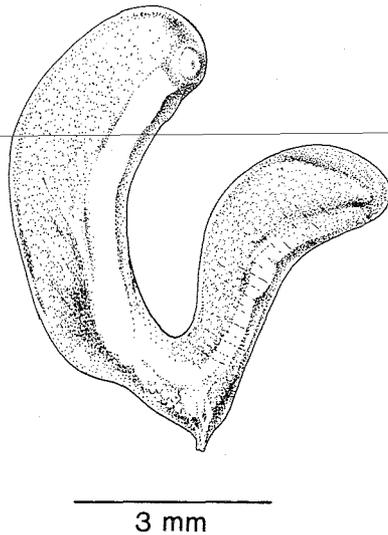


Fig. 4. *Boschmaia munidicola* Reinhard, viewed from the mesenterial side.

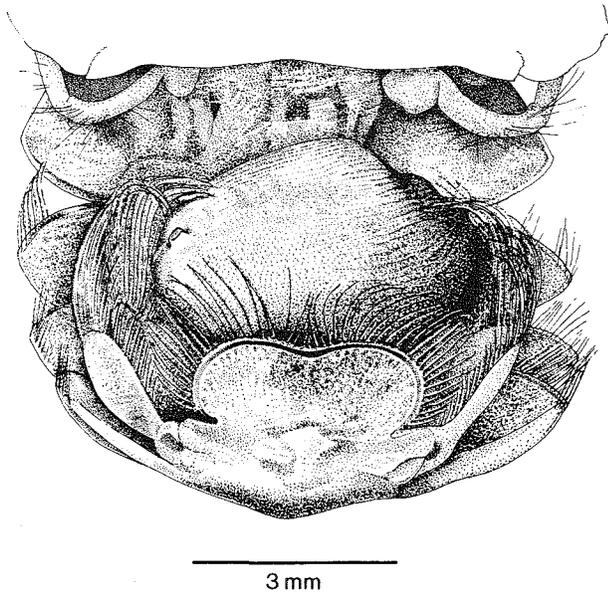


Fig. 5. *Galatheascus babai* n.sp. Latero-ventral view of holotype, attached to the abdomen of *Uroptychus nigricapillis* from S. of Kyushu, Japan (1125 m).

Diagnosis: Mantle opening at end of a short, ventrally directed tube. Stalk in front of middle of body. External cuticle with very fine longitudinal grooves.

Description: The single ovigerous specimen (holotype) is attached near the centre of the ventral side of the host's 3rd abdominal segment with the parasite's long axis perpendicular to the long axis of the host abdomen and the mantle aperture directed towards the right side of the host.

The specimen is almost oval, with a length of 5.2 mm, and the greatest width and height 3.6 and 2.0 mm, respectively. The colour in alcohol is yellowish orange. The mantle opening is small and circular; it is located at the end of a minute siphon that is placed anteriorly and directed towards the ventral side. The stalk is short but comparatively stout and issues slightly in front of the middle of the dorsal side. The cuticle is very finely plicated longitudinally and so thin and transparent that the eggs in the mantle cavity are visible through it.

The external appearance of the specimen and the way it is attached to the host are so characteristic of specimens of *Galatheascus*, that its relegation to this genus can not be doubted. Two species of *Galatheascus*, *G. striatus* Boschma and *G. minutus* Boschma, have been described, differing mainly in size (Boschma 1958) and presumably conspecific (Høeg & Lüt-

zen 1985). They parasitize shallow-water species of *Galathea* (family Galatheidae) and are known from European and South African waters and, if Reinhard's (1958) identification is correct, also from West Atlantic species of *Munida* and *Munidopsis*. Wenner (1982) further reports on a *Galatheascus* sp. from the Atlantic *Munida valida* Smith. The present species differs from the hitherto described species of *Galatheascus* by the ventral direction of its mantle aperture. The fact that it parasitizes a member of another family (Chirostylidae) of the Galatheidea also indicates that it belongs to a different species. A few species of *Uroptychus* have previously been reported to bear unidentified rhizocephalans: van Dam (1933) observed *U. australis* Henderson var. *indicus* Alcock and *U. scandens* Benedict to be parasitized. A specimen of *U. naso* van Dam (from the Kei Islands, 5°39'S, 132°23'E, 268 m) was also reported to be infected (van Dam, 1939) by a rhizocephalan. The latter is in the collections of the Zoological Museum, Copenhagen, and when inspected by the present author, also proved to belong to the genus *Galatheascus*.

***Briarosaccus callosus* Boschma, 1930**

Faxon (1895: 48) reported a specimen of the lithodid crab *Paralomis aspera* to bear what he considered to be a "huge *Peltogaster*". It was taken at "Albatross" St. 3353, 07°06'15"N, 80°34'W, Gulf of Panama, at 695 fathoms (1271 m). I have not seen the specimen, but it doubtless belongs to *Briarosaccus callosus*, a peltogastrid of very large size found on four species of *Lithodes* and on *Paralithodes camtschatica* and *Paralomis granulosa*. Faxon's find was overlooked by Arnaud & Do-Chi (1977), who listed all other records. *P. aspera* is the second species of *Paralomis* found to be parasitized, and *B. callosus* has only once been taken at greater depths, namely at 1299-1318 m, off the northern coast of Columbia, on *Lithodes agassizii*.

Family LERNAEODISCIDAE

***Lernaeodiscus triangularis* n.sp.**

Fig. 6

Material:
"Galathea" St. 314, Bay of Bengal (15°54'N, 90°17'E), 2600 m, 3 May 1951. Brownish ooze. - 1 specimen.

Diagnosis: Body regularly triangular in outline; several prominent rounded ridges radiating from region of mantle opening. Hold-fast of stalk without internal sclerotized projections.

Description: Attached to the ventral side of the 3rd abdominal segment of a female *Munidopsis granosa* Alcock. The parasite was positioned so that the mantle aperture faced posteriorly (with respect to the host). This is presumably an anomaly since in species of *Lernaeodiscus* it is typically directed forward. In 4 among 190 individuals of *L. ingolfi* Brinkmann, the body was turned opposite the usual way (Brinkmann, 1936).

Body of regular triangular outline, broadest (10.5 mm) in the posterior half; average thickness 3.5 mm. The surface is comparatively smooth, except for many very fine wrinkles and a number of prominent, rounded ridges radiating from the region of the mantle opening. The mantle opening is rather small, surrounded by a thick, protruding and much crenulated lip and placed at some distance from the anterior extremity.

Left and right parts of the body are separated in the median plane by deep dorsal and ventral clefts that run from the mantle aperture to the stalk region.

The stalk is short and broad. The sclerotized, yellowish hold-fast lacks internal projections. The cuticle surrounding the stalk exhibits a number of closely adjacent concentric lines similar to those known from other species of *Lernaeodiscidae*; they arise as a result of moulting of the externa's cuticle. Casting of the externa's cuticle was apparently imminent, as it had already detached over most of the body.

The two receptacles lie immediately beneath the dorsal surface; they are short and curved; both vasa deferentia run towards the midline and pass ventrad in a simple, short curve.

Firmizi (1966: 210) noted that the larger of two males of *Galacantha trachynotus* Anderson was infected with a large rhizocephalan emerging between abdominal segments 4 and 5. It was taken by the John Murray Deep Sea Expedition in the northern area of the Arabian Sea (22°53'30"N, 64°56'10"E), 1893 m. I have seen the specimen, which is deposited in the British Museum (Natural History), London. It belongs to the genus *Lernaeodiscus* and has an outline quite similar to *L. triangularis* n.sp., but it is in fairly poor condition, so the question of its identity can not be decided.

Dr. Elizabeth L. Wenner, Marine Resources Research Institute, South Carolina, has kindly fur-

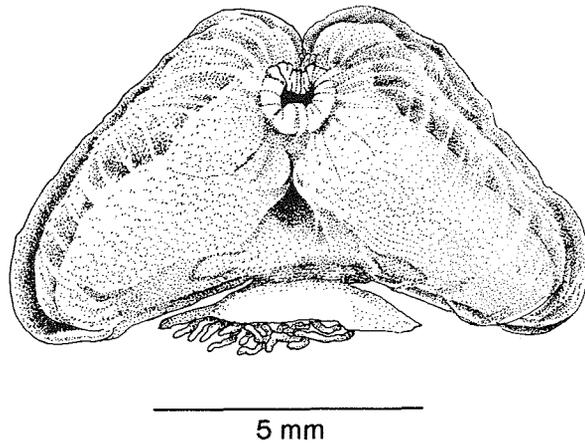


Fig. 6. *Lernaeodiscus triangularis* n.sp., dorsal view.

nished me with sketches made by professor A. Veillet, Nancy, France, of *Lernaeodiscus* sp. (C) from *Munidopsis rostrata* A. Milne Edwards (see Wenner 1982). It is interesting to note that it resembles *L. triangularis* n.sp. in general outline as well as in the presence of the characteristic rounded ridges radiating from the mantle opening. The parasitized hosts were taken in the Middle Atlantic Bight at depths ranging from 2165 to 2767 m.

Triangulus sp.

Material:

"Galathea" St. 626, Tasman Sea (42°10'S, 170°10'E), 610 m, 20 Jan. 1952. Globigerina ooze, ca. 7.6°C. - 1 specimen.

Description: The specimen is so small (1.8 mm in width) that it cannot be identified, but the asymmetrically placed slit-like mantle opening is characteristic of *Triangulus*. It is attached to the underside of the abdomen of a small female *Munida gracilis* Henderson.

Family SACCULINIDAE

Sacculina abyssicola Guérin-Ganivet, 1911

S. abyssicola Guérin-Ganivet, 1911, p. 63, pl. I, figs 10 & 11.

Material:

"Galathea" St. 192, off Durban (32°00'S, 32°41'E), 3530 m, 5 Feb. 1952. Globigerina ooze, 1.2°C. - 1 specimen.

"Galathea" St. 217, Mozambique Channel (14°20'S, 45°09'E), 3390 m, 27 Feb. 1952. Globigerina ooze, 1.6°C. - 1 specimen.

"Galathea" St. 238, off Kenya (03°23'S, 44°04'E), 3960 m, 13 Mar. 1952. Globigerina ooze, 1.8°C. - 2 specimens.

Description: The species occurs singly on the crab *Ethusina abyssicola* Smith. At St. 192 one among 3 male crabs was parasitized, at St. 217 one male crab among 3 males and 1 female was parasitized, and at St. 238 2 parasitized females occurred among 3 males and 7 females. The size of the externa ranges from 6.0 mm high and 6.5 mm long (St. 217) to 12.5 mm in both height and length (St. 238). Sectioning of one of the parasites from St. 238 failed almost completely.

Two of the specimens were non-ovigerous; the two other contained newly laid eggs (length 145 μ m).

Guérin-Ganivet (1911) stated that the smaller of his two parasitized male crabs was heavily feminized. The male from St. 217 (carapace 12.5 mm broad, 13.0 mm long) has the abdomen very slightly broader than usual, but is masculine in all other respects. The male from St. 192 (12.5 mm broad, 14.0 mm long) has a broad feminized abdomen, all segments of which are movable; the copulatory appendages are normal (lost in one side), but are succeeded by 3 pairs of pleopods. The two parasitized females look quite normal.

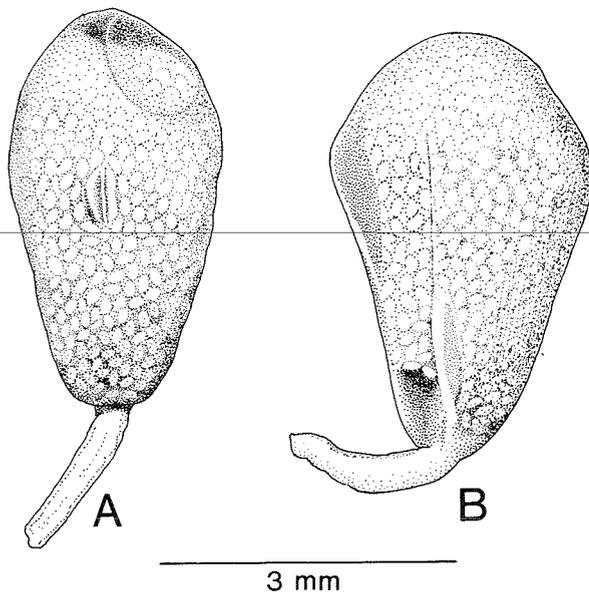


Fig. 7. *Pirusaccus socialis* n.gen., n.sp. Ventral view (A) and dorsal view (B) of ovigerous specimen with advanced embryos in the mantle cavity.

Earlier records, also on *E. abyssicola*, are from the North Atlantic Ocean, viz. the Cape Verde Islands (15°48'N, 22°43'W), 3655 m, and the Azores (42°15'N, 23°37'W), 3975 m (Guérin-Ganivet, 1911).

INCERTAE SEDIS

Pirusaccus n.gen.

Diagnosis: Externae gregarious, pear-shaped; stalk distinctly separated from body. Visceral sac fused with inner mantle wall along a short distance in the ventral midline. Two colleteric glands. Sperm enclosed in single-layered cellular capsules that lie free in the mantle cavity.

The generic name derives from *pirum* = pear (L), and *saccus* = sac (L).

Pirusaccus socialis n.sp.

Figs 7 & 8, Pl. 14, Figs 2-5

Material:

"Galathea" St. 314, Bay of Bengal (15°54'N, 90°17'E), 2600 m, 3 May 1951. Brownish ooze. - 53 specimens.

Diagnosis: With the characters of the genus. Externae 3-4 mm in length. Parasitic on *Munidopsis rostrata* A. Milne Edwards.

Description: Attached to the ventral side of the abdomen of two males of *Munidopsis rostrata* A. Milne Edwards. In one of the hosts (specimen A) 30 externae, apparently all with advanced embryos, emerge from the three first segments; in the other host (specimen B) 23 externae, most of them with very young embryos, are attached to segments 3-6. Attachment is mainly to a median zone occupying 1/3 of the width of the segments involved.

The externae are pear-shaped, 3-4 mm in length, 2-2.5 mm in greatest width. The body is distinctly set off from the stalk which is straight or slightly twisted and 2-2.5 mm long. The stalk is of equal diameter throughout, except near its base which, upon entering the host's tissue, is slightly swollen.

The externae are smooth-walled and bilaterally symmetrical; the latter fact is most apparent in the specimens from host A, which had well advanced embryos in the mantle cavity. In them the line of fusion between the mesentery and the mantle is seen to extend from the base of the body and along at least 2/3 of the dorsal midline (Fig. 7B), and a short dou-

ble line in the mantle is evident on the opposite side a little in front of the middle of the body (Fig. 7A). In the specimens from host B these details are more difficult to distinguish.

The stalks appear to arise from a mat of apparently interconnecting roots lying immediately beneath the host's skin.

Two externae from host A and one from host B were embedded in paraplast and cut in 10 μ m thick sections and stained with hematoxylin + eosin. One further specimen from host A and 8 from host B were embedded in epon and cut into 2 μ m thick sections and stained with toluidine-blue. Only one of the epon section series (host B) was complete; in the others, smaller or larger parts of each externa were left unsectioned. The type-specimen was selected from host A.

The visceral sac in both ovigerous and non-ovigerous specimens has almost the same shape as the externa, but is relatively smaller in the former specimens. It is attached to the dorsal mantle by means of a thin mesentery (mentioned above). Ventrally a short protruding ridge arising from the visceral sac is intimately adjoined to the mantle wall at the area delimited by the short double lines, but this coalescence is not a permanent one (see later). Everywhere else the visceral sac is separated from the mantle by a mantle cavity, narrow in the (only examined) non-ovigerous specimen, rather spaceous in the ovigerous ones. The mantle cavity is everywhere lined by a distinct and unmistakable cuticle.

The stalk contains a meshwork of connective tissue traversed by a discrete central haemocoelic tube without epithelial walls. Numerous peripherally placed longitudinal muscle fibers indicate that the externa is quite movable in the stalk region. The stalk tube and its envelope of connective tissue continues into the body and, upon entering the visceral sac, takes the shape of a narrow septum which bisects the visceral sac. Near the middle of the body this septum and the slit-shaped haemocoelic space it contains separate into a larger and longer dorsal and a smaller and shorter ventral part (Fig. 8). Along the periphery of the visceral sac each of the haemocoelic slits widens into a longitudinal channel.

The remainder of the visceral sac is occupied by the ovary, which towards the externa's base becomes divided into right and left parts by the haemocoelic spaces described above. In the specimen which had not spawned, only a single generation of ova, and no oogonia, could be distinguished in the ovary. In all of the 11 examined ovigerous specimens, the ovary had completely vanished; neither oogonia nor ova of a second batch could be detected, and the space of the spent ovary was filled with an abundant fluid. These facts suggest that the brood in the mantle cavity was the last and, since this was true of the externae from both hosts, perhaps the only one produced.

Two extremely short and narrow winding channels, equivalent to oviducts or colleteric glands, unite the ovary and the mantle cavity at the level of the presumed prospective mantle opening (Fig. 8).

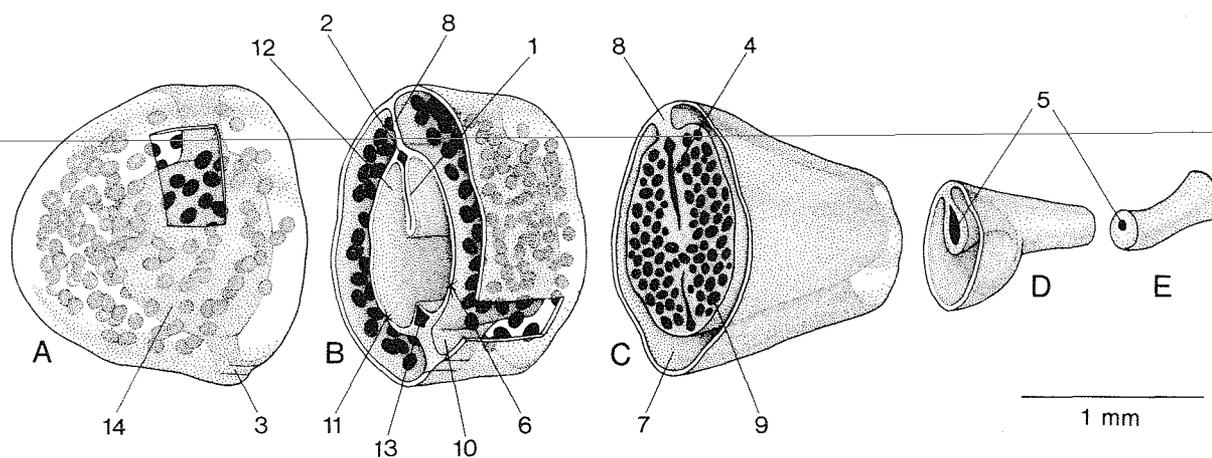


Fig. 8. Anatomy of *Pirusaccus socialis* n.gen., n.sp., composite exploded side view, dorsal side towards the top, A & B after an ovigerous specimen, C-E after a non-ovigerous specimen. 1, connective tissue septum; 2, dorsal haemocoelic channel; 3, fusion between mantle and visceral sac; 4, haemocoelic space; 5, haemocoelic tube; 6, left colleteric gland; 7, mantle cavity; 8, mesentery; 9, ovary; 10, projection from visceral sac; 11, right colleteric gland; 12, space of spent ovary; 13, ventral haemocoelic channel; 14, visceral sac.

Some of the cells lining the two channels are obviously glandular; all of the embryos in the mantle cavity were surrounded by a non-cellular secreted capsule as is usual in rhizocephalans provided with colleteric glands.

A mantle aperture did not occur in any of the specimens, but quite likely an opening of some sort will form at a later stage along the two ventral double lines that can be seen from outside. Just inside this small restricted area the inner mantle wall is seen to be in very close contact with a short, ridge-like prominence of the visceral sac. At high magnification the cuticles of the two structures are observed to adjoin each other intimately except for a narrow median zone along which the inner cuticle and mantle tissue are wanting (Pl. 14, Fig. 5); as a consequence, along this zone the cuticle of the visceral sac is fused to the interior of the outer mantle cuticle. Since the latter is continuous with the remaining outer mantle cuticle, the absence of a mantle at this place must be secondary; it has perhaps vanished by sealing off of the area through establishment of a contact with the outgrowth from the visceral sac.

It can not be proven that the structure described above will eventually produce an opening from the mantle cavity to the exterior, since it rather seems to support and strengthen the mantle; nevertheless, in many of the externae the mantle had split at one or both sides of the structure (Pl. 14, Fig. 5); one may imagine that the mantle could be torn open at this particular place if the circular muscle fibers of the mantle wall all contracted vigorously.

In 7 of the 8 externae that had spawned recently, packages of sperm cells were discovered in the mantle cavity, lying unattached between the embryos. The sperm cells of each package were confined within a capsule of a single layer of rounded or irregularly shaped cells which contained numerous inclusions and vacuolae (Pl. 14, Figs 3 & 4). There was no exterior cuticle around the cells. The sperm cells lay un-oriented within the packages and had long nuclei and filiform tails typical of cirripedian spermatozoa. The shape of the packages varies and depends apparently on the space left by the embryos. Sizes of a few packages, including their cellular exterior, were measured at 95×130 , 80×170 , 92×180 , and $132 \times 208 \mu\text{m}$.

The number of sperm packages found per externa was 1, 1, 1, 1, 2, 2, and 4, but since several of the section series were highly incomplete, the number was in all probability higher. No packages were found in the 3 sectioned externae with advanced embryos, nor

in the single non-ovigerous externa examined, in spite of the fact that these specimens were all cut into complete section series.

Among the embryos of all externae occurred a large number of cells, singularly or a few attached loosely together, which were indistinguishable from the cells that enclose the sperm packages (Pl. 14, Figs 3 & 4). No such cells, nor cells at all, were found in the mantle cavity of the non-ovigerous externa.

From external inspection alle specimens on each of the two hosts appeared to be in the same stage of the reproductive cycle and, with the exception of the single non-ovigerous externa, this was confirmed by the section series. One way that stimuli resulting in synchronization of the reproductive activity may spread is through a common root system, but section series designed to detect whether the roots of all externae interconnect, failed because of the insufficient preservation of the material. They showed, however, a thin layer of roots placed superficially beneath the host's skin and further, that some roots penetrated deeper into the abdomen to ramify among the muscles and around the intestine.

Remarks: *Pirusaccus* n.gen. represents a type of rhizocephalan not encountered before. The structure of the mantle aperture, if this is actually what the secondary fusion between mantle and visceral sac represents, is unparalleled. There are no male receptacles as in the Clistosaccidae, Lernaediscidae, Peltogastridae and Sacculinidae. A mesenterial canal such as exists in *Chthamalophilus*, *Boschmaella*, *Duplorbis*, *Mycetomorpha*, and *Cryptogaster* (Bocquet-Védrine & Bourdon 1984) is absent. There is some resemblance to species of *Thompsonia* in the shape of the externa and the fact that both genera are gregarious; however, with the possible exception of *T. cubensis* Reinhard & Stewart, a true mantle cavity never develops in *Thompsonia*. Moreover, not even in the few species of that genus where a space resembling a mantle cavity appears between the mantle and the visceral sac, does development occur there; in every case where reproduction has been studied in *Thompsonia*, the eggs are apparently fertilized *in situ* in the ovary and complete their development until the cypris stage there (see, e.g., Yanagimachi & Fujimaki 1967).

The nature of the peculiar sperm packages in *Pirusaccus* is obscure. It seems a likely conclusion, however, that when the eggs are discharged into the mantle cavity, the packages disintegrate and the

spermatozoa become liberated; in two instances the wall of a package was observed to have ruptured into the more or less individual cells that lie scattered among the embryos, and the large number of these cells in all of the ovigerous externae is evidence that the packages recorded are the only leftover of an earlier, much larger number. An assumed disintegration of the sperm packages after egg-laying is also consistent with the absence of packages in the 3 externae with advanced embryos while many free cells were present. On the other hand, one would expect a high number of packages to occur in the externae before or at the time of ovulation, but none occurred in the single non-ovigerous externa which, judging from the size of its ova, was just about to ovulate. If each sperm packet represents an introduced male organism, their absence in some of the externae, however, becomes quite explainable.

In most rhizocephalans the sperm cells develop in receptacles. In species of *Thompsonia* they mature in the mantle while being nourished by large cells (Yanagimachi & Fujimaki 1967). In a few aberrant genera spermiogenesis takes place in discrete bodies in the mantle cavity (Bocquet-Védrine & Bourdon 1984). The origin of these bodies has not been determined with certainty in all cases, but in two of the genera, *Chthamalophilus* and *Boschmaella*, both parasites of barnacles, they are believed to be budded off from a thickening of the mantle wall (Bocquet-Védrine 1961, 1968). The sperm-containing bodies of *Chthamalophilus* (Bocquet-Védrine: "îlots testiculaires") are fundamentally similar to the sperm packages of *Pirusaccus* in that the sperm cells (or spermatogonia and spermatids) are enveloped by a

peripheral capsule of rounded cells; however, the sperm cells in *Chthamalophilus* become liberated without rupturing of the capsule, and Bocquet-Védrine presumed that, following discharge of the sperm, the body enters a new spermatogenetic cycle. The total disappearance of the sperm packets in the specimens of *P. socialis* should be viewed in light of the fact that the brood in the mantle cavity was the last, and perhaps only one produced.

Records of unidentified Rhizocephala from the deep sea

Host: *Galacantha diomedea* Faxon

According to Faxon (1895: 81) a male of *Galacantha diomedea* was infested with "a *Peltogaster*". The specimen was collected at "Albatross" St. 3371, between Panama and the Galapagos Islands (05°26'20"N, 86°55'W), 770 fathoms (1408 m). This rhizocephalan, together with the following one, were removed from their hosts and entrusted to Dr. E. G. Reinhard, but can no longer be located (information kindly provided by Dr. C. Kessler, Museum of Comparative Zoology, Harvard University, U.S.A.).

Host: *Munidopsis hendersoniana* Faxon

A female infested with "a *Peltogaster*" (Faxon, 1895: 100). It was taken in the Gulf of Panama by the "Albatross" at St. 3393 (07°15'N, 79°36'W), 1020 fathoms (1865 m); the specimen could not be traced (see above).

GENERAL REMARKS

The species or specimens of rhizocephalans that have been recorded from depths greater than 600 m are listed in Table 1. Ignoring the unidentified species of *Cyphosaccus*, four of these species are truly abyssal: *Triangulopsis abyssorum* Guérin-Ganivet, *Sacculina abyssicola* Guérin-Ganivet (5 records), *Cyphosaccus jensi* n.sp., and *Trachelosaccus hymenodora* Boschma. Two of these genera, *Triangulopsis* and *Trachelosaccus*, appear to be endemic to this zone.

Most of the hosts involved belong to the anomurans, particularly the Galatheidae, a family that is richly represented in the deep sea. By comparison,

crabs are much less frequent there; Dahl (1946) demonstrated that the three genera of sacculinized crabs from great depths (*Ethusina*, *Dorhynchus* and *Geryon*) are also among the four or five genera that are most frequently recorded in deep-sea samples.

The depth records of rhizocephalans from crabs and anomurans are relatively close to those of their groups, and when the small number of records is allowed for, the generalization can be made that nothing but the absence of suitable hosts limits the vertical distribution of the parasites. Members of all three dominant families of rhizocephalans are known from the abyssal zone.

Adaptations to life in the deep sea have not yet been discovered with certainty in the Rhizocephala. Dahl (1946) remarked that the eggs of *Trachelosaccus hymenodora*, as described by Boschma (1928), contained extraordinarily large lipid vacuoles. This is apparently also the case in *Angulosaccus tenuis* Reinhard (1944, Fig. 1C, D), in *S. abyssicola* (serial sections of specimen from St. 238) and in *Lernaeodiscus* sp. from *Galacantha trachynotus*.

Compared with other Cirripedia, all rhizocephalans produce very small eggs with a length and diameter that are subject to rather minor variations from one species to another. The eggs of 14 species from the deep sea (Table 1) lie within the normal range for the group (100-200 μm in length for 52 species of lernaeodiscids and sacculinids, and 125-275 μm for 14 species of peltogastrids).

Dahl (1946) expected that the deep-sea rhizocephalans would show the same tendency to abbreviate the pelagic larval stage as that exhibited by so many cold-water invertebrates. He emphasized, on the other hand, that since the larvae of rhizocephalans do not feed, shortage of food in the deep sea represents no serious obstacle to a normal life. There are, however, quite other aspects of the pelagic larval phase which ought to be considered in this context.

In the majority of the rhizocephalans the larvae are discharged as nauplii which undergo two or three moults before they develop into the final larval stage, or cyprid. The minimum duration of the larval stages is 8-10 days in sublittoral species. But in a few genera and species the nauplius stage is suppressed, and the eggs develop directly into the cyprid stage. The time spent by the larvae in the water masses is probably shorter in these cases; according to Høeg (in press) it is 1-2 days in male cyprids of *Clistosaccus paguri*.

The behaviour and significance of the two larval types differ greatly, a fact that should be kept in mind when one tries to explain why the larval stage has been shortened in some species. The nauplius is heavier than sea water and possesses no hydrostatic devices, except that in some species the periphery of the body is surrounded by a hollow, water-filled annulus, which probably delays sinking (Schram 1972). Most nauplii have a nauplius eye and react to light by swimming towards it. Compared to passive transport by the water masses, movements in the horizontal plane caused by the larva's own locomotion are probably indifferent (due to the modest size of the body), and the significance of upward swimming,

stimulated by light, is undoubtedly that the larva constantly remains afloat. The chief function of the nauplius is thus to act as a non-feeding stage of dispersal, adapted to being more or less passively transported along with the water currents.

The cyprid, in contrast, is a site-selection organism. Equipped with chemo-sensory appendages on the antennae it seeks towards the bottom and is actively or passively attracted by a host or, in the male sex, an already established virginal female externa. In the few examined cases (species of *Sacculina* and *Lernaeodiscus*) the length of time in the plankton is shorter in the cyprid stage (3-5 days) than in the nauplius stages (4-5 days).

In littoral and sublittoral rhizocephalans parasitizing hosts that often show a discontinuous distribution it would seem advantageous to have an exploring stage of dispersal. But one may envisage at least two situations where the advantage of dispersal is more than counterbalanced by the hazards of the planktonic life:

1) When the habitat is restricted in area as it is in freshwater, migrations of the host would satisfy the parasite's need of being dispersed; long-lived larvae would even risk being carried along with the current into a hostile environment. Not surprisingly, therefore, the only three rhizocephalans that are true freshwater dwellers, *Ptychascus glaber* Boschma (rivers; Boschma 1967) and *Sesarmaxenos monticola* Annandale and *S. gedehensis* Feuerborn (mountain streams; Annandale 1911, Feuerborn 1933) have suppressed the nauplius stage and their larvae hatch as cyprids. Okada & Miyashita (1935) reported that *Sacculina gregaria* reproduces when its migratory freshwater host crab, *Eriocheir japonicus*, approaches the river mouth. They observed nauplii in the mantle cavity, but it is actually not known whether the larvae are emitted as nauplii or not.

2) When the habitat is uniform over vast areas, and the occurrence of the host(s) not too patchy in combination with the absence of strong transport currents, dispersal in the parasitic stage by random movements of the host could well be far superior to that effected by the nauplii. Such conditions are encountered more often in the deep sea than anywhere else in the marine environment.

The larvae of *Lernaeodiscus ingolfi* and *Triangulus galathea* are known to be emitted as nauplii (Brinkmann 1936; Veillet 1945), while those of *Clistosaccus paguri* and *Sylon hippolytes* are discharged as cyprids (Boschma 1928), but all four species have their chief distribution in the sublittoral

zone. *Tortugaster fistulatus* (bathymetrical distribution 402 to 512-549 m) hatches its larvae as cyprids (Reinhard 1948) and so does *Cyphosaccus chacei* (146-364 m; Reinhard 1958); none of these, however,

are true deep-sea species. The larvae of *C. norvegicus* (ca. 200-1242 m), on the other hand, hatch as nauplii (pers. comm. by Dr. Jens Høeg). I have reexamined 7 of the existing specimens of *Sacculinaatlan-*

Table 1. Species of Rhizocephala known from bathyal and abyssal depths (>600 m). Egg length calculated from serial sections are corrected for shrinkage. Brackets around bathymetrical distribution indicates depth range of host, not parasite. (A) Anomura, (B) Brachyura, (C) Caridea, and (D) Cumacea.

Species	Egg length (μm)	Bathymetrical distribution (m)	Host	References
Peltogastridae				
<i>Angulosaccus tenuis</i>	185	1603	(A) <i>Parapagurus armatus</i>	Reinhard 1944
<i>Boschmaia muniticola</i>	160	14-610	(A) <i>Munida irrasa</i> (A) <i>Munida gracilis</i>	Reinhard 1958 present study
<i>Briarosaccus callosus</i>	200	0-1318	(A) <i>Lithodes</i> spp. (A) <i>Paralithodes camtschatica</i> (A) <i>Paralomis</i> spp.	Arnaud & Do-Chi 1977 Faxon 1895 present study
<i>Cyphosaccus cornutus</i>	—	590-604	(A) <i>Munidopsis erinacea</i> (A) <i>Munida militaris</i>	Reinhard 1958 present study
<i>Cyphosaccus jensi</i> n.sp.	140	3800	(A) <i>Munidopsis antonii</i>	present study
<i>Cyphosaccus norvegicus</i>	—	c.200-1242	(A) <i>Munidopsis serricornis</i>	Doflein & Balss 1913 Boschma 1962
<i>Cyphosaccus</i> sp.	—	2257	(A) <i>Munidopsis rostrata</i>	Wenner (pers. comm.)
<i>Cyphosaccus</i> sp.	—	(2532-5315)	(A) <i>Munidopsis crassa</i>	Mayo 1974, Wenner 1982
<i>Cyphosaccus</i> sp.	—	5179-5184	(A) <i>Munidopsis bermudezi</i>	Wenner (pers. comm.)
<i>Galatheascus babai</i> n.sp.	—	1125	(A) <i>Uroptychus nigricapillis</i>	Baba 1981, present study
<i>Galatheascus</i> sp.	—	660-846	(A) <i>Munida valida</i>	Wenner (pers. comm.)
<i>Tortugaster boschmai</i> nov. comb.	—	50-670	(A) <i>Munida</i> spp.	Høeg & Lützen 1985
<i>Trachelosaccus hymenodora</i>	125-140	2356-3350	(C) <i>Hymenodora glacialis</i>	Boschma 1928
Lernaeodiscidae				
<i>Lernaeodiscus ingolfi</i>	160	100-1438	(A) <i>Munida</i> spp.	Dahl 1946
<i>Lernaeodiscus triangularis</i> n.sp.	130	2600	(A) <i>Munidopsis granosa</i>	present study
<i>Lernaeodiscus</i> sp.	175	1893	(A) <i>Galacantha trachynotus</i>	Tirmizi 1966
<i>Lernaeodiscus</i> sp.	—	2165-2767	(A) <i>Munidopsis rostrata</i>	Wenner (pers. comm.)
<i>Triangulopsis abyssorum</i>	—	4255	(A) <i>Munidopsis parfaiti</i>	Guérin-Ganivet 1911
<i>Triangulus galathea</i>	150 & 200	0-1710	(A) <i>Galathea</i> spp.	Dahl 1946
<i>Triangulus</i> sp.	—	610	(A) <i>Munida gracilis</i>	present study
Sacculinidae				
<i>Sacculina abyssicola</i>	145	3390-3975	(B) <i>Ethusina abyssicola</i>	Guérin-Ganivet 1911 present study
<i>Sacculina atlantica</i>	125	1180-1275	(B) <i>Dorhynchus thomsoni</i>	Boschma 1928
<i>Sacculina benedeni</i> (?)	—	1236	(B) <i>Geryon affinis</i>	Dahl 1946
<i>Sacculina elongata</i>	—	1463	(B) <i>Ethusina gracilipes</i>	Boschma 1933
<i>Sacculina muricata</i>	—	720	(B) <i>Sphenocarcinus stimpsoni</i>	Boschma 1931
<i>Sacculina sulcata</i>	—	1300	(B) <i>Ethusina gracilipes</i>	van Kampen & Boschma 1931
Clistosaccidae and Sylonidae				
<i>Clistosaccus paguri</i>	135	0-970	(A) <i>Pagurus</i> spp.	Dahl 1946
<i>Sylon hippolytes</i>	150	9-875	(C) various Caridea	Høeg & Lützen 1985
Incertae sedis and unidentified species				
<i>Cryptogaster cumacei</i>	—	2644-2895	(D) <i>Paralamprops semiornata</i>	Bocquet-Védrine & Bourdon 1984
<i>Pirusaccus socialis</i> n.g., n.sp.	120	2600	(A) <i>Munidopsis rostrata</i>	present study
Species not identified	—	1865	(A) <i>Munidopsis hendersoniana</i>	Faxon 1895
Species not identified	—	1408	(A) <i>Galacantha diomedea</i>	Faxon 1895
Species not identified	—	828	(A) <i>Uroptychus australis</i>	van Dam 1933

tica (1180-1275 m) and found nauplii with fully developed appendages in one of them. No additional information on the subject can be extracted from the other deep-sea material, including that collected by

the Galathea Expedition, and for the present one must conclude that there is no indication that the deep-sea rhizocephalans have abbreviated their planktonic larval stage.

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