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Crustacea Ascothoracida

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ABSTRACT

Females and larvae of an ascothoracid crustacean, *Endaster hamatosculum* gen. et sp. nov., are described. They live in large cysts in arms of the sea-star *Zoroaster carinatus philippinensis* Fisher, 1916. The new genus belongs to the previously monotypic Ctenosculidae and is distinguished from *Ctenosculum* Heath, 1910, primarily by its wider than long, ellipsoidal carapace, and features of the thorax. The peculiar nauplii have well developed but uniramous antennae and mandibles, and the sexes are separable by the end of naupliar development. The first ascothoracid larva is more generalized than the same stage of other echinoderm-infesting ascothoracids. *Endaster*'s possible utility as a model of the evolutionary grade between *Ctenosculum* and *Ulophysema* Brattström, 1936, is discussed.

RESUMÉ

Endaster hamatosculum gen. et sp. nov., crustacé ascothoracide parasite de l'astéroïde *Zoroaster carinatus philippinensis* Fisher, 1916, est décrit. Une étoile de mer infestée d'*Endaster* porte dans un bras un kyste interne qui s'ouvre à l'extérieur par un petit trou. C'est la deuxième espèce connue de Ctenosculidae, la femelle se distinguant du *Ctenosculum* Heath, 1910, par sa carapace en forme d'éllipsoïde latéralement élargi et par son thorax. Les larves naupliennes ont des antennes et des mâchoires uniramées et natatoires, et les sexes sont distincts avant la fin de ce stade. La première larve ascothoracidienne se révèle plus primitive que celles d'autres ascothoracides parasites d'échinodermes. *Endaster* peut représenter le niveau évolutif entre *Ctenosculum* et *Ulophysema* Brattström, 1936.

INTRODUCTION

The Ascothoracida are a small group of maxillopodan crustaceans that parasitize anthozoans and echinoderms. WAGIN (1976) provides the most recent review, and GRYGIER (1983 c) cites most of the subsequent literature. The MUSORSTOM Expeditions to the Philippines in 1976 and 1980 have produced a new asteroid-infesting ascothoracid, *Endaster hamatosculum* gen. et sp. nov., with a life style not heretofore observed.

Other Philippine ascothoracids recorded to date are : *Dendrogaster ludwigi* Le Roi, 1905, in the coelom of the asteroid *Echinaster fallax* Müller & Troschel, 1840 (LE ROI, 1907) ; an undescribed species of *Dendrogaster* in the asteroid *Sidonaster vaneyi* Koehler, 1909 (FISHER, 1919) ; *Waginella axotremata* Grygier, 1983, an ectoparasite of stalked crinoids of the genus *Saracrinus* A. H. Clark, 1926 (GRYGIER, 1983 a) ; *Thalassomembracis orientalis* Grygier, 1984, parasitizing an unidentified species of the gorgonian *Chrysogorgia* Duchassaing & Michelotti, 1864 (GRYGIER, 1984).

The present specimens were brought to my attention by P. ILLG (University of Washington). A. GUILLE (Muséum National d'Histoire Naturelle) lent me preserved specimens, and M. JANGOUX (Université libre de Bruxelles) sent dried ones. All are deposited in the Muséum in Paris.

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SYSTEMATIC ACCOUNT

Family CTENOSCULIDAE Thiele, 1925

Genus **Endaster** gen. nov.

DIAGNOSIS

Carapace in females a large, oval, laterally produced sac with spines and hooked setae near protruding aperture, inner lining with pair of setose ridges flanking body. Antennules vestigial. Thorax arched, 6-segmented with transverse ridge on greatly enlarged first segment, dorsal humps and paired dorsolateral protrusions on other segments. Six pairs of thoracopods ; first pair biramous (endopod variable) with large filamentary appendage at base ; rami of other limbs vestigial setose lobes, lost in sixth pair. Abdomen 4-segmented, penis rudiment minute or absent. Furcal rami elongate with short distal and medial setae. Metanauplii with long, setose, uniramous antennae and mandibles. Sexes separable by end of naupliar development, adult males unknown.

ETYMOLOGY

From Greek *endon* (within) and *aster* (star), referring to the relationship with the sea-star host. Gender masculine.

Endaster hamatosculum sp. nov.

DIAGNOSIS

As for genus, since this is the type-species.

ETYMOLOGY

From Latin *hamatus* (hooked) and *osculum* (little mouth), referring to the hooked setae near the carapace aperture.

MATERIAL

MUSORSTOM I

Station 43. — 24.03.1976, 13°50.5′-52.3′ N, 120°28.0′-28.6′ E, 484-448 m, 2 ♀♀ (holotype and paratype), both brooding late metanauplii.

MUSORSTOM II

Station 11. — 21.11.1980, 14°0.1′-0.4′ N, 120°19.9′-19.7′ E, 194-196 m, 2 ♀♀ (paratypes), brooding nauplii and metanauplii, respectively.

Station 12. — 21.11.1980, 14°01.0′-02.0′ N, 120°19.7′-21.0′ E, 197-210 m, 1 ♀ (paratype).

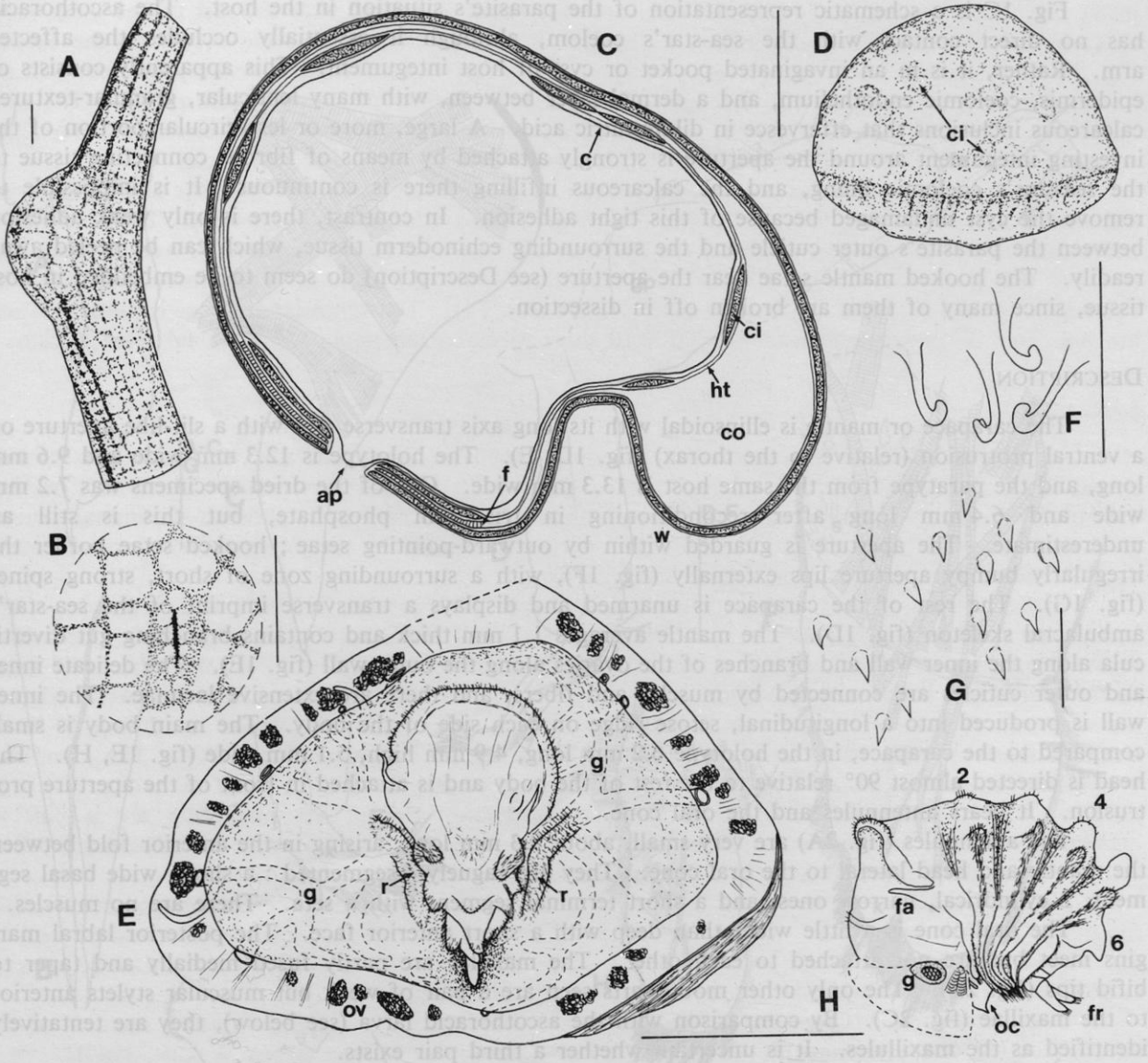

FIG. 1. — *Endaster hamatosculum* gen. et sp. nov. : A, infested arm of host sea-star, *Zoroaster carinatus philippinensis* : B, cyst opening, raised areas unstippled ; C, diagrammatic cross-section of infested sea-star arm ; D, parasite in situ ; E, female holotype, dorsal half of carapace removed, same orientation as D ; F, hooked aperture setae ; G, carapace spines ; H, female holotype, main body, some thoracomeres numbered. Abbreviations : ap, aperture ; c, carapace of *Endaster* ; ci, calcareous inclusion ; co, host's coelom ; f, fibrous material ; fa, filamentary appendage ; fr, furcal rami ; g, gut diverticulum ; ht, host tissue ; oc, oral cone ; ov, ovary ; r, setose ridge ; w, host body wall. Scale bars 0.05 mm in f, g, otherwise 0.5 mm.

RELATION TO HOST

The host asteroid in all cases is *Zoroaster carinatus philippinensis* Fisher, 1916. Two sea-stars (one from each station) had two parasites, the other just one. The ascothoracids are located no more than one per arm at various distances from the disc. They are detectable externally by a large swelling, as much as doubling the normal arm diameter (fig. 1A). Each swelling has a vertically oriented, slit-like hole laterally above or below midheight of the arm, with raised, bumpy edges (fig. 1B). The parasite's mantle aperture protrudes into this slit from within, so there is a connection between the external environment and the mantle cavity.

Fig. 1C is a schematic representation of the parasite's situation in the host. The ascothoracid has no direct contact with the sea-star's coelom, although it essentially occludes the affected arm. Rather, it is in an invaginated pocket or cyst of host integument. This apparently consists of epidermis, coelomic endothelium, and a dermal layer between, with many lenticular, granular-textured calcareous inclusions that effervesce in dilute nitric acid. A large, more or less circular portion of the investing integument around the aperture is strongly attached by means of fibrous connecting tissue to the sea-star's coelomic lining, and the calcareous infilling there is continuous. It is impossible to remove the cyst undamaged because of this tight adhesion. In contrast, there is only weak adhesion between the parasite's outer cuticle and the surrounding echinoderm tissue, which can be peeled away readily. The hooked mantle setae near the aperture (see Description) do seem to be embedded in host tissue, since many of them are broken off in dissection.

DESCRIPTION

The carapace or mantle is ellipsoidal with its long axis transverse and with a slit-like aperture on a ventral protrusion (relative to the thorax) (fig. 1D, E). The holotype is 12.3 mm wide and 9.6 mm long, and the paratype from the same host is 13.3 mm wide. One of the dried specimens was 7.2 mm wide and 6.4 mm long after reconditioning in trisodium phosphate, but this is still an underestimate. The aperture is guarded within by outward-pointing setae ; hooked setae border the irregularly bumpy aperture lips externally (fig. 1F), with a surrounding zone of short, strong spines (fig. 1G). The rest of the carapace is unarmed and displays a transverse imprint of the sea-star's ambulacral skeleton (fig. 1D). The mantle averages 1.1 mm thick and contains branching gut diverticula along the inner wall and branches of the ovaries along the outer wall (fig. 1E). The delicate inner and outer cuticles are connected by muscles and fibers, and there are extensive lacunae. The inner wall is produced into a longitudinal, setose ridge on each side of the body. The main body is small compared to the carapace, in the holotype 6.2 mm long, 4.9 mm high, 5.1 mm wide (fig. 1E, H). The head is directed almost 90° relative to the rest of the body and is attached in front of the aperture protrusion. It bears antennules and the oral cone.

The antennules (fig. 2A) are very small, about 0.3 mm long, arising in the anterior fold between the mantle and head lateral to the oral cone. They are vaguely 4-segmented : a short, wide basal segment, 2 cylindrical, narrow ones, and a short terminal segment with a seta. There are no muscles.

The oral cone is a little wider than deep with a short anterior face. The posterior labral margins meet but are not attached to each other. The maxillae are partly fused medially and taper to bifid tips (fig. 2B). The only other mouthparts seen are a pair of weak but muscular stylets anterior to the maxillae (fig. 2C). By comparison with the ascothoracid larva (see below), they are tentatively identified as the maxillules. It is uncertain whether a third pair exists.

The 6-segmented thorax is arched, most of the bend occuring in the enormous first segment (fig. 1H). Each segment has a pair of limbs and some dorsal ornamentation, which are described from the holotype. The first segment is distinct from the head, with a low, poorly setose ridge marking the boundary (ridge not evident in all specimens). Farther posteriorly is a prominent, setose, transverse ridge that in posterior view (fig. 1E) encompasses more than a semicircle and marks the broadest part of the body.

Segments 2-5 are progressively narrower, with a dorsal hump (more prominent posteriorly, first three setose) and a pair of short, dorsolateral protrusions. These latter, and the sides of the segments below them, are setose, the lower setae apparently meshing with those on the inner carapace ridges.

The first thoracopods are relatively narrow, with a long, curved, laterally and distally setose exopod, and an endopod that is small or absent in the holotype (fig. 2D, E), but somewhat longer with 2 distal setae in a paratype. These limbs have the female genital apertures and filamentary appendages at their base. The latter are approximately as long as the limbs and uniramous with a few setae in the holotype (fig. 1D), but in a paratype one is biramous ; they extend anteriorly on each side of the body.

Thoracopods 2-5 are extremely wide, flattened, and biramous (exopod narrower) with dense fine hairs down both edges and short, setulate setae on the rami (fig. 2F). The medial edges of each pair

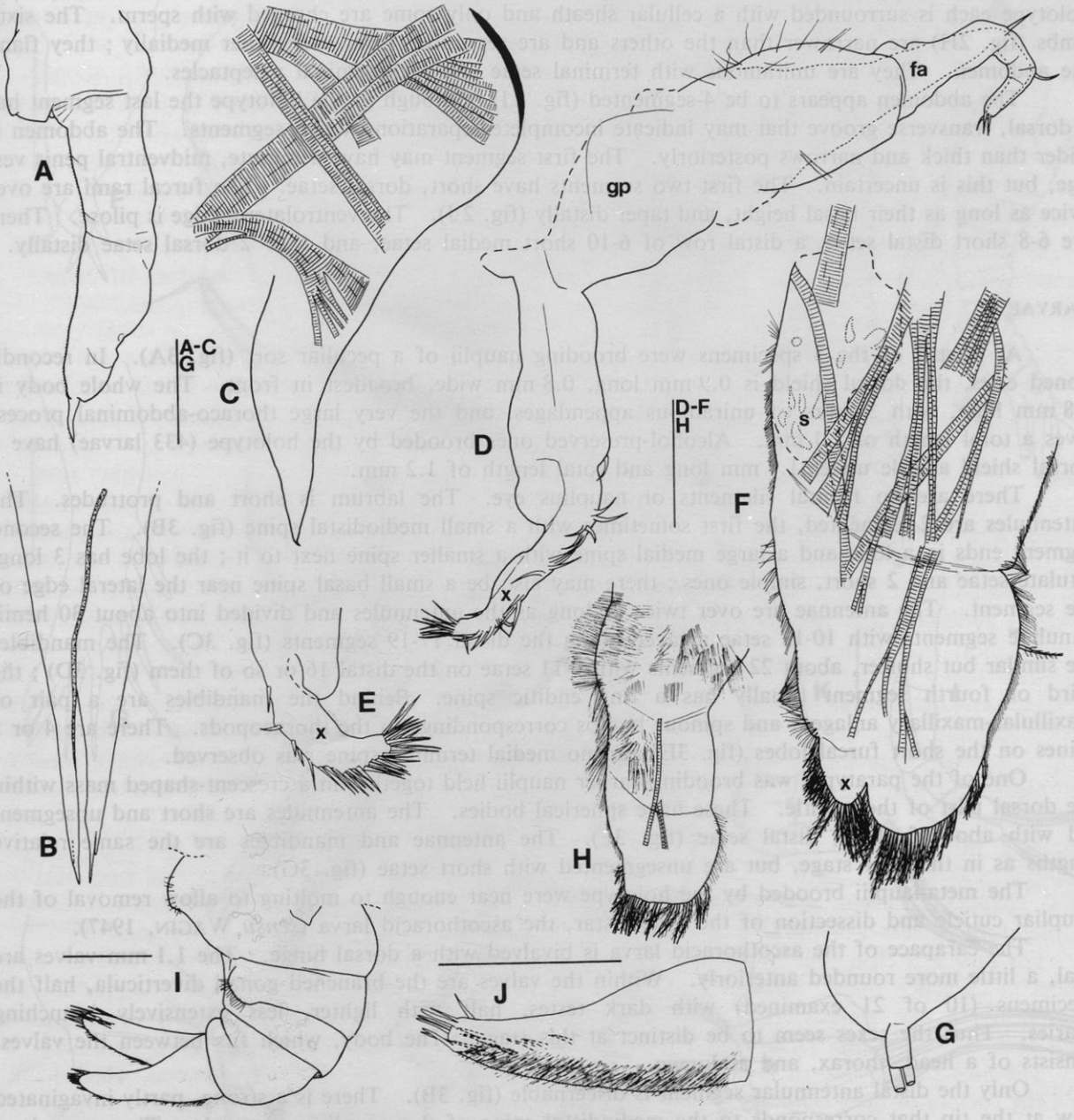

FIG. 2. — *Endaster hamatosculum* gen. et sp. nov., female holotype except J (female paratype) : A, antennule ; B, distal part of maxillae ; C, paired mouthpart (maxillule ?) ; D, right thoracopod 1, genital papilla, and filamentary appendage ; E, tip of left thoracopod 1 ; F, thoracopod 3 with muscles, dotted line shows extent of seminal receptacles ; G, exopod of thoracopod 2 with vestigial second segment ; H, thoracopod 6 ; I, abdomen ; J, furcal ramus, lateral view. Abbreviations : fa, filamentary appendage ; gp, genital papilla ; s, seminal receptacles ; x, exopod. Scale bars 0.1 mm in a-c, g, otherwise 0.5 mm.

meet. Articulations are vague and the rami are very small compared with the rest of the limb, especially in the fifth pair, but occasionally a vestigial distal segment with 2 setae occurs on the exopod (fig. 2G). There are a number of elongate seminal receptacles basolaterally in the protopods ; in the holotype each is surrounded with a cellular sheath and only some are charged with sperm. The sixth limbs (fig. 2H) are narrower than the others and are separated from each other medially ; they flank the abdomen. They are uniramous with terminal setae and lack seminal receptacles.

The abdomen appears to be 4-segmented (fig. 2 I), although in the holotype the last segment has a dorsal, transverse groove that may indicate incomplete separation of two segments. The abdomen is wider than thick and narrows posteriorly. The first segment may have a minute, midventral penis vestige, but this is uncertain. The first two segments have short, dorsal setae. The furcal rami are over twice as long as their basal height, and taper distally (fig. 2 J). The ventrolateral edge is pilose. There are 6-8 short distal setae, a distal row of 6-10 short medial setae, and 1 or 2 dorsal setae distally.

LARVAE

At least 4 of the 5 specimens were brooding nauplii of a peculiar sort (fig. 3A). In reconditioned ones, the dorsal shield is 0.9 mm long, 0.8 mm wide, broadest in front. The whole body is 0.8 mm high, with 3 pairs of uniramous appendages, and the very large thoraco-abdominal process gives a total length of 1.1 mm. Alcohol-preserved ones brooded by the holotype (433 larvae) have a dorsal shield a little under 1.1 mm long and total length of 1.2 mm.

There are no frontal filaments or nauplius eye. The labrum is short and protrudes. The antennules are 2-segmented, the first sometimes with a small mediodistal spine (fig. 3B). The second segment ends in a lobe and a large medial spine with a smaller spine next to it ; the lobe has 3 long, setulate setae and 2 short, simple ones ; there may also be a small basal spine near the lateral edge of the segment. The antennae are over twice as long as the antennules and divided into about 30 hemiannulate segments with 10-12 setae arrayed along the distal 17-19 segments (fig. 3C). The mandibles are similar but shorter, about 22 segments with 9-11 setae on the distal 16 or so of them (fig. 3D) ; the third or fourth segment usually has a tiny enditic spine. Behind the mandibles are a pair of maxillular-maxillary anlagen, and spinous bumps correspondings to the thoracopods. There are 4 or 5 spines on the short furcal lobes (fig. 3E) and no medial terminal spine was observed.

One of the paratypes was brooding earlier nauplii held together in a crescent-shaped mass within the dorsal part of the mantle. These have spherical bodies. The antennules are short and unsegmented with about 5 short, distal setae (fig. 3F). The antennae and mandibles are the same relative lengths as in the later stage, but are unsegmented with short setae (fig. 3G).

The metanauplii brooded by the holotype were near enough to molting to allow removal of the naupliar cuticle and dissection of the next instar, the ascothoracid larva (*sensu* WAGIN, 1947).

The carapace of the ascothoracid larva is bivalved with a dorsal hinge. The 1.1 mm valves are oval, a little more rounded anteriorly. Within the valves are the branched gonad diverticula, half the specimens (10 of 21 examined) with dark testes, half with lighter, less extensively branching ovaries. Thus the sexes seem to be distinct at this stage. The body, which fits between the valves, consists of a head, thorax, and abdomen.

Only the distal antennular segment is discernable (fig. 3B). There is a strong, partly invaginated claw at the tip that corresponds to the mediodistal spine of the naupliar antennule. There are three setae at the base of the protrusion in which the claw rests, one of them toward the rear. A protrusion behind the claw (the presumptive claw guard) has two setae, and behind that are two setae arising from the segment itself. These latter four setae seem to correspond to the distal setae of the naupliar antennule, but the specific homologies are unclear.

The labrum is a thick, curved lobe anterior to the other mouthparts : short, conical mandibles, tapered maxillules (which resemble the adult's mouthparts), and tapered, medially unfused maxillae with minutely bifid tips (fig. 3H).

There is no thoracic ornamentation except a small pair of epaulets at the base of the sixth legs. There are 6 pairs of biramous, natatory thoracopods. The first are the smallest, the biarticulate rami

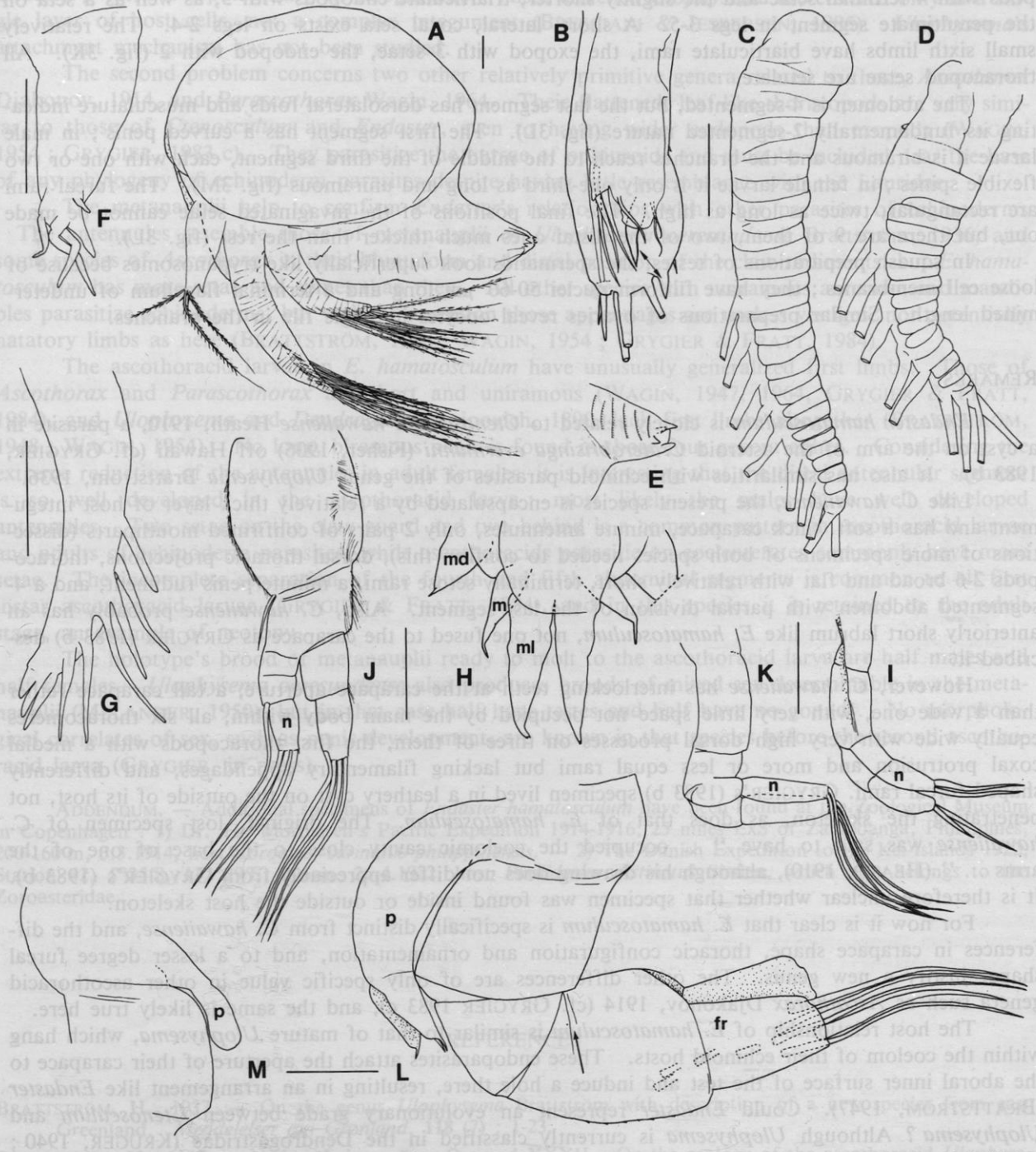

FIG. 3. — *Endaster hamatosculum* gen. et sp. nov., larvae : A-E, metanauplii ; A, lateral view ; B, antennule, ascothoracid larval antennule, within, arrow linking spine and claw ; C, antenna ; D, mandible ; E, furcal lobe ; F, G, antennule and mandible of earlier naupliar stage ; H-M, first ascothoracid larva ; H, paired mouthparts, rear view ; I, thoracopod 1 ; J, thoracopod 2 ; K, thoracopod 6 ; L, male abdomen, arrow pointing to incomplete separation of segments 4 and 5, only bases of some furcal setae shown ; M, female abdomen, first two segments. Abbreviations : fr, furcal ramus ; m, maxillule ; md, mandible ; ml, maxilla ; n, endopod ; p, penis. Scale bars 0.1 mm.

each with 2 terminal setae (fig. 3 I). The next four pairs are almost alike (fig. 3J), the biarticulate exopods with 4 terminal setae and the slightly shorter, triarticulate endopods with 3, as well as a seta on the penultimate segment in legs 3-5. A short, lateral, coxal seta exists on legs 2-4. The relatively small sixth limbs have biarticulate rami, the exopod with 3 setae, the endopod with 2 (fig. 3K). All thoracopod setae are setulate.

The abdomen is 4-segmented, but the last segment has dorsolateral folds and musculature indicating its fundamentally 2-segmented nature (fig. 3L). The first segment has a curved penis ; in male larvae it is biramous and the branches reach to the middle of the third segment, each with one or two flexible spines ; in female larvae it is only one-third as long and uniramous (fig. 3M). The furcal rami are rectangular, twice as long as high. The final positions of the invaginated setae cannot be made out, but there are 9 of them, two of the distal ones much thicker than the rest (fig. 3L).

In squash preparations of testes, the spermatids look superficially like trypanosomes because of loose cell membranes ; they have filiform nuclei 50-60 μm long and a terminal flagellum of undetermined length. Similar preparations of ovaries reveal oocytes in single file in the branches.

Remarks

Endaster hamatosculum is closely related to *Ctenosculum hawaiiense* Heath, 1910, a parasite in a cyst on the arm of the asteroid *Craterobrisinga evermanni* (Fisher, 1906) off Hawaii (cf. Grygier, 1983 b). It also has similarities with echinoid parasites of the genus *Ulophysema* Brattström, 1936.

Like *C. hawaiiense*, the present species is encapsulated by a relatively thick layer of host integument and has a soft, thick carapace, minute antennules, only 2 pairs of confirmed mouthparts (dissections of more specimens of both species needed to confirm this), dorsal thoracic projections, thoracopods 2-6 broad and flat with relatively short, terminally setose rami, a minute penis rudiment, and a 4-segmented abdomen with partial division of the last segment. Also, *C. hawaiiense* probably has an anteriorly short labrum like *E. hamatosculum*, not one fused to the carapace as Grygier (1983 b) described it.

However, *C. hawaiiense* has interlocking teeth at the carapace aperture, a tall carapace rather than a wide one, with very little space not occupied by the main body within, all six thoracomeres equally wide with very high dorsal processes on three of them, the first thoracopods with a medial coxal protrusion and more or less equal rami but lacking filamentary appendages, and differently shaped furcal rami. Grygier's (1983 b) specimen lived in a leathery cyst on the outside of its host, not penetrating the skeleton, as does that of *E. hamatosculum*. The original, lost specimen of *C. hawaiiense* was said to have " ... occupied the coelomic cavity close to the base of one of the arms ... " (Heath, 1910), although his drawing does not differ appreciably from Grygier's (1983 b). It is therefore unclear whether that specimen was found inside or outside the host skeleton.

For now it is clear that *E. hamatosculum* is specifically distinct from *C. hawaiiense*, and the differences in carapace shape, thoracic configuration and ornamentation, and to a lesser degree furcal shape, justify a new genus. The other differences are of only specific value in other ascothoracid genera such as *Ascothorax* Djakonov, 1914 (cf. Grygier 1983 c), and the same is likely true here.

The host relationship of *E. hamatosculum* is similar to that of mature *Ulophysema*, which hang within the coelom of their echinoid hosts. These endoparasites attach the aperture of their carapace to the aboral inner surface of the test and induce a hole there, resulting in an arrangement like *Endaster* (Brattström, 1947). Could *Endaster* represent an evolutionary grade between *Ctenosculum* and *Ulophysema* ? Although *Ulophysema* is currently classified in the Dendrogastridae (Krüger, 1940 ; Newman et al, 1969 ; Wagin, 1976), it has some resemblance to the Lauridae, parasites of zoanthids (Brattström, 1937 ; Okada, 1938). Grygier (1983 b) noted possible laurid affinities of *Ctenosculum*. An attractive evolutionary pathway modelled after extant forms is Lauridae → *Ctenosculum* → *Endaster* → *Ulophysema*. This is an improvement over Grygier's (1983 b) assigning the Ctenosculidae to the Lauroidida, since it does not require two distinct lineages of echinoderm parasites.

There are two problems with this scheme. First, the relationships to the host in *Endaster* and *Ulophysema* are not really the same. Young *Ulophysema* are usually free-floating in the echinoid's

coelom, having entered the host through the gonopores (BRATTSTRÖM, 1947). This cannot be true for *Endaster*, which is topologically an ectoparasite. Also, attached *Ulophysema* are covered only in a single layer of host cells, not a complex integument (BRESCIANI & JESPERSEN, 1985). *Ulophysema*'s attachment mechanism has not been studied.

The second problem concerns two other relatively primitive genera related to these, *Ascothorax* Djakonov, 1914, and *Parascothorax* Wagin, 1964. Their flattened, leaf-like thoracopods are very similar to those of *Ctenosculum* and *Endaster*, even to having wider endopods than exopods (WAGIN, 1954 ; GRYGIER, 1983 c). They parasitize the bursae of ophiuroids and must be included near the base of any phylogeny of echinoderm parasites despite having little resemblance with the Lauridae.

The metanauplii help to confirm *Endaster*'s relationships with other parasites of echinoderms The antennules resemble those of metanauplii of *Ulophysema oeresundense* Brattström, 1936, and some species of *Ascothorax* in their blunt form and distal position of the claw rudiments, but *E. hamatosculum* has more setae and spines than they. All other species with uniramous antennae and mandibles parasitize echinoderms, but without exception those appendages are useless vestiges, not potentially natatory limbs as here (BRATTSTRÖM, 1948 ; WAGIN, 1954 ; GRYGIER & FRATT, 1984).

The ascothoracid larvae in *E. hamatosculum* have unusually generalized first limbs. Those of *Ascothorax* and *Parascothorax* are short and uniramous (WAGIN, 1947, 1964, GRYGIER & FRATT, 1984), and *Ulophysema* and *Dendrogaster* Knipovich, 1890, lack first limbs altogether (BRATTSTRÖM, 1948 ; WAGIN, 1954). No long, biramous penis is found in those four genera either. Considering the extreme reduction of the antennules in adult females, it is interesting that the distal antennular segment is so well developed in the ascothoracid larva ; most likely the males have well developed antennules. Two setae on the claw guard and two behind is a common pattern in ascothoracid larvae and adults of echinoderm parasites, while ascothoracids parasitic on coelenterates commonly have more setae. The incomplete separation of the fourth and fifth abdominal segments is common to all first instar ascothoracid larvae (GRYGIER & FRATT, 1984), and in this species it is retained to the adult stage, an example of neotony.

The holotype's brood of metanauplii ready to molt to the ascothoracid larva are half males and half females. *Ulophysema oeresundense* also produces broods of mixed sex determinable in the metanauplii (MELANDER, 1950), but in that case half have testes and half have no gonads. No morphological correlates of sex, such as penis development, are known in that species before the second ascothoracid larva (GRYGIER, in press).

ADDENDUM. — Additional specimens of *Endaster hamatosculum* have been found at the Zoological Museum in Copenhagen : 1) Dr. Th. Mortensen's Pacific Expedition 1914-1916, 25 miles ExS of Zamboanga, Philippines, 200-160 m, 3.3.1914, host *Zoroaster carinatus philippinensis*. — 2) The Danish Expedition to the Kei-Islands 1922, Station 42, 5°35′S, 132°29′E, 225 m, 26.4.1922, host *Pholidaster distinctus* Sladen, which also belongs to the Zoroasteridae.

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