

TWO SPECIES OF *DENDROGASTER* (CRUSTACEA: ASCOTHORACIDA) PARASITIC IN PORCELLANASTERID STARFISHES

MARK J. GRYGIER

*Institute of Cell Biology and Anatomy, University of Copenhagen,
Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark*

ABSTRACT

Dendrogaster specimens infesting *Hyphalaster inermis* collected by the "Galathea" (4040 m, Indian Ocean) are compared to *D. beringensis* Wagin, 1957. Other specimens, infesting *Sidonaster vaneyi* collected by the "Albatross" (1370 m, Philippines), are a new species, *D. sagittaria*.

INTRODUCTION

Apparently the only ascothoracid crustaceans collected by the "Galathea" were endoparasites of sea-stars. Madsen (1961) reported such parasites (or suspected parasites) from several porcellanasterids: *Hyphalaster inermis* Sladen, Sts. 282 and 52 ("Ascothoracids were found ..."), St. 30 ("... large calcified tumor ventrally, which probably also indicates the presence of an ascothoracid parasite?"); *Eremicaster crassus* (Sladen), St. 238 ("A dendrogate ascothoracid with nauplius larvae ..."); *E. gracilis* (Sladen), St. 716 ("... appears to be infested with an ascothoracid, since in one radius of the disc there is a pair of close-set holes surrounded by a thickened wall of the integument?"; photograph in Madsen's pl. XIII, 1).

All the infested sea-stars were handed over to a zoologist who has since left science. For the present study only the *H. inermis* from Sts. 282 and 30 could be recovered from his former institute. The calcified tumor on the latter turns out not to contain any metazoan parasite, but the two specimens from St. 282 were indeed infested with the ascothoracid *Dendrogaster*. The *E. crassus* probably also had been,

but the pair of holes in *E. gracilis* is not typical of *Dendrogaster* or other known ascothoracids, although members of the Ctenosculidae leave a single hole to the exterior of their asteroid hosts (Heath 1910, Grygier 1983a, 1985b).

There are over twenty described species of *Dendrogaster*, as well as several records of unidentified specimens, from various sea-stars in all parts of the world and down to 4000 m. They are endoparasitic, occupying a greater or lesser part of their host's perivisceral coelom. In females the carapace or mantle is greatly enlarged into a branching brood sac up to 85 mm across in some species, and there remain only cephalic appendages on the reduced body. Males and brooded young inhabit the mantle cavity. The literature on this genus is compiled in Wagin (1976) and Grygier (1982), the most important works of recent decades being Wagin (1950, 1954). Besides the single available "Galathea" species, the present paper also treats a porcellanasterid-infesting *Dendrogaster* mentioned by Fisher (1919) that was collected by the "Albatross".

Dendrogaster cf. beringensis Wagin, 1950
(Figs 1-3)

Material:

"Galathea" St. 282, south of India between Sri Lanka and Maldives, 5°32'N, 78°41'E, 4040 m, 11 Apr. 1951, blackish mud, ca. 1.4°C. — Three females endoparasitic in two specimens of porcel-

lanasterid sea-star *Hyphalaster inermis*; single one with at least one male; one of other two with nauplii and at least one male, other not brooding and not examined for males or otherwise dissected (other females and males dissected). All specimens deposited in Zoological Museum, Copenhagen.

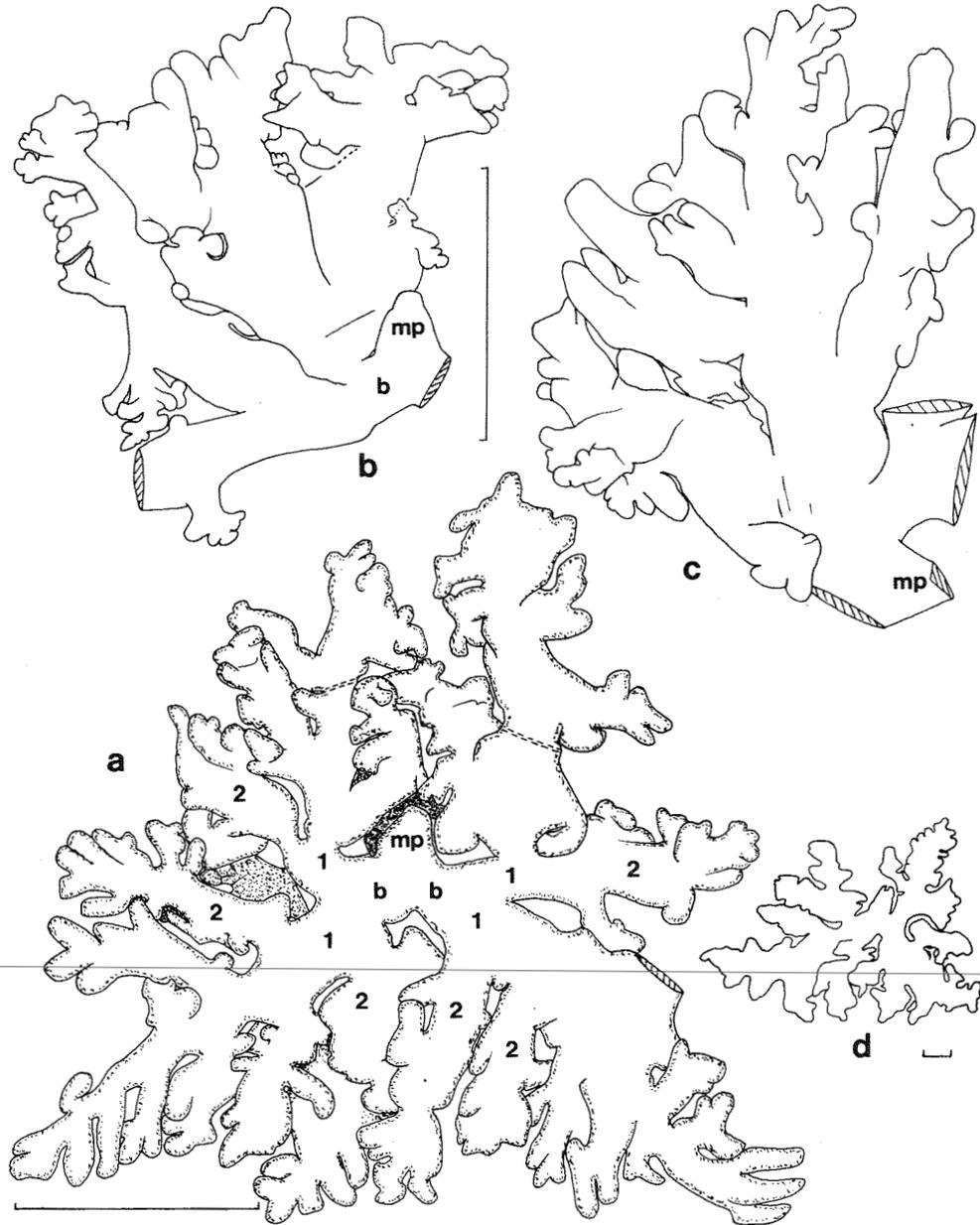


Fig. 1. a-c, *Dendrogaster cf. beringensis*, females; a, habitus of specimen found alone, two branches marked by double dashed lines were broken off and are shown in their most likely original positions; b, part of topmost of two specimens from single host, including middle piece, anterior primary branch and part of posterior primary branch; c, part of lower of two specimens found together, including middle piece and posterior primary branch, oriented 90° clockwise relative to a and b; d, syntype of *D. beringensis* redrawn from Wagin (1957). Scale bars 10 mm in a-c, 1 mm in d. Abbreviations: b, main branch; mp, middle piece; 1, primary branch; 2, secondary branch (only a few labelled).

Disposition in hosts: All three specimens were flattened between the aboral surface of the starfish and its mud-filled stomach. Those sharing a host were one atop the other, the lower one lying ventral side up (orientation of other specimens not determined).

Description:

Females: Maximum carapace span of single specimen 32 mm, larger of other two 40 mm (Fig. 1a-c). Middle piece small, subconical, only slightly longer than basal width, housing animal's main body within distal, slitlike opening. Main branches and unbranched basal parts of primary branches very short, no longer than wide. All four primary branches approximately equally developed except for a rudimentary posterior one on one specimen. Secondary branches arising alternately or irregularly, larger basally. Distal parts of primary and secondary branches generally thin-walled, distended, varying in degree among specimens. Terminal branches usually arising directly from secondary branches, but sometimes from short tertiary branches, either as small, thick-walled lobes or trefoils, or as thin-walled, finger-like projections. Mantle texture smooth except on leathery-appearing middle piece, muscle strands readily visible in thin-walled areas.

Antennules four-segmented, first three segments telescoping alternately (Fig. 2a). First segment as large as rest combined. Second rectangular. Third longer than wide with two long setae on anterior edge, segment outline only slightly bent at that point; anterobasal fusion seam on lateral side with accompanying muscle. Fourth segment a little longer than broad with a movable terminal claw; a single seta below claw in two of four antennules examined, but no flanking setae clearly seen (a single small one sometimes ambiguously seen, included in Fig. 2a); claw guard cylindrical with variously two or three setae, two setae behind it.

Oral cone typical, with posteriorly open labral sheath, and maxillae as only well developed mouthparts. Maxillae fused for most of length, bifid tips spread laterally (Fig. 2b). Tips of distal prong bent medially, posterior hooks bent straight back. Subterminal parts of maxillae broadened posteriorly, distal edge sometimes with delicate protuberance. Anterior side with transverse rows of short cuticular ctenae.

Males: Positioned in mantle cavity with main body at or near base of middle piece, posterior rami reach-

ing into a posterior primary branch. Total length respectively 8.5 and 11 mm, posterior rami tubular, testes basically longitudinally within them but with short, lobular branches (Fig. 2c). Original carapace valves easily distinguished, ventral rims produced into thickened, sometimes wrinkled shields that enclose male's main body in large chamber (Fig. 2d, e). Boundary between shields and thin-walled posterior rami marked by deep folds in cuticle. Body attached to carapace by extensive cephalic attachment zone, so cephalic appendages and thoracic limbs well separated, as in *D. punctata* Grygier (cf. Grygier 1982).

Antennules with four roughly equal segments (Fig. 2f); first two unarmed; third with two long, spine-like setae on anterodistal corner, anterobasal fusion seam and accompanying muscle; distal segment with movable claw, a seta at its base and on ridge to each side (one of latter missing on one of four antennules studied), claw guard with three distal setae, small proximal process with long seta and comb of short hairs, no strap-like aesthetasc (possibly ripped off, remnant visible in one case; Fig. 2f).

Labral sheath of oral cone open posteriorly. Pair of vestigial mandibles or maxillules (latter, judging from position) seen on one specimen (Fig. 2g). Maxillae fused for half of length, tips trifid with normal terminal prong and recurved posterior hook, but also with a blunt process directly behind terminal prong (Fig. 2g).

Five pairs of typically-constructed thoracopods on segments II-VI, with diagonal coxal-basal articulation, two-segmented exopods, three-segmented endopods (two-segmented in last pair). Setation of one male: legs II and III with lateral coxal seta, medial basal seta, four terminal exopod setae, two terminal endopod setae; terminal setae the same on all but leg VI, with three on exopod. Legs IV and V lacking coxal and basal setae, but with seta on second endopod segment.

Abdomen five-segmented, U-shaped, second and fifth segments longest, fourth shortest. Penis rudiment not clearly observed. Furcal rami slightly oblong with three mediobasal setae, one mediobasal seta, a terminal spine, and one short and at least two, probably three, long distal setae (latter not clearly observed).

Nauplii: In process of molting, so two instars available. Dorsal shield dome-like, 1.01 mm long, 0.63 mm wide (mean of eight), rounded at front and rear, but front wider and often with slight medial indentation (Fig. 3a). Thick, rigid, dorsal cuticle extends

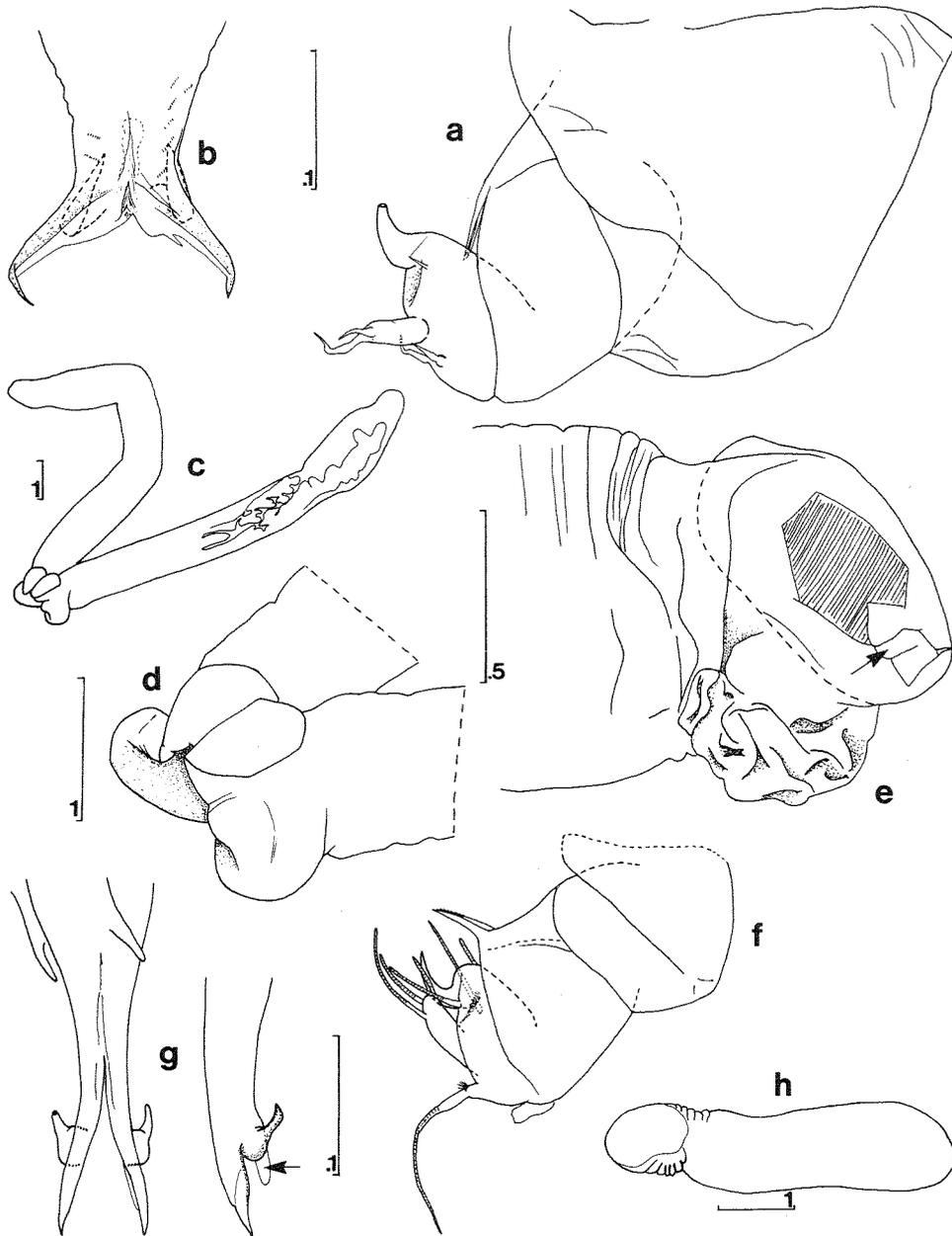


Fig. 2. a-b, *Dendrogaster cf. beringensis*, female appendages; a, antennule (composite drawing); b, distal part of maxillae, anterior view, posterior hooks shown as dashes; c-g, *D. cf. beringensis*, males; c, habitus, some testes shown in one posterior ramus; d, enlargement of body end of c, showing original, oval carapace valves and shields; e, medial view of valve of another male, part of antennule in situ (arrow); f, antennule; g, anterior and lateral views of maxillae, former with pair of vestigial mouthparts at base, extra distal prong shown by arrow; h, *D. beringensis*, male carapace valve and posterior ramus, redrawn from Wagin (1957). Scale bars in mm.

partly onto ventral surface, its edges marked by band of equatorial pores. Short cephalic appendages not reaching to edge of shield. Frontal filaments papilliform, often with short projections, tiny papilla between them (Fig. 3b). Labrum spade-shaped. Antennules unsegmented (Fig. 3c). Earlier instar with three medial setae (first two short, distal one long), a short laterodistal seta, and three unequal distal setae. Next instar the same, but setae thinner and base of

longest terminal seta sticking out beyond other two. Antennae and mandibles resembling each other (Fig. 3d): earlier instar with short, unarmed coxa and longer, unarmed basis; unsegmented, cylindrical endopod with long medial seta at midlength, two long setae and spine distally; exopod unsegmented with five setae. Next instar with exopods divided into 12-17 annuli and bearing seven setae on distal ones (one seta added terminally, one proximally). Anten-

nae with more annuli than mandibles. Maxillular rudiments as pair of sharp spines in later instar; no external evidence of more posterior limbs. Pair of unarmed furcal lobes in both instars, texture scaly in later one, terminal seta dorsal to them.

Remarks: The present specimens can be compared to *D. beringensis*, whose original description is a little sketchy (Wagin 1957, 1976), and whose type-specimens (Zoological Institute, Leningrad) have unfortunately not been made available for examination. The host of *D. beringensis* is the porcellanasterid *Eremicaster tenebrarius* Fisher (= *E. gracilis* and is probably a subspecies of *E. crassus* according to Madsen 1961) from the Bering Sea (3940 m) and the Kurile-Kamchatka Trench (2590 m). The missing "Galathea" *Dendrogaster* parasitizing *E. crassus* might therefore also have been the same species.

Some parts of the present specimens' mantles are as distended and irregular as in the type specimens

(Fig. 1d), and the degree of branching, only up to a limited number of tertiary branches, is the same. All have a short middle piece and very short main and primary branches before the secondary branching begins. Wagin, however, emphasized the prominent lips of the mantle aperture, and his mature animals were smaller, no more than 18 mm across. The female antennules agree in having the third segment longer than wide and the fourth segment short with three setae on the claw guard and two behind. This setation is common in *Dendrogaster*, however, and Wagin drew the third segment's setae shorter than in the present specimens. He drew only the tip of a maxilla, not mentioning a subterminal broadening or whether the distal prongs diverge.

Only one male was available to Wagin. It had posterior rami 3-4 mm long, shorter than in the present males, but like them had testes with short branches and a thickened, wrinkled region between the original valves and the posterior rami (Fig. 2h). No other male *Dendrogaster* has anything similar

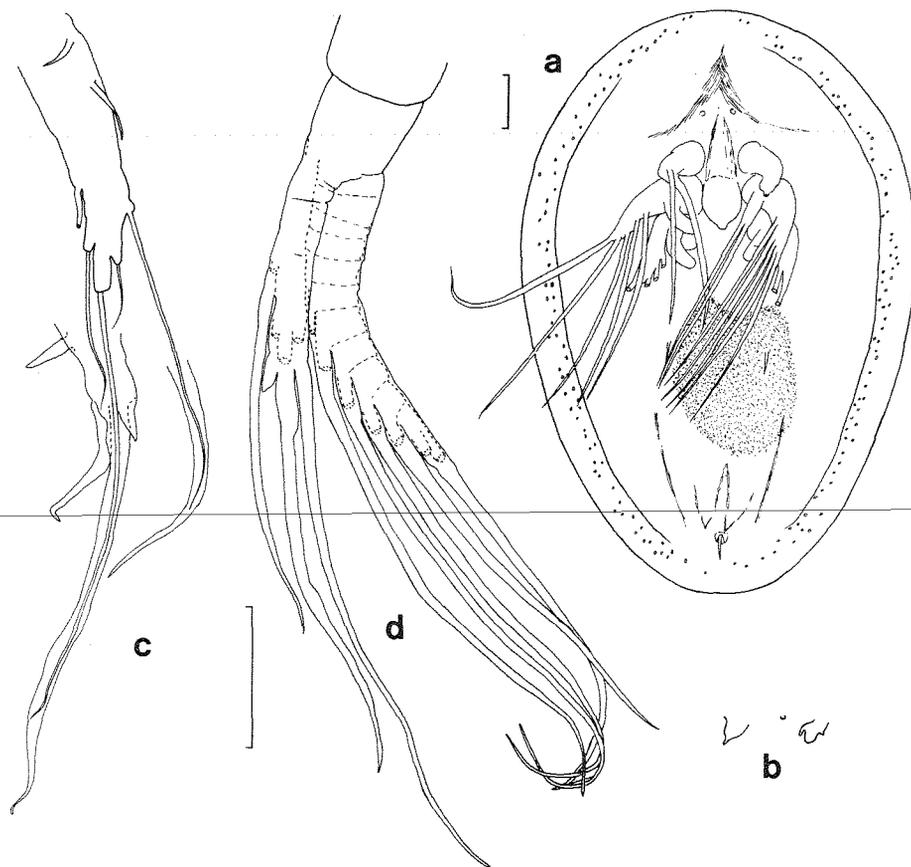


Fig. 3. *Dendrogaster* cf. *beringensis*, brooded nauplii. a, ventral view, many setae omitted, yolk stippled; b, representative pair of frontal filaments and medial knob; c, antennule, that of later instar partly enclosed by earlier instar's cuticle; d, antenna, earlier instar's cuticle still in place, only bases of later instar's setae shown. Scale bars 0.1 mm.

except for sucker-like valve protrusions in *D. astropectinis* Yosii (sensu Wagin 1950), which parasitizes the astropectinid *Psilaster pectinatus* Fisher. In *D. beringensis* Wagin did not describe a third distal prong on the maxilla, but he drew this mouthpart with the posterior hook pointing distally, which would have hidden the more medial extra prong, which is otherwise unique to the present males. Wagin (1957, 1976) put taxonomic weight on the direction of the posterior hook, but since it is movable through the action of basal maxillary muscles on a tendon, its orientation has no taxonomic importance. The male antennules are like the present ones except for two setae to one side of the claw instead of one to each side, an obvious lapsus. Wagin did not see an anterobasal muscle in the third antennular segment of either sex, but this muscle is sometimes almost transverse and very difficult to see. Absence of it or of the segmental fusion seam associated with it is not a reliable taxonomic character. Wagin did not describe the male's limb or furcal setation. Two females had large metanauplii with well developed, setose limbs, but no details were given.

A more definite identification of the "Galathea" *Dendrogaster* awaits a re-examination of the type-specimens of *D. beringensis*, particularly of their

maxillae. Those of the present specimens, especially of the males, are distinctive and potentially specifically diagnostic. This would best be done as part of a general restudy of all of Wagin's (1950) *Dendrogaster* species.

***Dendrogaster sagittaria* n. sp.**

(Figs 4, 5)

Material:

"Albatross" St. 5491, between Leyte and Mindanao, Philippines, 9°24'N, 125°12'E, 1370 m, 1 July 1909. — Holotype female with male and nauplii (USNM 213944; dissected), paratype female with nauplii (USNM 213945; not dissected) intertwined in perivisceral coelom of porcellanasterid starfish *Sidonaster vaneyi* Fisher (USNM 40830).

Diagnosis: Mantle generally with long anterior primary branches, each with large, basal, secondary branch anteriorly; short, quickly bifurcating, posterior primary branches: tertiary branching irregular, not highly developed. Third antennular segment in females with single, large spine. Thoracopods in males with three terminal setae on exopods, two on endopods.

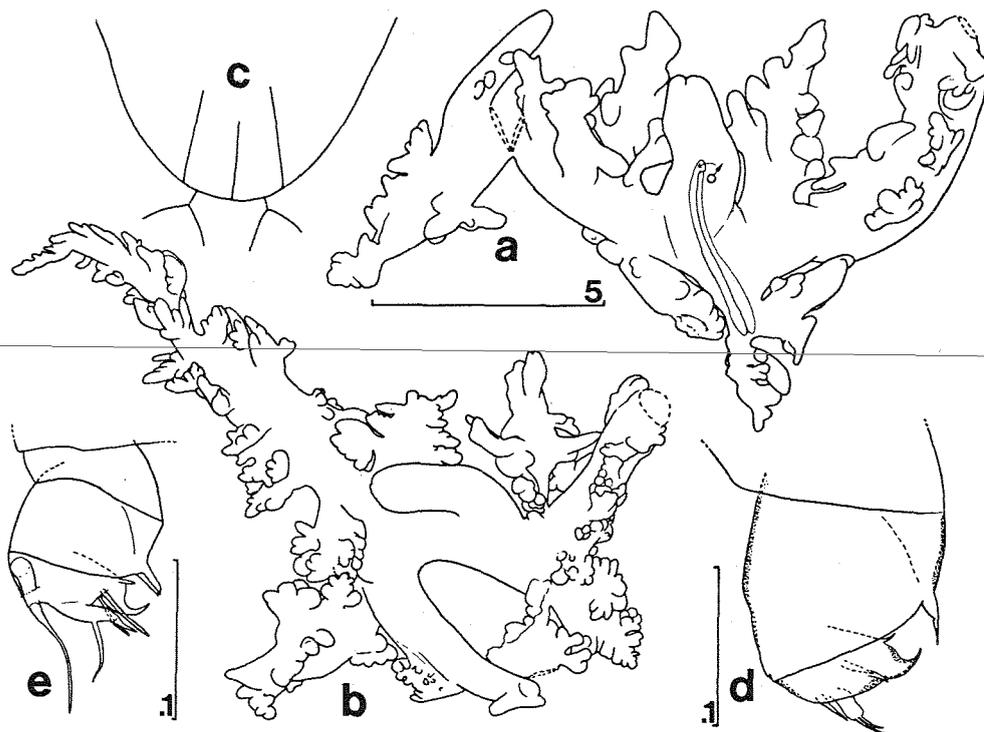


Fig. 4. *Dendrogaster sagittaria* n. sp. a, holotype female (USNM 213944), showing position of male within mantle; b, paratype female (USNM 213945); c, schematic mantle branching pattern; d, distal part of holotype's antennule; e, male antennule. Scale bars in mm.

Description:

Females: Both specimens illustrated in Fig. 4a, b and branching pattern shown in Fig. 4c. Middle piece of mantle little more than twice as long as wide (2.5-2.7 mm long), almost equalling span of main branches. Anterior primary branches 8-10 mm long, straight or anteriorly curved, with large, basal, anterior secondary branches. Posterior primary branches usually dividing quickly into short secondary branches about as long as basal anterior secondary branches. Short, foliose tertiary branches arranged alternately or irregularly, somewhat better developed basally, with round or slightly elongate terminal branches.

Antennules (Fig. 4d) four-segmented, basal two segments wider than rest. Third about as wide as long, with lateral fusion seam and muscle proximal to it; large anterodistal spine, bifid on at least one antennule in holotype. Fourth segment with claw, three basal setae (lateral one longer than medial), cylindrical claw guard with two terminal setae, and short seta behind claw guard. Maxillae with posterior hooks.

Male: Somewhat shrivelled. Main body in female's middle piece, both posterior rami of carapace going into same posterior primary branch (Fig. 4a). Rami cylindrical, about 5 mm long, no other modifications of carapace valves. Body tagmosis normal for genus (5-6-5).

Antennules (Fig. 4e) with two small basal segments; two spines and fusion seam on third segment; fourth segment with movable claw, three setae at base of claw, lateral one longest, terminal and subterminal seta on claw guard, posterior seta, and aesthetasc. Maxillae with posterior hooks. Five pairs of thoracopods (II-VI), segmentation as in preceding species, lateral coxal seta on thoracopods II and III, three terminal setae on exopod and two on endopod in all legs, medial limb setation unknown. Furcal rami approximately square with four medial setae (three basal, one dorsodistal), terminal dorsal spine, and four terminal setae, ventral one shortest.

Nauplii: Early metanauplii with elliptical, bowl-shaped dorsal shield averaging 0.54×0.39 mm (mean of seven) and bordered by equatorial pores (Fig. 5a). Frontal filaments well developed, sometimes tapered or branched, with small knob between (vestigial nauplius eye?) (Fig. 5b). Labrum spade-shaped. Antennules with two short and one long medial setae, the last with a medium-long, lateral seta opposite it, and three unequal terminal setae

(Fig. 5c). Antennae and mandibles alike (Fig. 5d), protopod with two medial knobs, endopod with one long medial seta and one short and two long terminal setae, exopod with approximately ten annuli and five long setae. Rudiments of maxillules represented by pair of large spines. Posterior end of body conical; next instar will acquire pair of furcal lobes (Fig. 5e).

Etymology: Named for Sagittarius, the archer, since the mantle's anterior primary branches and middle piece resemble a bow and arrow.

Remarks: The mantle branching pattern is similar to *D. murmanensis* Wagin and *D. asterinae* Achituv in having one set of primary branches much better developed than the others, which are relegated to the role of basal side branches (cf. Wagin 1950, Achituv 1971). In those two species the longest branches sweep backward, not forward. Such a biaxial mantle may be primitive, since the mantle is an outgrowth of an originally bivalved carapace. A single spine on the

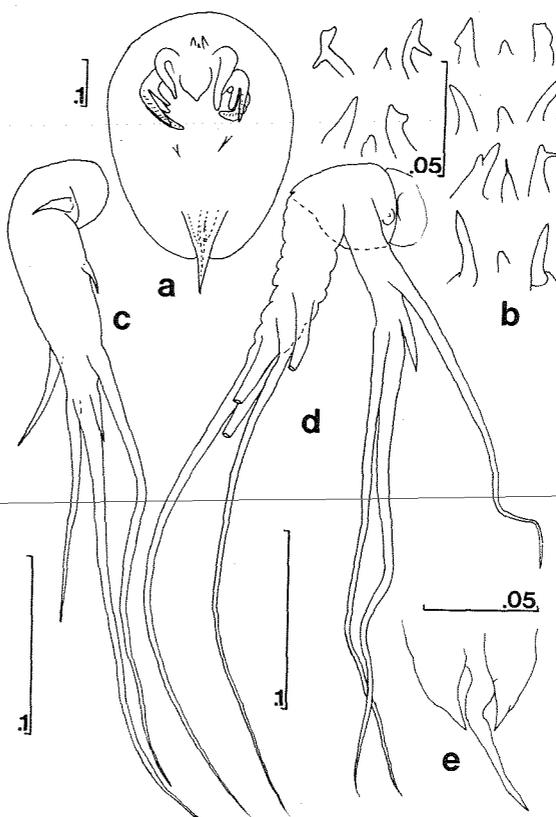


Fig. 5. *Dendrogaster sagittaria* n. sp., brooded nauplii. a, ventral view, setae omitted; b, frontal filaments and medial knobs of several nauplii; c, antennule; d, mandible; e, terminal spine and furcal lobes of next instar. Scale bars in mm.

third antennular segment occurs in female *D. arbusculus* Fisher, *D. punctata* Grygier, and on one antennule of the holotype of *D. fisheri* Grygier (not counting a more distal seta unique to that species) (cf. Grygier 1982). The first two species have highly branched mantles, and the last has equal anterior and posterior primary branches. Since the spine was here observed to be bifid in one case, it may actually be a projection from the segment with two small setae at the tip. Such a "chin" is common in *Ascothorax*, parasites of ophiuroids (Grygier 1983b), but has not been reported in *Dendrogaster*. The males of the new species are unremarkable except for their distal limb setation. *Dendrogaster* males usually have four terminal setae on the exopods and three on the endopods in legs II-V. Some other species have fewer on one ramus or the other, but not both. The present nauplii together with those of the preceding species are the only *Dendrogaster* nauplii in which maxillular spines have been described. Better developed maxillular rudiments are so far only known to occur in the Lauridae, parasites of zoanthids (Yosii 1931, Grygier 1985a). *D. sagittaria* is heterochronic in the late appearance of the furcal lobes.

Dendrogaster beringensis (the type lot and the present specimens) and *D. astropectinis* sensu Wagin (1950) may form a monophyletic subset of the genus, defined by the special elaborations of the carapace valves in the males, that is parasitic in deep-water asteroids of two suborders. The male of *D. sagittaria* has no unusual structures between the original valves and the posterior rami; therefore it does not belong to this group despite a deep-sea habitat and having a porcellanasterid host like *D. beringensis*. Once again a lack of correlation of host taxonomy and intrageneric relationships of *Dendrogaster* is evident (see Grygier 1981).

Acknowledgments

This work was partly supported by a postdoctoral fellowship from the American-Scandinavian Foundation. Thanks go to F. J. Madsen, T. Wolff, and R. Elofsson for locating the parasitized "Galathea" sea-stars, and to M. Downey for loaning me the "Albatross" material.

REFERENCES

- Achituv, Y., 1971: *Dendrogaster asterinae* n. sp., an ascothoracid (Cirripedia) parasite of the starfish *Asterina burtoni* of the Gulf of Elat. — *Crustaceana* **21**: 1-5.
- Fisher, W. K., 1919: Starfishes of the Philippine seas and adjacent waters. — *U. S. Nat. Mus. Bull.* **100**, 3: 1-712.
- Grygier, M. J., 1981: A representative of the genus *Dendrogaster* (Cirripedia: Ascothoracida) parasitic in an Antarctic starfish. — *Antarct. Res. Ser.* **32**, 1: 1-15.
- 1982: *Dendrogaster* (Crustacea: Ascothoracida) from California: sea-star parasites collected by the *Albatross*. — *Proc. Calif. Acad. Sci.* **42**, 18: 443-454.
- 1983a: *Ctenosculum hawaiiense* Heath: confirmation of its affinities (Crustacea: Ascothoracida — ex Mollusca: Gastropoda). — *J. Crust. Biol.* **3**: 257-265.
- 1983b: *Ascothorax*, a review with descriptions of new species and remarks on larval development, biogeography, and ecology (Crustacea: Ascothoracida). — *Sarsia* **68**: 103-126.
- 1985a: Lauridae: taxonomy and morphology of ascothoracid crustacean parasites of zoanthids. — *Bull. Mar. Sci.* **36**: 278-303.
- 1985b: Crustacea: Ascothoracida. — *Résultats des Campagnes Musorstom 2* (in press).
- Heath, H., 1910: A new genus of parasitic gastropods. — *Biol. Bull.* **18**: 99-108.
- Madsen, F. J., 1961: The Porcellanasteridae, a monographic revision of an abyssal group of sea-stars. — *Galathea Rep.* **4**: 33-174.
- Wagin, V. L., 1950: [On new parasitic crustaceans of the family Dendrogasteridae (order Ascothoracida)]. — *Trudy Leningr. Obshch. Estestvoispyt.* **70**, 4: 3-89 (in Russian).
- 1954: [On the structure, larval development and metamorphosis of dendrogasterids (parasitic crustaceans of the order Ascothoracida)]. — *Uchen. Zap. Leningr. Gos. Univ.* **172**, Ser. Biol. Nauk **35**: 42-89 (in Russian).
- 1957: Dendrogasteridae (Entomostraca, Ascothoracida) aus den Asteroidea der Beringsee. — *Trudy Leningr. Obshch. Estestvoispyt.* **73**, 4: 58-63 (in Russian, German summary).
- 1976: Meshkogrudyje Raki [Ascothoracida]. — *Kazan' University Press, Kazan', USSR.* 141 pp. (in Russian).
- Yosii, N., 1931: Note on the organisation of *Bacallaureus japonicus*. — *Annot. Zool. Jap.* **13**: 169-187.