

Description and Complete Larval Development of a New Species of *Baccalaureus* (Crustacea: Ascothoracida) Parasitic in a Zoanthid from Tanabe Bay, Honshu, Japan

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ABSTRACT—An unidentified species of *Zoanthus* from Tanabe Bay, Honshu, Japan, is the host of an endoparasitic ascothoracid crustacean, *Baccalaureus falsiramus*, new species. This is the first record of this zoanthid genus serving as the host of an ascothoracid and the second species of *Baccalaureus* from Japan. The morphology of the adult females, nauplii, and ascothoracid larva is described based upon a detailed study combining light microscopy and SEM. The female of this new species is characterized by a coiled carapace but very short, more or less distally upturned thoracic horns, and very long, ventrally directed papillae for seminal receptacle ducts lateral to thoracopods II–IV. Much variability is recognized in the antennule, thoracopods, penis, and abdominal ornamentation. Larval specimens were individually reared in the laboratory. Six lecithotrophic naupliar instars with rudimentary endites on the antennae and mandibles are present before the ascothoracid larva. The nauplii swam for about one month without feeding until the metamorphosis to the ascothoracid larva. Naupliar instars II–VI have a sculpture of concentric cuticular ridges on the marginal area of the dorsal shield. A nauplius eye is present through all naupliar instars as well as in the ascothoracid larva. Setae are gradually added to the antennules, but the antennae and mandibles remain essentially unchanged after instar III; rudimentary maxillules appear in instar II. The ascothoracid larva is a “Tessmann’s larva” similar to one recently described from Hawaiian plankton, but lacking central pores within the carapace reticulations. Morphological and developmental features of the nauplii and ascothoracid larva are discussed.

INTRODUCTION

One of us (T. I.) has been conducting an extensive parasitological survey in Tanabe Bay, Japan, to discover the adults of *Facetotecta* Grygier (Crustacea, Maxillopoda), which are currently known only from so-called y-larvae [1]. An unidentified *Zoanthus* (Hexacorallia) examined in this survey was infested by a previously unknown species of *Baccalaureus* Broch (Crustacea, Ascothoracida, Lauridae), which is described in this paper.

The present paper also reports the first successful study of a generalized larval history in an ascothoracid, based upon larvae of the new

species individually reared in the laboratory. The only other complete report is that of Brattström [2] on *Ulophysema oeresundense* Brattström, 1936, a species with abbreviated development. Wagin [3] and Karande and Oguro [4] gave more or less complete accounts of the larvae of *Ascothorax ophioctenis* Djakonov, 1914, and *Dendrogaster* (= *Myriocladus*) *astropectinis* Yosii, 1931, respectively, but in neither case were naupliar instars clearly determined, just arbitrary stages.

MATERIAL AND METHODS

Five adult females and one possible male of the new species were collected from a single colony of *Zoanthus* sp. (Japanese name: mame-sunagincha-ku) that was found on a rocky cliff on the north side of Toshima Rock in Tanabe Bay (33°41'N,

135°21'E), at a depth of 4 m. Parts of this zoanthid colony that yielded ascothoracidans were sampled on several occasions by one of us (T. I.) using SCUBA. Three females that were examined by light microscopy have been designated as the type series (data given later). The other two females and the possible male were examined by SEM. One of the females (SEM-1; collected 22-I-1989), which was accompanied by the possible male, was fixed with 10% Formalin-sea water solution; the other female (SEM-2; collected 5-II-1989) was pre-fixed with 2% glutaraldehyde (phosphate-buffered, with sucrose to adjust osmotic pressure) for 4 hr, treated with a mixture of 2% tannic acid and 2% guanidine hydrochloride solution for 8 hr, and then post-fixed with 2% osmic acid for 8 hr. An instar I nauplius collected from the brood chamber of SEM-2 was similarly treated for SEM study. Four instar II nauplii obtained from a paratype and two ascothoracid larvae metamorphosed in the laboratory were fixed with Formalin-sea water, and were also used for SEM study. After fixation, all the specimens used for SEM study were dehydrated through a graded series of ethanol, transferred into isoamyl acetate, and desiccated in a critical point dryer using CO₂. Dried specimens were sputter-coated with gold, and examined in a scanning electron microscope (JEOL, JSM T-220) at accelerating voltages of 5 to 15 kv.

Several instar I nauplii from the holotype and instar II nauplii from a paratype were dissected in glycerine for examination of appendages. Three nauplii obtained from the same paratype were reared in the laboratory. Initially, as shown later by examination of their exuviae, two were second instar and one was third. They were kept in small dishes individually at 19°C, with daily changes (twice a day) of sterilized dishes containing fresh, paper-filtered sea water until the metamorphosis to the ascothoracid larva. Exuviae were removed from the dishes when present, fixed in Formalin-sea water, and mounted on glass slides in glycerine for light microscopical examination. One of the resulting ascothoracid larvae was dissected and mounted first in glycerine, then in glycerine jelly for microscopical examination; the other two were prepared for SEM study as described above.

Due to the extensively modified body and

appendages in *Baccalaureus*, there has historically been considerable disagreement about the number of thoracic segments and the identity of most of the cephalic and anterior thoracic appendages and bodily projections. The morphological terminology adopted here is that of Brattström [5] as modified by Gryier [6].

Part 1. Taxonomy

Baccalaureus falsiramus sp. nov.

Diagnosis. Adult female: *Baccalaureus* round in side view, with coiled lateral carapace lobes making almost two full revolutions, and with spines on edges of coils. Anterior thoracic horns shorter than thorax, naked, either distally upturned or almost straight. All three pairs of mouthparts well developed. Small plate-like organ at base of first thoracopod, or just a swelling instead, barely or not extending dorsally over lateral chitinous ridge of thorax. Thoracopod 1 variform, represented by a papilla or cylindrical process, with 0–2 apical setae. Thoracopods 2–4 containing seminal receptacles, each limb flanked laterally by prominent, ventrally directed, conical papilla with apical opening. Thoracopod 5 variform. Thoracopod 6 variform, or absent. Dorsal setae only on last thoracomere and first abdominal segment. Penis uniramous, variform, often with distal spines. Furcal rami as long as first two abdominal segments combined, narrow, with 2–3 hirsute terminal setae, no medial setae or sensilla, lateral side partly bare of cuticular ctenae.

Nauplii: lecithotrophic, six instars, with bowl-shaped dorsal shield after instar I, four-segmented antennules at instar VI, vestigial protopodal endites on antennae and mandibles, caudal armament barely protruding beyond end of dorsal shield. Ascothoracid larva: a "Tessmann's larva", carapace valves without central pores in polygonal cells delineated by chitinous, mesh-like ridges.

Type series. Holotype: adult female, fully dissected, brooding eggs and nauplii, trunk and carapace lobes preserved in ethanol, dissected appendages and part of carapace mounted onto slide glasses with glycerine jelly. Paratype-1: adult female, brooding eggs, carapace partly torn, specimen otherwise intact, preserved in ethanol. The

holotype and paratype-1 were recovered by M. J. G. from host material that had been fixed (10-IX-1988) and preserved in 70% ethanol by T. I. after

being kept in an aquarium (Original collection date 26-VII-1988). Paratype-2: adult female (fully dissected), brooding eggs and nauplii, recovered

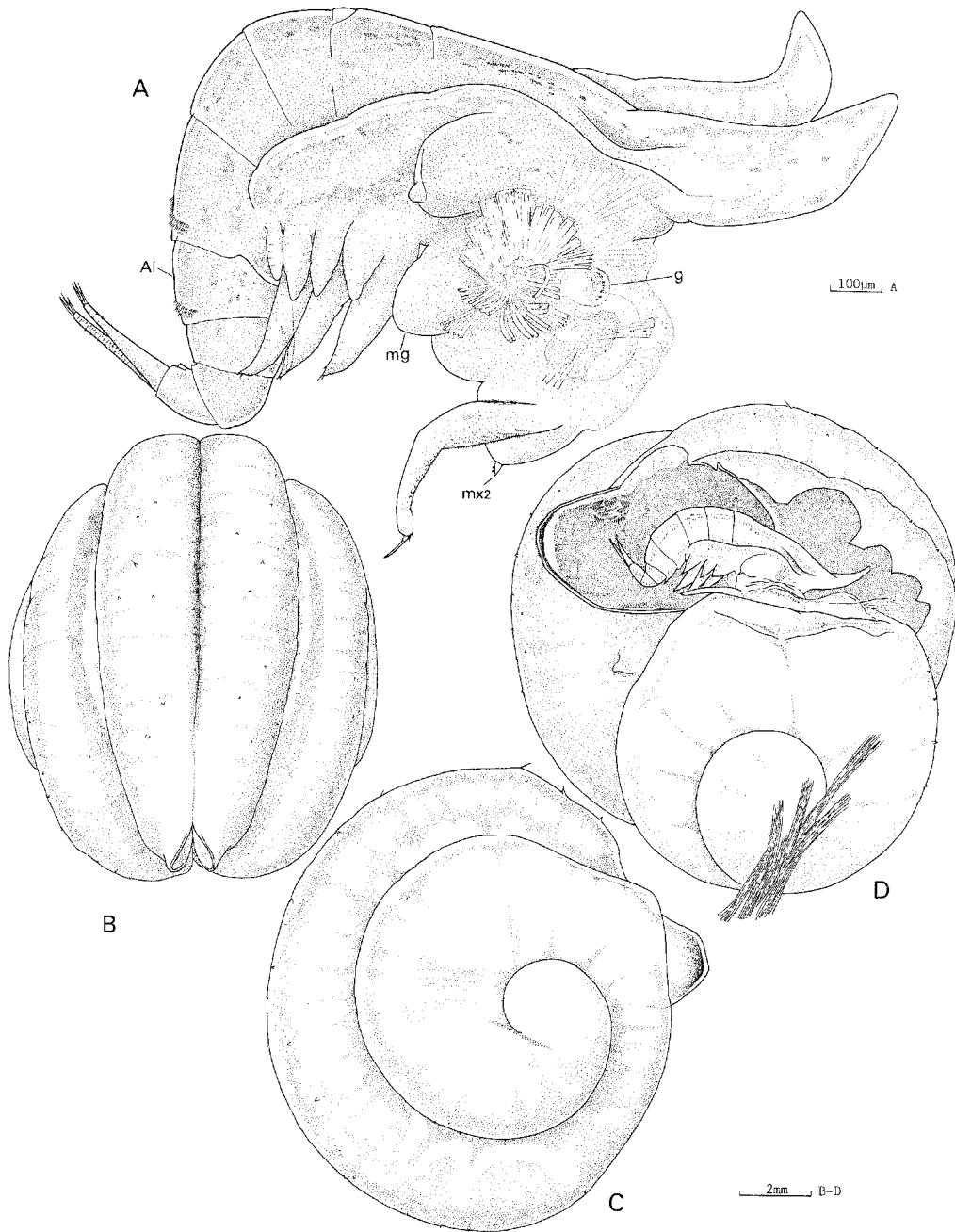


FIG. 1. *B. falsiramus* sp. nov. A, lateral view of holotype (carapace removed; AI, first abdominal segment; g, gut diverticulum; mg, maxillary gland; mx2, maxilla). B-D, paratype-1. B, dorsal view of carapace; C, lateral view of carapace; D, lateral view of habitus with partly torn carapace.

by T. I. from living host material (26-VII-1988), cephalic area and much of carapace missing, remainder of carapace removed from trunk, preserved in ethanol, dissected appendages mounted onto slide glass with glycerine jelly. Type locality: Tanabe Bay, Honshu, Japan. The type series is deposited in the Seto Marine Biological Laboratory, Kyoto University.

Etymology. The specific name (from Latin "*falsus*" = false plus Latin "*ramus*" = branch) refers to the extraordinarily large papillae at the bases of thoracopods 2-4.

1-1. DESCRIPTION OF HOLOTYPE

Carapace with small, medial body chamber connected to pair of large, coiled, lateral lobes serving as brood sacs (see Fig. 1B-C of paratype-1), tintured with reddish brown along aperture lips, other parts with very faint tinge of yellowish brown. Outer coils nearly circular in side view, 6.0 mm high, 5.1 mm long, subsequent coiling of diminishing radius, up to nearly two full revolutions altogether (± 675). Exposed lateral faces of coils with sparse, simple papillae, edges with widely spaced spines sometimes exceeding 0.15 mm long, outer part of hidden medial faces with similar but smaller tubercles (Fig. 3C). Gut diverticula and ovaries readily visible through carapace wall, with radially arranged side branches from main central coil, side branches dividing once or twice. Body chamber protruding beyond outer coil posteriorly, with vertical posterior aperture; aperture lips bearing adherent exuviae of four earlier instars (partially shown in Fig. 3A). Lips with short marginal spines, inner sculpturing of cuticular ridges forming hexagons, and dense interior lining of fine cuticular hairs (Fig. 3B). Ventral margins of lateral sides of body chamber adjoining but readily separable as far forward as oral cone; no special armament.

Body attitude as shown in Figure 1A; almost colorless but scattered spots of faint purple. Distance from tips of horns to tips of furcal rami 3.7 mm. Body cuticle loose, animal preparing to molt. Head bearing oral cone, posteriorly directed antennules, and pair of lobes representing maxillary glands. Thorax six-segmented, boundary of first and second segments not expressed externally,

that of second and third segments weakly expressed. Pair of anterior horns arising from first segment, parallel, shorter than thorax, laterally flattened, tapering to rounded, upturned tips, naked, semitransparent. Dorsoproximal part of each horn markedly swollen laterally in connection with anterior part of lateral chitinous ridge, latter present from basal part of horn to middle of sixth thoracomere, consisting of at least four or five separate, segmentally arranged thickenings and forming outer edge of trough along side of body, highest point near supposed boundary of first two thoracomeres. Transverse band of short rows of hairs on rear of sixth thoracomere and first abdominal segment. Five pairs of thoracopods present. Abdomen four-segmented, each segment narrower and less high than preceding one, ornamented with many small pores among sparse, delicate spinules (Fig. 3D). First abdominal segment with ventral penis.

Antennules (Fig. 4A, C) strap-like, about 0.9 mm long, curved or sharply bent, indistinctly divided into about four segments and apical process, hairy all over surface, transverse rows of longer hairs along anterior (ventral) face of proximal half. Terminal segment with two short, subapical setae, one medial and one anterior; medial seta apparently folded or bipartite (Fig. 4B, D). Apical process small, with trifurcate aesthetasc and short seta.

Labrum (Fig. 1A) deeper than long, short posterior edges adjoining behind other mouthparts but readily separable.

Mandible (Fig. 4E) narrow, distal half tapered with many short, basally directed spinules on proximal two-thirds of anteromedial margin, four arched rows of spinules posterolaterally.

Distal part of maxillule (Fig. 4F) represented by conical process with hairs of different lengths.

Maxillae (Fig. 4G) largely fused, their tips protruding through distal labral aperture; tips separate, bifid, each accompanied subterminally by basally bent, triangular, lateral plate.

Thoracopod 1 represented by a small papillary process arising from basal swelling, with no seta. Right one (Fig. 3E) shorter and wider than left one (Fig. 3F). Basal swelling hemispherical, somewhat inflated but not extending as "plate-like organ"

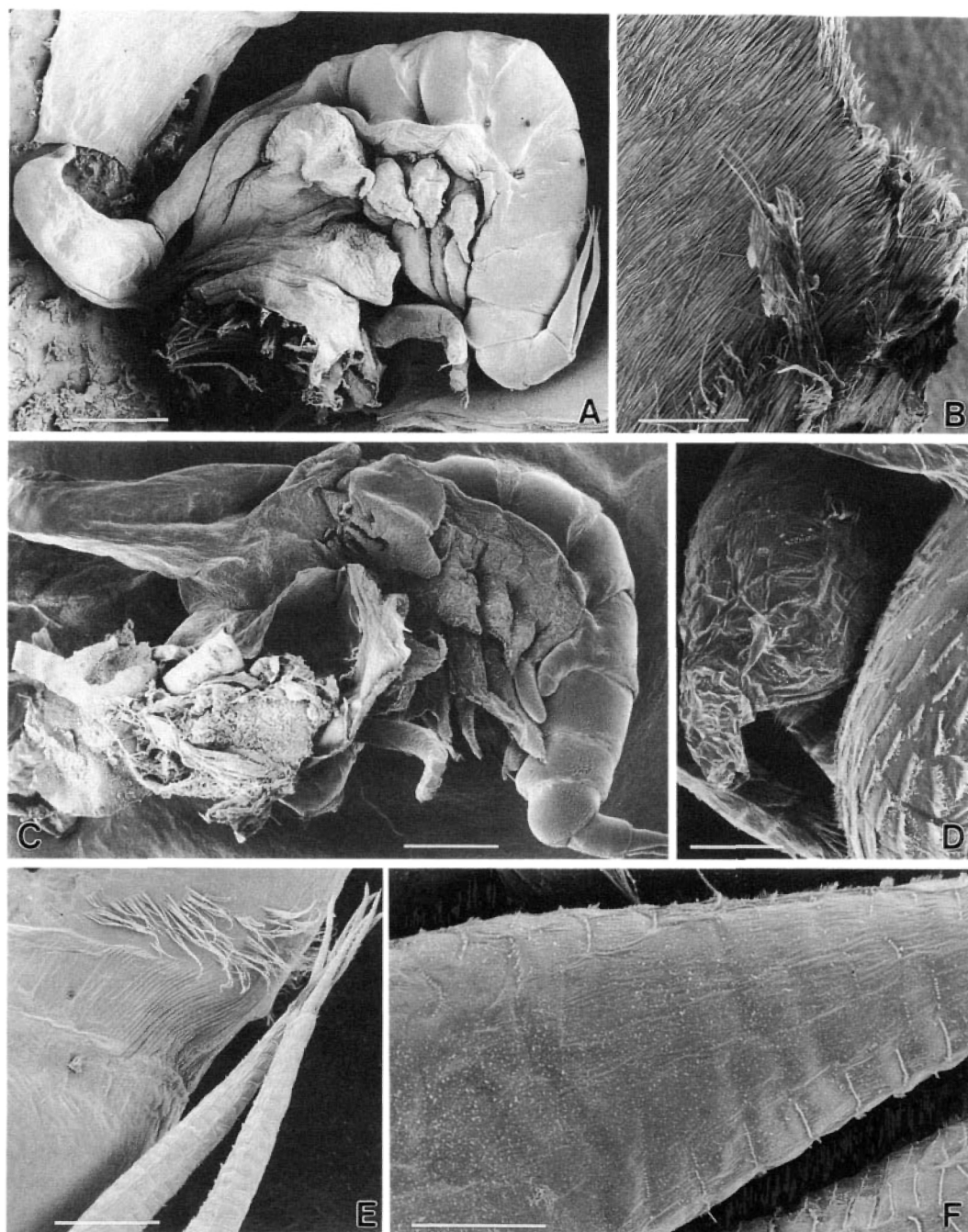


FIG. 2. SEM photomicrographs of *B. falsiramus* sp. nov. C-D SEM-2, otherwise SEM-1. A, habitus, lateral; B, internal side of carapace near aperture lip; C, habitus, lateral; D, penis and first abdominal segment; E, apical portion of furcal rami and first abdominal segment with hairs; F, furcal rami, lateral. Scales: A, C 500 μm ; B, E 100 μm ; D, F 50 μm .

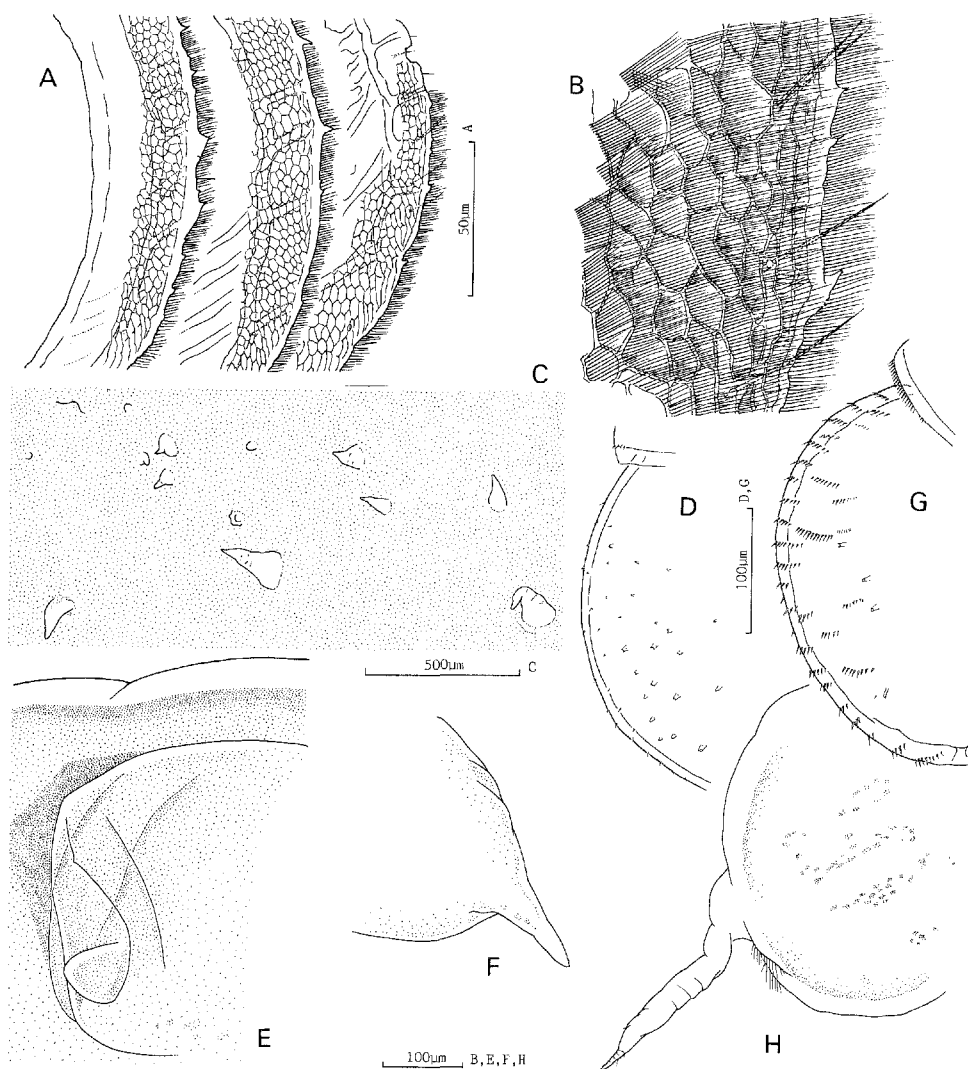


FIG. 3. *B. falsiramus* sp. nov. A-C, paratype 1. A, internal view of aperture lip, showing adherent exuvia; B, detail of marginal part of A; C, carapace spination, 3 large spines (below) on edge of coil, smaller ones (above) on inner face below edge. D-F, holotype. D, lateral view of third abdominal segment; E-F, right and left thoracopods 1 with basal swelling. G-H, paratype-2. G, lateral view of third abdominal segment; H, right thoracopod 1 with basal swelling.

dorsally over chitinous ridge.

Thoracopod 2 (Fig. 6A) large, well-developed, appearing biramous because of presence of prominent lateral papilla; leg itself unsegmented, but tiny distal, setose "ramus" distinguishable from "protopod" filled with seminal receptacles, "ramus" armed apically and laterally with four (right) or five (left) short setae or spiniform pro-

cesses together with cuticular ctenae and hairs (Fig. 6B, C). Lateral papilla conical, pointing ventrally, almost bare, extending to about middle of "protopod", terminating in relatively large opening (Fig. 6D), apparently many much smaller pores on sides of papilla, precise relationships to seminal receptacle ducts unclear. Seminal receptacles bottle-shaped, the number estimated at 14-17,

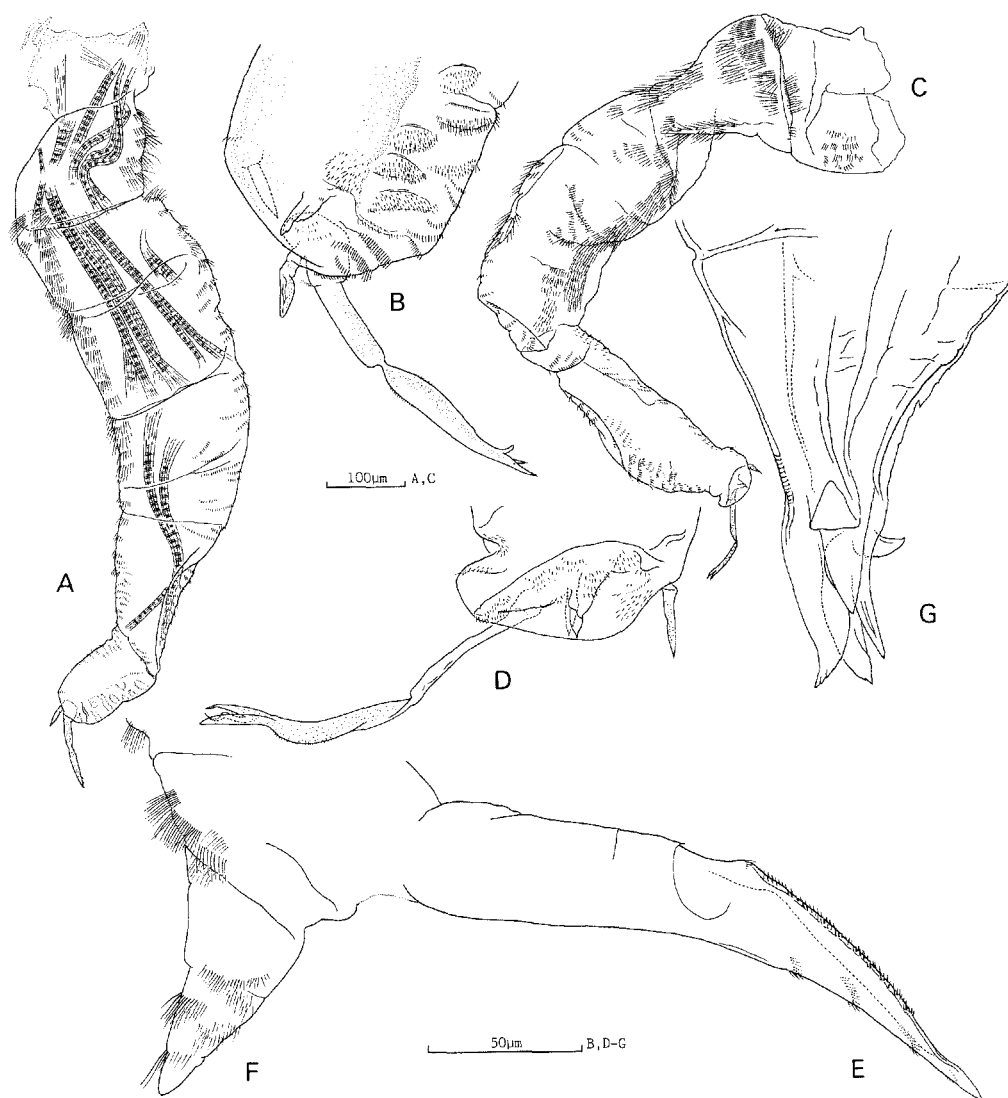


FIG. 4. *B. falsiramus* sp. nov. Holotype, A, right antennule, showing musculature; B, apical part of A; C, left antennule; D, apical part of C; E, mandible; F, maxillule; G, maxillae.

with long, extremely narrow ducts sheathed in cells. Within receptacles, sperm usually in small knot near duct entrance (see Fig. 6J, paratype), some sperms with elongate heads 42 μm long expressed from them.

Thoracopods 3–4 similar to thoracopod 2. Thoracopod 3 armed with spiniform processes or short setae on each ramus, three lateral and two terminal on the left (Fig. 6E), five lateral, two terminal, and one medial on the right (Fig. 6F), each con-

taining 14–15 seminal receptacles. Right thoracopod 4 (Fig. 7A) armed with one terminal and three short lateral setae, left thoracopod 4 (Fig. 7B) armed apically with one strong spine and one seta, 8–11 seminal receptacles in each “protopod”.

Left thoracopod 5 (Fig. 7C) sausage-shaped, right one tapered, both same size, less than half as long as preceding three pairs, lacking seminal receptacles and lateral papilla, ornamented with delicate cuticular ctenae almost all over its surface,

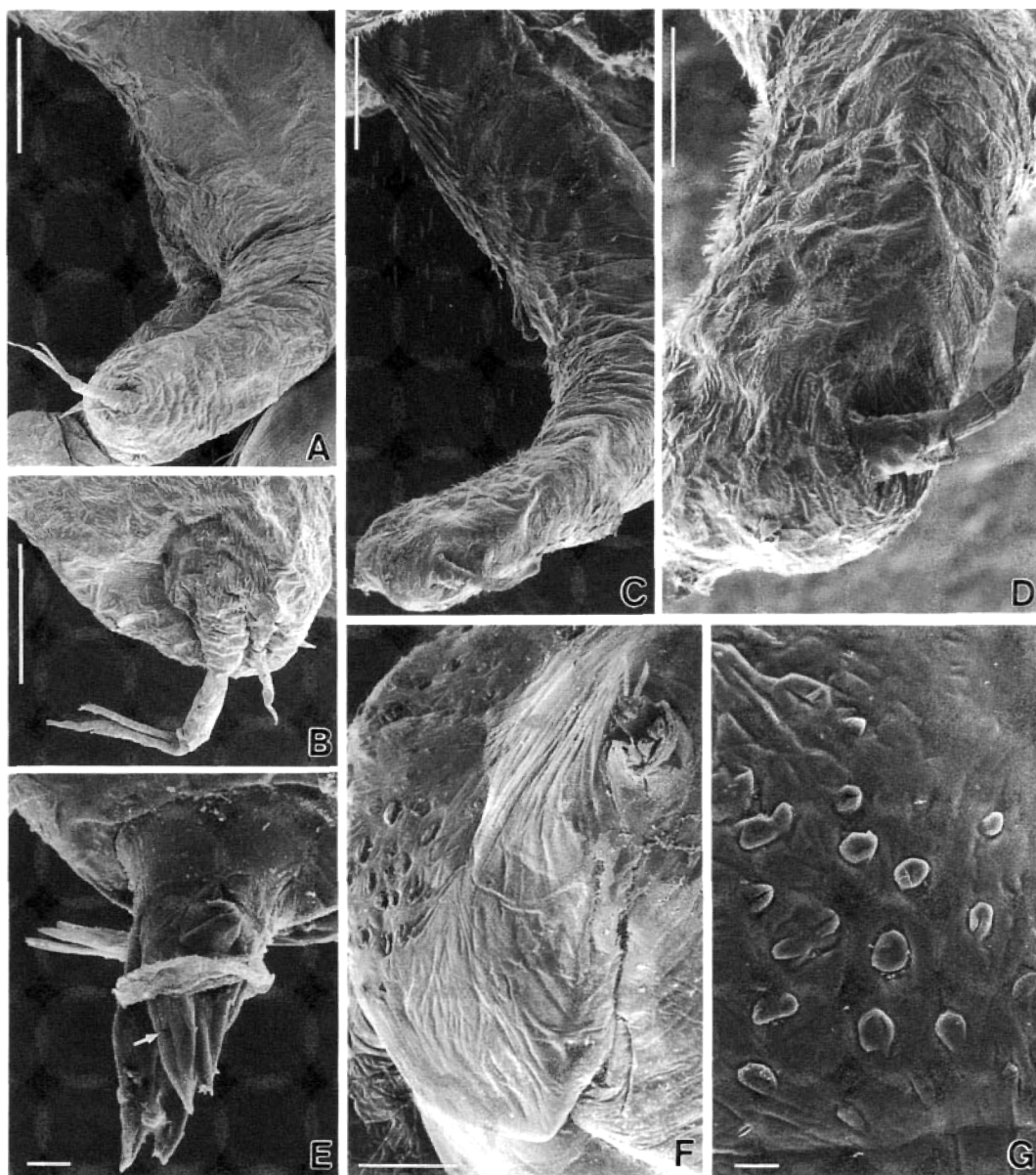


FIG. 5. SEM photomicrographs of *B. falsiramus* sp. nov. A-B SEM-1, otherwise SEM-2. A, left antennule; B, apical part of A; C, left antennule; D, apical part of C; E, tips of maxillae (arrow indicating duct opening); F, ventral view of labrum and maxillae; G, round papillae of labrum. Scales: A, C 100 μm ; B, D, F 50 μm ; E, G 10 μm .

with neither setae nor spines.

Thoracopod 6 absent, though ventral side of sixth thoracomere produced into transverse fold.

Penis (Fig. 7D) vermiform, reaching end of second abdominal segment, tapering toward two

sharp spines. Possible duct opening between spines.

Furcal rami (Fig. 7E) 0.50 mm long, basal height 0.13 mm, tapering and weakly sigmoidal. Three hirsute terminal setae, no medial setae or sensilla.

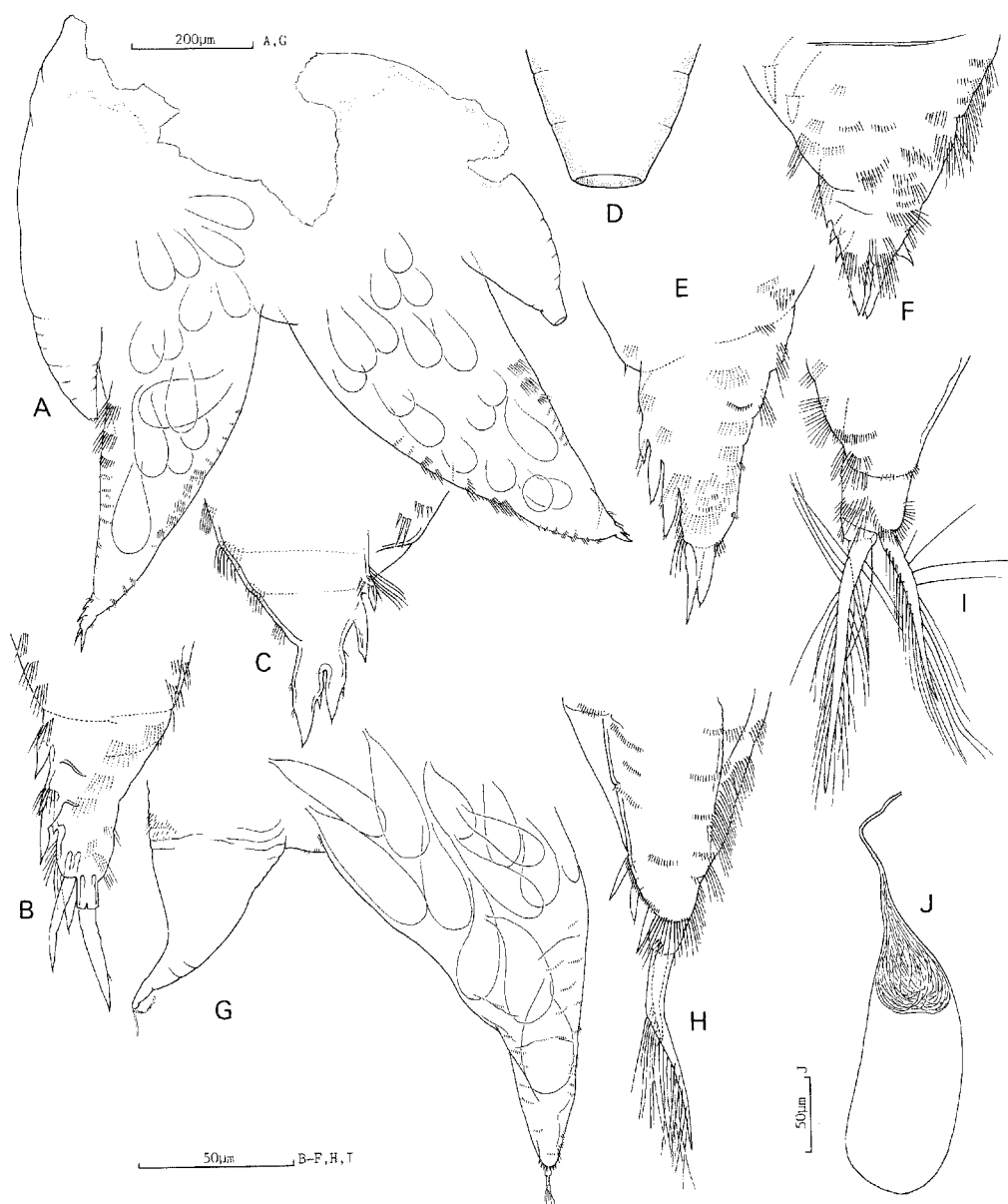


FIG. 6. *B. falsiramus* sp. nov. A-F, holotype. A, thoracopod 2; B, apex of right thoracopod 2; C, apex of left thoracopod 2; D, apex of lateral papilla of left thoracopod 2; E, left thoracopod 3, posterior; F, right thoracopod 3. G-J, paratype-2. G, thoracopod 2; H, apex of thoracopod 2; I, apex of thoracopod 3; J, seminal receptacle.

Short cuticular ctenae present on whole medial surface, distal quarter of lateral surface, and dorsal and ventral edges. Thickened dorsal and ventral margins appearing scalloped internally.

1-2. DESCRIPTION OF OTHER FEMALES

Outer coils of carapace of paratype-1 (Fig. 1B-D) 6.9 mm high, 6.2 mm long, paratype-2 indeterminate in this respect due to damage. Pair of dense patches of hairs dorsolaterally within body

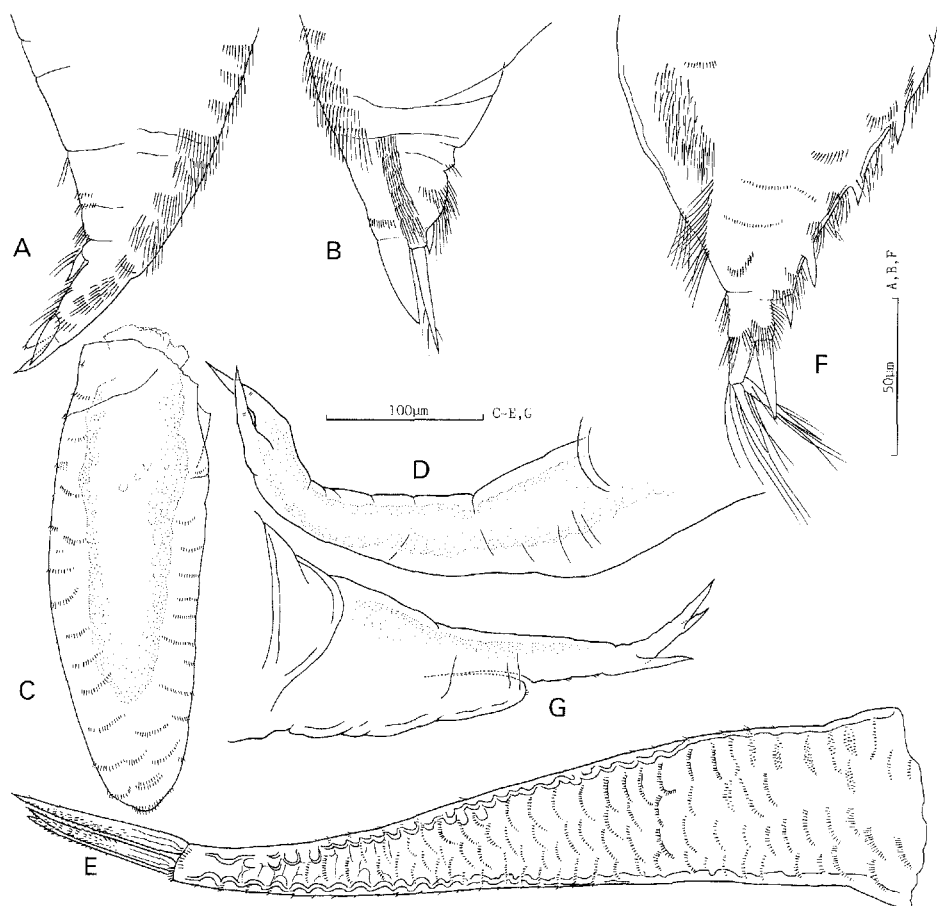


FIG. 7. *B. falsiramus* sp. nov. A-E, holotype. A, apex of right thoracopod 4; B, apex of left thoracopod 4; C, thoracopod 5; D, penis; E, medial view of furcal ramus. F-G, paratype-2. F, apex of left thoracopod 4; G, penis.

chamber (Fig. 1C; see also Fig. 2B). Bands of filamentous material firmly attached to a carapace coil of paratype-1 (Fig. 1C), probably pieces of host tissue.

Body attitude in all these females almost the same as in holotype, but horns of SEM-2 extending straight forward, not particularly upturned (cf. Fig. 2A and C). Distance from tips of horns to tips of furcal rami 3.9 mm in paratype-1, 4.2 mm in paratype-2, about 5 mm in SEM-1, 5.5 mm in SEM-2.

Thoracic segmentation of SEM-1 more obvious than in type specimens, evident as five tergites (thoracomeres 2-6) separated by wide areas of thinner cuticle (Fig. 2A). Wide band of thin cuti-

cle separating lateral chitinous ridge from bases of thoracopods (Fig. 2C), probably collapsed within longitudinal groove visible in SEM-1 (Fig. 2A). Paratype-2 and SEM-2 with prominent, dense cuticular ctenae on ventral half of abdomen (Figs. 3E, 2D), SEM-1 lacking such prominent ctenae but with many small pores instead (Fig. 8D, E), similar to holotype. In both specimens examined with SEM, dorsal setal patches on the last thoracic and first abdominal segments composed of many rows of hairs (Fig. 2E).

Antennules of SEM-1 similar to those of holotype in principal armature of apical segment and its process (Fig. 5A, B), though details of branching of terminal aesthetascs somewhat different. Apic-

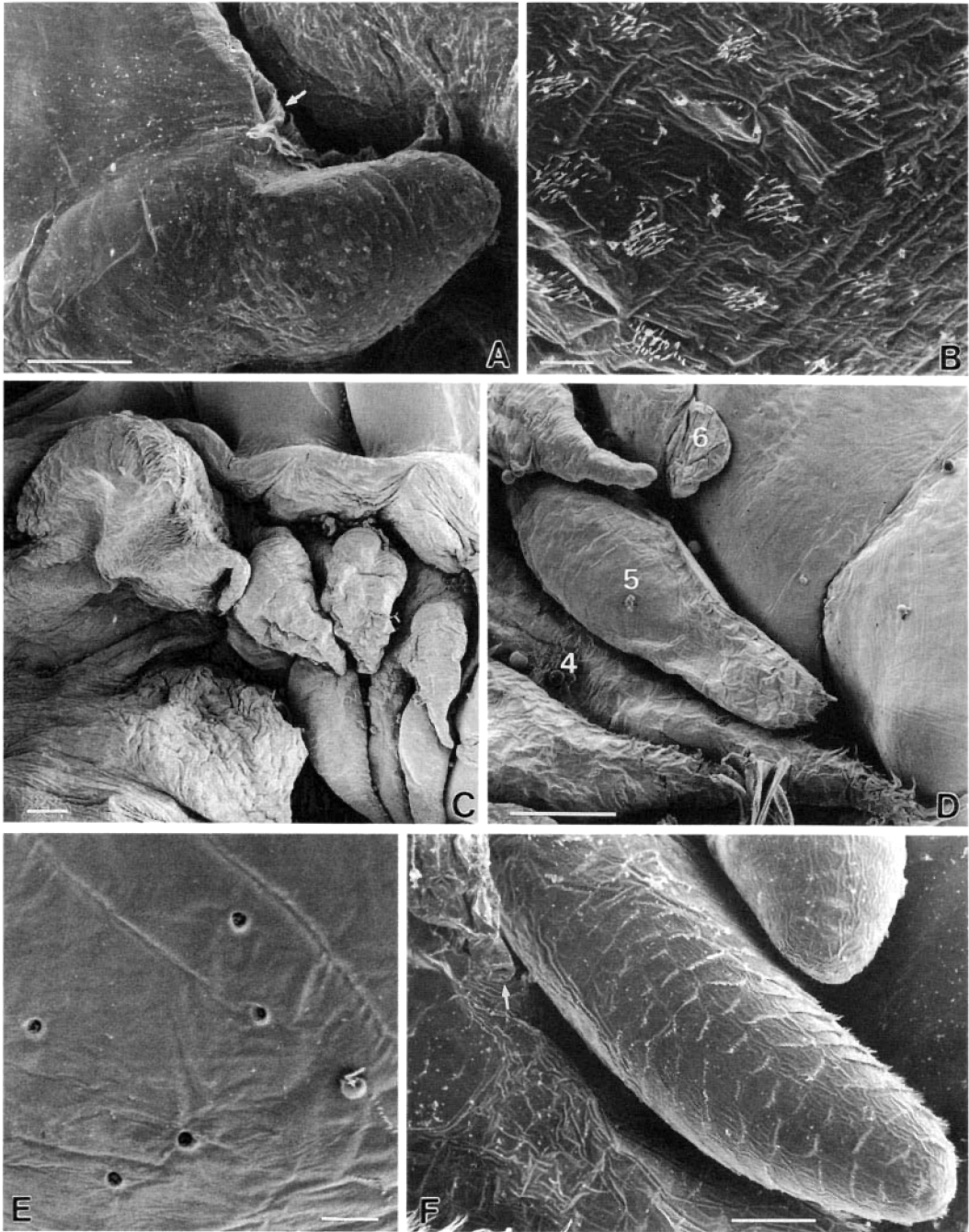


FIG. 8. SEM photomicrographs of *B. falsiramus* sp. nov. A, B and F SEM-2, otherwise SEM-1. A, thoracopod 1 with basal swelling (arrow indicating membranous structure with hairs); B, enlarged view of A, showing patches of hairs; C, thoracopods 1-4; D, thoracopods 4-6 (labeled as 4-6); E, pores on third abdominal segment; F, thoracopods 4-6 (arrow indicating apical opening of lateral papilla of thoracopod 4). Scales: A, C, D 100 μm ; B, E 10 μm ; F 50 μm .

al process clearly delimited from apical segment, but no other segmentation detected, at least externally. Apical process ornamented with cuticular ctenae as in apical segment. Left antennule of SEM-2 (right one lost) distinct in many respects (Fig. 5C, D), lacking distinct apical process but ending in rounded apex with delicate hairs and very small, closely set setae on frontal side. Unbranched aesthetasc arising from subapical, posterior side, small seta attached to thick basal part of aesthetasc.

Labrum bearing many flat, round, proximolateral papillae (Fig. 5F, G).

Apical part of maxillae protruding from labrum in SEM-2 with at least partial ring of unknown material distal to triangular lateral plates, and two closely set, spiniform structures extending anterior, that may be debris (Fig. 5E). Duct opening on anterior prong of bifid tip. Left triangular plate ending in two minute points.

Thoracopod 1, including its basal swelling, quite variform. In paratype-2, right one similar to holotype but left one a narrow, hairy, cylindrical process arising from semicircular swelling, armed with small apical seta (Fig. 3H). In paratype-1 (Fig. 1C), right one apparently similar to left one of paratype-2, but details not determined. Thoracopod 1 in SEM-1 similar to elongate ones in paratypes, but basal swelling more massive, reaching dorsal limit of lateral chitinous ridge of thorax and covered with long, dense hairs, especially abundant on dorsal edge (Figs. 2A, 8C). Basal swelling of this specimen apparently separated into two parts by shallow slit along dorsal edge (Fig. 8C). Left thoracopod 1 of SEM-2 represented by thick, papillary process arising from ventroposterior portion of discoidal plate (Fig. 2C) and armed with two dorsoapical setae (Fig. 8A); plate extending a little over dorsal limit of lateral chitinous ridge and equipped with numerous patches of short hairs (Fig. 8A, B). Membranous structure fringed with dense hairs (female gonopore ?) arising from dorsal gap between plate-like organ and trunk (Fig. 8A).

Terminal armament of thoracopods 2-4 variable. In paratype-2 thoracopods 2-4 bearing two or three prominent, apical setae in addition of lateral spines (Figs. 6H, I; 7F).

Lateral papillae of thoracopods 2-4 in SEM-1 almost naked (Fig. 8C), but those in SEM-2 ornamented with numerous patches of fine hairs. Papilla of right thoracopod 2 of paratype-2 with two cylindrical projections at tip rather than usual opening (Fig. 6G); each projection with internal duct and apparently extending from inside papilla, though its origin unclear. Apical opening of lateral papilla clearly seen in thoracopod 4 of SEM-2 (Fig. 8F).

In SEM-1, thoracopod 5 somewhat like thoracopods 2-4 except for absence of lateral papilla (Fig. 8C, D). This specimen with rudimentary thoracopod 6 (Fig. 8D). In SEM-2, thoracopod 5 represented by long, cylindrical process with round tip, ornamented with numerous cuticular ctenae (Fig. 8F). This specimen with prominent thoracopod 6 similar to thoracopod 5 in general appearance, including ornamentation, but shorter (Figs. 2C, 8F).

Penis of paratype-2 abruptly narrowing beyond duct opening at about middle of ventral side, terminating in two spiniform processes with single subapical spiniform process (Fig. 7G). Penis of paratype-1 also with spines but details unknown; penis of SEM-1 hidden in preparation. Penis of SEM-2 with narrow, nozzle-like apex with terminal opening and transversely arranged, fine spinules (Fig. 2D), short spine at least on right side proximal to nozzle.

Furcal rami examined with SEM ornamented with fine, longitudinal wrinkles (Fig. 2F). Furcal rami of SEM-2 slimmer than in SEM-1. Right ramus of paratype-1 with only two terminal setae.

1-3. POSSIBLE MALE

A possible male was found in association with a female (SEM-1), located near the aperture lips of the female, partially embedded in the host (Fig. 9A). This is similar to the positional relationship of males and females in *Baccalaureus japonicus* Broch, 1929 [7]. Since the main body was not visible, the possibility that this specimen is a settled ascothoracid larva cannot be wholly excluded.

Carapace apparently bivalved, about 0.60 mm long, surface ornamented with polygons delineated by chitinous ridges and lacking central pores

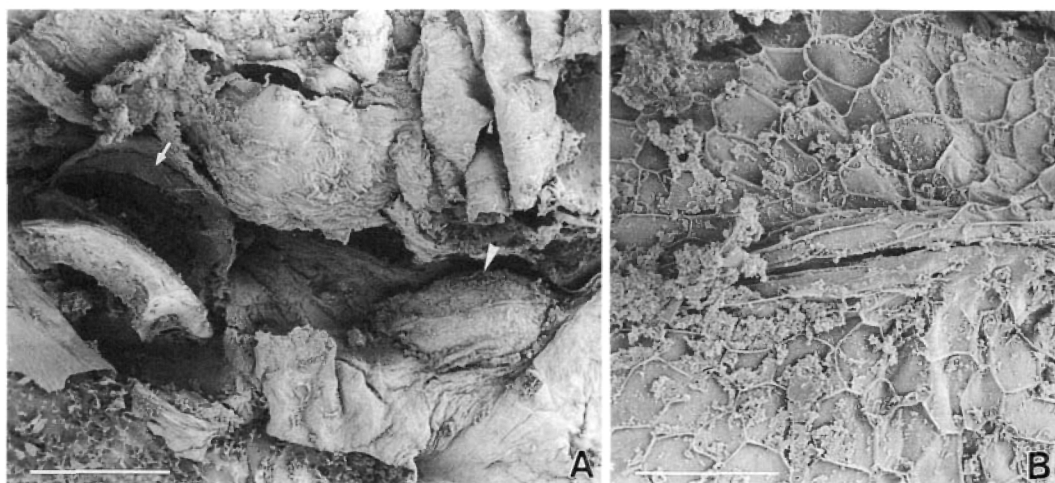


FIG. 9. SEM photomicrographs of *B. falsiramus* sp. nov. A, aperture lip of SEM-1 female (arrow) and possible male (arrowhead); B, enlarged view of carapace of possible male. Scales: A 500 μm ; B 50 μm .

(Fig. 9B).

1–4. COMMENTS ON HABITS

The adult females except for SEM-2 occurred individually in nodules at the bases of groups of 5–6 polyps, but each nodule's inner cavity seemed to be connected to only one or two polyps' gastro-vascular cavities. In one case, an external hole for the carapace aperture was evident between the bases of two nodule-associated polyps. SEM-2 occurred inside a spherical nodule formed of the basal portion of a single polyp, and the lips of its carapace aperture were clearly seen externally.

1–5. TAXONOMIC AND MORPHOLOGICAL REMARKS

The present new species, *Baccalaureus falsiramus*, is easily distinguished from the nine described species of the genus. None of the previous descriptions [5–14] mentions such enormous papillae lateral to the three major pairs of thoracopods, only sometimes small, nipple-like protrusions [e.g., 6]. Elsewhere in the Lauridae, *Laura bicornuta* Grygier, 1985 [6], as moderately large, laterally directed, conical papillae at the bases of thoracopods 2–5, and *Polymarsypus digitatus* (Pyefinch, 1939) [12] has flat lateral lobes at the bases of thoracopods 3 and 4; seminal receptacle ducts pass through both structures [6].

The coiled carapace lobes of *B. maldivensis* Pyefinch, 1934 [9], *B. hexapus* Pyefinch, 1936 [10], *B. torrensis* Pyefinch, 1937 [11], *B. argalicornis* Brattström, 1936 [14], and *B. durbanensis* Brattström, 1956 [5], all make over 1.5 turns like the present new species, but these species all also have long, downturned, coiled thoracic horns that wrap around the columellae of the carapace lobes and the horns are usually said to have short, retrorse hairs; in *B. falsiramus* the horns are short, more or less upturned, and naked. *B. verrucosus* Pyefinch, 1939, is the only species with horns as short as *B. falsiramus*, but they are still downturned and hirsute [12]. Carapace spines like those in the present new species have not been reported before.

The apical process or isolated aesthetasc on the antennules of *B. falsiramus* as well as the “terminal spine” in the unidentified specimen studied by Grygier [6], the “lobe” in *B. japonicus* [7], and the long, thin, spine-like tips observed by Pyefinch [12] in *B. pyefinchi* Brattström, 1956 [5], and *B. disparcaudatus* Pyefinch, 1939 [12], are probably homologous to the claw guard and/or proximal sensory complex of the distal antennular segment of other ascothoracidans, including male laurids.

In the maxillae, the bent, triangular plates presumably correspond to the posterior, movable hooks of many other ascothoracidans; if so, the bifid distal tip is unusual, and a duct has never

been observed there before.

The small, narrow furcal rami of *B. falsiramus* are most similar to those of *B. argalicornis* and *B. torrensis*, although in the last species they are terminally unarmed. There are apparently different kinds of furcal armament in *Baccalaureus*: terminal spines, terminal setae, tiny medial setae and sensilla, cuticular ctenae. The true distribution of these elements among the species is not clear from semantically ambiguous and incomplete descriptions, but true setae terminally, lack of medial armament aside from ctenae, and partial lack of lateral ctenae may be peculiar to the new species.

The variable structure of thoracopod 1 in *B. falsiramus* is problematic. The first thoracopod in *Baccalaureus* is usually accompanied by a "plate-like organ" (interpreted by Grygier as a form of filamentary appendage [6]). Only *B. pyefinchi*, which has little carapace coiling but long thoracic horns, has been previously known to have such small swellings hardly extending dorsally over the lateral chitinous ridge. However, the present material of *B. falsiramus* exhibits marked variability, and SEM-2 has a prominent structure that may be called a "plate-like organ". Thoracopod 1 proper in the present material appears as either a small papillary process, a cylindrical process with an apical seta, or a prominent papillary process with two setae. Hence, thoracopod 1 morphology might not be easily used as a diagnostic character within this genus.

The number of thoracopods has been one of the primary features used to diagnose species of *Baccalaureus* [e.g., 11], but since the sixth pair is not always present in *B. falsiramus*, this feature is actually not reliable at the species level.

The type specimens are smaller than the specimens examined by SEM. The largest one (SEM-2) has the best developed basal swelling (plate-like organ) of thoracopod 1 and the most prominent thoracopod 6. In SEM-1, the basal swelling is less developed than in the largest specimen but more so than in smaller specimens, and it has a rudimentary thoracopod 6 while the smaller specimens do not. These size-correlated morphological differences may reflect, at least in part, differences between adult instars.

Up to the present, most ascothoracidans have not been subjected to detailed studies of morphological variability. *Dendrogaster astropectinis* would be an exceptional case, in which variation of antennular morphology was studied by Karande and Oguro [15]. As mentioned above, the examined females of *B. falsiramus* show enormous variability, not only in the antennule but also in the thoracopods, penis, abdominal ornamentation, etc. Although this suggests that they may not all be conspecific, we treat them for the time being as conspecific because they share a characteristic thoracic horn morphology, their thoracopods 2–4 are always associated with prominent lateral papillae, and they lived in a single host colony.

Most of the identified hosts of *Baccalaureus* have been various species of *Palythoa*, but *B. japonicus* parasitizes a species of *Parazoanthus* and Muirhead and Ryland [16] recorded *Isaurus* as the host of an undescribed species. Hence the present report is the first confirmed occurrence of this parasite in a species of *Zoanthus*. The host of the type species, *B. japonicus*, has been recorded under several names in Japan, including *Zoanthus cnidosus* [7], but the name now used for this zoanthid is *Parazoanthus gracilis* (Lwowsky) [e.g., 17].

Baccalaureus is most widely recorded in the Indian Ocean [5, 9, 10, 12, 14, 18], with Pacific records limited to Japan [7, 8, 13, 17], Vietnam [19], northeastern Australia [11, 16], and French Polynesia [6]. The present finding adds a second species to the Japanese fauna of this genus and family.

Part 2. Larval Development

2-1. NAUPLII-GENERAL

Brood sizes are somewhat uncertain, but the holotype had over 375 brooded eggs and nauplii and paratype-1 had about 325 eggs in half of its carapace plus part of the other half, perhaps 550–600 in all.

There are six naupliar instars (one orthonauplius and five metanauplii) before the ascothoracid larva. In culture, the duration of instar I could not be determined. When one of us (T. I.) removed a

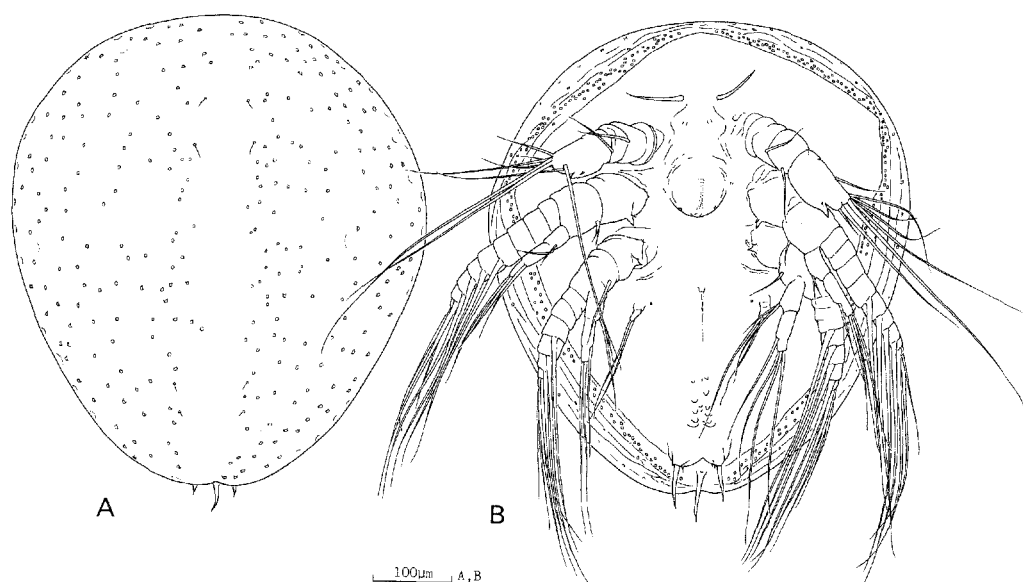


FIG. 10. *B. falsiramus* sp. nov. Exuvium of instar VI nauplius. A, dorsal view; B, ventral view.

female (paratype-2) from the host, it released a number of instar I nauplii together with eggs and possibly some instar II nauplii. The released nauplii immediately started to molt. None of the three nauplii isolated for individual culture from this batch of nauplii within 30 min. after release was still in the first instar. They were put in culture on 26 July, 1988, and metamorphosed into the ascothoracid larva on either 22 (one) or 23 (two) August, 1988. At 19°C, instar II lasted at least 3 days, and instars III-VI respectively 3, 2.5, 4, and 14-15 days. Molts were nearly synchronous, differing by at most one day. Thoracic limb buds of the ascothoracid larva were first recognized on the 8th-10th day of the last naupliar instar. The nauplii continued to swim during this period of about one month without feeding.

Eggs oval, 0.48 mm × 0.35 mm. Late instar I and newly molted instar II nauplii about 0.59 mm long (excluding caudal armament), 0.45 mm wide, 0.28 mm thick (excluding labrum). Instar VI nauplii 0.60 mm long, 0.52 mm wide.

Body of instar I oval, with no ventral depression where appendages occur, without distinct dorsal shield. Cuticle of instar I very delicate (Fig. 11E), with wrinkles, most likely separated from cuticle of internally formed, succeeding instar. Body of

instars II-VI with broad depression where appendages occur, and with bowl-shaped dorsal shield (Figs. 10, 11), broader in front, cuticle only significantly thickened in instar VI. Border of shield outlined by equatorial pores (sensu Grygier [6]) on inner "brim" of "bowl". No equatorial pores in instar I (Fig. 11B, E). At each molt after instar II, cuticle splits ventrally along border of thin, ventral cuticle and innermost edge of "brim" of dorsal shield, except for short, caudal region (Fig. 15). Nauplii escape from exuvia through gap formed by widening of this fissure. Exuvia of instar I always crumpled, often torn into pieces, uncertain whether definite fissure line exists.

Dorsal shield of instars II-VI ornamented with about three concentric, cuticular ridges on ventral and outer face of "brim" (Figs. 10A, 11A, D), some ridges connected with each other. No such ridges in instar I (Fig. 11B, E). Instars II-VI with small dorsal pores except along midline (Fig. 10A). Four pairs of hairs on dorsum of instar VI, two anterior pairs in instar II. Instars III-V unknown in this respect. No such pores or hairs on dorsum of instar I.

Nauplius eye present in front of antennules in all instars, with two obvious, red pigment cups. Pair of simple frontal filaments 90-100 μm long in

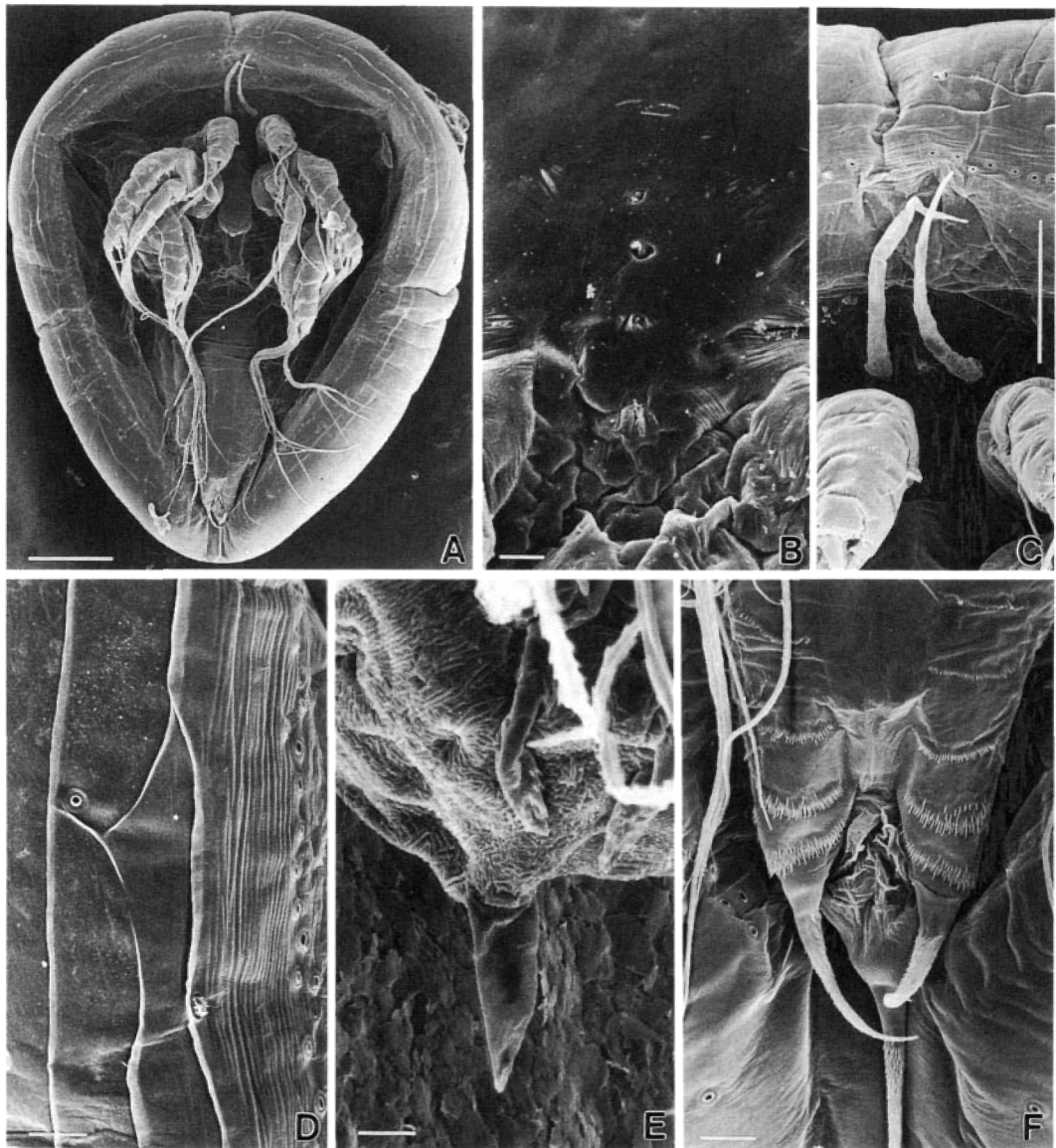


FIG. 11. *B. falsiramus* sp. nov. SEM photomicrographs of nauplii. A, ventral view of instar II; B, ventral surface between and anterior to antennules of instar I; C, frontal filaments of instar II; D, chitinous ridges of instar II; E, caudal region of instar I; F, caudal region of instar II. Scales: A 100 μm ; B, D-F 10 μm ; C 50 μm .

instars II-VI (Figs. 10B, 11C). Cylindrical, internal "cord", possibly a sensory organ, extending dorsally from point under cuticle between frontal filaments in at least instar II. No frontal filaments in instar I (Fig. 11B), but longitudinal row of three pit-like, sensory structures at midline, at least frontal two with rod-like sensillum, possibly diffe-

rent manifestation of internal "cord" of instar II.

Labrum small and triangular in all instars, with two apical pores and two widely spaced pores on hind surface at least in instars III-VI (Fig. 10). Short, cuticle-lined duct extending anteriorly from hind base of labrum in at least instars II-VI, probably representing rudimentary mouth.

Relatively well-developed antennules, antennae, and mandibles present in all instars, rudimentary maxillules also present from instar II. Caudal armament terminal in instar I, subterminal on ventral side in instar II-VI (Fig. 15).

2-2. ANTENNULES

Instar I (Fig. 12A): Short apical segment defined, with patch of spinules, but otherwise segmentation indistinct, about five additional patches of spinules marking possible future segments. Setation matching Grygier's [22] basic pattern for brooded ascothoracidan nauplii: two single median setae (a, b), grossly unequal pair of more distal median setae (long-d, short-e) opposite a lateral seta (f), and three unequal terminal setae (g). Except for seta "c", and shortest, medial "g" seta, these setae thick and spinulose.

Instar II (Fig. 12B): five-segmented, three basal segments subequal in length, next twice as long, last very small, setation 0-1-1-(2+1)-3, relative lengths of setae as in instar I but narrower; lateral "g" seta subterminal. Two setae, "d" longest "g",

plumose in this and later instars.

Instar III (Fig. 12C): Four-segmented due to fusion of distal two segments of previous instar, segments weakly marked, distal one spinulose, setation 0-1-1-7 with new setae (h_1) on lateral side, presumably the most proximal one there, a little shorter than seta "f". Medial "g" seta, formerly very short, now almost as long as "d" and setulose. Lateral "g" seta, now the shortest of the three, distally spinulose, perhaps in this instar only.

Instar IV (Fig. 12D): Similar to foregoing; segmentation less distinct, setation 0-1-1-8 with very short seta " h_2 " added proximal to " h_1 ".

Instar V (Fig. 12E): Unchanged except for addition of tiny lateral seta " h_3 " next to somewhat longer " h_2 ".

Instar VI (Fig. 12F, G): Clearly four-segmented, with unarmed basal segment, seta "a" on second, seta "b" on third, each accompanied by rudimentary new seta; fourth segment with subterminal claw rudiment (c) on medial side accompanied by small, anterior seta (i), three groups of distal setae: setae "d" and "e" medially terminal,

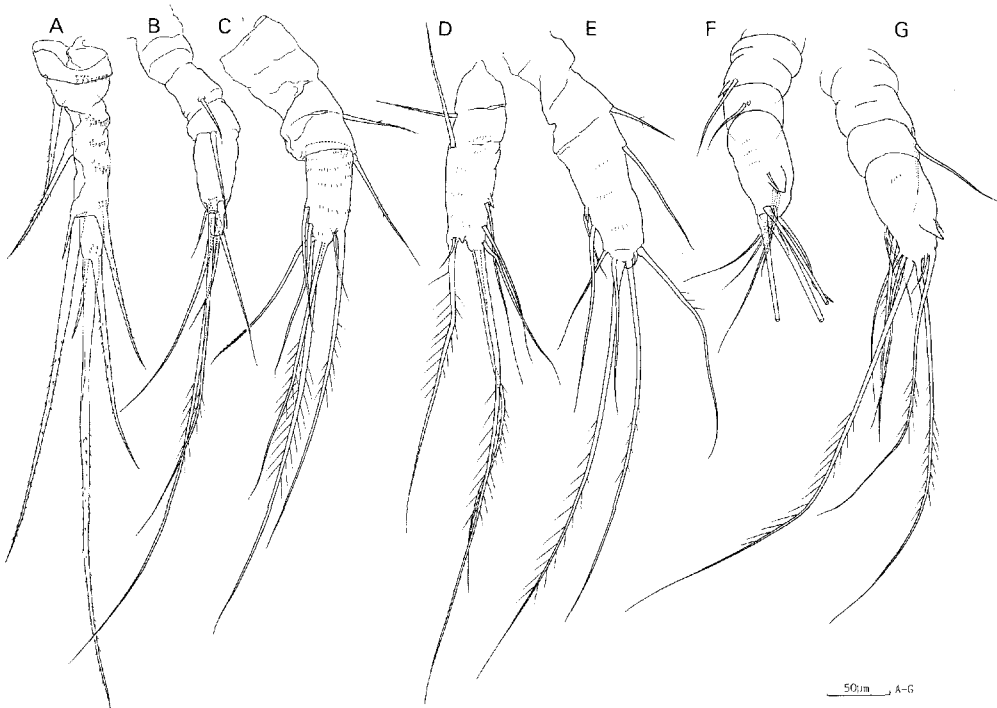


FIG. 12. *B. falsiramus* sp. nov. Antennules of naupliar exuvia. A-E, instars I-V; F-G, instar VI.

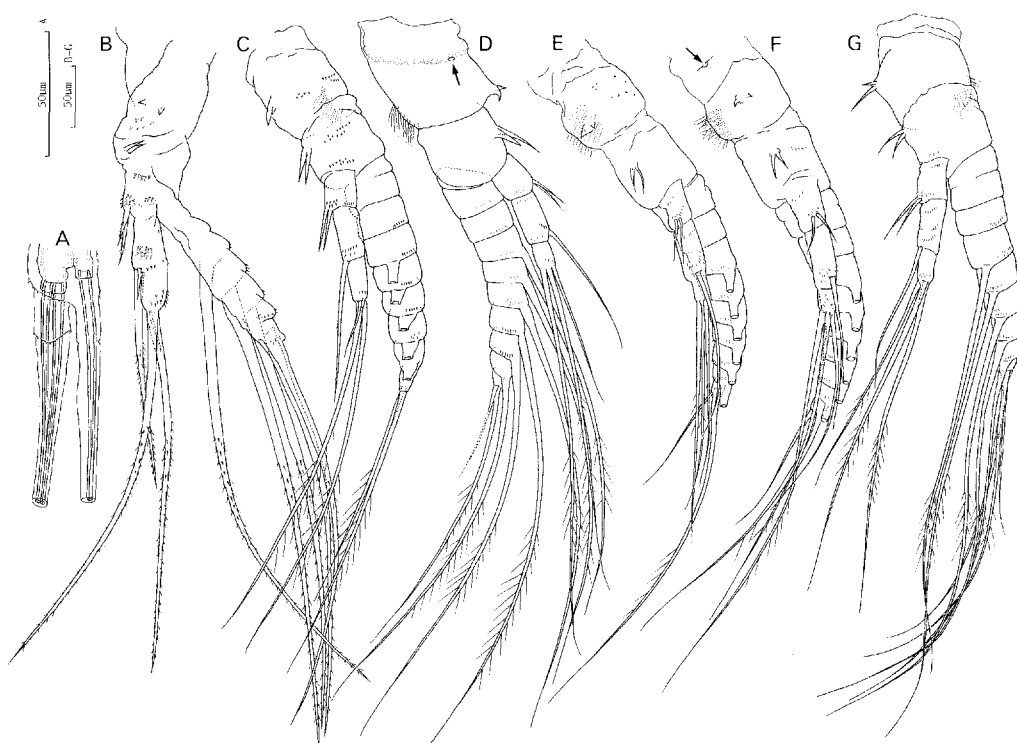


FIG. 13. *B. falsiramus* sp. nov. Naupliar antennae. A, apical part of exopod of instar I, showing two apical setae of instar II formed inside single terminal seta. B-G, exuvia of instars I-VI (some setae of C, E, and F omitted) (arrows indicating openings of possible antennal gland).

three "g" setae laterally terminal, setae "f" and "h₁₋₃" subterminolateral, none of these setae very short.

2-3. ANTENNAE

Instar I (Fig. 13B): Biramous, segmentation indistinct. Coxal area with two small, widely spaced, enditic spines and scattered spinules. Basal area with two closely set, enditic spines. Endopod as long as protopod, stepped at two points along medial edge; two subequal short setae on proximal step, thin seta on distal step; two long and one short, thin setae arising from apex; most setae spinulose but short, thin ones on distal step and apex simple; minute spinules occurring about stepped edges and apex. Exopod twice as long as endopod, indistinctly annulated, bearing from midlength five, thick spinulose setae up to 380 μm long. In individuals ready to molt to instar II, basal seta and distal seta of exopod each contain-

ing two setae of next instar (Fig. 13A).

Instar II (Fig. 13C): Boundary between coxa and basis clear. Coxa with two tiny, unequal, enditic spines, pore (? opening of antennal gland) on medioproximal edge, and fine hairs laterally. Basis with two equal, simple spines longer than coxal ones. Endopod equally three-segmented, first with two equal, simple setae, second with one narrow seta (clearly basally setulose only in this instar and one individual of instar VI), third with three apical setae, two of them well-developed and setulose. Exopod nine- or exceptionally ten-segmented, sometimes varying within a specimen, first segment short and indistinctly demarcated from second; segments 1-3 with no seta, segments 4-8 (5-9 on ten-segmented exopods) each with one seta, last segment with two apical setae; all setae well-developed and setulose.

Instar III (Fig. 13D): Unchanged except exopod ten-segmented due to splitting of terminal segment

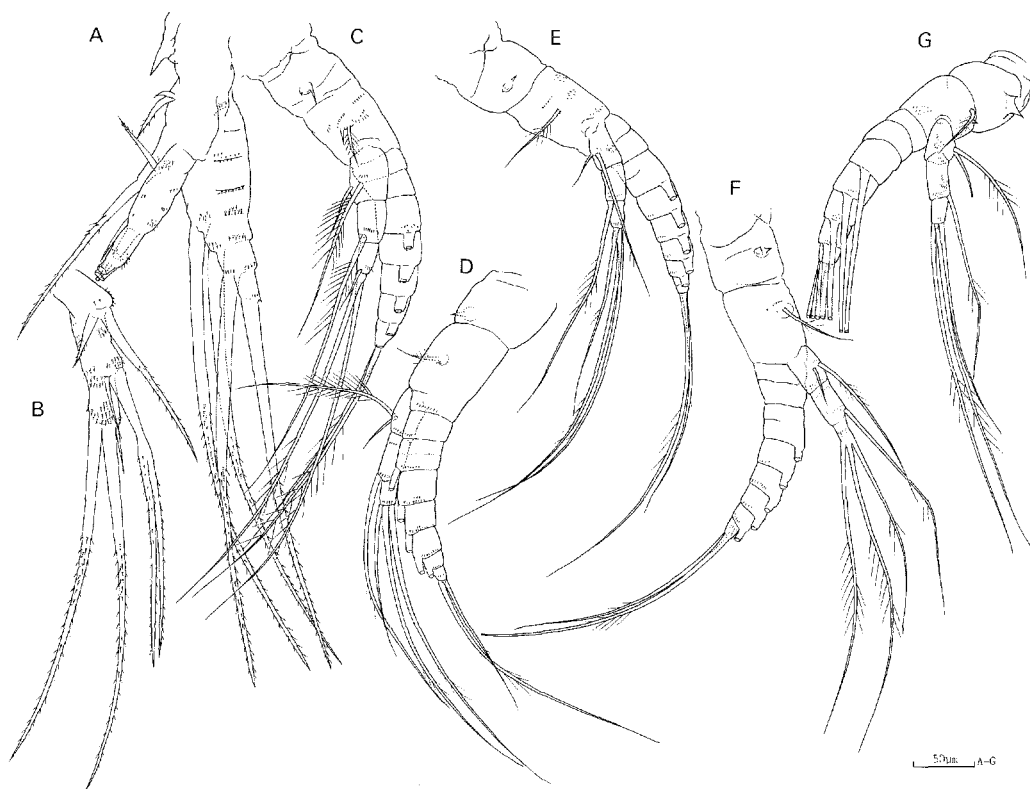


FIG. 14. *B. falsiramus* sp. nov. Naupliar mandible, exuviae. A, instar I (four endopodal setae omitted); B, endopod of instar I, with bifid aberrant seta; C-G, instars II-VI (some exopodal setae omitted).

and bearing eight setae, segments 4-9 with one each, terminal segment with two, including short, probably simple one; shortest apical endopod seta longer than before.

Instars IV-V (Fig. 13E, F): Unchanged from instar III in major ornamentation.

Instar VI (Fig. 13G): Coxal spines longer, one of them rather setiform, shortest terminal endopod seta setulose and grown to two-thirds length of other two, otherwise unchanged.

2-4. MANDIBLES

Instar I (Fig. 14A): Segmentation indistinct. Coxal region with thick enditic spine and much smaller one. Basis region with two short, enditic spines, longer one spinulose. Endopod stepped at two places along medial edge, two thick unequal setae on first step, one thin and one thick setae on second step, two thick setae and short, thin one apically; all thick setae spinulose, thin ones naked.

Abnormal, bifurcate setae seen on one endopod (Fig. 14B). Exopod a little longer than endopod, indistinctly annulated, with patches of fine spinules, bearing from midlength four thick, spinulose setae. In nauplii preparing to molt to instar II, basal seta and terminal seta of exopod each containing two setae of next instar.

Instar II (Fig. 14C): Segmentation clear. Coxa with distinct, medial, condylic articulation to ventral body surface, not seen in antennae. Coxal endite represented by low protuberance bearing spinule on anterior margin and, probably, very minute spinule posteriorly. Endite of basis represented by spine and short, setulose seta. Endopod three-segmented, first segment with two setae, longer one plumose, second segment with well-developed, plumose seta, third with two well-developed, plumose setae and hairlike seta. Exopod 1.5 times as long as endopod, seven-segmented; segments 1-2 short, with no seta;

segments 3–6 each with one well-developed seta; segment 7 with two well-developed apical setae; all setae setulose.

Instars III–V (Fig. 14D–F): Coxa as in instar II except enditic spine shorter. Enditic spine of basis reduced to spinule, seta unchanged. On endopod, hairlike apical seta of instar II now well-developed

and bearing some setules, though shorter than other two apical setae, otherwise unchanged. Exopod eight-segmented due to splitting of terminal segment and bearing seven setae, segments 3–7 with one each, terminal segment with two, including relatively short, simple one. Indistinct partial division of third segment.

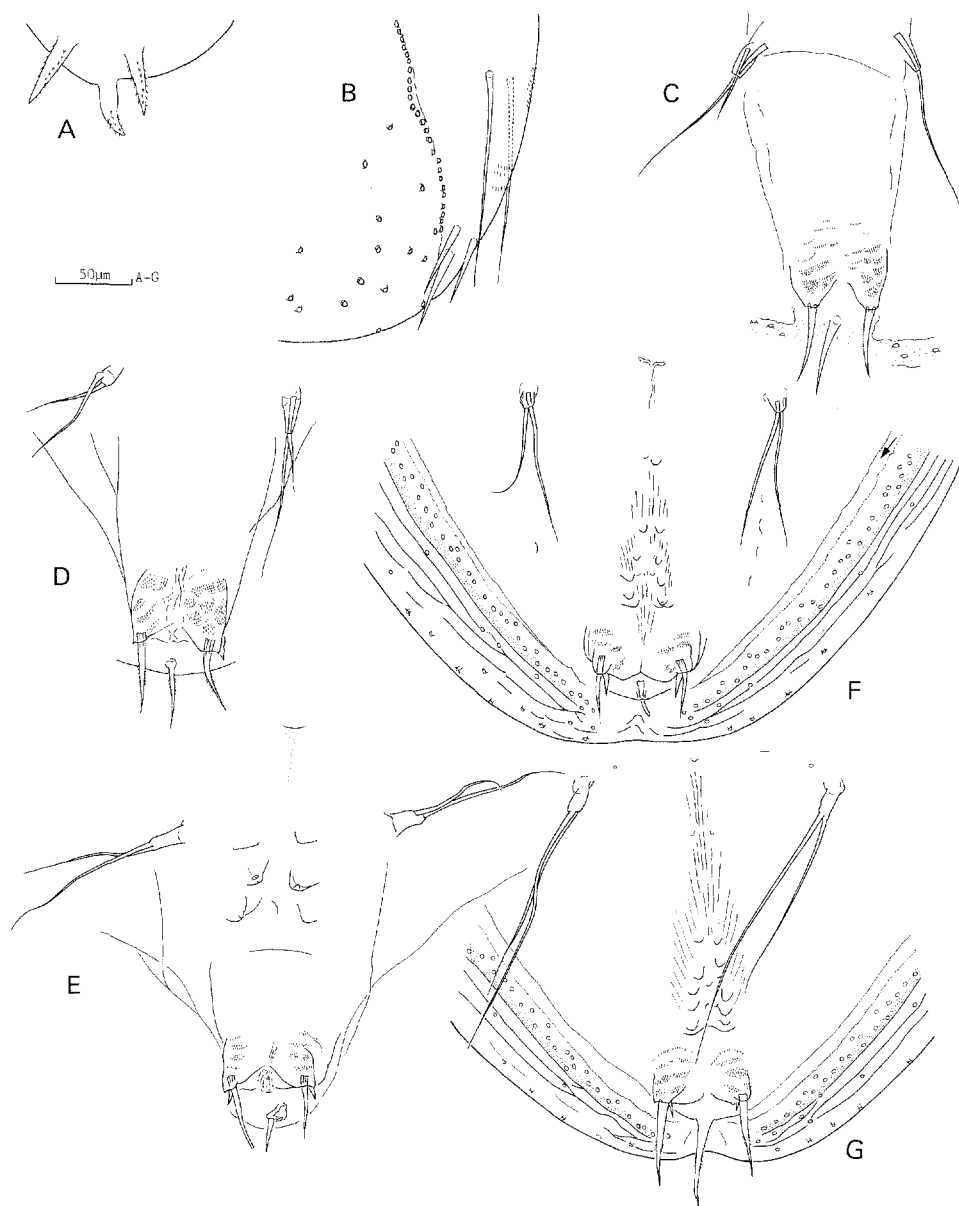


FIG. 15. *B. falsiramus* sp. nov. Caudal region and rudimentary maxillules of nauplii. A, instar I; B–E, exuvia of instars II–V with maxillules; F–G, exuvia of instar VI with maxillules and other rudimentary appendages (arrows indicating fissures).

Instar VI (Fig. 14G): Coxa with short, wide, enditic spine with two apical points. Otherwise unchanged.

2-5. MAXILLULES AND OTHER POSTERIOR APPENDAGES

Instar I: No maxillules.

Instar II (Fig. 15B): Maxillules represented by pair of long, simple setae. No sign of more posterior limbs, though seven or eight pairs of transverse rows of spinules or spinular bands between maxillular bases and furcal spines (Fig. 11F).

Instars III-IV (Fig. 15C, D): Maxillules represented by pair of small, papillary processes, each normally bearing two simple setae (only one seta on left in one of three instar series: see Fig. 15C). No sign of more posterior limbs.

Instar V (Fig. 15E): Maxillules unchanged, though setal lengths varying. Two or three pairs of conical, posteroventral bumps representing more posterior limbs.

Instar VI (Fig. 15F, G): Maxillules unchanged in principal structure, though setal lengths varying. In two cases formed as one-segmented rudiments on short, non-articulated bases. Five or six pairs of smaller and more posterior bumps than in instar V.

2-6. CAUDAL ARMAMENT

Instar I (Figs. 11E, 15A): Terminal spine and furcal setae equal in length (35 μ m), but terminal spine thicker, all more or less spinulose.

Instar II (Figs. 11F, 15B): Terminal spine extending slightly beyond rear of dorsal shield, usually longer than furcal setae, all thinner and more pointed than in instar I, with very delicate spinules.

Instars III-VI (Fig. 15C, D): Terminal spine and furcal setae as in instar II, length variable among specimens, patches of fine spinules anterior to furcal spines.

Instar V (Fig. 15E): Additional short spine or seta appearing dorsal to each furcal seta.

Instar VI (Figs. 10, 15F, G). Unchanged.

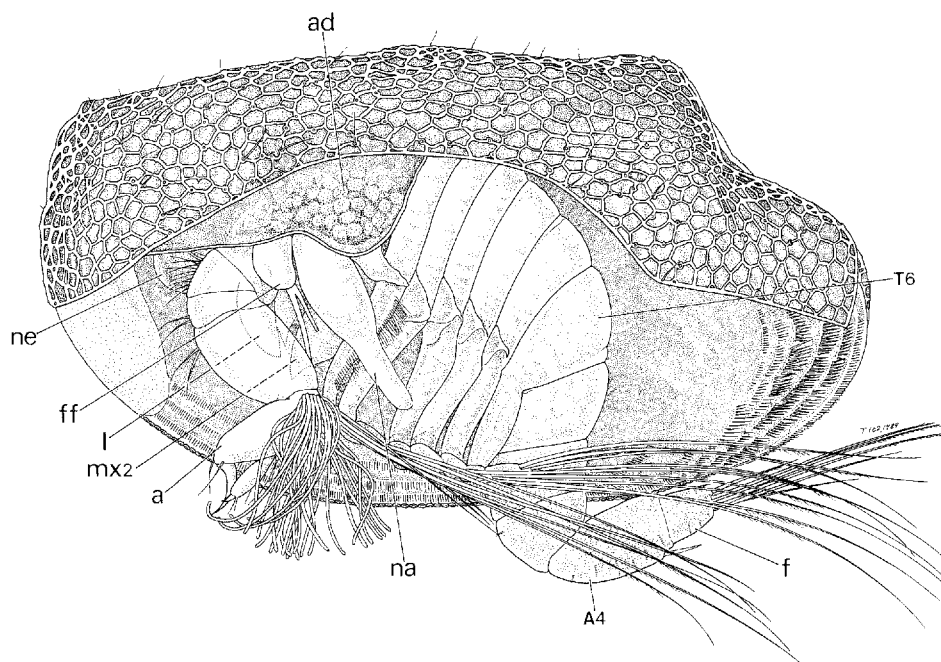


FIG. 16. *B. falsiramus* sp. nov. Scheme of ascothoracid larva, with carapace optically cut away. a, antennule; ad, adductor muscle; A4, fourth abdominal segment; f, furcal ramus; ff, frontal filament complex; mx2, maxilla; l, labrum; na, nauplius antenna; ne, nauplius eye; T6, sixth thoracic segment.

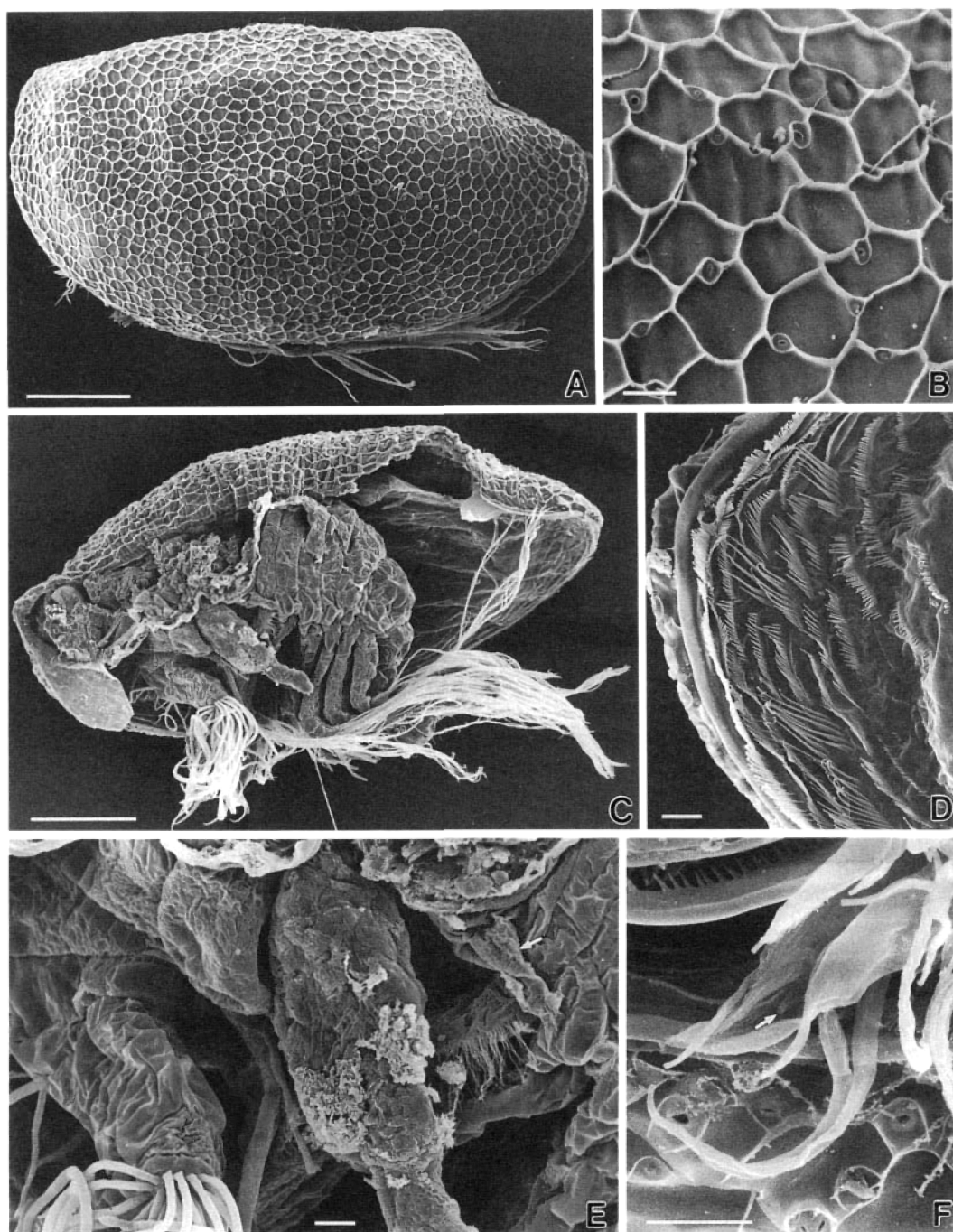


FIG. 17. *B. falsiramus* sp. nov. SEM photomicrographs of ascothoracid larva. A, habitus lateral; B, posterolateral portion of carapace; C, habitus (left carapace removed); D, internal view of posterior portion of carapace; E, antennule, frontal filament complex, and naupliar antenna (arrow indicating possible naupliar mandible); F, apical hood of antennular claw guard (arrow indicating possible gland opening). Scales: A, C 100 μm ; B, D-F 10 μm .

2-7. SUMMARY OF NAUPLIAR DEVELOPMENT

There are six naupliar instars. The greatest morphological changes take place at the molt from instar I to instar II: equatorial pores and frontal filaments appear, the dorsal shield takes form, the appendages become well segmented and set in a deep ventral depression, the exopods of the antennae and mandibles gain two setae each, the natatory setae become setulose, maxillular rudiments differentiate, and the caudal armament moves ventrally. At later molts there are only minor changes: addition of another segment and seta to

the antennal and mandibular exopods at instar III along with incorporation of the distal antennular segment into the penultimate one; gradual addition of lateral setae and a claw rudiment to the antennule (Fig. 20); appearance of postmaxillular limb buds and a second pair of furcal spines at instar V; thickening of the dorsal shield of instar VI.

2-8. ASCOTHORACID LARVA

The ascothoracid larvae (Fig. 16) are active swimmers. They open their carapace valves to extend their antennules and abdomen when swimming. The red nauplius eye was easily seen ven-

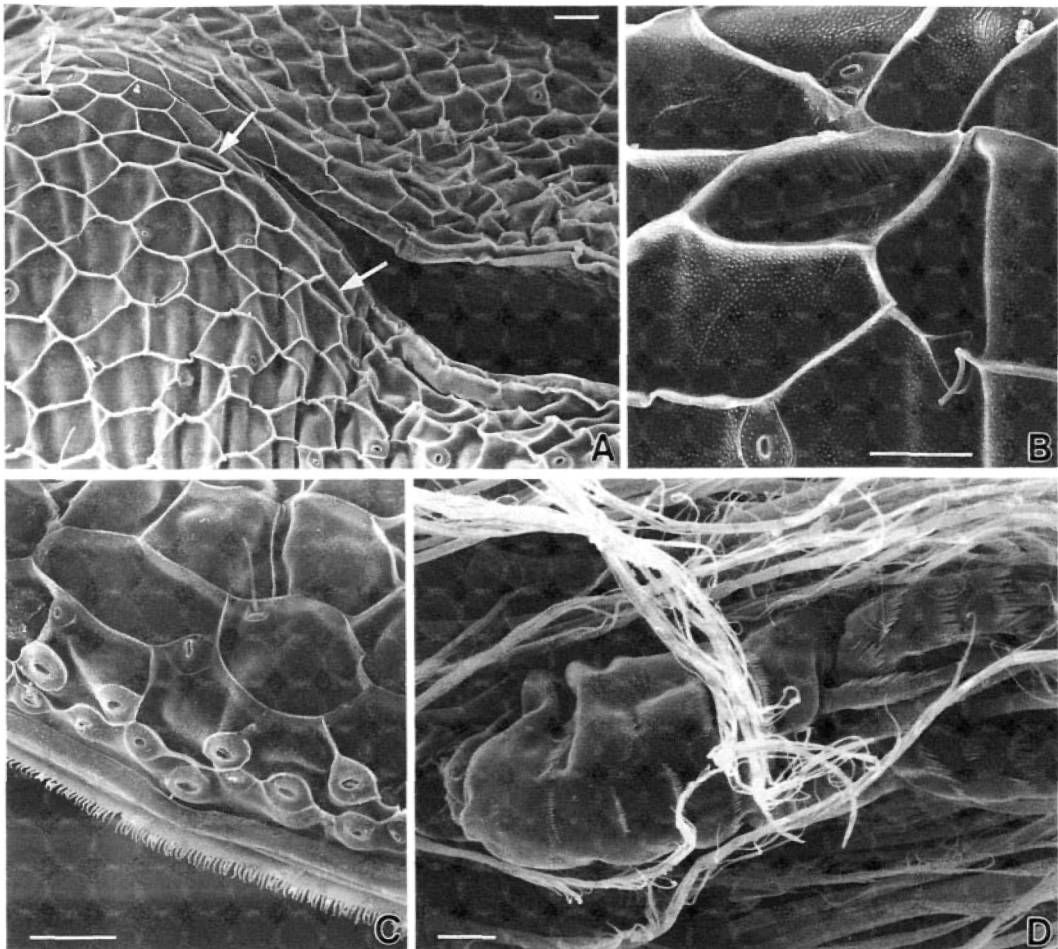


FIG. 18. *B. falsiramus* sp. nov. SEM photomicrographs of ascothoracid larva. A, dorsocaudal region of carapace, showing cardiac organs (arrows); B, enlarged view of cardiac organ; C, ventral margin of carapace; D, last abdominal segment and furcal rami. Scales: A, C, D 10 μ m; B 5 μ m.

trally while they were swimming. The furcal rami are movable, often splaying apart from each other laterally.

Carapace bivalved, 0.51 mm long, 0.31 mm high, 0.30 mm wide (Fig. 17A). Dorsal hinge line

thickened, somewhat interdigitated, recessed. In side view, valve outline slightly convex dorsally, rounded anteriorly and posteroventrally, almost straight mid-ventrally, concave posterodorsally below angle formed by protrusion above hinge line.

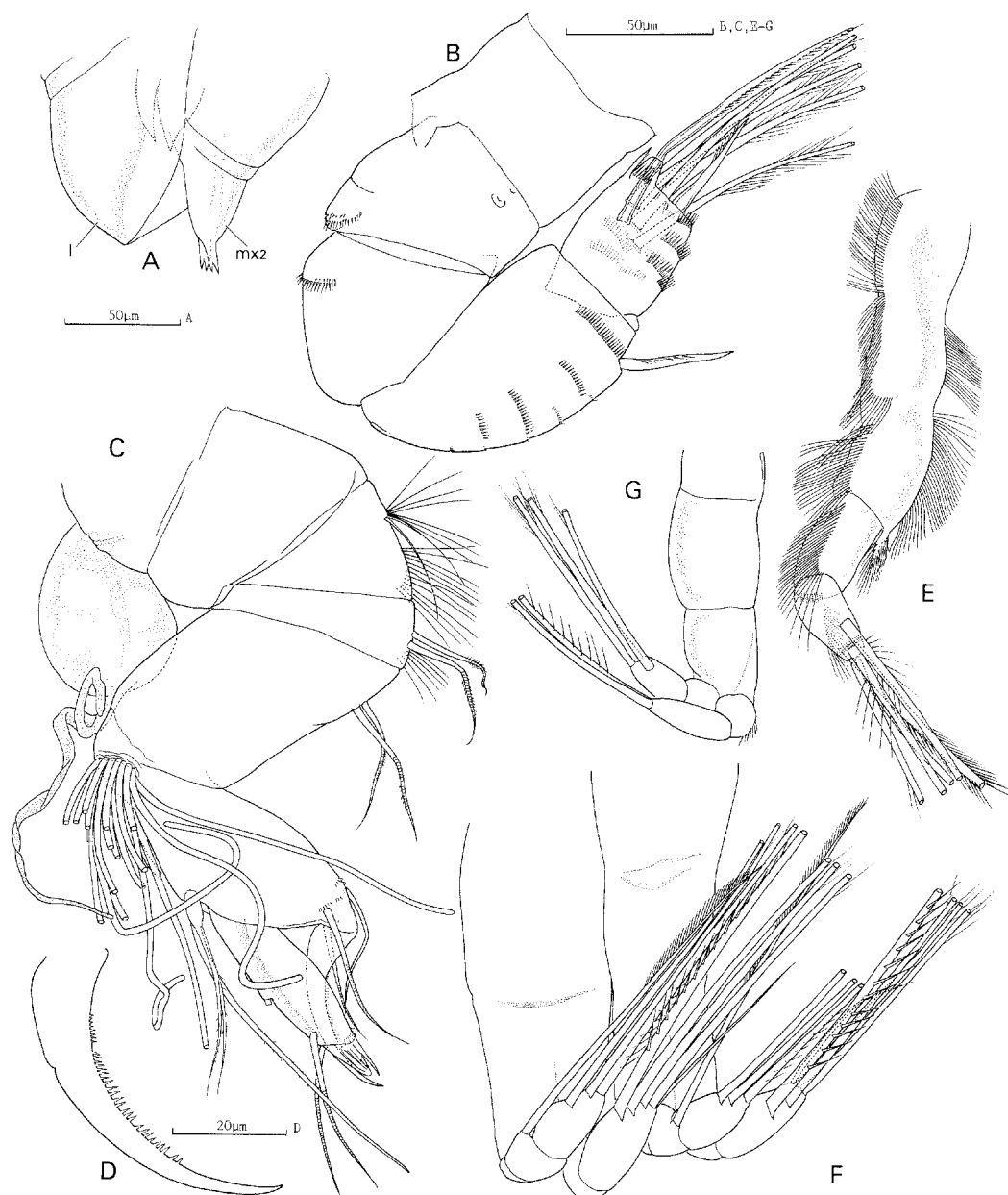


FIG. 19. *B. falsiramus* sp. nov. Ascothoracid larva. A, oral area (l, labrum; mx2; maxilla); B, abdomen (penis broken); C, antennule (most aesthetascs broken during dissection) and frontal filament complex; D, antennular claw; E, thoracopod 1; F, thoracopods 4-5; G, thoracopod 6.

Outer surface of valves with polygonal (principally hexagonal) meshes averaging $13\text{ }\mu\text{m}$ across and outlined by low, cuticular ridges (Fig. 17B). No pits or pores in centers of meshes, but meshwork often interrupted or adjoined by small, rounded, ridge-bounded meshes $3\text{--}5\text{ }\mu\text{m}$ across, with either central pore surrounded by elevated rim or seta about $25\text{ }\mu\text{m}$ long; these features absent in area overlying adductor muscle attachment. Entire outer surface, except certain areas as described below, with very fine granulation (Fig. 18B). On each valve, five narrow, polygonal meshes equidistant from hinge line, three flanking front of hinge, two near its rear (Fig. 18A); each with tube arising from anterior pit, running longitudinally along bottom of mesh, and opening at posterior end (Fig. 18B). Bottoms of these five meshes with no granulation.

Band of prominent pores, derived from naupliar equatorial pores, along entire free margin of valves outside marginal cuticular ctenae (Fig. 18C). Inner surface of valves with several cuticular ridges parallel to edge, additional posterior armament of fine fringes of cuticular ctenae and several arrays of long guard spines (Fig. 17D).

Body completely enclosed by carapace when abdomen retracted, 0.40 mm from antennule to tip of furcal rami in retracted position, with head, six-segmented thorax, and four-segmented abdomen with furca (Figs. 16, 17C). Large nauplius eye with two obvious red pigment cups in hemispherical ventral protrusion of "forehead" anterior to labrum.

Frontal filament complex hanging just lateral to rear base of antennule, with rounded, rather pyriform basal part ($42\text{ }\mu\text{m}$ long, $32\text{ }\mu\text{m}$ wide in SEM specimen) and biramous sensory process; branches unequal, main one about $100\text{ }\mu\text{m}$ long, shorter, thinner one arising near its base (Figs. 17E, 19C).

Antennule composed of six major segments, Z-shaped (Fig. 19C). First segment short, next three together not much bigger than fifth, third one triangular with long hairs on anterior edge, fourth and fifth each with two nearly equal anterior setae. Sixth segment with thin, movable claw with bump on convex side and row of distally longer denticles on concave side (Fig. 19D); three long setae at base of claw. Laterally flanged claw guard

with one seta distal and two proximal to small apical hood, latter a membrane armed marginally and externally with many spinules and protecting short, protruding tubule on end of claw guard (Fig. 17F); shelf at mid-length of claw guard on free side, bearing short tubule (? broken seta) on one antennule of dissected specimen only. Proximal sensory process near base of claw guard short and cylindrical, with three setae, one long and thick, other two replaced by bifid seta in one case, all three setae with delicate spinules. Cluster of about 25 long aesthetascs arising on sixth segment from basolateral, oval region with thick, chitinous border (Figs. 17C, E; 19C).

Pair of vestigial but large naupliar antennae (Fig. 17C, E) posterior to frontal filament complexes; medial sides, including possible endopods, not clearly seen; internal musculature present; vestiges of 5–6 setae on narrow distal part, presumably representing exopod. Another, much smaller and badly shrunken structure apparent behind antenna in SEM specimen (Fig. 17E), possibly vestige of naupliar mandible.

Oral cone imperfectly formed (Fig. 19A). Labrum a rounded lobe partly enclosing other mouthparts. Mandibles and maxillules spiniform, but latter thicker. Maxillae relatively large, tips narrow and bifid.

Thorax demarcated from head by distinct suture (Fig. 17C), first segment shorter than segments 2–4, segments 5 and 6 much longer dorsally due to body curvature; segments 2–4 with small external swelling anteriorly above limb articulations.

Six pairs of thoracopods biramous. First limb narrower than others; coxa and basis lined on both sides by long hairs (Figs. 17E, 19E); exopod two-segmented, with hairs on lateral edge of first segment and medial edge of second one, armed with five setae, medialmost one thicker than others and with dense, fine spinules bilaterally, others more or less plumose; endopod represented by small, hairy, setiform process. Limbs 2–5 (Fig. 19F) similar to each other; posterior border between coxa and basis unclear; basis with shallow, lengthwise groove on at least distal half of anterior surface; exopod two-segmented, first segment with no seta, second one with five setae, lateralmost seta thin, short, and minutely spinulate, others

equally thick and long, medialmost one markedly spinulate while others plumose; endopod three-segmented, with no seta on first segment, markedly spinulate seta on second segment, three more or less plumose setae on third segment. Limb 6 (Fig. 19G) smaller than previous limbs; coxa and basis distinct, both naked; lengthwise, anterior groove of basis clear, reaching near coxa; rami two-segmented; exopod with no seta on first segment, three similar, more or less plumose setae on second segment; endopod with short spinules on medial edge of first segment, two terminal setae on second segment.

When observed in whole mount, first abdominal segment seemed to bear lobe-like penis, but penis lost from dissected abdomen so details unknown (Fig. 19B). Fourth abdominal segment longer than others, with ventral and ventrolateral cuticular ctenae and pair of lanceolate, movable, somewhat setiform telsonic spines (Figs. 18D, 19B).

Furcal rami (Fig. 19B) slightly longer than high in lateral view, flattened laterally, slightly curved with concave medial faces, closer together dorsally than ventrally. Armament consisting of transverse cuticular ctenae laterally; lanceolate, short spine on dorsal edge near posterior end; four apical and

three medial setae, dorsalmost seta inserted into short process, both it and ventral seta dorso-ventrally flattened and lanceolate, other setae setulose.

2-9. DISCUSSION

Nauplii. -The present study has demonstrated that lecithotrophic nauplii of ascothoracids can be raised at least to the ascothoracid larva in the laboratory by using the culturing method that was originally developed to raise *y*-larvae [20]. This kind of laboratory culture is essential for the identification of larval instars and for a precise analysis of their morphological changes. Although Grygier [21, 22] reported without full descriptions a minimum of five naupliar instars in *Gorgonolaureus muzikae* Grygier, 1981, and *Parascythorax* cf. *synagogoides* Wagin, 1964, and Wagin [3] described seven "stages", one hypothetical, in the naupliar development of *Ascothorax ophiocetis*, the present results are the first that shows conclusively that some ascothoracids have six naupliar instars. This number is generally regarded as plesiomorphic in at least some maxillopodan taxa, such as Copepoda and Cirripedia.

It is not clear when the nauplii in the present

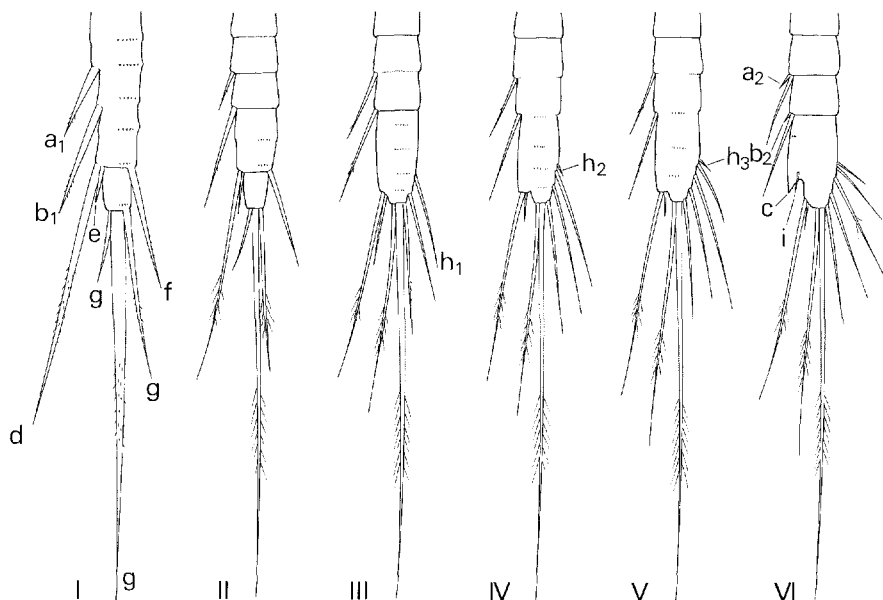


FIG. 20. *B. falsiramus* sp. nov. Schematic representation of antennular development through six naupliar instars (I-VI). Arrows indicating newly added setae and claw, other labels used for explanation in the text.

species normally leave the female's brood chambers. However, the cuticle of instar I nauplii is very thin and delicate and tore easily, and they immediately molted into the next instar after being released into sea-water. Instar I nauplii are not active swimmers, but instar II nauplii have setulose natatory setae and are good swimmers. These observations suggest that, like cirriped nauplii, they normally leave the female's brood chambers at the end of instar I, whereupon they may molt immediately to instar II and remain planktonic until the metamorphosis to the ascothoracid larva.

Early instar nauplii have been described in several laurids (list in [22]). Most have apparently planktotrophic nauplii with very strong antennal and mandibular endites. The present nauplii are considerably larger than those previously reported in *Baccalaureus*. Nauplii of *B. japonicus* are 0.4 mm long and 0.3 mm wide [7], and *B. pyefinchi* and *B. argalicornis* have nauplii only about 0.3 mm long [12, 14]. These might not all be the same instar. Nonetheless, the present nauplii differ additionally from those of *B. japonicus* in never developing large, enditic spines on the antennae and mandibles and in not having a long, protruding terminal spine flanked by three pairs of posterior dorsal shield papillae. Nauplii of *B. maldivensis* and *B. hexapus* seem to have weakly armed limbs according to schematic diagrams and a setation table [9, 10]. However, they differ from *B. falsiramus* by the large, pointed, rear end of their bodies and the much longer limbs relative to the body. Within the Lauridae, *Polymarsypus digitatus* has nauplii most similar to the present ones [6]; these are probably instar I ready to molt to instar II. They are nearly the same size as the equivalent stage in the present material (0.62×0.44 mm), have similar, weak armament of the antennae and mandibles, and a rounded rear end. However, they reportedly have frontal filaments and equatorial pores already, clear appendage segmentation, and somewhat different proportions of the protopods and rami. But the frontal filaments and equatorial pores might actually have belonged to the fully developed instar II within; their absence in the present instar I nauplii was only confirmed on the basis of exuviae and SEM. Such a misinterpretation may also explain the supposed presence

of these structure in some other first instar nauplii like those of *Laura bicornuta* [cf., 6].

In comparison to the few known planktonic ascothoracidan metanauplii tentatively attributed to the Lauridae [22, 23], the present sixth instar nauplii have less well-developed antennules (four segments instead of six), little development of complex appendage armament for feeding, and little elaboration of the furcal armament. The pattern of dorsal pores and setae on the last instar differs from that of Boxshall and Böttger-Schnack's [23] Red Sea metanauplius type I, which has three pairs of setae toward the rear instead of two pairs each at front and rear, and three longitudinal pore-free strips instead of one. In both, the pores are most dense in a row to either side of the central bare zone.

Development of naupliar antennules in *B. falsiramus* is summarized in Figure 20. The addition of several setae (h_{1-3}) proximal to the original lateral seta (f) of the penultimate antennular segment has not been observed in ascothoracidan development before. Its occurrence in *B. falsiramus* suggests that the lateral spine on the naupliar antennule of *Endaster hamatosculum* Grygier, 1985 [22, 24], which is not homologizable with any of the previously recognized setae in ascothoracidan antennules, might be an "h" seta. In the six-segmented antennules of the planktonic ascothoracidan metanauplii cited above, the fourth segment has a claw rudiment and two setae, one of which is probably equivalent to the small seta (i) next to the claw rudiment in the present species, and the other to an "h" seta.

The present study revealed that some ascothoracidan nauplii have cuticular ridges at least on the marginal area of their dorsal shield. More broadly developed, cuticular ridges have long been known to occur in so-called, nauplius y larvae [e.g., 25–27] and the possession of such prominent cuticular ridges has been believed to define, at least in part, the Facetotecta in which these larvae are accommodated [21]. Despite ignorance of the presence of such ridges in the Ascothoracida, Bresciani [28] suggested, and Itô [1] seconded, a possibility that y-larvae are the larval stages of certain ascothoracidans, but Grygier [22, 29] has disagreed. The present finding of cuticular ridges

in an ascothoracidan appears to bridge over one of the morphological gaps between these two thecostrocan groups. However, it has recently been reported that the thoracican cirripede *Ibla* has marginal ridges on its nauplii [30]. Now it is apparent that variously developed, cuticular ridges are widely distributed within the Thecostroca.

Ascothoracid larva. Ascothoracid larvae similar to this species' have been reported several times before and tentatively assigned to the Lauridae, which is strongly supported by the present study. Tessmann [31] first described one from the Indian Ocean, and thus such larvae can be called "Tessmann's larvae" [32]. McKenzie [33] schematically illustrated a similar larva from the eastern Indian Ocean, and Bonaduce *et al.* ([34]: FIG. 2, fig. 4) found an isolated carapace valve in Red Sea sediments, which they mistakenly attributed to an ostracod. Grygier [6] found a single larval carapace valve together with adults of the laurid *Zoanthoeus cerebroides* Grygier, 1985, and later [32] gave a detailed, SEM-assisted description of a shallow-water, Hawaiian form. The carapaces all have a reticulate pattern of chitinous ridges and a posterodorsal emargination like the present examples, and the three forms with described appendages [31, 32; herein] have a proximal cluster of aesthetascs on the claw-bearing segment of antennules. Additional common features of the present larvae with Grygier's [32] Hawaiian form are the antennular claw with a comb-like row of spinules, an imperfectly formed oral cone, the thoracopodal setation, including a setiform endopod on the first limb, and the frontal filament complex with a bifid filament. Some of these features may eventually prove to be universally characteristic of Tessmann's larvae.

Tessmann's description of the distal antennular and thoracopodal structures [31] seems incomplete (thoracopodal rami uniformly two-segmented, exopods with two setae, endopods with one), and the supposedly four-segmented antennules and five-segmented abdomen (equivalent of first segment in other larvae drawn with discontinuous tergite) are at odds with the other descriptions. Grygier's Hawaiian larvae [32] are larger than the present ones (0.60×0.35 mm), their carapace meshes each have a deep pit with a pore instead of a flat surface,

and the polygons are smaller, about $11 \mu\text{m}$ across. On the antennule, the setae on segment 5 are unequal, the distal setae on segment 6 much shorter, the claw more deeply curved, and the claw denticles less numerous than in *B. falsiramus*; there are fewer proximal aesthetascs (only up to 13). There are no vestigial naupliar appendages, although this might not be a stable character because Tessmann's original larva might have such vestiges ([31]: "röhrenförmiges Gebilde") and reduction of vestigial naupliar appendages is known in facetotectan cyprids [20]. In the Hawaiian form the first thoracomere is not well delineated from the head, and the furcal rami are longer with supposedly non-setulate setae. Thus, Tessmann's larvae from Hawaii differ from the larvae of *B. falsiramus* in many morphological features, which may become taxonomically useful once more forms are linked to their adults.

In the echinoderm-infesting, ascothoracidan order Dendrogastrida, many species have two ascothoracid larval instars (e.g., [2, 35]; review in [21]). Such a relatively gradual transition from the nauplius to the adult has been assumed to be plesiomorphic relative to the single cypris larva in the Cirripedia [21, 36], but it is important to be sure that it is not a secondary development in a single ascothoracidan clade. The dendrogastridan first instar is characterized by inflated, poorly hinged carapace valves; antennules in an intermediate state between the metanaupliar and adult conditions (e.g., [22]; Fig. 6a); the labrum not fully surrounding the other mouthparts; sometimes remnants of the naupliar antennae and mandibles; short, simple setae on the legs, usually only distally; and a four-segmented abdomen. The ascothoracid larva of *B. falsiramus* has an incompletely developed oral cone, a pair of naupliar appendages, and lacks protopodal setae on the legs, but in other respects it is as well developed as typical dendrogastridan late ascothoracid larvae (in this species the adults have four-segmented abdomens, so that is not significant in the larvae). This circumstantial evidence suggests, but certainly does not prove, that this species has a single ascothoracid larval instar.

The presence of a large nauplius eye in these ascothoracid larvae, as well as in the nauplii, is

significant because it confirms Tessmann's identification of a nauplius eye in his original larva [31] and because only previous record of an eye in an ascothoracid nauplius concerned the first recorded species, *Laura gerardiae* Lacaze-Duthiers, 1865 [37].

The presence of up to three setae proximal and one distal to a poorly understood apical structure (herein formally termed the apical hood) on generalized claw guards in the Ascothoracida has long been noted [e.g., 38]. There is a "spinulose tip" on the claw guard in *Isidascus bassindalei* Moyse, 1983 [39] and many short hairs on the "articulating tip" of the claw guard in *Cardomanica andersoni* Lowry, 1985 [40], but the microstructure of the apical hood has not previously been examined. In the present larva it proves to be a spinulose cloak around a previously unsuspected tubule. Grygier [32] may have seen the tubule in the Hawaiian Tessmann's larva, mistaking it for a sensillum on the "distal flange." The function of the tubule, whether chemosensory or a gland duct, is unclear.

The subterminal position of the antennular claw rudiment (c) in naupliar instar VI supports Grygier's assertion [22] that the claw-bearing segment (sixth segment in the present ascothoracid larva) is not really the most terminal one in ascothoracid antennules. Rather, at least the proximal sensory process on the claw-bearing segment is assumed to be equivalent to the palp (apical segments distal to the claw-bearing segment) in facetotectan antennules [22, 41].

The five pairs of peculiar organs near the carapace hinge line have been recorded in other ascothoracidan, though usually only four pairs. We would like to formally call them "cardic organs" (from Latin *cardo*=hinge). The second ascothoracid larva of *Ascothorax gigas* Wagin, 1968, has two pairs of "slit-like pores or sensory organs" at either end of the hinge [35], and so does the last (second ?) instar ascothoracid larva of *Parascothorax ?synagoides* [21] and an unidentified ascothoracid larva from the Virgin Islands, in which they are called "oval pits" [32]. Adult *Waginella sandersi* (Newman, 1974) have at least two pairs [38]. Due to their position near the hinge, the cardiac organs might be interpreted as proprioceptors. However, they may also be parts of

glands, because they involve an externally produced tube.

Cardic organs may be homologous to similarly placed, supposedly chemoreceptive "lattice organs" recently described in detail in a lepadomorph cirriped cyprid [42], and whose morphology has been summarized for 28 other cirriped species as well [43]. There are usually five pairs of these narrow, elongate structures symmetrically disposed near the carapace midline, two pairs anteriorly, three posteriorly. They have a porose floor ("sensory field") with a single large pore anteriorly in the front two pairs, posteriorly in the rear ones, and the sensory field is surrounded by a ring of non-porose, often thickened cuticle. The cardiac and lattice organs are also somewhat similar in form and especially position to the "dorsal compound organs" on the midline of the carapaces of pelagic eucarids and at both ends of the carapace midline in the leptostracan *Nebaliopsis typica* Sars, 1887, for which a photosensitive capacity has been postulated [44]. The malacostracan organs consist in part of paired pores and often slits, the latter at least superficially reminiscent of cardiac and lattice organs. The ultrastructure and neurology of all these organs need to be investigated.

ACKNOWLEDGMENTS

This study was supported by Grant-in-Aid for Scientific Research No. 62540567 from the Ministry of Education, Science and Culture of Japan to T. I., by a travel grant from the Seto Marine Biological Laboratory to M. J. G., and by the Sesoko Marine Science Center of the University of the Ryukyus, where M. J. G. was Visiting Foreign Researcher in 1988–89.

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