

Larval and Juvenile Ascothoracida (Crustacea) from the Plankton

By

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With Text-figures 1-5

Abstract Two kinds of previously recorded ascothoracid larvae from plankton over coral reefs in Hawaii and the Virgin Islands are redescribed as possible representatives of the Lauridae and Petrarciidae, respectively. A bathyal, tropical Atlantic ascothoracid larva from an epibenthic sled sample cannot confidently be identified to family. A planktonic, juvenile ascothoracidan from the eastern Indian Ocean belongs to the genus *Synagoga*.

Ascothoracida are parasitic crustaceans which as adults infest echinoderms and anthozoans. Grygier (1987b) recently revised their classification. Adult females brood their young, so the early stages of larval development are fairly well known (e.g., Grygier, 1987a), but no complete life cycles are known due to a paucity of information about post-brooding larvae. Sometimes the larvae are released as nauplii, but more often as bivalved, ascothoracid larvae. I described a damaged, planktonic ascothoracid larva from the Virgin Islands (Grygier, 1983a), and could only cite three previous records, none of which were from the Pacific Ocean. Four different sorts of post-brooding ascothoracidans are the subject of the present report, including Tessmann's (1904) larva from Hawaii and undamaged specimens of the Virgin Islands form. This is also the first scanning electron microscopical study of a larval ascothoracidan.

Three specimens of Tessmann's larva were critical point dried, mounted on metal stubs, sputter-coated with carbon and gold, and examined in a Cambridge Stereoscan 100 scanning electron microscope.

Tessmann's Larva

(Figs 1-2)

Tessman (1904) described an ascothoracid larva from the North Equatorial Current of the Indian Ocean. A large number of a very similar larva have now been taken inshore at Hawaii. All specimens were collected by Tony Chess in Honaunau Bay on the Kona Coast of the island of Hawaii by pushing a 0.5 m net of 0.165 mm mesh up and down through the water column over 4-10 m deep *Porites* reefs interspersed with sand patches: 8 specimens taken 12-IX-1984; 14 specimens taken 1700 hrs, 38 taken 1957 hrs, 14-IX-1984, unexamined specimens present in other samples taken at night but not after sunrise, highest density (26/100 m³) about 2 hrs after sunset. Bodies of several individuals were

removed from their carapaces and examined in glycerine and lactic acid mounts; 3 specimens were examined with a scanning electron microscope. Some specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM 229987).

Description. Carapace bivalved, about 0.60 mm long, 0.35 mm high (Figs 1A, 2A). Dorsal hinge line nearly straight and depressed below level of dorsal carinae. Front of valves broadly rounded, ventral side shallowly curved, rear with posterodorsal emargination. External face of valve with primarily hexagonal pattern of deep pits separated by narrow ridges, with large pores at bottom of pits, other pores and short setae at some vertices of polygonal ridge network (Fig. 2B). Inner carapace lining with cuticular ridges parallel to whole free margin, posteroventral rows of short guard setae (Fig. 1A), and anterior arrays of cuticular ctenae (Fig. 2C). Eyes absent. Antennules 6-segmented, Z-shaped, sparse hairs on third segment, variably 1–2 setae on fourth, fifth with 2 unequal basal setae (Fig. 1A). Sixth antennular segment with spinulate, movable claw; 3 setae proximal to claw; elongate claw guard with 2 short setae behind and 1 in front of distal, sensillum-bearing flange; sensillum and small proximal sensory process with 3 unequal setae just behind claw guard; and proximal cluster of at least 9 (up to 13 seen) long aesthetascs (Figs 1A, 2D). Frontal filament with thick base and bifid aesthetasc arising from inner face of each carapace valve lateral to anterior base of antennule (Figs 1A, B, 2E). Oral cone much smaller than antennules, curved labrum partially enclosing large, terminally bifid maxillae and minute, pointed mandibles and maxillules (Fig. 1C). Thorax 6-segmented,

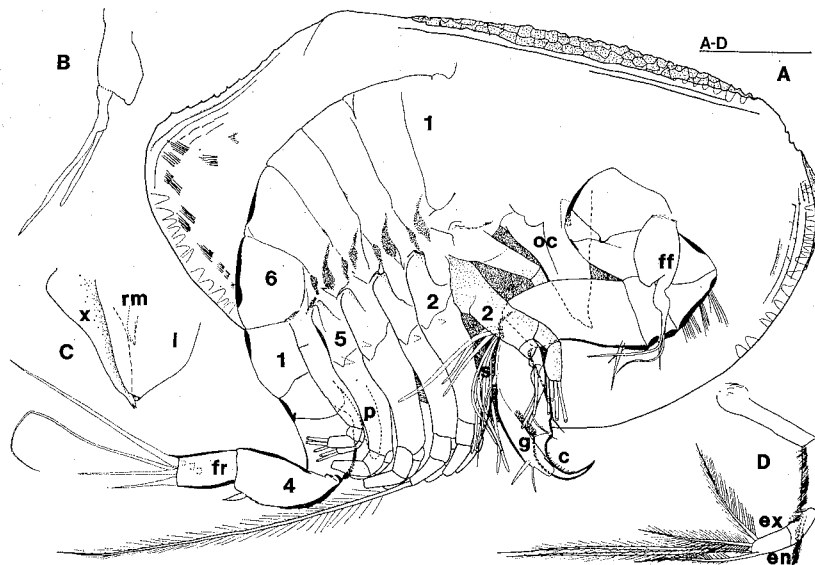


Fig. 1. Tessmann's (1904) larva from Hawaii. A, habitus, right carapace valve removed, some thoracomeres, abdominal segments, and thoracopods numbered, most natatory setae omitted or cut short for clarity; B, frontal filament; C, oral cone; D, first thoracopod (mostly hidden behind antennule in A). c, claw; en, endopod; ex, exopod; ff, frontal filament; fr, furcal ramus; g, claw guard; 1, labrum; oc, oral cone; p, penis; rm, rudimentary mandibles and maxillules; s, aesthetascs; x, maxillae. Scale bar 0.1 mm.

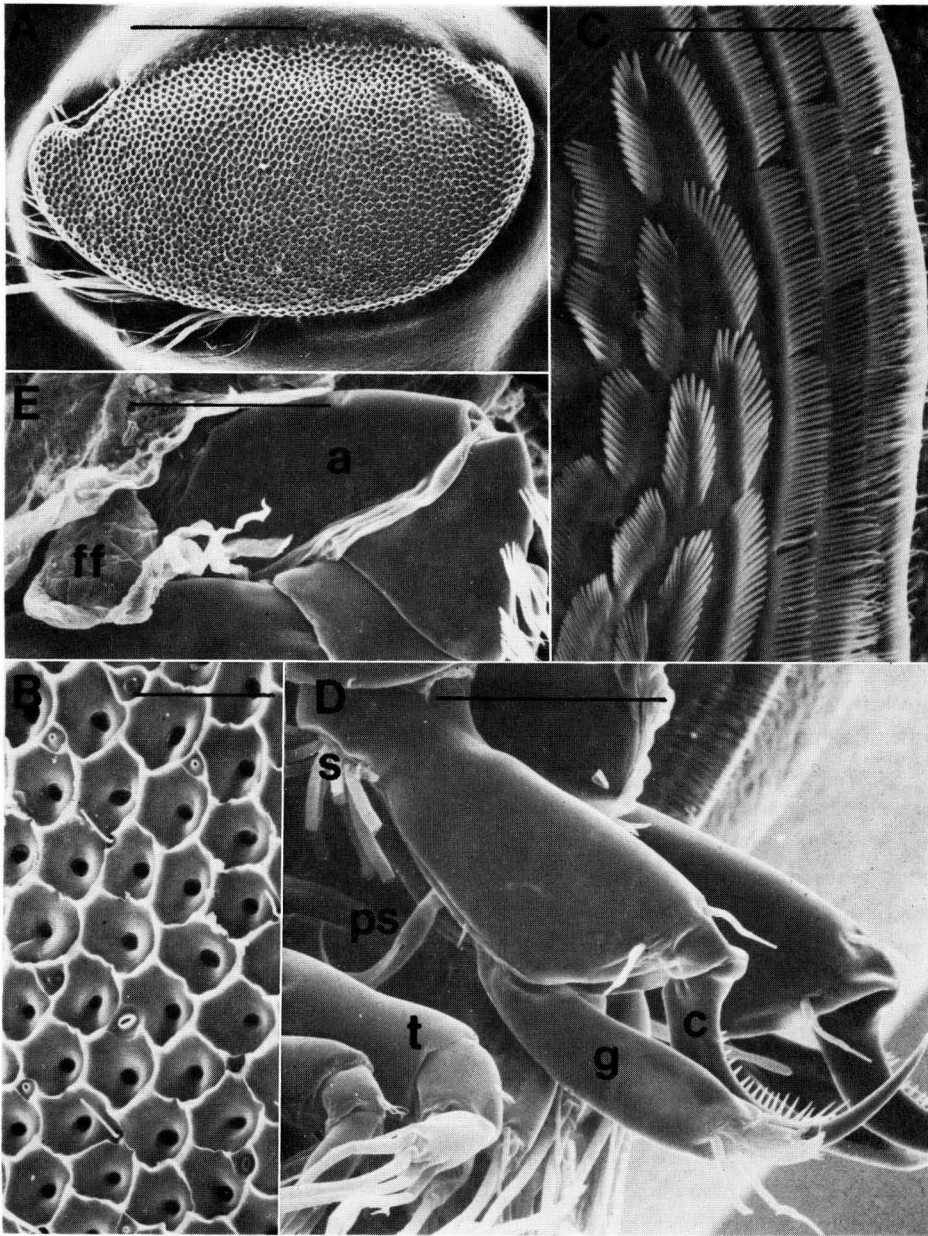


Fig. 2. Tessmann's (1904) larva from Hawaii, SEM micrographs. A, external view of carapace, anterior end right; B, detail of carapace sculpturing; C, cuticular ctenae on anterior inner surface of carapace; D, sixth antennular segment; E, frontal filament at base of antennule. a, antennule; c, claw; ff, frontal filament; g, claw guard; ps, proximal sensory process; s, aesthetascs; t, thoracopod. Scale bars 200 μm in A, 20 μm in B, C, 50 μm in D, E.

front edge of first segment not obviously delineated, first 4 segments otherwise alike, fifth and sixth successively longer and less high (Fig. 1A). Six pairs of biramous thoracopods, with coxa, basis, 2-segmented exopod and 3-segmented endopod,

latter setiform in leg 1 (Fig. 1D), 2-segmented in leg 6. Leg 1 thinner and leg 6 shorter and thinner than others. Protopods lacking setae. Exopod of leg 1 with variably 4–5 distal setae, 2 twice as long as rest (Fig. 1D). Five terminal exopod setae in legs 2–5, one short and thin, at least 2 terminal setae on endopods (3 confirmed on leg 2 of 2 specimens) plus 1 seta on penultimate segment (Figs 1A, 2D); leg 6 with 3 terminal setae on exopod, 2 on endopod; long thoracopodal setae setulate. Abdomen 4-segmented, initially directed downwards, but bent rearwards between segments 3 and 4 (Fig. 1A), segment 4 longest, then segments 1, 3, and 2. First segment with uniramous, unarmed penis (Fig. 1A). Last segment with pair of spinulate, posteroventral spines and rectangular furcal rami twice as long as high, latter with 3 mediobasal setae, dorsobasal spine, and 4 unequal terminal setae, all furcal setae unarmed (Fig. 1A).

Remarks. Aside from the very low, probably mistaken, setal counts in the earlier description, these specimens differ from Tessmann's (1904) only in lacking any structure that could be identified as an eye; Tessmann reported a nauplius eye positioned where compound eyes would be expected. Otherwise, the similar outer carapace sculpturing and antennular armament, especially the unusual cluster of aesthetascs, show that they are very closely related if not identical. Tessmann proposed that his larva was related to the Mediterranean ascothoracidan *Laura gerardiae* Lacaze-Duthiers, since it resembled a possible male described by Lacaze-Duthiers (1883). Grygier (1985a) described an ascothoracid larval carapace associated with the laurid *Zoanthoeus cerebroides* Grygier from bathyal depths in the Hawaiian Islands that had the same shape and external sculpturing and also discussed another such carapace that had been found in Red Sea sediments. The 4-segmented abdomen and uniramous penis are laurid features, but are not restricted to that family. No shallow-water Lauridae have yet been reported from Hawaii, but this family includes numerous species of the genus *Baccalaureus* that infest shallow-water zoanthids in the Indo-West Pacific (literature in Grygier, 1985a), and one of these may be responsible here.

The most striking morphological specializations of this larva are the carapace sculpturing and aspects of the antennular armament. Presumably the pores at the bottom of the pits represent glands, but their function is unclear; perhaps they secrete a protective substance when the larva settles upon its cnidarian host. Spinulate antennular claws occur in *Synagoga* (Synagogidae) and in ascothoracid larvae of *Ulophysema* (Dendrogastridae) and *Gongylophysema* (Ctenosculidae) (Grygier, 1983b, 1987b, 1987d, respectively), and the antennular aesthetasc cluster is most similar to the trifold antennular aesthetascs of male ascothoracid larvae in *Ulophysema oeresundense* Brattström (Grygier, 1987b). The setiform endopod of the first thoracopods is unique to this larva.

Grygier's Larva

(Fig. 3)

Grygier (1983a) described an ascothoracid larva from near-shore plankton in the Virgin Islands.

The single, damaged specimen (USNM 227068) had an oval, bivalved carapace and stalked compound eyes, each bearing a long frontal filament. The distalmost of 5 incompletely divided antennular segments had 3 setae at the base of the claw, a claw guard with 4 short setae, and a proximal sensory process with an aesthetasc and 2 unequal setae; the fourth segment had 2 spine-like setae. Biramous thoracopods were present on the 6-segmented thorax, and the 5-segmented abdomen ended in posteroventral telsonic spines and tapered furcal rami with 4 medial setae and 3 terminal and ventral setae. Hallberg et al. (1985) described the compound eye: about 13 ommatidia (not about 100 as originally reported), tripartite crystalline cones, peripheral nuclei, and irregular rhabdomes. I originally compared this larva to *Synagoga* (Synagogidae), but additional specimens now allow me to complete the description and revise this identification.

Two undamaged specimens were collected by Tony Chess at the same locality as the original one but a year later (outer reef of Tague Bay, St. Croix, mid-water over 9 m deep bottom, 7–8 June, 1988), using diver-manipulated plankton nets. The redescription is based on the dissected specimen which also provided one of the compound eyes described by Hallberg et al. (1985).

Supplementary description. Carapace 0.71 mm long, 0.51 mm high, larger than original specimen. Four oval pits on each valve, 2 near each end of dorsal hinge, front 2 spaced farther than rear 2. Claw guards of this specimen with 3 setae. Large, flabby, biramous, asetose vestiges of naupliar antennae and mandibles present; small labrum, spiniform maxillules, and short, pointed maxillae also present (entire ventral head region and part of thorax missing in original specimen). Form of anterior thoracopods originally misconstrued; first pair setiform, other 5 pairs biramous with 2-segmented exopods, 2-segmented endopods in pairs 2 and 6, 3-segmented endopods in pairs 3–5; thoracopods 2–6 with 3 terminal, setulate setae on exopods, 2 on endopods.

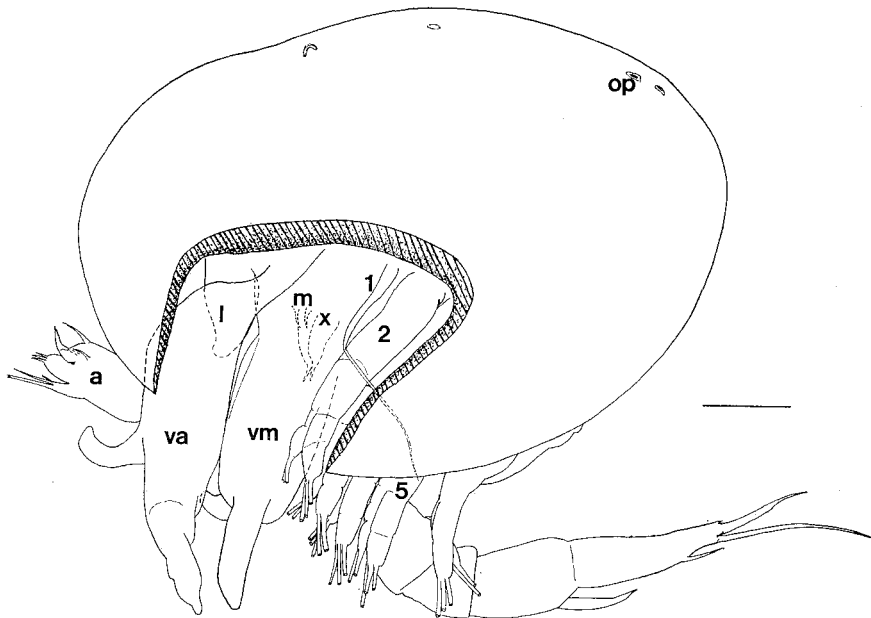


Fig. 3. Grygier's (1983a) ascothoracid larva from St. Croix, cutaway view with compound eye removed, thoracopods 1, 2, and 5 numbered. a, antennule; l, labrum; m, maxillules; op, oval pits; va, vestigial antenna; vm, vestigial mandible; x, maxillae. Scale bar 0.1 mm.

Remarks. The incomplete antennular segmentation, the non-functional vestiges of the naupliar antennae and mandibles, and the meager count of thoracopodal setae are characteristic of first instar ascothoracid larvae of many members of the echinoderm-infesting order Dendrogastrida (Grygier, 1984; Grygier & Fratt, 1984), but the fully bivalved carapace, complete distal antennular armament, fully developed abdomen, and setulate natatory setae betoken a later developmental stage, and the present larvae show no sign of developing the typical dendrogastridan subchelate antennule. They probably belong to the other order, Laurida. The setiform first thoracopods exclude the Synagogidae *sensu* Grygier (1987b) from consideration, since all synagogids have primitive, biramous first legs as adults; reduction of the second thoracopod's endopod to two segments is a very unusual feature. The Lauridae and Petraridae, parasites of zoanthids and scleractinians respectively, always have reduced, often setiform or absent first thoracopods as adults (Grygier, 1985a, b), so they are the best candidates. Known or suspected laurid ascothoracid larvae have prominent hexagonal sculpturing on their posterodorsally emarginate carapace (Grygier, 1985a; herein above), unlike the present larvae. Petrarids have 5-segmented antennules with only distal armament as adults, like these larvae, and the closest antennular and furcal match is with *Introcornia conjugans* Grygier (1983c). Unfortunately, there is no record yet of Petraridae from the tropical western Atlantic (Zibrowius & Grygier, 1985), and only brooded nauplii have been described in this family (Grygier, 1985b).

Bathyal Tropical Atlantic Larva

(Fig. 4)

One specimen (USNM Acc. no. 263223, uncatalogued), "Atlantis II" Cr. 31, stn. 162, 8°2.0'–7°56.0'S, 34°3.0'–9.0'W, 1439 m, 19–II–1967, epibenthic sled. The specimen was examined whole in a glycerine mount and some parts of the main body were not exposed to clear view.

Description. Carapace bivalved, 0.80 mm long, 0.43 mm high, bluntly produced at front and rear, each valve with distinct brim most of way around, valve edges with small, polygonal tessellations and numerous pores (Fig. 4A). Eyes absent. Antennules 6-segmented, Z-shaped (Fig. 4B); segment 3 with fine hairs anteriorly; segment 4 with 2 unequal setae; segment 5 with 3 setae along proximal half; segment 6 with movable claw, seta at base and to each side of claw, 3 setae on claw guard, 3 unequal setae and lobe with aesthetasc of uncertain length on proximal sensory process set apart from claw guard. Frontal filament possibly present (Fig. 4B), although observed structure may have been seta of first thoracopod. Oral cone much smaller than antennule, apparently with labrum in front of massive maxillae, details unclear. Six pairs of thoracopods. Leg 1 with biarticulate rami, minute endopod with 1 terminal seta, exopod with 4 setae (Fig. 4C). Details of other legs unclear; legs 2–3, at least, with 1 seta on penultimate endopod segment and few terminal setae on each ramus; thoracopodal setae setulate. Abdomen 4-segmented, last segment with furcal rami and spinose, posteroventral spines as long as rami (Fig. 4D). Furcal rami

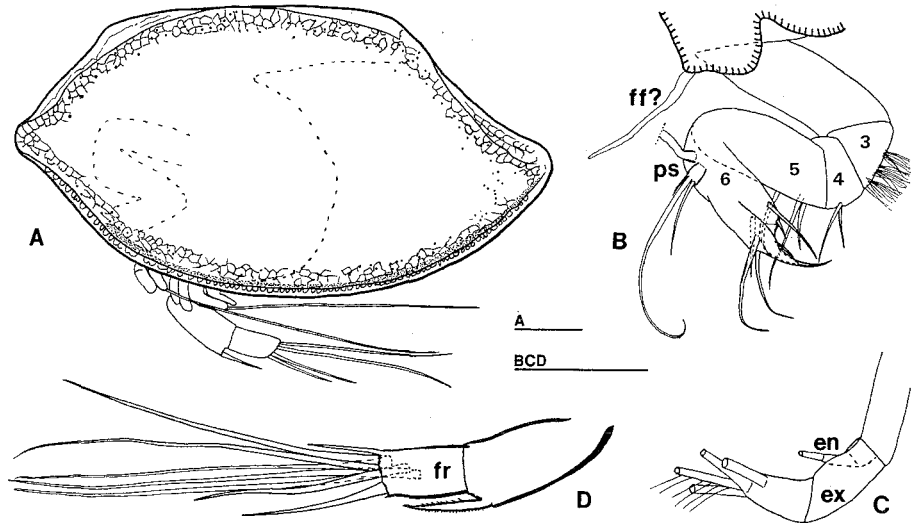


Fig. 4. Bathyal tropical Atlantic larva. A, external view of carapace, anterior end left, with dashed outline of body and antennule; B, antennule, some segments numbered; C, distal part of first thoracopod; D, last abdominal segment. en, endopod; ex, exopod, ff?, frontal filament?; fr, furcal ramus; ps, proximal sensory process. Scale bars 0.1 mm.

rectangular, over 1.5 times as long as high, with diagonal row of 3 mediiodistal setae, long dorsodistal spine, and 4 terminal setae, dorsal 2 twice as long as ventral 2 and reaching posteriorly as far as medial setae do (Fig. 4D).

Remarks. All known ascothoracid larvae in the order Dendrogastrida have simple, oval carapace valves (Grygier, 1984; Grygier & Fratt, 1984). Carapaces with posterodorsal excavations like the present one are so far known with any certainty from the family Lauridae (Gryger, 1985a; herein above) and must be suspected to occur in other representatives of the order Laurida. The restriction of external sculpturing to the rim of the valves is different from Tessmann's larva, but the rudimentary endopod of the first thoracopod, the furcal rami, and the 4-segmented abdomen are similar. The antennular armament is quite different from Tessmann's larva; a space between an aesthetasc-bearing, proximal sensory process and the claw guard is found in some synagogids and in male *Zoanthoecus* (Lauridae) (e.g., Grygier, 1983b, 1985a; herein below).

McKenzie's Larva

(Fig. 5)

McKenzie (1972) schematically illustrated a planktonic ascothoracidan identified by him as a laurid. It was taken in 1962 during CSIRO Division of Fisheries and Oceanography Cruise G 4/62 along the 110°E transect between Java and the level of Fremantle, Western Australia; no more specific data is available. The drawing shows a posterodorsally excavated carapace valve with reticulate ornamentation and pores at the vertices like Tessmann's larva. McKenzie sent some of his material

to P. Illg (University of Washington), and the specimen Dr. Illg forwarded to me is a *Synagoga* that does not resemble McKenzie's drawing. A remark on the label suggests that two different kinds of ascothoracidans were indeed present in McKenzie's material and that he tentatively but mistakenly interpreted the present one as a later stage of the illustrated one. Although some details are obscured, a reasonably complete description of the present specimen can be given.

Stained slide preparation (Australian Museum Reg. no. P 38268) of carapace valves and main body of juvenile *Synagoga* sp. labelled "G 4/62 700E", "marine crustacean 'cypris' larva cirripede", and "2nd post-larval stage?".

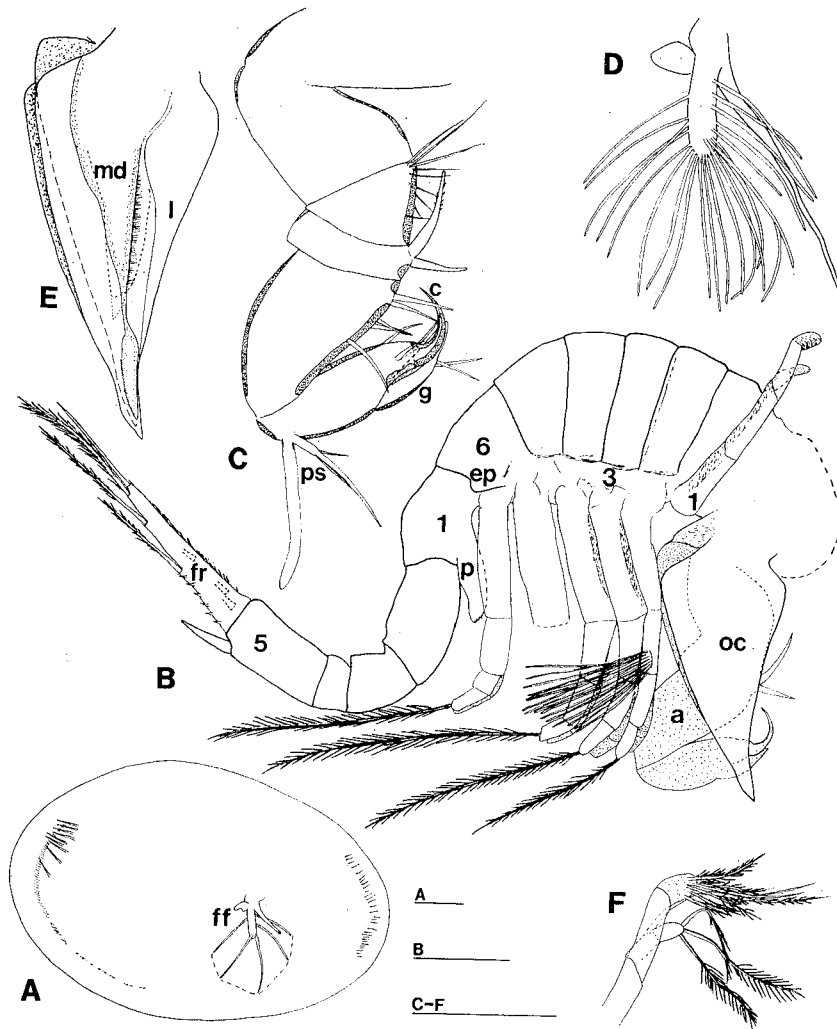


Fig. 5. McKenzie's juvenile *Synagoga* from the Indian Ocean. A, inner view of left carapace valve, anterior end right; B, body removed from carapace, most antennular and thoracopodal setation omitted, upraised position of first thoracopod an artifact, some thoracomeres and abdominal segments numbered; C, left antennule; D, right frontal filament; E, oral cone; F, distal part of right first thoracopod, second exopod segment foreshortened due to angle of view. a, antennule; c, claw; ep, epaulet; ff, frontal filament; fr, furcal ramus; g, claw guard; l, labrum; md, mandible; oc, oral cone; p, penis; ps, proximal sensory process. Scale bars 0.1 mm.

Description. Carapace valves oval, 0.79 mm long, 0.53 mm high, highest point behind midlength (Fig. 5A). External surface with closely spaced, conical pits not forming a reticular pattern, each with a pore. Posteroventral quarter and front end lined internally with cuticular guard hairs, some longer guard setae posteriorly. Body consisting of head, 6-segmented thorax, and 5-segmented abdomen, with anterodorsal cephalic attachment zone (Fig. 5B). Thoracomere 1 distinctly articulated with head, thoracomeres 1-4 alike, 5 and 6 progressively longer and less high, 6 with pair of very small, lateral epaulets. Abdomen J-shaped, segments 2 and 5 longest, then 1, 3, and 4, last segment with long, posteroventral spines and furcal rami.

Folded antennule as long as oral cone, 6-segmented (Fig. 5A, C). Third segment with sparse anterior hairs, fourth with 2 strong anterior setae, fifth tapering with curved posterior margin and 5 setae along basal half of anterior margin. Sixth segment narrower and shorter than fifth, ending in movable claw with seta at base and to each side, lateral seta twice as long as medial; partly obscured claw guard with at least 2 setae and lateral flange; proximal sensory process near base of segment, with basal aesthetasc and 3 distal setae, one longer than others. Frontal filaments arising from inner lining of each valve (Fig. 5A, D), consisting of plumose main axis (i.e., ventral ramus) with many aesthetascs, basal appendix, and strong basal aesthetasc as long as main axis. No posterior ramus seen except maybe as tuft of aesthetascs seemingly arising from basis of first thoracopod (Fig. 5A), which is normally unarmed in ascothoracidans. Oral cone with labral sheath surrounding paired mouthparts, including harpoon-shaped mandibles (Fig. 5E); details of mouthparts not visible, but general appearance agreeing with earlier reports on *Synagoga* (Norman, 1913; Grygier, 1983b). Thoracopods 1-6 approximately equally long, proportional length of coxa increasing posteriorly (Fig. 5B); exopods 2-segmented, endopods 3-segmented (2-segmented in thoracopods 1 and 6). Setae plumose and twice as long as thoracopods proper, except short in first pair (Fig. 5B, F). Setal count only available for first pair, although no lateral coxal seta on any thoracopod; first endopod segment with 1 seta, second with 3, endopod about as long as first exopod segment; second exopod segment with about 11 setae with short setules. Short, uniramous penis on first abdominal segment (Fig. 5B). Posteroventral spines on last segment rough but not spinulose. Furcal rami straight but tapered, 4 times longer than basal height (Fig. 5B), with cuticular ctenae along dorsal margin, 6 spines along proximal half of ventral margin, 2 long ventral and 2 long terminal setae, and at least 3 very long medial setae, 2 arising basally, 1 at midlength (possibly others in between); ventral and terminal setae setulate to varying degrees.

Remarks. The antennular and furcal morphology, the type of mouthparts, lack of lateral coxal setae on the thoracopods, and small epaulets identify this specimen as *Synagoga* sensu Grygier (1983b). The small size, lack of gonads in the carapace, few hairs on proximal antennular segments, and small number of ventral spines on the furcal rami suggest that the animal is a juvenile; it is similar enough to adults not to be regarded as an ascothoracid larva. One species of this genus is known from

the Indian Ocean, *S. normani* Grygier from an alcyonacean host near Mombasa, Kenya (Grygier, 1983b).

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References

- Grygier, M.J. 1983a. A novel, planktonic ascothoracid larva from St. Croix (Crustacea). *J. Plankton Res.*, 5: 197-202.
- . 1983b. Revision of *Synagoga* (Crustacea: Maxillopoda: Ascothoracida). *J. nat. Hist.*, 17: 213-239.
- . 1983c. *Introcornia conjugans* n. gen. n. sp., parasitic in a Japanese ahermatypic coral (Crustacea: Ascothoracida: Petrarciidae). *Senckenberg. biol.*, 63: 419-426.
- . 1984. Comparative morphology and ontogeny of the Ascothoracida, a step toward a phylogeny of the Maxillopoda. 417 pp. Ph. D. dissertation, University of California San Diego.
- . 1985a. Lauridae: taxonomy and morphology of ascothoracid crustacean parasites of zoanthids. *Bull. mar. Sci.*, 36: 278-303.
- . 1985b. New ascothoracid crustacean endoparasites of Scleractinia. *J. nat. Hist.*, 19: 1029-1043.
- . 1987a. Nauplii, antennular ontogeny, and the position of the Ascothoracida within the Maxillopoda. *J. crust. Biol.*, 7: 87-104.
- . 1987b. Reappraisal of sex determination in the Ascothoracida. *Crustaceana*, 52: 149-162.
- . 1987c. Classification of the Ascothoracida (Crustacea). *Proc. biol. Soc. Wash.*, 100: 425-458.
- . 1987d. Antarctic records of asteroid-infesting Ascothoracida (Crustacea), including a new genus of Ctenosculidae. *Proc. biol. Soc. Wash.*, 100: 700-712.
- . & D.B. Fratt 1984. The ascothoracid crustacean *Ascothorax gigas*: redescription, larval development, and notes on its infestation of the Antarctic ophiuroid *Ophionotus victoriae*. *Antarct. Res. Ser.*, 41: 43-58.
- Hallberg, E., R. Elofsson & M.J. Grygier 1985. An ascothoracid compound eye (Crustacea). *Sarsia*, 70: 167-171.
- Lacaze-Duthiers, H. de 1883. Histoire de la *Laura gerardiae* type nouveau de Crustacé parasite. *Mém. Acad. Sci. Inst. France*, (2)42(2): 1-160.
- McKenzie, K.G. 1972. Contribution to the ontogeny and phylogeny of Ostracoda. In: Proceedings of the International Paleontological Union, XXIII International Geological Congress, Prague 1968. Pp. 165-188.
- Norman, A.M. 1913. *Synagoga mira*, a crustacean of the order Ascothoracida. *Trans. Linn. Soc. Lond.*, 2nd Ser., Zool., 11: 161-166.
- Tessmann, M. 1904. Beiträge zur Entwicklungsgeschichte der Cirripeden. 38 pp. Inaugural-Dissertation, Universität zu Leipzig.
- Zibrowius, H. & M.J. Grygier 1985. Diversity and range of scleractinian coral hosts of Ascothoracida (Crustacea: Maxillopoda). *Ann. Inst. océanogr.*, Paris, 61: 115-138.