Late Planktonic Naupliar Development of an Ascothoracidan Crustacean (?Petrarcidae) in the Red Sea and a Comparison to the Cirripedia

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ABSTRACT. Three metanaupliar instars, evidently NIV–VI (or maybe NIII–V), of one or more closely related species of ascothoracidans tentatively identified as Petrarcidae (endoparasites of Scleractinia) are described on the basis of five larvae caught at 0–250 m depth in the central and southern Red Sea. Besides increases in size and in the number of pores and sensilla on the dorsal shield, there are minor increases in the complexity of the appendage armament. Four specimens have abnormalities of at least one appendage. The normal antennae and mandibles are compared with those of NIV–VI in the Cirripedia Thoracica. Unlike cirripeds, the petrarcids have a seta on the antennal coxa and a corolla of claws on the enditic spine of the mandibular basis. The exopods of both limbs have more segments in the petrarcids and, in the mandibles, more setae as well. The antennal basis and first endopodal segment have feathered setae like chthamaloid and some lepadomorph nauplii. There are fewer apical setae on the antennal endopod and more setae on the first segment of the mandibular endopod than in cirriped nauplii. The possibility of homology between cirriped frontolateral horns and a pair of marginal dorsal shield processes in petrarcid nauplii is reconsidered.

INTRODUCTION

Comparative larval development can be of great use in clarifying and corroborating relationships among crustaceans. Recent comparative ontogenetic studies in the Cirripedia include Kado (1982), Moyse (1987), Elfimov (1988), Korn (1988), and Egan and Anderson (1989). In the parasitic group Ascothoracida, which is closely related to the Cirripedia within the maxillopodan subclass Thecostraca, the most accessible nauplius larvae have been brooded ones (reviewed by Grygier, 1987a). Except for the earliest stages, these nauplii are not very useful for comparative study. They do not develop complex appendage armament and, indeed, sometimes have vestigial appendages. Grygier (1987a, 1987b) published some hypotheses about homologous structures and phylogeny in the Maxillopoda based mostly on such larvae, but the dearth of information about free-swimming ascothoracidan nauplii, especially planktotrophs with complex appendage armament, has hindered further progress.

Planktotrophic nauplii seem to occur in three families of Ascothoracida, but no complete planktotrophic naupliar series have been documented. Several Lauridae and Petrarcidae have brooded NI nauplii with large enditic spines on the antennae and mandibles (e.g., Grygier, 1985a, 1985b, 1990c) and so does one species of Synagogidae (Grygier, 1990b), but the corresponding NII is known in detail only in two laurids and one petrarcid (Yosii, 1931; Grygier, 1990a). On the basis of those few cases, Grygier (1990a) listed several differences between the appendages of ascothoracidan NII and cirriped NII nauplii. Three last-instar metanauplii of possible laurids have been described (Grygier, 1987a; Boxshall and Böttger-Schnack, 1988); these should be NVI if the six naupliar instars of the lecithotrophic laurid *Baccalaureus falsiramus* Itô and Grygier (1990) are also typical for planktotrophs. Boxshall and Böttger-Schnack (1988) also described a purported earlier instar (NIII or NIV; discussed by Grygier, 1990a) of one of their forms.

Here I report on a series of three metanaupliar instars of what is probably a petrarcid ascothoracidan collected in plankton in the Red Sea. The Petrarcidae are endoparasites of scleractinian corals. Though this material provides only half the story for this particular species (or set of closely related species), in combination with the known NI and NII of *Zibrowia* sp. (see Grygier, 1990a), five of the supposed six naupliar instars of planktotrophic petrarcids are now known and available for comparison to cirriped nauplii.

METHODS AND MATERIALS

Five specimens were sorted and sent to me by R. Böttger-Schnack, and they are deposited in the Natural History

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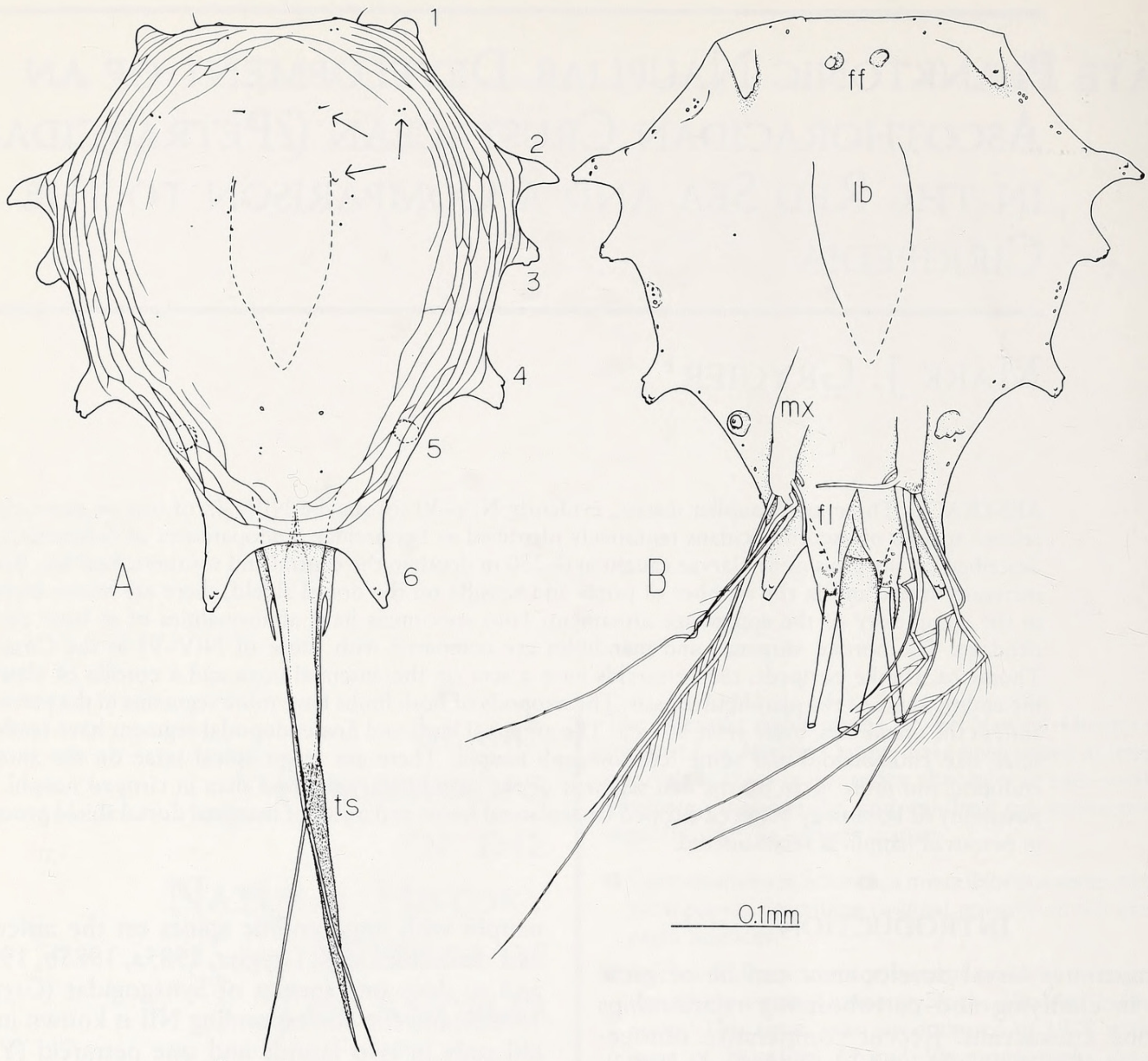

Figure 1. Petrarcid metanauplius NIV (or NIII?) from Red Sea, sta. 703. **A,** dorsal view, appendages omitted, marginal processes numbered, ventral position of labrum indicated by dashed line, two dorsal sensilla and double pore indicated by arrows; **B,** ventral view, first three pairs of appendages and distal parts of caudal armament omitted, broken distal half of labrum marked by dashed line. Abbreviations: ff, frontal filaments; fl, furcal lobe; lb, labrum; mx, maxillule; ts, terminal spine.

Museum of Los Angeles County (LACM). They were taken in vertical hauls of multiple opening–closing nets equipped with 55 μm mesh during "Meteor" Cruise 5, leg 5 in the Red Sea during the summer of 1987 (Weikert, 1988, as cited in Böttger-Schnack, 1991): one NVI (or NV?), sta. 682, central Red Sea, haul 28/4, July 25, 1987, 17:17–17:30, 21°14.1′N, 38°05.3′E, 50–100 m fraction over 1,888 m depth (LACM 87-407.1); one NV (or NIV?), sta. 703, southern Red Sea, haul 39/1, August 3, 1987, 17:29–17:40, 15°34.1′N, 41°54.9′E, 200–250 m fraction over 953 m depth (LACM 87-408.1); one NIV (or NIII?) and two NVI (or NV?), sta. 703, haul 39/5, same data as previous entry but 0–50 m fraction (LACM 87-409.1, 87-409.2, 87-409.3).

Each specimen was drawn in dorsal view in glycerine. Each was also examined in ventral view before dissection, but details of the appendages were difficult to see. Therefore, the three anterior pairs of appendages of all five specimens, and usually also the labrum, were dissected free with a needle and fine forceps and, together with the remaining naupliar body (in ventral view), mounted in glycerine jelly and drawn using standard optics with an open diaphragm, supplemented with phase contrast. The oil immersion lens was used with anisole.

In the following descriptions any seta with two opposing rows of long setules is called plumose except for a few with very closely spaced setules, which are called feathered. Simple setae so-called herein have no long setules but in some cases have rows of very tiny spinules (e.g., on the long furcal setae). The letter designations (a–h) of the antennular setae follow Grygier (1987a) and Itô and Grygier (1990).

DESCRIPTIONS

Description of Nauplius IV (NIII?)

Figures 1, 2

DORSAL SHIELD (Fig. 1A). Kite-shaped, 404 μm long along dorsal midline, 358 μm wide between second and third pairs of marginal processes, shallowly convex. Six pairs of blunt marginal processes: one anterior pair, two lateral pairs, two posterolateral pairs, one posterior pair. Processes directed radially outwards and downwards except fifth pair (straight downwards or even medially; differing from others in its ventral submarginal position) and sixth pair (straight posteriorly). Sixth pair of processes longest, then first and second; third and fifth processes shortest. Number of apical and subapical pores per process: first—4 or 5, second—4, third—3, fourth—4, fifth—2, sixth—5; almost all subapical pores ventral or lateral. Ventral side of shield margin with scattered pores between processes, one anterior pair of pores being slightly raised. Concentric ridge pattern with many oblique connections on outer 40% of shield, possibly some very weak ridges closer to center. Three pairs of short, hairlike sensilla, located on anterior margin, anterodorsally, and mid-dorsally above anterior end of labrum. Dorsal pores not always in precise pairs; on each side two pores behind and medial to first sensillum, two closely set large pores (double pore) lateral to second sensillum, three pores behind third sensillum, and one large and one or two small, posterior pores at about level of fifth pair of marginal processes.

MID-VENTRAL STRUCTURES (Fig. 1B). Pair of papilliform frontal filaments just behind anterior margin, with pore between. Labrum about twice as long as wide, rear half acutely pointed. Setal armament of labrum and ornamentation of ventral body surface unknown due to damage in dissection.

ANTENNULE (Fig. 2A). Long, slender, and cylindrical with slight taper; four-segmented, but fourth segment obviously representing three undifferentiated segments. All setae plumose. First segment short and unarmed. Second segment as long as wide, with postaxial (i.e., medial) a-seta and three preaxial (i.e., lateral) rows of spinules. Third segment as long as second, with postaxial b-seta. Proximal third of fourth segment with two preaxial h-setae (h_1, h_2); middle third with very long postaxial d-seta, shorter postaxial e-seta, and long preaxial f-seta; distal third with three long, apical g-setae.

ANTENNA (Fig. 2B). Composed of coxa, basis, 11-segmented exopod (first two segments incompletely separated), and three-segmented endopod. Coxa and basis each partly subdivided along lateral margins. Endopod slightly shorter than exopod, distal three-quarters of each ramus extending beyond margin of dorsal shield (also in mandible). Coxal endite (gnathobase) ending in bifid spine with proximal prong longer and biserially toothed; curved, setiform spine on proximal face of endite, short plumose seta on distal face; row of 10–11 bristles between seta and bifurcation. Basal endite prominent, with long, fine hairs along distal face and with styliform, plumose apical spine and two or three apical setae (one seta apparently lost from each antenna in dissection and all setae broken so armament and length uncertain). First endopodal segment with three feathered setae at midlength; second segment with two long, plumose, distal setae and one shorter, simple seta; third segment with three long, plumose, apical setae. Exopod with posterolateral, longitudinal row of fine hairs on first two segments and 10 long, plumose, natatory setae, one seta each on segments 3–10 and two setae on apical segment; distal four setae progressively shorter than others.

MANDIBLE (Fig. 2C). About two-thirds as long and wide as antenna. Divided into coxa, basis, eight-segmented exopod (first segment an incomplete annulus), and three-segmented endopod as long as exopod and with first segment as long as other two segments combined. Coxa and basis each with partial lateral subdivisions. Coxal endite with conical, bristly spine and somewhat longer plumose seta with stiff setules. Basal endite very complex: simple seta on rear base; plumose seta and array of long, fine hairs on distal face; another plumose seta on posterior side and very short, simple sensillum on anterior side, both just proximal to semicircular corolla of at least seven stout claws; comb of about 15 somewhat flattened, modified setules arising along posteroproximal face of tip of enditic spine and at least two similar setules on anterodistal face near tip. First endopodal segment with two plumose setae and one short, simple seta at midlength of medial margin, another slightly more distal, simple seta on posterior face; second segment with two plumose setae and one simple seta; third segment of right mandible with four long, basally plumose, apical setae and one short, simple seta, but three plumose setae and one simple seta on left mandible. Exopod with posterolateral, longitudinal row of fine hairs along whole length. Seven long, plumose setae distributed one per segment on segments 3–7 and two setae on apical segment; distal setae somewhat shorter than proximal ones.

MAXILLULES (Fig. 1B). Pair of oblong lobes between fifth pair of marginal processes. Proximal region not clearly seen, thus presence of articulation questionable. Distally armed with spinules, four long apical setae (medialmost shortest and, unlike others, simple rather than plumose), and two subapical, probably simple, medial setae of uncertain length (proximal one very short).

CAUDAL REGION (Fig. 1). Furcal lobes each with pore, two arcs of spinules, short, biserially spinulose, lateral apical spine, and long apical seta with rows of minute spinules. Apical seta reaching end of long, thin, medial terminal spine, latter extending 394 μm beyond posterior margin of dorsal shield and bearing "fur" of minute spinules on distal three-quarters.

Description of Nauplius V (NIV?)
Figures 3, 4

DORSAL SHIELD (Fig. 3A). As in NIV but larger, 470 μm long along dorsal midline, 446 μm wide at level between two lateral pairs of marginal processes. Marginal processes arranged as in NIV, sixth pair longest, fifth pair smallest. Number of apical

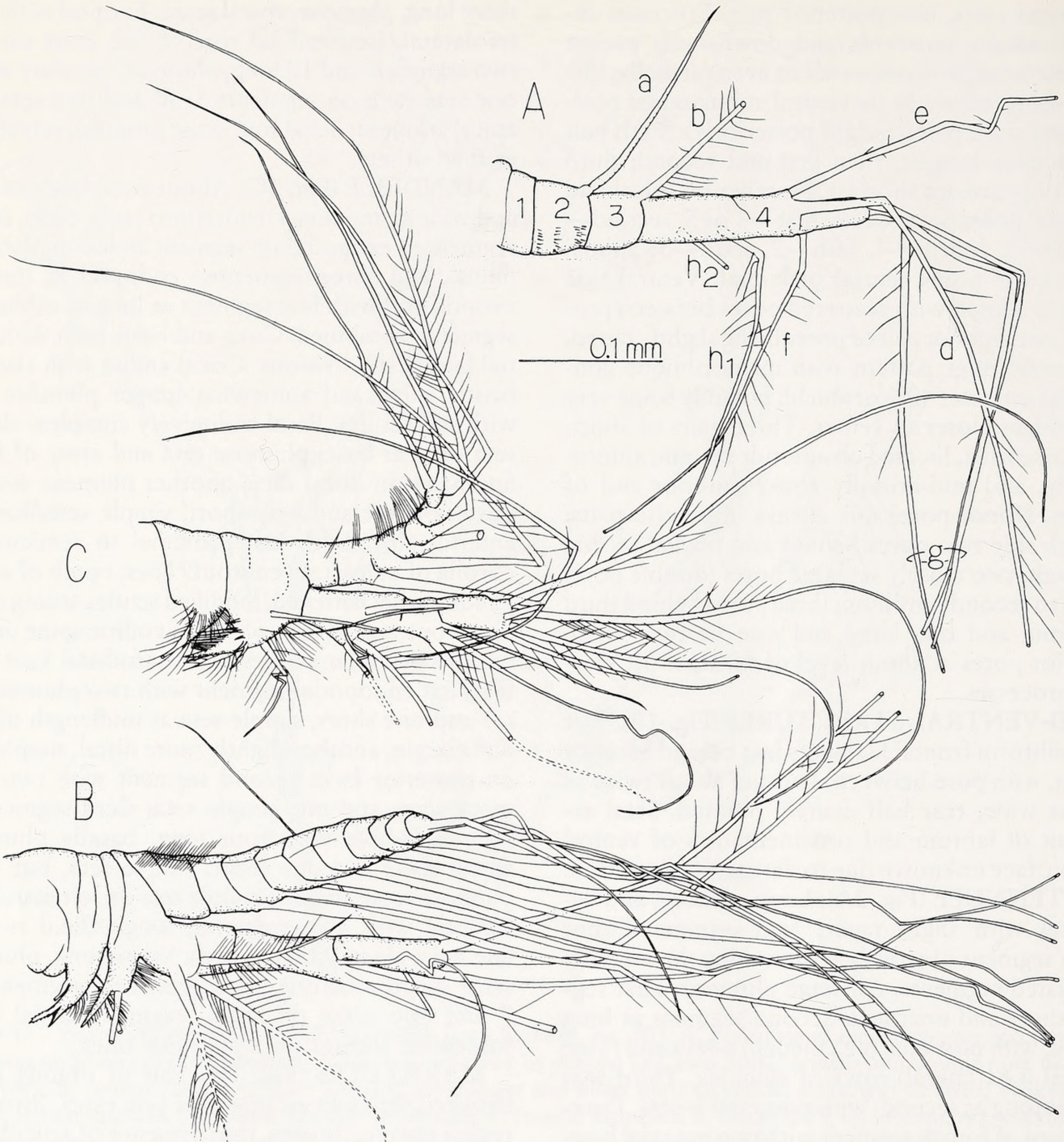

Figure 2. Petrarcid metanauplius NIV (or NIII?) from Red Sea, sta. 703. **A,** right antennule, anterior view, segments numbered and setae designated by letters; **B,** right antenna, posterior view; **C,** right mandible, posterior view. Many setae cut short in A and B, dashed setae in B and C reconstructed based on left member of pair.

and subapical pores per process: first—3 or 4, second—5, third—3?, fourth—4 or 5, fifth—2, sixth—5 or 6. Ventral marginal pores between processes more numerous than in NIV, raised anterior pair present. Dorsal concentric ridges present on outer 25% of shield, with oblique connections usually at levels of marginal processes. Three pairs of short, hairlike sensilla: one pair on anterior margin (left sensillum only seen), one pair anterodorsally, and a posterodorsal pair not present in NIV; no mid-dorsal sensilla observed. Number of dorsal pores increased relative to NIV, 14–15 in discontinuous row on each side of dorsal midline, 7–9 in more lateral position on each side, including double pore retained from NIV.

MID-VENTRAL STRUCTURES. Pair of papilliform frontal filaments just behind anterior margin, with pore between (Fig. 3A). Labrum as in NIV, with sparse, subapical row of long setae on each side (Fig. 3A). Ornamentation of ventral body surface (Fig. 3B, based on NVI but the same as NV): field of tiny cuticular bumps just behind mouth, paired oblique row of spinules extending posteriorly away from mouth, paired longitudinal row of setae (anterior setae stout and in two rows laterally flanked by spinules, middle setae fine, posterior setae again stout), a gap, and paired small field of spinules followed by paired field of fine hairs leading onto bases of maxillules.

ANTENNULE (Fig. 4A). Generally similar to NIV but clearly five-segmented, fifth segment representing two undifferentiated segments. All setae plumose. First segment very short and unarmed. Second and third segments slightly wider than long, with postaxial a-seta and b-seta, respectively; second segment also with single row of spinules. Fourth

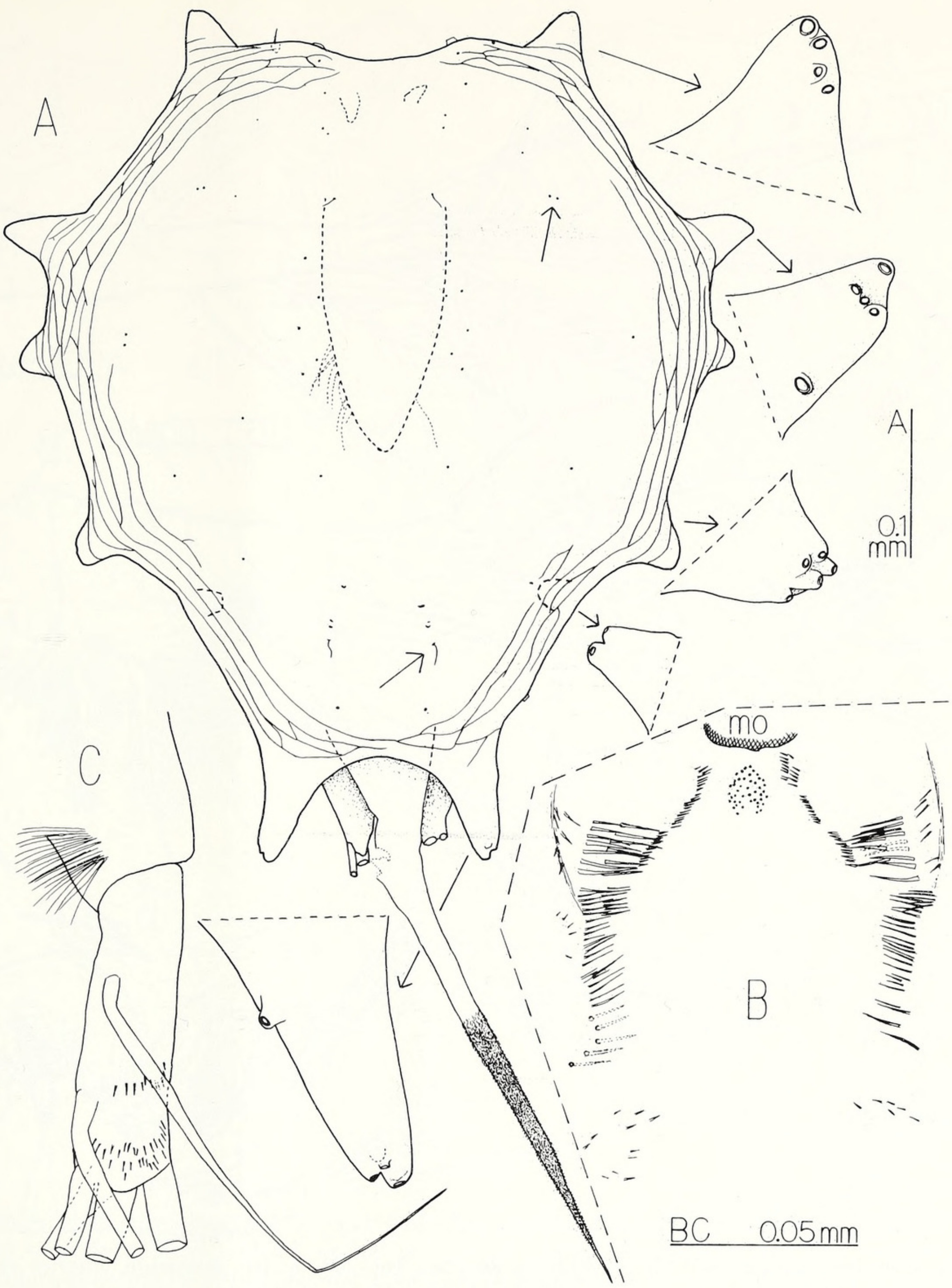

Figure 3. Petrarcid metanauplius NV (or NIV?) from Red Sea, sta. 703. **A,** dorsal view with details of ventral sides of most right marginal processes, appendages omitted, ventral positions of frontal filaments and labrum marked with dashed lines, dorsal double pore and new posterior sensillum marked by arrows. **B,** ventral body ornamentation between mouth (mo) and bases of maxillules, a few missing setae dotted (drawing based on smaller NVI from sta. 703, but condition same in NV); **C,** left maxillule, most setae cut short.

segment with three preaxial h-setae (h_{1-3}), proximal one presumably new in this instar, and new postaxial i-seta. Proximal half of fifth segment with postaxial d-seta and e-seta, and preaxial f-seta; distal half with three long, apical g-setae.

ANTENNA (Fig. 4B–D). Composed of coxa, basis, 12-segmented exopod (first two segments incompletely separated; abnormal right exopod nine-segmented), and three-segmented endopod with all segments equally long. Endopod slightly shorter than exopod. Coxal endite as in NIV. Basal endite apically armed with styliform, plumose spine, two somewhat longer, feathered setae, and one simple seta; distal face with long, fine hairs. Endopod armed as in NIV except for distal patches of spinules on first two segments and new, simple seta on second segment for total of four setae there. Exopod with proximal row of fine hairs as in NIV. Left exopod with 11 plumose, natatory setae, one more than in NIV, with one seta each on segments 3–11 and two on apical segment. Abnormal right exopod also with 11 setae, one seta each on segments 3–5, two setae each on more distal segments, some of latter setae short and of abnormal form.

MANDIBLE (Fig. 4E–H). About two-thirds as long and wide as antenna. Divided into coxa, basis,

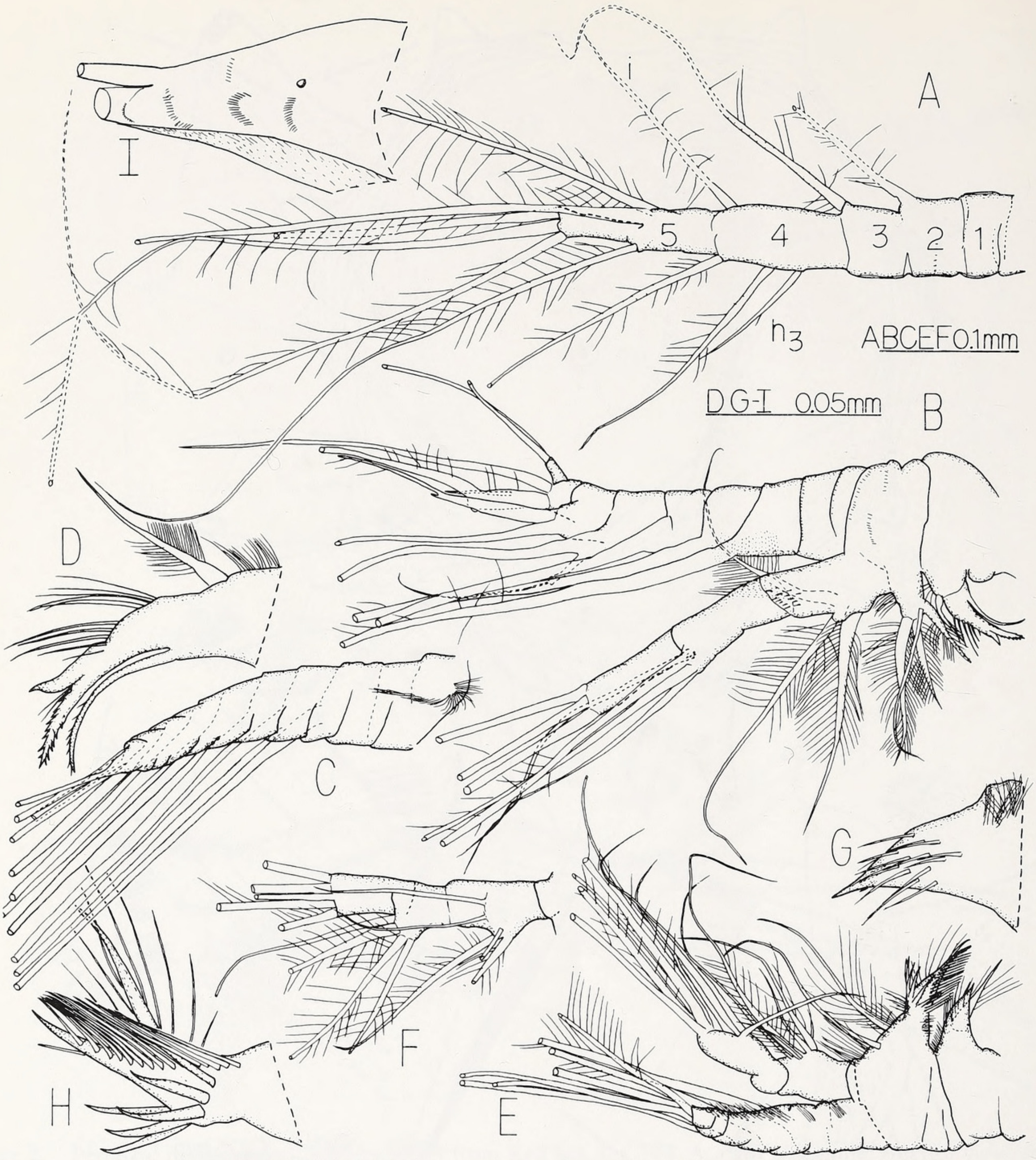

Figure 4. Petrarcid metanauplius NV (or NIV?) from Red Sea, sta. 703. **A,** left antennule, anterior view, segments numbered, letter designations of new setae shown, dashed setae reconstructed from other antennule; **B,** right antenna with abnormal exopod, anterior view; **C,** normal exopod of left antenna, posterior view; **D,** left antennal coxal gnathobase; **E,** right mandible, posterior view, endopod distorted; **F,** better displayed endopod of left mandible, posterior view; **G,** left mandibular coxal enditic spine; **H,** detail of mandibular basal endite from E; **I,** right furcal lobe, setae broken. Many setae cut short in A–C, E, F.

eight-segmented exopod (first segment an incomplete annulus), and three-segmented endopod as long as exopod and with first segment a little shorter than other two combined. Coxal and basal endites as in NIV (Fig. 4G, H). First endopodal segment with three medial setae at midlength, two of them plumose, the other short and simple, and two posterior simple setae, one of latter setae being new in this instar; second segment with three plumose setae, one of them new, and one simple seta (only three setae altogether observed on this segment on right endopod); third segment with five apical setae, number of simple setae among them unclear. Exopod as in NIV.

MAXILLULES (Fig. 3C). Not segmented, oblong, resting flat against ventral body surface and articulated to distinct, hirsute bases. Armed with two arc-shaped patches of spinules, four long, plumose, apical setae, and two probably simple medial setae arising at one-third and two-thirds length, proximal seta shorter than distal one.

CAUDAL REGION. Furcal lobes (Fig. 4I) each with ventral pore and three rows of spinules, one lobe also possibly with distal pore. Furcal setae

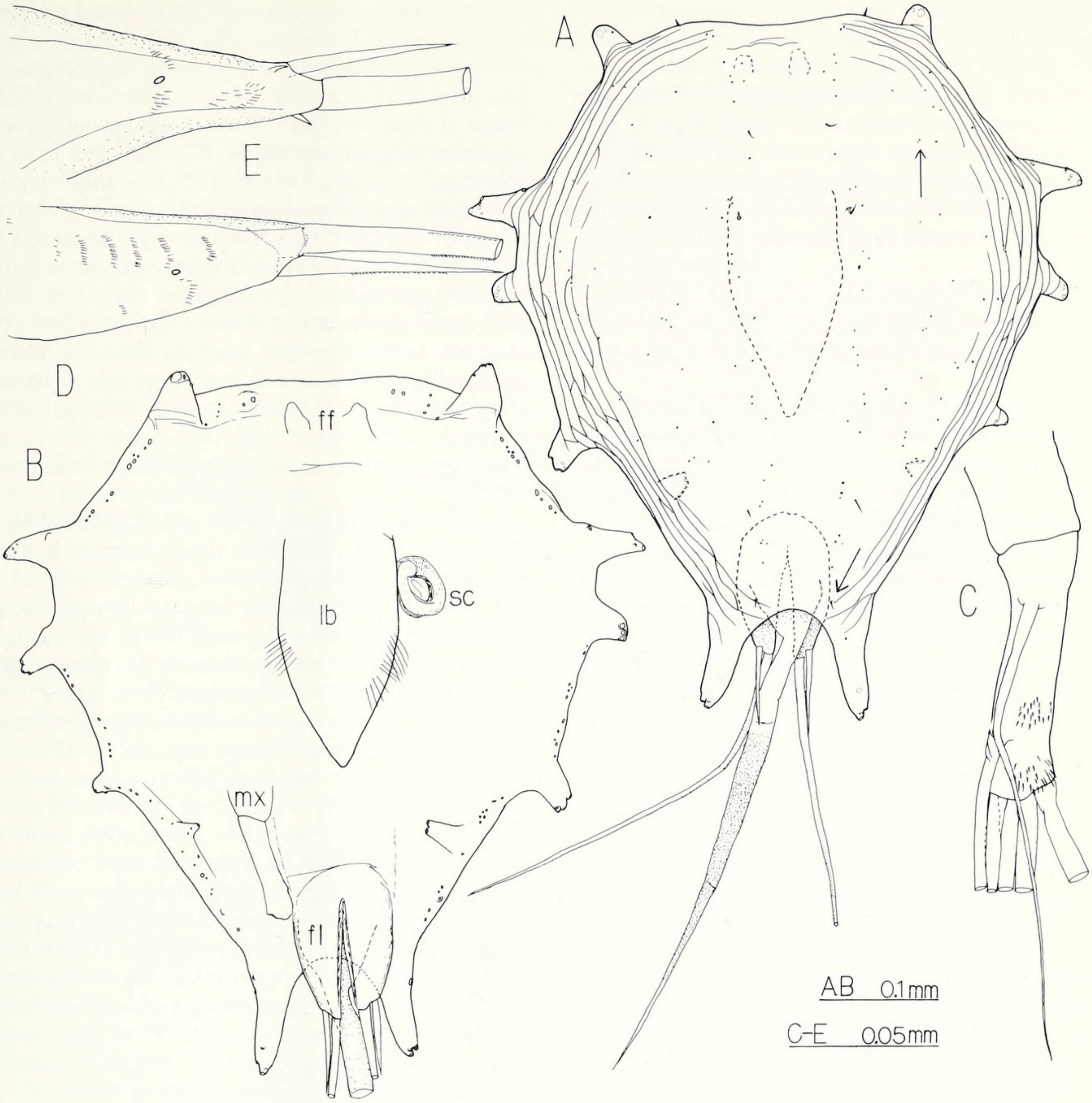

Figure 5. Petrarcid metanauplius NVI (or NV?) from Red Sea, sta. 682 except E, which is large specimen from sta. 703. **A,** dorsal view, appendages omitted, ventral position of labrum shown by dashed line, double pore and new posterior sensillum indicated by arrows; **B,** ventral view, most appendages omitted and caudal armament cut short; **C,** left maxillule, most setae cut short; **D, E,** right and left furcal lobes, respectively, medial apical seta cut short. Abbreviations as in Figure 1 except sc, scarlike vestige of left antenna.

broken off at base, probably two setae of unequal thickness on each lobe. Medial terminal spine (Fig. 3A) as in NIV but relatively shorter, extending 392 μm beyond rear margin of shield (83.4% of shield length versus 97.5% in NIV).

Description of Nauplius VI (NV?)

Figures 5, 6

DORSAL SHIELD (Fig. 5A, B). As in NV but larger, specimens from sta. 703 being 488 μm long by 455 μm wide and 520 μm long by 525 μm wide, specimen from sta. 682 being 490 μm long by 440 μm wide (455 μm wide when flattened); all measurements along same axes utilized above. Marginal processes as in NV. Number of apical and subapical pores per process in specimen from sta. 682: first—4; second—4; third—3 or 4; fourth—4; fifth—2; sixth—4 or 5. Dorsal concentric ridges present on outer 20–25% of shield, with occasional oblique connections. Five pairs of sensilla, including three anterior pairs as in NIV but third pair thicker and not hairlike, and two posterior pairs, rearmost being new in this instar (smaller specimen from sta. 703 seems to lack second and third pairs of anterior sensilla and one rearmost sensillum, other posterior pair accompanied by extra sensillum). Number of dorsal pores increased to 25–37 in discontinuous

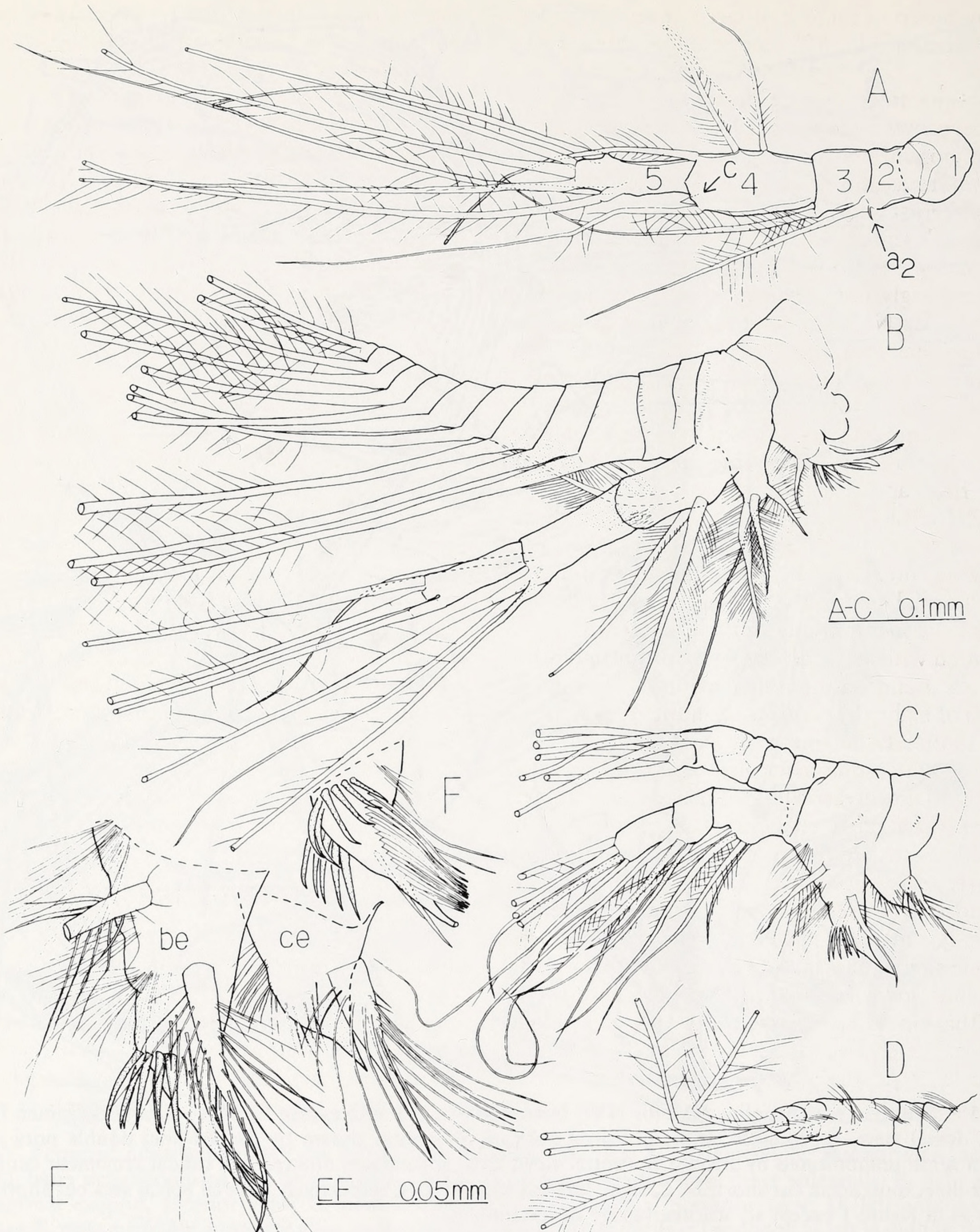

Figure 6. Petrarcid metanauplius NVI (or NV?) from Red Sea, sta. 682 except A, which is small specimen from sta. 703, and B, which is large specimen from sta. 703. **A,** right antennule, anterior view, segments numbered, letter designations of new spines shown, dashed seta reconstructed from other antennule; **B,** right antenna, anterior view; **C,** right mandible with abnormal exopod, anterior view; **D,** normal left mandibular endopod, posterior view; **E,** detail of C, showing endites of coxa (ce) and basis (be); **F,** distal part of left mandibular basal endite, posterior view. Many setae cut short in A–D.

row on each side of midline and 23–33 in more lateral position on each side, including double pore lateral to second sensillum.

MID-VENTRAL STRUCTURES (Fig. 5B). As in NV, except presence of pore between frontal filaments not confirmed in specimen from sta. 682 before dissection.

ANTENNULE (Fig. 6A). Descriptions of paired appendages based on specimen from sta. 682, followed by variability in other specimens; drawings based on all three specimens. Antennules similar to those of NV; setation the same except for new small spine (a_2) next to a-seta on second segment and new claw rudiment (c) next to i-seta on fourth segment (claw rudiment not seen on left antennule).

ANTENNA. Left antenna absent, represented only by bump in middle of circular scar (Fig. 5B). Right antenna (Fig. 6B) composed of coxa, basis, 12-segmented exopod (first two segments incompletely separated, seventh partly subdivided), and three-segmented endopod. Endopod slightly shorter than exopod, with all segments equal in length. Coxal endite as in NIV and NV. Basal endite armed as in NV. First and third endopodal segments as in NV; second segment with one simple and four plumose setae, one more than NV (three of plumose setae seemingly uniserially plumose; one plumose seta replacing NV's newly arisen simple seta). Posterolateral hairs on basal part of exopod not confirmed in this specimen due to unfavorable orientation on slide. Exopod with 12 plumose, natatory setae, one more than NV, one on each segment from third on, except two setae each on apical and fourth from apical segments.

MANDIBLE (Fig. 6C–F). Left mandible with abnormal exopod. Each mandible about two-thirds as large as antenna, with endopod longer than exopod; normal exopod eight-segmented with first segment an incomplete annulus, endopod three-segmented with second segment shorter than other two. Coxal and basal endites as in NIV and NV. Corolla of eight claws on basal endite of right mandible, 11 on left, and several short bristles on distal part of enditic spine opposite comb of modified setae; fine hairs on distal face of this endite clustered in three tufts. First endopodal segment of right mandible with five setae as in NV, two plumose and three simple (latter including one short medial seta and two posterior setae); posterior setae not seen on left mandible. Second endopodal segment with one simple and three plumose setae as in NV. Third endopodal segment with six apical setae, one more than in NV, one of them simple and five plumose. Exopod bearing longitudinal row or tufts of fine hairs posterolaterally. Setation of normal left exopod as in NV. Abnormal right exopod six-segmented (first two segments incompletely separated, fourth rather long and possibly representing two or three segments) with one plumose, natatory seta each on fourth and fifth segments, four on apical segment, total of six setae being one fewer than normal.

VARIABILITY IN APPENDAGES. Small specimen from sta. 703 with distal half of right fifth antennular segment abnormally short. Twelve setae on 13-segmented antennal exopods, first two exopodal segments incompletely separated and bearing posterolateral row of fine hairs; apparently one natatory seta each on segments 3–12, two on apical segment. On mandibles, left basal endite with corolla of 10 clawlike setae, right one with eight. Right endopod developed normally, with one simple and three plumose setae on second segment, five setae on third segment, one of them simple; abnormal left endopod with one plumose and one simple seta on second segment and four setae, all plumose, on very short third segment.

In large specimen from sta. 703, a_2-spine unconfirmed on antennule due to orientation on slide. Antennae with 11 setae on 12-segmented exopods, one seta each on segments 3–11 and two on apical segment; proximal two segments with posterolateral row of hairs. On antennal endopod, second segment bearing one simple and three plumose setae (latter perhaps uniserially plumose or nearly so). On mandibular endopod, short medial seta of first segment at least uniserially plumose (simple in other two specimens).

MAXILLULES (Fig. 5C). As in NV except more spinules in already existing patches and first medial seta, a simple one, arising more proximally than in NV.

CAUDAL REGION (Fig. 5A, D, E). Furcal lobes of specimen from sta. 682 with about eight rows of spinules, including some anterior to pore, but no spinules observed anterior to pore in other two specimens. Each lobe bearing short, minutely spinulose, spinelike seta and long, minutely spinulose seta reaching to end of terminal spine. Large specimen from sta. 703 exhibiting two additional spinules apically on left furcal lobe (not seen on other specimens, but generally tips of furcal lobes not fully exposed to view). Medial terminal spine extending 418 μm beyond rear margin of dorsal shield in specimen from sta. 682, 337 μm in smaller specimen from sta. 703, 456 μm in larger specimen (85.3%, 69.1%, and 87.7% of shield length, respectively).

SUMMARY OF NAUPLIAR DEVELOPMENT (Table 1)

From NIV to NV there is an increase in body size and number of dorsal pores. One pair of dorsal sensilla is added to the posterior part of the dorsal shield. Two setae are added to the antennule, and the fourth segment separates from the fifth. The antennal exopod adds one segment and one seta to make 12 segments and 11 setae, while the endopod adds one seta to the second segment, resulting in four setae. On the mandible the endopod adds one seta each to the second and third segments, making five and four setae, respectively, though the latter addition occurs only unilaterally here. The medial setae on the maxillules become longer.

From NV to NVI there is an increase in body size and in the number of dorsal pores. Another pair of posterior dorsal sensilla is added. A small spine and a claw rudiment are added to the antennule. In the antennal exopod there is an inconsistent addition of one segment or one seta to make 12 segments or 13 setae, and one seta may be added to the second endopodal segment; each of these states was observed in only one of three specimens. On the mandibular endopod, a simple seta on the first segment changes to plumose (in one of three specimens) and one apical seta is added to make six (in two out of three specimens). The proximal medial seta on the maxillule moves toward the base.

Spinule rows may be added proximally and small spines apically to the furcal lobes (each seen in one of three specimens).

DISCUSSION

AFFINITIES

Among all known crustacean nauplii, the present specimens are most similar to the NII of *Zibrowia* sp. (Ascothoracida: Petrarcidae) described by Grygier (1990a). Notable features in common include large size; a kite-shaped dorsal shield with pore-bearing marginal processes; three pairs of sensilla on the anterior half of the shield (also true of NII in another ascothoracidan, *Baccalaureus* sp.; Grygier, 1990a); papilliform frontal filaments; elongate, basically six-segmented antennules with imperfect distal segmental divisions; elongate endopods on the antennae and mandibles, and the mandibular endopod longer than the exopod; posterolateral hairs on only the first two segments of the antennal exopods; and a long, pilose, medial terminal spine flanked both by a long pair of furcal setae that arise from sessile furcal lobes and by long maxillular setae. Differences in the present specimens that are not solely attributable to their later ontogenetic stage include a larger dorsal shield relative to the appendages, six rather than four pairs of marginal shield processes, dorsal cuticular ridges, no obvious nauplius eye (preservation artifact?), no band of setae crossing the labrum, and a semicircular corolla of claws on the mandibular basal endite. A tentative assignment of these specimens to the Petrarcidae seems reasonable despite uncertainty about the true significance of these differences.

There is no *a priori* reason to expect that all five specimens belong to the same species. Only about 12 species of Petrarcidae have been named or partly described, none yet from the Red Sea, but this family is known to infest a great number of mostly ahermatypic scleractinian corals in the Indo-West Pacific (Zibrowius and Grygier, 1985; Grygier, 1991). Many undiscovered petrarcids undoubtedly inhabit the Red Sea, and some of them may have nearly identical larvae. Several differences between the two supposed NVI from sta. 703 suggest that they, at least, belong to different species: their great size difference; the somewhat different distribution of dorsal pores on their shields (large specimen with fewer pores parallel to the midline but more pores laterally than small one); the large specimen's extra apical furcal spinules; and the small specimen's lack of some dorsal shield sensilla (possibly an artifact), 13-segmented instead of 12-segmented antennal exopods, and relatively short terminal spine. The more extensive spinulation of the furcal lobes in the supposed NVI from sta. 682 is suggestive of yet a third species. However, the high rate of appendage abnormalities in the present sample (four of five specimens with at least one deformed or missing limb) suggests that a single species might exhibit considerable variability in more subtle features as well. All five specimens are so similar compared to other known nauplii that in the following discussion I will treat them as one species.

DETERMINATION OF INSTARS

Antennular armament provides an easy way to distinguish naupliar instars NII–NVI in ordinary, planktotrophic Cirripedia, since the setae are added in a nearly fixed order. For the time being I am assuming that the same is broadly true for the Ascothoracida. Antennular armament shows that three instars are represented in the present material, the youngest one with two h-setae, the middle one with three h-setae, and the latest one with, in addition to three h-setae, a claw rudiment and a spine accompanying the a-seta. This setal criterion correlates pretty well with the size of the dorsal shield and the abundance of dorsal pores and sensilla in the present material except that one of the supposed NVI is much bigger than the others. Perhaps it is the only true NVI and the other four specimens represent NIII–NV. If so, the only morphological changes besides growth at the molt from NV to NVI are the change of one short seta on the mandibular endopod from simple to (uniserially?) plumose and perhaps the addition of apical spines to the furcal lobes.

The h-setae and the a_2-spine in the present antennular setal patterns match NIV–NVI of *Baccalaureus falsiramus*, which is the only available ascothoracidan species in which all six naupliar instars are known (Itô and Grygier, 1990). However, in that species the very small i-seta first appears at NVI and a small seta joins the b-seta as well as the a-seta at NVI. Therefore, there are incongruities between antennular development in *B. falsiramus* and in the present nauplii.

One might expect to find a cypridiform ascothoracid larva developing within the NVI cuticle of any ascothoracidan. In the present material no well developed ascothoracid larva is yet formed; the NV and NVI specimens have only internal tissue blocks representing the early stages of formation of the ascothoracid larva's thoracomeres and thoracopods and no obvious compound eyes. This, together with the lack of ventral spines representing the thoracopodal setae, suggests that the oldest metanauplii on hand may only be NV, and not NVI. The presence of a claw rudiment does not disprove this, because Grygier (1992) found a small claw rudiment in NV of a lecithotrophic naupliar series similar to that of *Baccalaureus falsiramus*. If the present material does not truly include NVI, then the youngest specimen must represent the next instar after Grygier's (1990a) NII of *Zibrowia* sp. If so, some rather important changes seem to take place at the molt from NII to NIII (Table 1), namely the addition of three segments to the antennal exopods and the change from a single seta representing the maxillule to a large, possibly articulated

Table 1. Setal formulae of naupliar appendages of Petrarcidae in cirriped literature-based format (e.g., Egan & Anderson, 1985), NI–II based on Grygier (1990a) and NIV–VI on present study. Symbols: E, enditic spine and subsidiary armament; F, feathered seta; P, plumose seta (spinulose in NI); S, simple seta; s, small spine; ?, armament element of uncertain nature; italics, preaxial setae. Parentheses recording variation (or . . .) or doubt (?).

Antennule	
NI	*S*:SPS:P:S
NII	*P*:PPP:PP:P:P
NIV	*PP*:*P*:PPP:PP:P:P
NV	*PPP*:*P*:PPP:PP:P:P:P
NVI	*PPP*:*P*:PPP:PP:sP:P:sP

Antenna		
Exopod		Endopod and protopod
NI	P:4P	sPP:SS:EE:Es:Es
NII	PP:5P	PPP:SP:PP:EsP:EP
NIV	PP:8P	PPP:SPP:FFF:E??(?):EsP
NV	PP:9P	PPP:SSPP:FFF:ESFF:EsP
NVI	PP:10P(or 9P) (or PP:P:P:PP:6P)	PPP:SPPPP(or S3P):FFF:ESFF:EsP

Mandible			Maxillule
Exopod		Endopod and protopod	
NI	P:3P	sPP:SP:Es:Es:ss	Absent
NII	PP:4P	sPPP:SP:SPPP:EPP:sP	P
NIV	PP:5P	SPPP(or S4P):SPP:SSPP:ESPP:sP	SPPP:S:S
NV	PP:5P	5?:SPPP(or 3?):SSSPP:ESPP:sP	PPPP:S:S
NVI	PP:5P	S5P:SPPP:SSSPP(or SPP):ESPP:sP	PPPP:S:S

maxillule with six setae. In *B. falsiramus* the molt from NII to NIII is less drastic, involving the addition of at most one segment to the antennal exopod (9- to 10-segmented) and a change from a sessile maxillular seta to two setae on a small, nonarticulated lobe, smaller changes than those postulated here. Nonetheless, *B. falsiramus* has lecithotrophic nauplii, so some simplification in ontogeny relative to planktotrophic forms might be expected.

The following treatment of the present nauplii as NIV–NVI in a comparison with the Cirripedia is conservative. If there is an unknown later instar representing the true NVI, it must have appendages at least as complex as those of the oldest specimen on hand, and perhaps more complex. The same trends documented below would still apply, but merely be amplified.

COMPARISON WITH CIRRIPEDIA (Table 2)

There is a voluminous literature on the naupliar development of Cirripedia. Some recent large-scale works and reviews include Lang (1979), Kado (1982), Moyse (1987), Korn (1988), and Egan and Anderson (1989), which can be consulted for additional literature sources. The present comparison (Table 2) is limited to the review of lepadomorph nauplii by Moyse (1987), a series of papers by Egan and Anderson (1985, 1986, 1987, 1988, 1989) in which larvae representing all the major groups of balanomorph barnacles are described and compared, and an unpublished thesis (Kado, 1982) in which the larvae of 18 diverse thoracicans are described and information on chaetotaxy, including literature data, is concisely and usefully summarized. I have prepared a separate reevaluation of the segmental and setal homologies of the antennules of cirripedes and ascothoracidans (see Grygier, in press) and so will not discuss antennules here.

Antennae (Table 2)

The antennal coxal gnathobases of the present metanauplii and all planktotrophic cirriped nauplii are similar, consisting of a bifid spine, one of whose prongs is biserially dentate (in the Cirripedia this prong may also have basal teeth), a curved setiform spine, and bristles [see Kado (1982) for a detailed survey of the cirriped gnathobase]. The smoothly curved form of the gnathobase in the petrarcids is more similar to that of balanoid nauplii than to the angular gnathobases of lepadomorph and chthamaloid nauplii. The present nauplii have a seta at the base of the coxal endite that cirriped nauplii lack. This seta is also present in NII of *Zibrowia* sp. and of another ascothoracidan in the family Lauridae, *Baccalaureus* sp. (Grygier, 1990a), but in these NII there is no curved, setiform spine. Apparently the latter spine develops in NIII or NIV in the Ascothoracida, while in the Cirripedia it is present from NII.

Table 2. Comparison of antennal and mandibular setal armament of petrarcid (Petr.) nauplii (present study) and cirriped (Cirr.) nauplii (Kado, 1982; Egan and Anderson, 1985, 1986, 1987, 1988, 1989; Moyse, 1987) at NIV–VI. Numerals represent setal counts, alternative states given in parentheses, short sensilla on petrarcid mandibular basis not included. Symbols: E, enditic spine and subsidiary armament; F, feathered seta; s, small spine.

	Exopod		Endopod and protopod				
Instar	Apical	Lateral	Seg. 3	Seg. 2	Seg. 1	Basis	Coxa
Antenna							
NIV							
Petr.	2	8	3	3	3F	E + (2–3?)	Es + 1
Cirr.	2 (3)	7 (6)	4–5	2–3	2 (2F + 1)	E + 3 (E + F + 2)	Es
NV							
Petr.	2	9	3	4	3F	E + 2F + 1	Es + 1
Cirr.	3 (2, 4)	8 (6–7)	4–5	3	2 (3F + 1)	E + 3 (E + F + 2)	Es
NVI							
Petr.	2	10 (9)	3	5	3F	E + 2F + 1	Es + 1
Cirr.	4 (2–3)	8 (6–7)	4–5	2–4	2 (3F + 1(2))	E + 3 (E + F + 2)	Es
Mandible							
NIV							
Petr.	2	5	4–5	3	4	E + 3	s + 1
Cirr.	2	3	4–5	3	E + (2–3)	E (+s) + (2–3)	s + 1
NV							
Petr.	2	5	5	3–4	5	E + 3	s + 1
Cirr.	2	4	5	4	E + (2–3)	E (+s) + (2–3)	s + 1
NVI							
Petr.	2	5	5–6	4	5 (3)	E + 3	s + 1
Cirr.	2	4	4–5	4	E + 3	E (+s) + (2–3)	s + 1

In cirriped NIV–NVI the basis has an enditic spine (referred to in cirriped literature as a cuspidate seta or, in chthamaloids, a hispid seta, both kinds unlike the present spine) and three setae, one of them simple, as in the present petrarcids. While the two non-simple setae are feathered at least in NV–VI in the petrarcids, only one of them is feathered in these instars in chthamaloids, and none in other barnacles.

The antennal exopods of planktotrophic cirriped nauplii have 8–9 setae at NIV, 10–12 at NV, and 9–12 at NVI, 12 being most common. Kado (1982) states that the first of these setae arises from either the second or third segment, often varying within a species, and that there are two setae on the apical segment at NIV, two or usually three setae at NV, and two, three, or usually four apical setae at NVI. Other papers cited above show as many as three apical setae at NIV and four at NV. The current NIV nauplius has 10 setae, the NV has 11, and the NVI larvae have 11 or 12 setae on the antennal exopods, and only two are apical in each instar. Thus the petrarcid NIV has more exopodal setae than the corresponding cirriped instar, but at NV and NVI both groups are usually equal. However, cirriped exopods have fewer segments, generally nine at NIV–VI versus 11–13 in the petrarcid metanauplii, and the greater number of apical setae in the Cirripedia shows that this is due to a suppression of distal segment division compared with the petrarcids. In a few cirripeds like *Lepas* NV–VI (see Moyse, 1987), the first exopodal seta is feathered, but not in the petrarcids. When posterolateral hairs are present on the antennal exopod in cirriped nauplii, they line the whole length, not just the first two segments as in the petrarcids.

It is uncommon in the cirriped literature for the antennal endopodal segments to be referred to by number; rather, setal clusters alone are usually noted and the basal endite may be inaccurately counted as part of the endopod. In planktotrophic cirriped nauplii there are three groups of setae which are clearly homologous to the setae on the three endopodal segments of ascothoracidan nauplii; these show that the first endopodal segment of the cirriped antenna is generally continuous with the basis, and the other segment boundaries, especially between the second and third segments, are often poorly expressed. According to the surveyed cirriped literature, NIV may have an endopodal setal count (from proximal to distal) of from 2-3-4 or 3-2-4 to 3-3-5, NV may have 2-3-4 to 4-3-5, and NVI may have 2-3-4 to 5-5-5. The present petrarcid nauplii have counts of 3-3-3 at NIV, 3-4-3 at NV, and 3-(4–5)-3 at NVI. Cirripeds never have three setae on the first segment in NV and NVI, only two or four to five; when there are four or five setae (in lepadomorphs, verrucomorphs, and chthamaloids), three of them are feathered as in the petrarcids, and the remaining simple ones are absent from the petrarcids. Coronuloids and balanoids lack feathered setae. Cirriped nauplii have more setae on the third segment in all three instars compared to the petrarcids (four or five versus three).

Mandible (Table 2)

The coxal endites of cirripeds and petrarcids are alike. The basal endite has three prominent setae, or four in some lepadomorphs like *Lepas* (see Moyse, 1987). This number includes the enditic spine, which is usually referred to as a cuspidate seta. The spine has some stiff bristles but completely lacks the corolla of claws that is present in the petrarcids. Thus the number of prominent true setae in cirripeds, as opposed to this spine, is either two or three, and three matches the condition in the present petrarcid nauplii. Many cirripeds, but not lepadids, have an additional small spine distally on the basis that petrarcids lack.

In cirriped mandibular exopods, five setae on four segments at NIV and six setae on five segments at NV and NVI seem to be nearly universal. In contrast, there are seven setae on eight segments at all three instars in the petrarcid metanauplii. A complete row of posterolateral hairs is common to both.

The cirriped naupliar mandibular endopod is rather like the antennal one except the two distal segments are often fully fused. Nonetheless, the setal clusters remain distinct. The terminology in the literature parallels that for the antennal endopods, and the setal counts (from proximal to distal) recorded there range from 3-3-4 to 4-3-5 at NIV, 3-4-5 to 4-4-5 at NV, and 4-4-4 to 4-4-5 at NIV. On the first segment one of the setae, usually called a cuspidate seta, is actually a spine that is more complexly armed than the enditic spine of the basis. In contrast, the petrarcid metanauplii have only true setae on this segment, and the total number of armament elements there in NV–VI is five in the petrarcids versus three or four in cirripeds. Six setae on the distal segment at NVI, occurring inconsistently in the present specimens, also surpasses cirripeds.

Maxillules

Maxillular rudiments gradually develop first as setal arcs and then as setose lobes on the sides of the body in cirriped nauplii. They generally do not become articulated until NVI at the earliest, while this occurs at NV or possibly NIV in the present petrarcids.

Caudal Armament

Unlike the present specimens, cirriped nauplii never have furcal setae but usually have a pair of furcal spines on a short or long stalk or, in a few lepadomorphs, sessile furcal spines.

Other Remarks

When there are differences in the numbers of segments or setae in the antennae and mandibles in the present petrarcid metanauplii and their counterpart instars in the Cirripedia, the former usually have more segments or more setae, as in the exopods of both limbs and the first endopodal segment of the mandible (Table 2). In such cases the petrarcid condition can be considered plesiomorphic by the criterion of oligomerization [see Huys and Boxshall (1991) for a detailed application of this criterion]. The only consistent exception, where the cirripeds always have more setae and perhaps the more plesiomorphic condition, is on the third endopodal segment of the antenna. Large subsets of cirriped nauplii exhibit two other features that might be plesiomorphies: one or two simple setae on the first endopodal segment of the antenna in addition to three feathered setae shared with the petrarcids and a small distal spine on the mandibular basis that petrarcids lack.

A separate topic is the question of a homologue of cirriped frontolateral horns in the Ascothoracida. A pair of frontolateral horns arising from the dorsal shield of the nauplius has been considered the single most diagnostic feature of the Cirripedia plus Rhizocephala. However, Grygier (1990a) has suggested that the anterior pair of marginal shield processes of the ascothoracidan *Zibrowia* sp. at NII might be homologous to frontolateral horns and represent their ancestral state. Besides having a corresponding form and position, both structures have two apical pores. Therefore it is significant that the marginal processes in the present metanauplii, except the fifth pair, have more than two and up to five pores (up to four pores in the first pair). Two pores at NII is just the first step in an ontogenetic series. For the previously recorded coincidence in the number of pores to retain any phylogenetic significance, it is necessary to regard the cirriped frontolateral horns as paedomorphic, maintained through all the naupliar stages in a condition equivalent to the ascothoracidan NII. In *Zibrowia* sp. NII, the pores on the processes were highlighted by the absence of pores between the processes. Now it is clear that pores are gradually added all around the margin of the shield, on and off the processes, as larval molts take place, and that all the pores are homologous to the equatorial pores of other ascothoracidan nauplii. Homology of the marginal processes with the marginal gland papillae of lepadomorph nauplii, as discussed by Grygier (1991a), remains a likely possibility.

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