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Scanning electron microscopy of acrothoracican cypris larvae (Crustacea, Thecostraca, Cirripedia, Acrothoracica, Lithoglyptidae)

Gregory A. Kolbasov[1], Jens T. Høeg[2] & Alexei S. Elfimov[1]
[1]Department of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow 119899, Russia; [2]Corresponding author. Department of Zoomorphology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen, Denmark, e-mail: jthoeg@zi.ku.dk

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Abstract

Scanning electron microscopy was used to provide a full morphological description of cypris morphology in the acrothoracican species *Lithoglyptes mitis* and *L. habei* (Lithoglyptidae). Special attention was given to lattice organs, antennules, thorax, thoracopods, abdomen, and furcal rami. Cypris larvae of the Acrothoracica share some putative plesiomorphic features with the cypris-like ascothoracid larvae of the non-cirripede taxon Ascothoracida. The most notable are traces of abdominal segmentation and carapace lattice organs without pore fields. Acrothoracican cyprids also share numerous synapomorphies with those of the Thoracica and the Rhizocephala. This list includes a four-segmented antennule with a triangular first segment of two sclerites set at an angle to each other, a cylindrical second segment, a small third segment functioning as an attachment organ, and a cylindrical fourth segment bearing homologous sensory setae. Further apomorphies are a pair of frontolateral horn glands exiting anteroventrally on the headshield (carapace), a pair of multicellular cement glands exiting on the attachment organs, a single stout, serrated and non-natatory seta on the thoracopodal exopods and a highly reduced abdomen with at best traces of segmentation. These synapomorphies in cypris morphology support a monophyletic taxon Cirripedia comprising the Acrothoracica, Thoracica, and Rhizocephala but excluding the Ascothoracida.

Contents

Introduction

The Cirripedia consist of the orders Acrothoracica, Thoracica, and Rhizocephala (Høeg, 1992; Høeg, 1995). Both the Thoracica and the Acrothoracica use thoracic limbs (cirri) for setose feeding, but the Acrothoracica deviate in inhabiting burrows and lacking an armament of mineralized shell plates. This cryptic mode of life has resulted in numerous modifications to their morphology.

The Acrothoracica have long been important in discussing both the evolution and phylogeny of the Cirripedia and of the Thecostraca in general (Glenner et al., 1995; Newman, 1971, 1974, 1987; Spears et al., 1994; Turquier, 1972). An origin from or, more precisely, a sistergroup relationship with various cirripede taxa has been suggested, such as the Iblidae (Tomlinson, 1969) and the scalpellid *Lithotrya* (Newman, 1982; Grygier & Newman, 1985). In spite of these studies the position of the

Acrothoracica within the Thecostraca remains unclear. The lack of mineralized shell plates and whether this is primary or due to secondary loss impedes comparison with the characters used in estimating the phylogeny of thoracican barnacles (Glenner et al., 1995, Newman, 1996). Spears et al. (1994) used molecular data in an effort to clarify cirripede phylogeny and their results suggested an affinity between the Acrothoracica and the Ascothoracida, which challenged even the basic monophyly of the Cirripedia. Despite the wide morphological differences among adult Thecostraca, most representatives of each group possess pelagic nauplius and cypris-like larvae. The similarity and unproblematic homology of these larvae including numerous details apparent under the scanning electron microscope make them eminently suited for resolving the phylogenetic relationships within the Thecostraca (Grygier, 1987a, b; Walossek et al., 1996). Jensen et al. (1994) used SEM on cypris larvae to study the recently discovered lattice organs in the carapace. They found putative plesiomorphic similarities between Ascothoracida and Acrothoracica and putative synapomorphies between Acrothoracica and the remaining two cirripede orders. Moyse et al. (1995) employed SEM on cypris attachment organs in a wide selection of cirripede cyprids. These two studies focussed on but a few selected organs, and all previous works on acrothoracican cyprids used only light microscopy (Kühnert, 1934; Tomlinson, 1969; Turquier, 1967, 1970, 1971, 1985; Wells & Tomlinson, 1966). For acrothoracican cyprids we therefore lack the level of detail now available from the two other cirripede orders (e.g., Elfimov, 1995; Glenner et al., 1989; Glenner & Høeg, 1995; Høeg, 1985; Jensen et al., 1994; Moyse et al., 1995; Walker, 1985; Walker et al., 1987). An ultrastructural study of the entire morphology of an acrothoracican cyprid is necessary for gathering the suite of larval characters that Glenner et al. (1995) advocated for future studies of cirripede phylogeny. Here we try to accomplish this in part by a study of cypris morphology in two species of the acrothoracican family Lithoglyptidae.

Material and methods

Most acrothoracican species brood their larva until the cypris stage is reached (Tomlinson, 1969). It is therefore possible to sample mature cypris larvae from the mantle cavities of females found in museum collections. Acrothoracican males are always dwarf forms attached to the females (Gotelli & Spivey, 1992; Kolbasov, 1996).

We examined the collections of mollusc shells stored in the Zoological Museum of Moscow State University and found more than 300 specimens containing Acrothoracica. Many of them hosted either *Lithoglyptes habei* or *L. mitis*, and some contained cypris larvae. Recently settled cypris stages of dwarf males (Fig. 2C) and females were also isolated.

All material was preserved in 70% alcohol. We investigated five *Lithoglyptes habei* cypris larvae and five *L. mitis* cypris larvae with SEM and we also mounted some for light microscopy after KOH treatment. All larvae for SEM investigation were post-fixed with 2% OsO_4 for 2 hrs, dehydrated in acetone, and critical point dried in CO_2. Dried specimens were sputter-coated with gold and examined at 15 kv accelerating voltage (with a JEOL JSM-840 SEM in Copenhagen and a HITACHI S405A SEM in Moscow). After investigation of external carapace features one "valve" of some larvae was removed to reveal the body.

The material studied came from the following localities. *Lithoglyptes habei*: Gulf of Aden, 13°59'5''N, 48°24'7''E, depth 3 m, coral reef, 1 female with 1 cypris inside, in *Turbo argirostomum*; Seychelles, Silhouette I., 4°36'S, 56°48'E, subtidal zone, 6 females and 1 free cypris in *Mancinella mancinella*; South China Sea, Vietnam 12°N, 109°E: depth 1.5 m, 3 females (1 with a cypris inside) in *Mancinella mancinella*; depth 2 m, 2 females and 1 free cypris in *Coralliophila deformis*; 2-4 m, 5 females (1 with a cypris inside) in *Drupa morum*.

Lithoglyptes mitis: Maldives: Feartu I., 3°48'N, 73°05'E, intertidal zone, coral reef, 8 females (1 with a cypris inside); Genego I., 3°49'N, 73°06'E intertidal and subtidal zones, coral reef, 2 females and 1 cypris with stretched antennules in *Trochus pyramis*, 17 females (2 with a cypris inside) in *Mancinella alauina*, 8 females (1 with a cypris inside) in *Latirolagena smaragdula*, 3 female specimens (1 with a cypris inside) in *Morula cavernosa*, 2 females (1 with a cypris inside) in *Hipponix* sp.

Results

We could not detect any morphological differences between cypris larvae of *Lithoglyptes habei* and *L. mitis*. We have therefore not distinguished between the two species in the following description, but the species name is provided for all figures.

Size and shape of the cyprids

In our material the adult females never contained more than a single cypris, while Tomlinson (1969) often found two brooded larvae in the same female. The brooded cypris larvae are located in the lower body part of the female and usually towards the dorsal margin of mantle cavity. They measure ca. 580-600 µm in length, which equals approximately 40% of the length of the brooding female. The size of the cypris relative to the female means that brood size is necessarily minute.

The cypris headshield, or carapace, has an elongated, spindle-shaped form with an anterior rounded end and a narrower and truncated posterior end (Figs. 1B,C, 2A). The dorsal margin is slightly curved. The ventral margins of the carapace are also slightly curved in the anterior half, whereas in the posterior half they are somewhat concave. The length : height ratio of the carapace is ca. 3 : 1. In lateral view the shape of the cypris resembles those of other cirripedes. However, the cyprids of both *Lithoglyptes* studied here and those of *Trypetesa lampas* studied by Jensen et al. (1994) deviate from other cirripede cyprids in having a very narrow carapace compared to the length (Fig. 2A,B). The functional significance of this shape is not clear. In *Trypetesa* it may relate to peculiarities of settlement within the narrow confines of gastropod shells inhabited by hermit crabs.

General morphology

The general morphology of *Lithoglyptes* cyprids agrees with that found in other cirripedes. The four-segmented antennules are located in the anterior mantle cavity, which occupies the anterior one third of the cyprid Godg. The cement glands lie at the basis of the first antennulary segments. They have a loboform shape and a brown colour (in alcohol), darker than the rest of the body. The paired compound eyes, associated with frontal filaments, lie in front of the cement glands (Fig. 1B,C). The nauplius eye is situated near the dorsal margin, one third of the length from the anterior end. Retractor muscles of the antennules and thorax extend through the anterior and middle parts of the cypris body and attach to the dorsomedial side of the carapace, but a complete description of the cypris musculature will require section series as in Walley (1969) and Høeg (1985). The undifferentiated oral (buccal) cone and the thorax lie within the posterior half of the carapace. The thorax carries six pairs of biramous limbs armed with long natatory setae. The abdomen is rudimentary but carries a distinct telson with a pair of furcal rami (Figs. 1B, 7). The thorax and the antennules can be partially extended outside the mantle cavity (Fig. 2B,D)

Carapace

There is no dorsal hinge line or posterior slit on the carapace. At lower magnifications its surface appears slightly wrinkled with small longitudinal and transversal ridges (Fig. 2A,B), but some of these ornaments may be artifacts produced during fixation or preparation for SEM. At higher magnification the carapace surface appears smooth (Fig. 3A-D) and without the cellular hexagonal patterning that characterizes some ascothoracid larvae (Itô & Grygier, 1990), facetotectan cypris-y (Schram, 1970), and some thoracican cyprids. The carapace also lacks large pores (except the frontolateral pores), papillae, and the wheel organs of Elfimov (1995). Unlike cyprids of *Cryptophialus* (unpublished data), there are no long setae but only minute (0.7 µm) setae sparsely distributed over the entire carapace (Fig. 3A,C,D). These carapace setae are single (Fig. 3A) or double (Fig. 3C,D) and are located in shallow, 1 µm wide depressions. Single setae occur most frequently on the anterior and lateral surfaces of the carapace. A longitudinal row of double setae extends from the anterior end along the dorsomedial line of the carapace (Fig. 3C,D). The carapace "valves" have deep longitudinal and transverse furrows at the anterior end (Figs. 2D, 3C).

Frontolateral pores

Lithoglyptes cypris larvae lack the frontolateral horns found in a few thoracican species, but sport a pair of conspicuous frontolateral pores near the

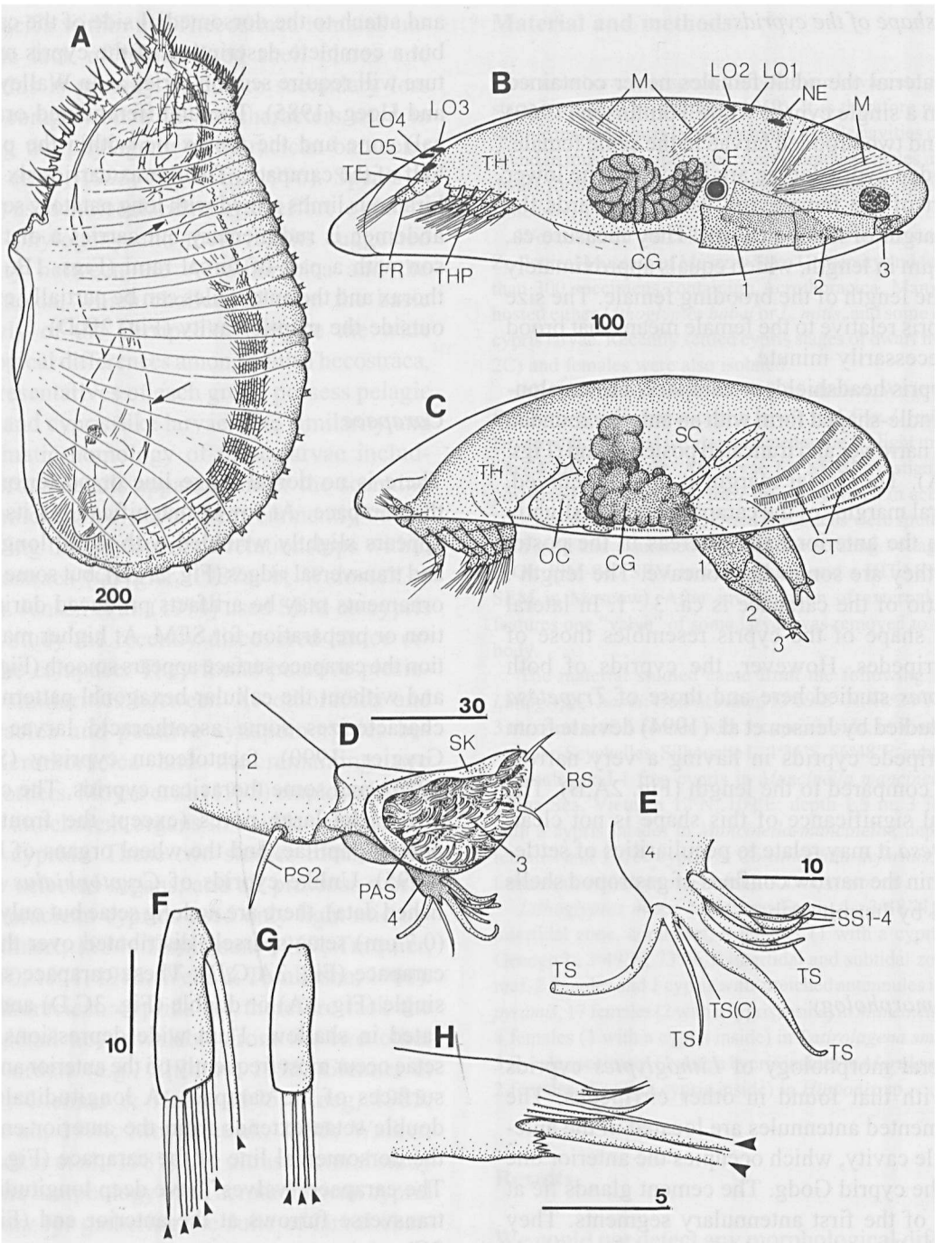

Fig. 1. A, *Lithoglyptes mitis*, adult female, lateral view, with a cypris (bottom arrow) and an unidentified copepod (top arrow) inside the mantle cavity, lateral view; B,C, *L. habei* cyprid, lateral view from light microscopy; D, terminal part of antennule showing attachment disc on 3rd segment (3) with dense carpet of cuticular villi (see Fig. 5D); E, Setation on fourth antennulary segment, among five terminal setae (TS) only minute seta C identified (See Fig. 6D); F, Setation (arrowheads) of terminal (2nd) segment in thoracopodal exopod, isolated basal seta, three subterminal and two terminal setae closely grouped; G, Setation (arrowheads) of terminal (3rd) segment of thoracopodal endopod, three terminal setae; H, Terminal end of furcal ramus with two setae (arrowheads) (See Fig. 7G). CE compound eye, CG cement gland, CT, rows of ctenes inside mantle cavity, FR furcal ramus, LO1-5 lattice organs 1-5, M extrinsic antennulary muscles, NE nauplius eye, OC, oral cone, PAS postaxial sensillum, PS2 postaxial seta 2, RS radial setae, SC proximal sclerite of 1st antennulary segment, SK skirt encircling attachment disc, SS1-4 subterminal setae 1-4, TE telson, TH thorax, THP thoracopods, TS terminal setae, 1-4 antennulary segments. Scale bars in μm.

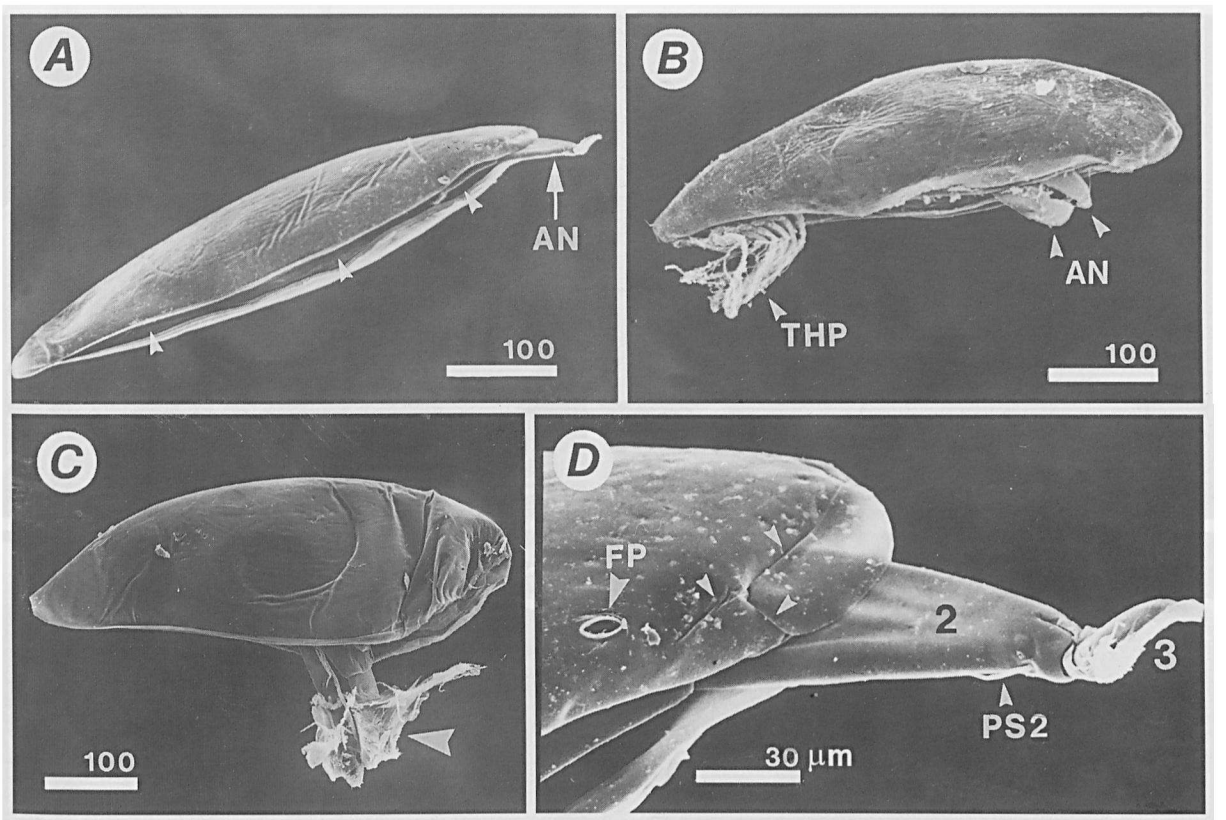

Fig. 2. Cyprids (A,D *Lithoglyptes mitis*; B,C *L. habei*). A, with extended antennule, ventrolateral view, arrowheads show entrance to mantle cavity; B, with both antennules and thoracopods extended, lateral view; C, settled male cyprid removed from female mantle cavity, female tissue remains around antennules (arrowhead); D, anterior end with extended antennule, ventrolateral view, arrowheads denote anterior furrows. AN antennule, FP frontolateral pore, PS2 postaxial seta 2, THP thoracopods, 2-3 antennulary segments. Scale bars in µm.

anteroventral margin of the carapace ca. 80 µm from the anterior end (Figs. 2D, 3B,E). The pores are elongate (3 by 4 µm) and surrounded by a 1.3 µm high cuticular ridge without any sculpture. They are the exits for the frontolateral glands that characterize cirripede cyprids.

Lattice organs

The carapace has five pairs of lattice organs (LO) in both *Lithoglyptes habei* and *L. mitis*. They have the same position and the same morphology of the individual organs as the five LO pairs found in *Trypetesa lampas* by Jensen et al. (1994).

Individual morphology: All individual lattice organs are shallow, 7-18 µm long and 0.8-1 µm wide depressions (Fig. 4). They may have a weak median keel or crest (in LO3 and LO4), but are never encircled by a cuticular ridge. This means that the LOs of *Lithoglyptes* have the same morphology ('keel in a trough') as found by Jensen et al. (1994) in cyprids of *T. lampas*. The elongate depression of the LOs has a latticed bottom due to minute perforations in the epicuticle, but a TEM investigation of similar organs in the acrothoracican *T. lampas* revealed that they lack pores in the underlying procuticle (Høeg et al., 1998).

Terminal pore: A conspicuous terminal pore (TP) lies at the posterior end of LO1 and LO3-5, but LO2 differs in having this pore sited at the anterior end (Fig. 4A-D).

Position and shape: The first (LO1) and second (LO2) pairs of lattice organs lie close (10 µm) together, ca. 200 µm from the anterior end and 5-13 µm from the dorsal midline (Fig. 4A,B). LO1 is straight

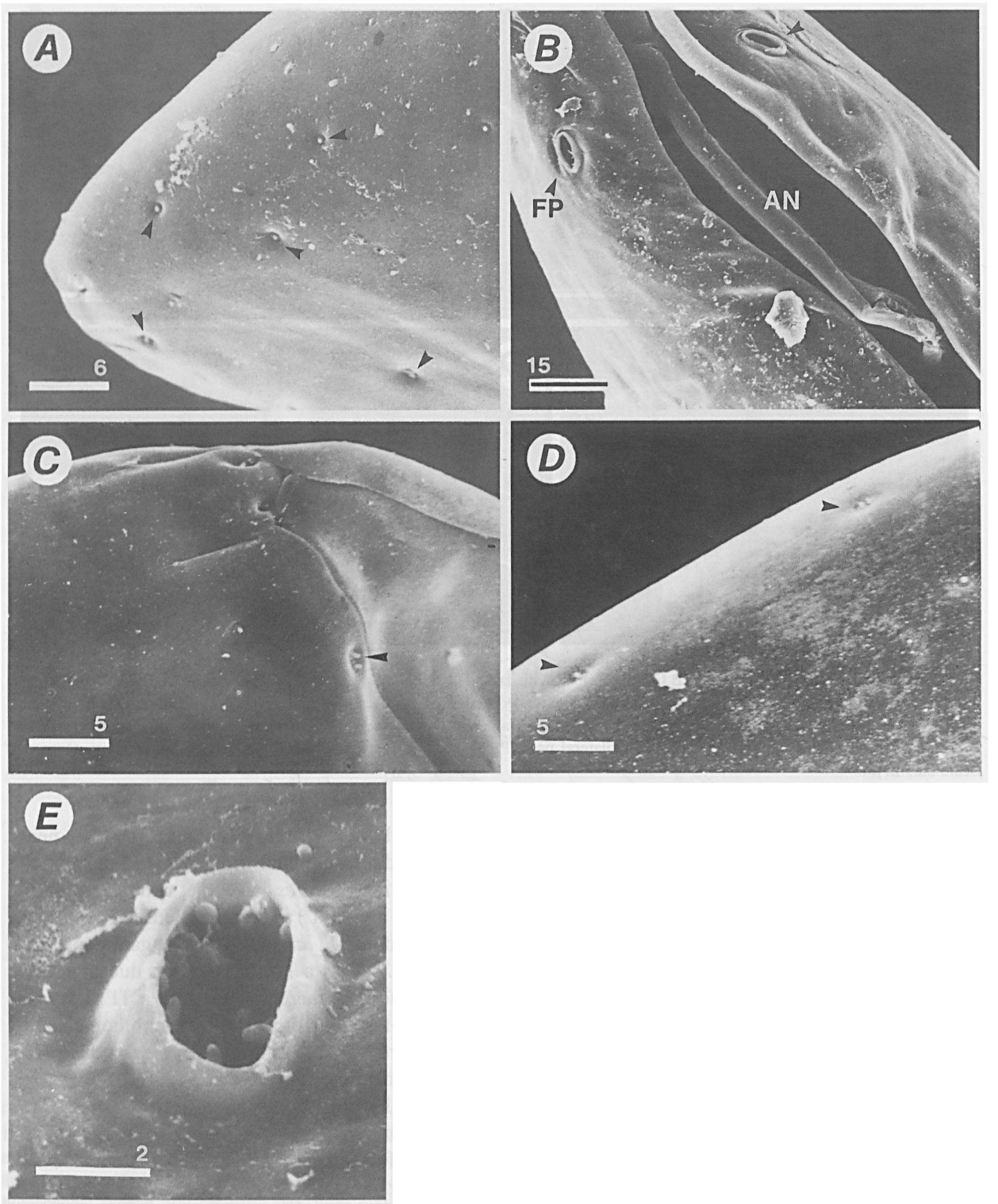

Fig. 3. Cyprids (A-B *Lithoglyptes mitis*, C-E *L. habei*). A, anterior end, oblique lateral view, setae arrowed; B, anterior end, ventral view showing entrance to mantle cavity with antennule (AN), front at upper left, C, anterior end, dorsal view of carapace, furrows and double seta (arrowed); D, dorsal margin of carapace, double setae arrowed; E, frontolateral pore (of frontolateral gland) with raised rim. AN antennule, FP frontolateral pore. Scale bars in μm.

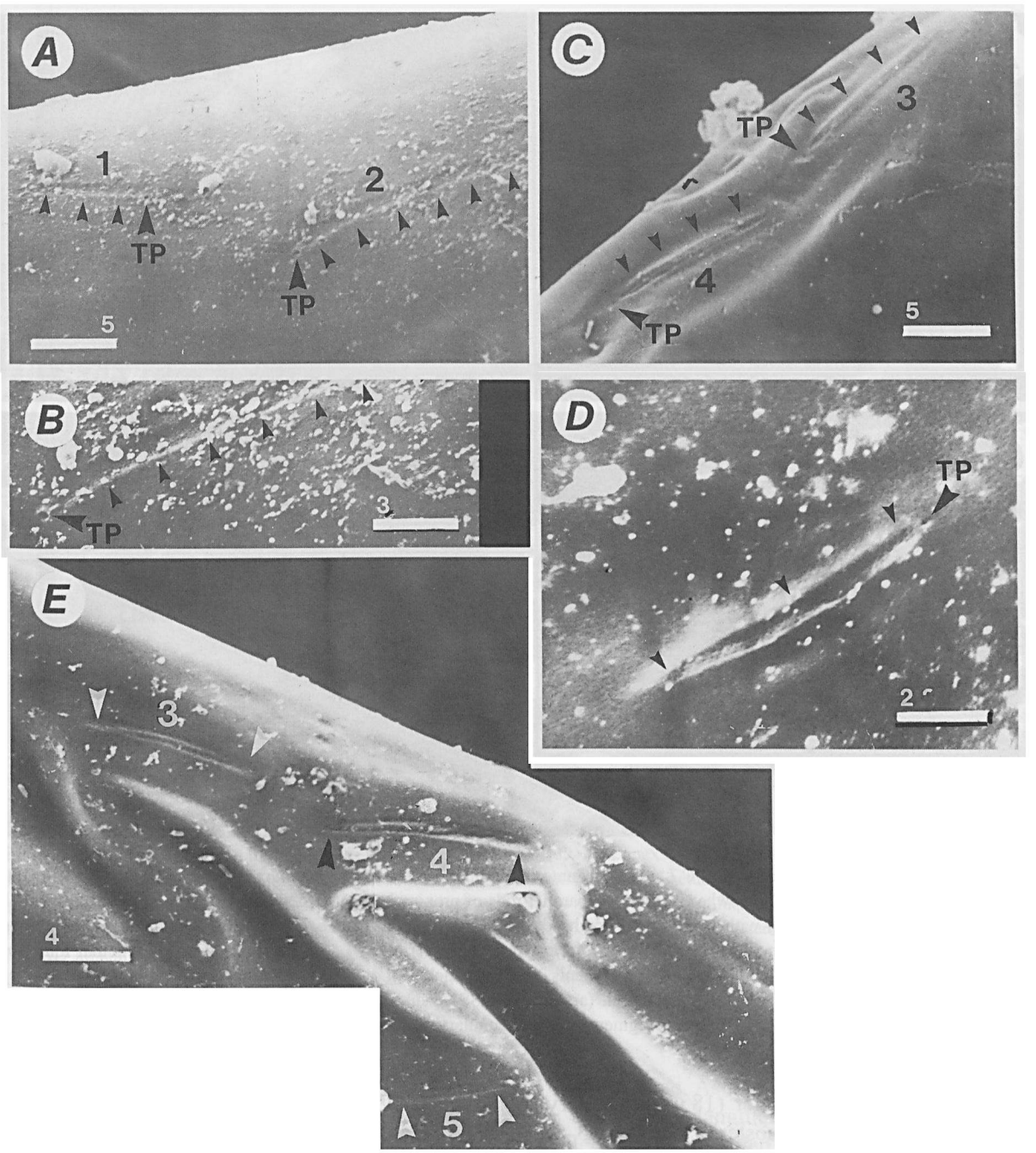

Fig. 4. Cyprid carapace, lattice organs numbered (A,B,D,E *Lithoglyptes mitis* cyprid; C *L. habei*). A, left side, lattice organs 1 and 2 (small arrowheads), anterior end is left, terminal pore (TP) posterior in lattice organ 1 but anterior in lattice organ 2; B, left side, lattice organ 2, terminal pore (TP) anteriorly sited, anterior end is left; C, posterior end, right side, lattice organs 3 and 4, both with posteriorly sited terminal pore (TP), anterior end is right; D, lattice organ 5, left side, posteriorly sited terminal pore (TP), anterior end is left; E, posterior end, showing relative position of lattice organs 3, 4 and 5, anterior end is left. Scale bars in μm.

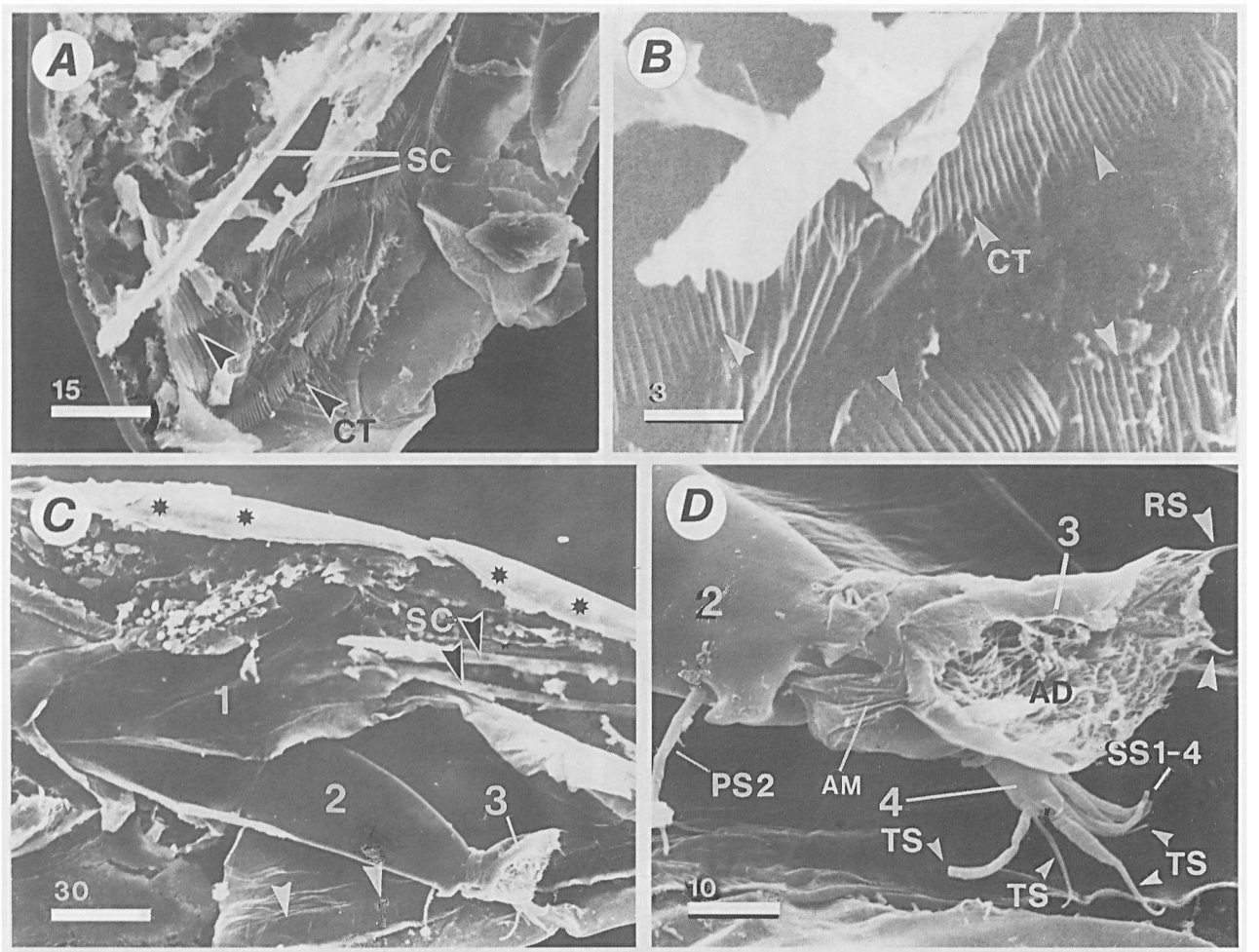

Fig. 5. Cyprids (A,B,D *Lithoglyptes habei*; C *L. mitis*). A, anterior end, left side of carapace removed to expose inner side of mantle with rows of cuticular ctenes (CT, arrowheads) and semiparallel rods of proximal sclerite (SC) of the first antennulary segment; B, detail of A, cuticle of mantle cavity with ctenes (CT, arrowheads); C, anterior end, right side of carapace and right antennule removed (breakage at *) exposing left antennule with anteriorly projecting proximal sclerite (SC), white arrowheads show cuticular fold close to ventral mantle margin; D, distal part of antennule (segments 2-4). AD attachment disc, AM arthrodial membrane (between segment 2 and 3), CT ctenes, PS2 postaxial seta 2, RS radial setae (arrowheads), SS1-4 subterminal setae (on segment 4), TS terminal setae (on segment 4), SC proximal sclerite of antennulary segment 1, 2-4 antennulary segments. Scale bars in μm.

and 7 μm long. LO2 is longer (18 μm) and very slightly curved. The three posterior pairs (LO3-5) are located ca. 300 μm behind the anterior pairs and are close (100 μm) to the posteriormost end of the cypris (Fig. 4E). LO3 and LO4 are separated by only 4 μm and lie approximately in line with LO1 and LO2 (4-5 μm from the dorsal midline). LO5 lie level with LO4 but are more distant (16-18 μm) from the midline (Fig. 4E). LO3 and LO4 are 8-10 μm long and straight or only slightly curved. LO5 is only 7 μm long.

Mantle and mantle cavity

The inner surface of the mantle has a longitudinal fold 18 μm distant from the ventralmost edge (Fig. 5C, white arrowheads). In the anterior mantle cavity the cuticle also has five longitudinal rows of cuticular ctenes running parallel to the ventral edge of the carapace. These rows are separated by about 11 μm and their 3-4 μm high ctenes consist of unfused fringes (Figs. 1C, 5A,B). We were not able to verify whether similar ctene rows occur in the

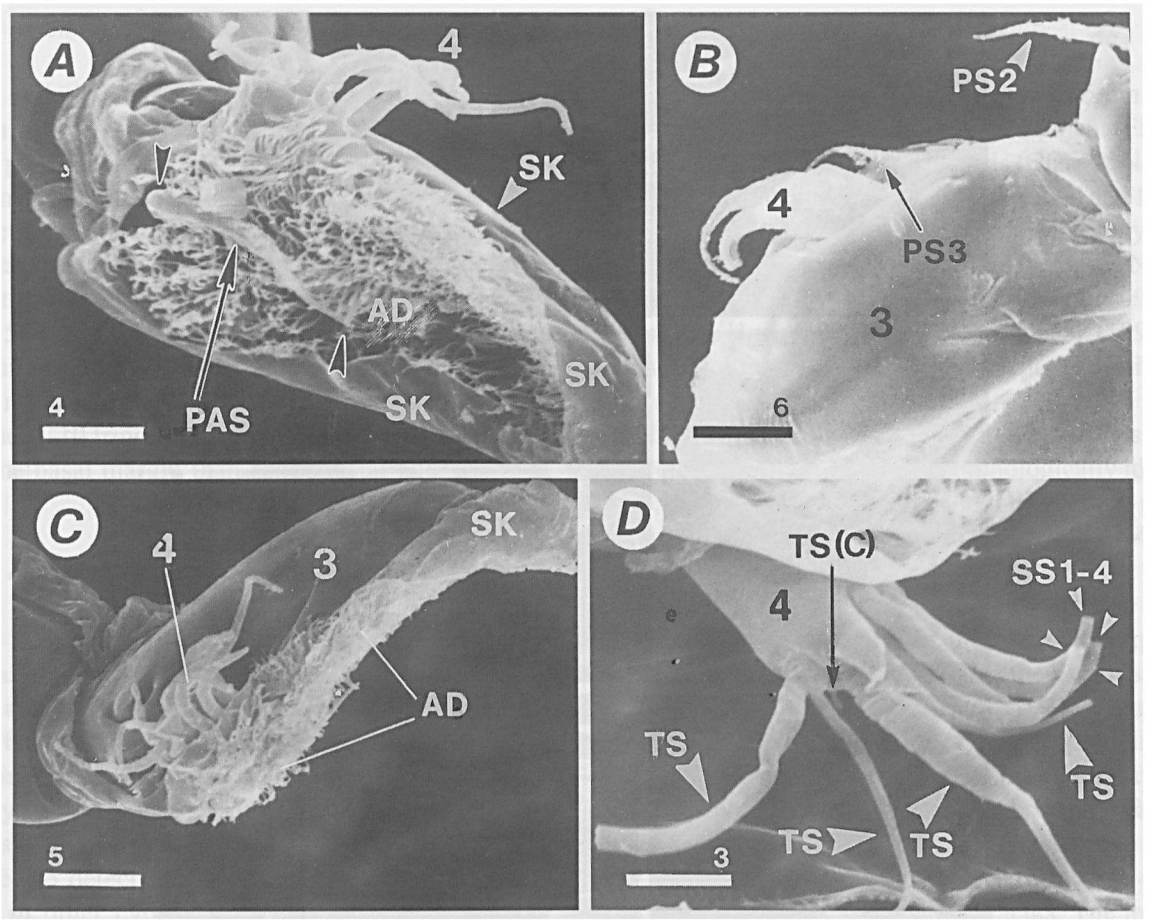

Fig. 6. Cyprid antennule (A,C *Lithoglyptes mitis*; B,D *L. habei*). A, attachment disc (AD) of segment 3 with dense carpet of cuticular villi and encircling skirt (SK), black arrowheads point to insertion (left) and apex (right) of postaxial sensillum (PAS); B, dorsal (preaxial) side of segment 3 showing insertion of segment 4 and diminutive postaxial seta 3 (PS3); C, segment 3, right lateral view of right antennule; D, distal end of segment 4, four subterminal setae (SS1-4), among five terminal setae (TS) only minute seta C named, other TS (see text) are clockwise: first long thin seta, seta with distended base and distal taper, second long, thin seta, thick cylindrical seta. AD attachment disc, (C) terminal seta C, PAS postaxial sensillum, PS2 postaxial seta 2, PS3 minute postaxial seta 3, SK cuticular skirt encircling attachment disc, SS1-4 subterminal setae (on segment 4), TS terminal setae (on segment 4), 3-4 antennulary segments. Scale bars in μm.

posterior part of the mantle cavity. (Terminology on ctenes and fringes adapted from Grygier (1987b) and Klepal & Nemeschkal (1995).)

1st antennulary segment

As in all other cirripede cyprids the antennules consist of four segments (Figs. 1B, 2D, 5C,D, 6). The first segment (Figs. 1C, 5C) is largest, about 80 μm long and 40 μm wide, flattened laterally and without setae. As in all cirripedes this segment has a conical or triangular shape and consists of two sclerites (see detailed description in Høeg, 1985 and Glenner, in press). The proximal sclerite forms the base of the cone and carries two anteriorly projecting rods (SC in Fig. 5C). The distal sclerite connects with the cylindrical second segment at the apex of the cone. The segment can be completely withdrawn inside the mantle cavity, but projects outside during exploratory walking and in attachment (Figs. 1C, 2C).

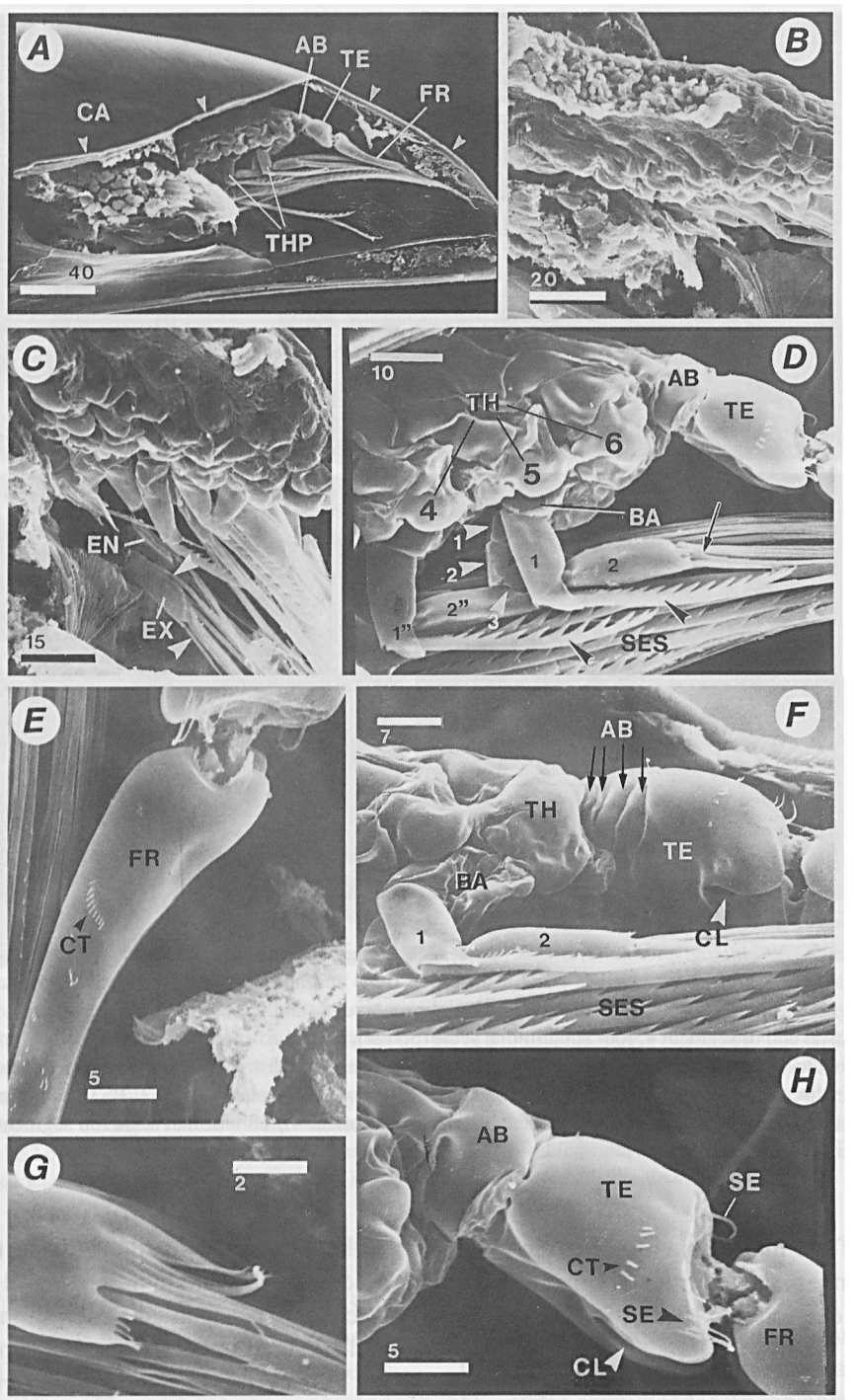

Fig. 7. Cyprid, posterior end (*L. habei*). A, posterior part of thorax and abdomen, part of left side carapace removed (arrowheads); B, thorax, dorsal view; C, thorax, dorsolateral view, terminal segments of exopod (EX) and endopod (EN) of left thoracopod 3, arrowheads indicate single basal seta and five terminal setae in exopod; D, detail of A, showing last three thoracic segments (TH 4-6) and thoracopods 5 and 6, thoracopod 6 may appear to originate from thoracic segment 5 (TH5) due to anteriorly directed basalmost limb part (BA), thoracopod 6 with three-segmented endopod (1-3, white arrowheads) and two-segmented exopod (1-2, black arrowheads), (1", 2" are exopod segments of thoracopod 5), exopod segments 1 with single long and serrated seta (SES arrowheads), arrow shows terminal natatory setae on exopod segment 2; E, proximal-middle part of furcal ramus, lateral view, distal end is down; F, posteriormost

→

2nd antennulary segment

The cylindrical second segment is ca. 75 µm long, with a straight ventral (postaxial) and curved dorsal (preaxial) margin (Fig. 5C). Its width decreases from 35-40 µm proximally to only 12-13 µm at the articulation to the third segment. A conspicuous postaxial seta 2, number 13 in the classification of Nott & Foster (1969), inserts ventrodistally (Figs. 1D, 5D) as in the groundpattern for cirripede cyprids (Glenner et al., 1989; Moyse et al., 1995). There are no other second segmental setae, but a small ctene (7-10 fringes) adorns its lateral surface closer to the basal margin than to the distal one.

3rd antennulary segment

The hoof-shaped third segment measures ca. 30 by 15 µm (Figs. 1D, 5D, 6A,C). All surfaces except the attachment disc lack setae. A well-developed skirt of thin cuticle (sensu Moyse et al., 1995) encircles the attachment disc, which is morphologically ventral (Figs. 5D, 6A,C) and is covered by a dense carpet of cuticular villi (Figs. 1D, 6A). We failed to detect an axial sense organ (sensillum), but in other cyprids it is often obscured by the cuticular villi (Moyse et al., 1995). A well-developed postaxial sensillum (PAS) inserts at the postaxial margin of the segment (Figs. 1D, 6A) between the skirt and the carpet of villi. Two setae situated at the distal, preaxial margin of the attachment disc (Figs. 1D, 5D) represent two of the radial sensilla of thoracican cyprids, but there could well be additional radial sensilla hidden in the carpet of villi. An indistinct structure inserts on the lateral surface near the base of the fourth segment (Fig. 6B). We interpret it as a rudimentary postaxial seta 3, which in thoracican and some rhizocephalan cyprids inserts at this place but is a very conspicuous sensillum (Nott & Foster, 1969; Moyse et al., 1995).

4th antennulary segment

The cylindrical fourth segment measures 5 µm by 4 µm and inserts laterally on the third segment (Figs. 5D, 6A-D). As in thoracican cyprids (Clare & Nott, 1994), the segment carries four subterminal and five terminal setae (Figs. 1E, 6D). Our terminology of these setae follows the scheme of Gibson & Nott (1971) and also used by Clare & Nott (1994), Glenner & Høeg (1995) and Walossek et al. (1996). All setae of the fourth segment, except the diminutive seta C, have an apical pore.

The four subterminal setae (setae 1-4) are situated close together. They are morphologically identical, approximately equal in length (9 µm), and resemble those in thoracican barnacles (SS1-4 in Fig. 6D).

The homologies of the five terminal setae are discussed below. They differ in regards to length, width, and morphology, but not to the extent seen in the Thoracica (Gibson & Nott, 1971; Clare & Nott, 1994; Glenner & Høeg, 1995). In particular, all terminal setae in *Lithoglyptes* are unsetulated, whereas in thoracicans two terminal setae (A & B) have long setules. In *Lithoglyptes*, two setae are 8-9 µm long, narrow, and of simple form. One seta (C) is vestigial, just as in the Thoracica. The longest seta (13 µm) has a distended basal half, but tapers rather abruptly at around 2/3rds of the way towards the tip; its surface shows a faint circular or spiral pattern that indicates a reinforcement structure in an otherwise very thin cuticle. Finally, one c. 9 µm long, cylindrical and isodiametrical seta has a width in between the two thin setae and the thick seta and terminates very abruptly.

Thorax and thoracopods

The ca. 120 µm long thorax forms the posterior third of the cypris body (Figs. 1A,B, 7). As in other cirripedes it consists of six segments each bearing a pair of biramous and natatory thoracopods. In

thorax (TH), abdomen (AB), and telson (TE), ventral view, furrows indicate four putative abdominal segments (arrows), telson with deep ventral cleft (CL); G, distal end of furcal ramus, lateral view; H, abdomen, telson and proximal part of left furcal ramus, left lateral view, single setae (SE) on dorsal margin and setae or fringes (arrowhead) on ventral margin of telson are duplicated on (unseen) right side. AB, abdomen (but see text), BA basis of thoracopod, CA carapace, CL cleft in telson, CT ctene, EN endopod, EX exopod, FR furcal ramus, SE, seta, SES serrated seta (on exopod segment 1), TE telson, TH thorax (segments numbered in D), 1-3(white) endopodal segments, 1-2(black) exopodal segments. Scale bars in µm.

rhizocephalan cypris larvae Walossek et al. (1996) found an unpaired medioventral process inserted between the sixth thoracic segment and the abdominal rudiment, and they speculated that it might be a rudimentary penis. The acrothoracican cypris has no such process (Fig. 7D,H).

We could not observe all details in each of the six individual pairs of thoracopods. Small differences, such as occur between the first and second pair in the Thoracica may therefore have gone undetected (Glenner & Høeg, 1995). The thoracopods in cyprids of *Lithoglyptes* resemble those described using light microscopy from cyprids of *Trypetesa nassaroides* (Turquier, 1967). The thoracopods consist of a protopod carrying a two-segmented exopod and a three-segmented endopod (Fig. 7C,D). In lateral view, pseudo-quadrangular sclerites (Fig. 7D) cover the insertion and the proximal part of the thoracopods, so we could not with certainty identify a coxa. The thoracopods bend strongly backwards in the joint between the first ramal segment and the basis before they insert on the thorax (Fig. 7D,F).

The first exopod segment carries a single, stout seta inserted laterodistally beneath a triangular projection and extending beyond the second segment (SES in Fig. 7D). It carries a basal row of small spines and a single row of 8-10 much larger spines on the surface facing the second segment. Extensive bending can occur between the first and second exopodal segments. The second segment bears five terminal simple setae and a single isolated simple seta inserted near the base (Figs. 1F, 7C,D).

The endopod is shorter than the exopod. The position of segments in preserved cyprids show that extensive bending can occur between segments two and three. We never saw any flexure between segments one and two in the fixed specimens and surmise that in the live larva little or no movement occurs between them at all (Fig. 7D). The setation of the endopod is difficult to observe due to obscuration by the exopods, but the second segment seems to carry one simple seta on the laterodistal margin, while the third segment (Figs. 1G, 7C) carries three simple, terminal setae. If correct, this setation corresponds exactly to that described by Turquier (1967) for the endopod of *Trypetesa nassaroides* cyprids.

Hindbody and furcal rami

The hindbody consists of a short, cylindrical (6 × 10 μm) abdomen, with four transverse furrows on the ventral side, that may indicate the presence of four segments, and a longer (18 × 13 μm) telson (Fig. 7A,D,F).

The lateral surface of the telson bears a row (ctene) of five elongate denticles (Fig. 7H). In addition there is a single, minute seta dorsodistally on each side of the telson and a small group of setae or fringes laterally on the ventrodistal margin (Fig. 7H). The ventral surface of the telson has a deep and distinct medial cleft (Fig. 7F).

The furcal rami in cyprids of *Lithoglyptes* have only a single 44 μm long segment (Fig. 7A,E,G). However, the partially cleaved telson can easily be mistaken as the basal segments of "two-segmented rami". The lateral surface of a caudal ramus bears a ctene of nine fringes and some sparsely spaced smaller fringes (Fig. 7E), while distally it terminates in two long setae (Fig. 1H). A comb of cuticular villi surrounds the furcal setae on the dorsal margin, but are almost vestigial along the ventral margin (Fig. 1H, 7G).

Discussion

This paper is the first SEM based description of all external features in acrothoracican cypris larvae. Jensen et al. (1994) and Moyse et al. (1995) have previously used SEM to describe individual organs in cyprids of *Weltneria spinosa* (lattice organs) and *Trypetesa lampas* (lattice organs, attachment organs). In addition, Turquier (1967) gave a good light microscopical account of cyprids of *T. nassaroides*.

The cyprids of *Lithoglyptes* agree in all important aspects with the scattered data available for the other acrothoracican species. We can confirm that acrothoracican cyprids show numerous similarities with cyprids of the remaining two cirripede orders while also in many respects resembling the cypris-like ascothoracid larvae of the Ascothoracida. We will first discuss the individual morphological features concerned before we summarize their phylogenetic significance.

Lattice organs

Lattice organs were first described by Elfimov (1986). They are chemoreceptors and known only from within the Thecostraca, where five pairs adorn the carapace of facetotectan cypris-y larvae and cirripede cypris larvae (Jensen, 1993; Jensen et al., 1994; Høeg et al., 1998; Hosfeld et al., 1998). Many ascothoracidans have fever lattice organs (Grygier, pers. comm.), but based on comparison with the fixed number in both the Facetotecta and the Cirripedia we consider such cases as apomorphic deviations from a thecostracan ground pattern with five pairs. Lattice organs (LO) vary between the thecostracan taxa both in their general morphology and in the position of the large terminal pore, which can be sited either anteriorly or posteriorly in the individual organ (Jensen et al., 1994).

Lithoglyptes habei, *L. mitis*, *Trypetesa lampas*, and *Weltneria spinosa* have lattice organs of near identical morphology ("keel in a trough" type) and in all of them the terminal pore is anterior in LO2 but posterior in LO1 and LO3-5. This stereotyped morphology of the lattice organs within the Acrothoracica makes them well suited for discussing large scale thecostracan phylogeny. The Acrothoracica have lattice organs of the "keel in a trough" morphology, but all the numerous thoracican and rhizocephalan species studied by Jensen et al. (1994) had lattice organs of the "pore field type", i.e., an oval or elongate area perforated by numerous small pores. This variation in lattice organ morphology found among the Cirripedia can be polarized by outgroup comparison with the Ascothoracida and the Facetotecta. Both outgroups have lattice organs of the keel "in a trough" type (Jensen et al., 1994; Hosfeld et al., 1998), which indicates that this morphology is plesiomorphic within the Thecostraca. The apomorphic "pore field" type shared by cypris larvae of the Rhizocephala and the Thoracica indicates that these two taxa are sister groups, a conclusion also supported by molecular data (Spears et al., 1994).

The variation in the position of the large terminal pore is more problematic. It is posterior in all five pairs (LO1-5) in the ascothoracidan *Ulophysema oeresundense*, whereas the Thoracica and Rhizocephala have an anteriorly sited pore in LO1 and LO2 but a posteriorly sited pore in LO3-5. Jensen et al. (1994) therefore suggested that the taxon Acrothoracica exhibits an intermediate character state in having an anteriorly sited pore in LO2 only. There is nothing in our data to question that conclusion. But Grygier & Ohtsuka (1995) found an anterior position of the terminal pore in LO1 and LO3 of *Synagoga millipalus* indicating that different ascothoracidan species vary with respect to the position of the terminal pore. We therefore need a third group to clarify the plesiomorphic position of the terminal pores within the Thecostraca. This highlights the importance of a detailed SEM investigation of the cypris-y larvae of the Facetotecta (Hosfeld et al., 1998).

Mantle cavity

Parallel longitudinal rows of cuticular ctenes line the inner lamellae of the carapace in both acrothoracican cyprids (present study), rhizocephalan cyprids (Walossek et al., 1996), thoracican cyprids (Høeg, unpublished) and ascothoracid larvae (Grygier, 1987b; Ito & Grygier, 1990). This indicates that such rows represent a ground pattern (apomorphic?) feature of the Thecostraca. We suggest that they function as combs for cleaning the antennules.

Antennules

Segments 1 and 2 have a morphology very similar to that seen in other cirripede cyprids. Segment 3 resembles the one Moyse et al. (1995) described from *Trypetesa lampas*, but with the differences noted below. In all cirripede cyprids, the radial setae are partially or wholly obscured by the microvilli carpeting the attachment disc, so an exact count requires TEM sections in a plane tangential to the disc. This has only been done in *Semibalanus balanoides*, where Nott & Foster (1969) found 8 radial setae. It is quite normal that two of the radial setae distally on the attachment disc are longer than the remaining ones (Moyse et al., 1995), as also seen here in *Lithoglyptes*, where they are the only ones visible at all. As in our study, Moyse et

al. (1995) failed to detect the axial sense organ in *Trypetesa lampas* using SEM only but revealed its presence with TEM. An axial sense organ could therefore also be present in our species.

In *T. lampas* Moyse et al. (1995) specifically mentioned the absence of a postaxial seta 3 (ps3), which in both the Thoracica and Rhizocephala is a conspicuous structure that inserts near the base of the 4th segment. In *Lithoglyptes* cyprids the rudimentary knob found adjacent to the insertion of segment 4 could represent a highly reduced ps3. If so, this indicates that the absence or extreme reduction of ps3 is an apomorphy for the Acrothoracica.

Antennulary segment 4

This segment has the same number and position of setae as in thoracican cyprids. The homology of the four subterminal setae with the similarly shaped and positioned ones in thoracican cyprids is straightforward. There is also little doubt that the five terminal setae correspond to the five terminal ones in the Thoracica. One terminal seta (C) is very short in both the Thoracica and Acrothoracica and clearly homologous in both groups. The remaining four much longer terminal setae differ in morphology between the two orders, so we hesitate to suggest any seta-by-seta homologies. The seta in *Lithoglyptes* with a distended basal part and tapered apex could well correspond to seta D in thoracicans (and rhizocephalans). In both acrothoracicans and thoracicans this seta exhibits a distinct pattern on its surface and Clare & Nott (1994) suggested that it is an aesthetasc.

Apomorphies in antennulary morphology

The unique structure and morphology of the cypris antennule involve several putative apomorphies which agrees with the claim that the Acrothoracica, Thoracica and Rhizocephala form a monophyletic taxon Cirripedia. In all three orders, the antennule consists of four segments with surprisingly similar shape and function. This probably reflects functional constraints posed on the antennule that functions both in exploratory walking prior to settlement and in permanent cementation. Important apomorphies are: a triangular or cone-shaped first segment consisting of two sclerites set at an angle to each other (see Høeg, 1985; Glenner, in press); a long, cylindrical second segment; a small third segment with the attachment organ and a cylindrical fourth segment bearing, in the ground pattern, 4+5 sensory setae. It is the third and fourth segments that vary most extensively among cirripedes. This is hardly surprising, since these two segments are in direct contact with the many different types of substrata used in settlement by cyprids of the different species. In acrothoracican cyprids, the most pronounced difference on the 3rd segment is the absence or at least extreme reduction of postaxial seta 3 (ps3). In thoracican cyprids, this seta is a long and conspicuous simple seta, while in rhizocephalan male cyprids it has the form of a long aesthetasc (Walker, 1985; Moyse et al., 1995). Otherwise, the third segment of acrothoracican cyprids has a fairly conventional morphology.

The fourth segment carries four subterminal and five terminal setae in both the Acrothoracica and the Thoracica (Clare & Nott, 1994), and this represents the cirriped ground pattern. Only the Rhizocephala have fewer setae on this segment, and this is probably an apomorphic condition (Høeg & Rybakov, 1996). However, the Acrothoracica do deviate in lacking setulation on any of the terminal setae, whereas the Thoracica have two setulose setae. Grygier (1987a) made a pioneering attempt in homologizing segments and setae in antennules of ascothoracids, facetotectan cypris-y, and cirripede cyprids. Further conclusions must await SEM studies of facetotectan antennules.

Thoracopods

Few studies have focused on the cypris thoracopods, despite their importance in the rapid swimming bouts during the pelagic phase of the larva. Cyprids of *Lithoglyptes* and *Trypetesa* have a three-segmented endopod and a two-segmented exopod just as in the ground pattern for ascothoracid larvae (Turquier, 1967, present paper). As discussed in detail by Grygier (1987b) and commented on by Glenner &

Høeg (1995), this signifies that such a segmentation scheme characterized not only the cypris-like larva of the urthecostracan but also the true cypris of the urcirripede. Our observation on *Lithoglyptes* also confirms Grygier's (1987b) character matrix in that the fusion in cirripedes occurred between endopodal segments 1 and 2. The Facetotecta have a three-segmented endopod in the ground pattern, but Schram (1970) and Grygier (1987b) found that some facetotectans have evolved a two-segmented state by fusion between endopodal segments 2 and 3. Obviously, the two-segmented endopods found in some cirripeds and facetotectans do not represent homologous states and again demonstrates how simple counting of limb articles can lead to erroneous conclusions as elegantly elaborated in Huys & Boxshall (1991).

The apparent lack of flexure between endopod segments one and two in *Lithoglyptes* cyprids indicates that it was these two segments that fused into one in the evolution of the Thoracica (and Rhizocephala?). In the Thoracica, a faint suture in the first segment of the endopod recalls the plesiomorphic three-segmented condition (Glenner et al., 1995).

All cirripede cyprids carry a single stout and serrated seta on the first exopod segment of all eight thoracopods (Glenner & Høeg, 1995; Walossek et al., 1996 Fig. 14B). These setae are always shorter than the natatory ones on the second segment, and they undoubtedly serve in grooming both the natatory setae and the limb bases. However, they are rarely if ever as large and strongly armed as in the acrothoracican cyprids studied here. Nothing comparable to these grooming setae exists in ascothoracid or cypris-y larvae, so they represent another of the many apomorphies characterizing the cirripede cyprid.

The single seta inserting on the 2nd endopod segment is also present in ascothoracid larvae, cypris-y, and in thoracican cypris larvae. But aside from this, it is premature to speculate on the ground pattern of thoracopodal natatory setae in the Thecostraca.

Tagmosis and hindbody

According to Grygier (1983, 1987a) and Grygier & Ohtsuka (1995) both the Thecostraca and the Maxillopoda in general have a 5-7-4 tagmosis scheme in the ground pattern. In cyprids of *Lithoglyptes* the presence of four, short abdominal segments and an elongate telson with unsegmented furcal rami dovetails with this pattern. The apparently 4-segmented abdomen is plesiomorphic compared to all other cirripedes (larval or adult). We found no trace of a 7th thoracomere, which in the thecostracan ground plan carries the penis, unless it forms part of the annulated region we here designate as abdomen. Unpublished SEM micrographs reveal that cyprids of some lepadomorphan Thoracica can have a three-segmented abdomen.

A more or less deeply cleaved telson bearing unsegmented caudal rami constitutes a ground pattern feature in cirripede cypris larvae. It occurs in the Acrothoracica (this study), the Rhizocephala (Walossek et al., 1996) and apparently also in cyprids of lepadid Thoracica (Grygier, 1987b). In contrast, Walker & Lee (1976) and Glenner & Høeg (1995) used SEM to claim that balanomorphan cyprids (*Balanus amphitrite*, *Semibalanus balanoides*) have two-segmented "caudal rami" inserted directly on the posteriormost end of the thorax and no visible abdomen or telson. We believe that also balanomorph cyprids have unsegmented rami inserted on a telson, but that the cleft has become so deep that the telson can easily be mistaken for "basal ramal segments". A similar error probably lead Turquier (1967) to describe two-segmented "furcal rami" in cyprids of the acrothoracican *Trypetesa nassaroides*. Support for our claim could come from serial sections revealing that the purported "first ramal segments" are united by a slim medial connection. The urthecostracan undoubtedly had unsegmented caudal rami, since we find this condition in both the Ascothoracida, the Facetotecta, and the outgroup Copepoda (Grygier, 1987b). Obviously, SEM and TEM studies of the hindbody in additional thoracican cyprids may provide characters useful for a phylogenetic analysis.

Conclusion

The data from SEM analysis presented here again highlight the value of larval characters in elucidating thecostracan and cirripede phylogeny (Grygier 1987a & b, 1994, 1995; Jensen et al., 1994; Elfimov, 1995; Moyse et al., 1995; Høeg et al., 1998). The cypris larvae of the Acrothoracica exhibit similarities both with the Ascothoracida and the Facetotecta, and with the two remaining cirripede orders. Although we await a full-fledged phylogenetic analysis, as in Glenner et al. (1995), we will here assume that the similarities with ascothoracid larvae and facetotectan cypris-y represent symplesiomorphies. They include: the "keel in a trough" shape of the lattice organ; three-segmented thoracopodal endopods; a five-segmented hindbody.

These plesiomorphies do not alter the fact that the Acrothoracica have a typical cirripede cypris with its numerous apomorphies compared to the thecostracan ground pattern, such as: a single pair of frontal (horn) gland pores on the carapace; very similar four-segmented antennules with a homologous attachment organ on the third segment and a 4+5 setation scheme on the fourth segment; paired cement glands terminating on the attachment organ; thoracopods with a stout, serrated seta on the first exopodal segment; abdomen highly shortened.

The status of some other characters remains more uncertain or insufficiently analysed: the position of the terminal pore in lattice organs; the presence of a penis rudiment; and the number and special morphology of thoracic natatory setae.

We have in this paper proposed some phylogenetic scenarios based on single characters sets, but we stress that they are meant at this point more as mental exercises than solidly built theories. Yet with studies such as the present one and those of Grygier (1994), Jensen et al. (1994), Moyse et al. (1995), Korn (1995), Elfimov (1995), and Walossek et al. (1996) we are approaching the point where we can enlarge the thecostracan character matrix of Grygier (1987b) and Glenner et al. (1995) with a wealth of new characters from larval morphology.

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