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Cypris larvae of acrothoracican barnacles (Thecostraca: Cirripedia: Acrothoracica)

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Abstract

We used SEM to investigate the morphology of the cypris larvae from a range of species of the Cirripedia Acrothoracica, representing all three families and including the first detailed account of cyprids in the highly specialized Cryptophialidae. Special attention was given to the head shield (carapace), the lattice organs, the antennules, the thoracopods, the telson and the furcal rami. The cypris larvae of the Acrothoracica fall into two morphological groups; those of the Trypetesidae and Lithoglyptidae have a well-developed carapace (head shield) that can completely enclose the body and sports fronto-lateral pores, numerous short setae and lattice organs perforated by numerous small, rounded pores and a single, conspicuous terminal pore. The fourth antennular segment has the setae arranged in subterminal and terminal groups. There is a developed thorax with natatory thoracopods and a distinct abdomen and telson. In comparison, the cyprids of the Cryptophialidae exhibit apomorphies in the morphology of the carapace, the antennules and the thorax, mostly in the form of simplifications and reductions. They have a much smaller head shield, leaving parts of the body directly exposed. The shield is conspicuously ornamented by deep pits and hexagonally arranged ridges and bears a few, very long setae but lacks fronto-lateral pores. The lattice organs have numerous elongated pores, but no large, terminal pore. The fourth antennular segment has all the setae clustered in one terminal group. The thorax and thoracopods are rudimentary and not suitable for swimming. These reductions and simplifications in morphology correlate with cryptophialid cyprids being unable to swim. They can only disperse by antennular walking resulting in small, but highly gregarious populations of adults. The variations in antennular morphology and telson structure were traced for the genera of the families Lithoglyptidae and Trypetesidae. The traditional non-cladistic taxonomy in the suborders Pygophora (Cryptophialidae + Lithoglyptidae) and Apygophora (Trypetesidae) was based largely on symplesiomorphies in adult morphology and cannot be upheld. The Lithoglyptidae and Trypetesidae may form a monophylum, but evidence remains scarce. We expect that the use of

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larval (cyprid) characters will in the future play an important part in more detailed phylogenetic analyses of the Acrothoracica and also shed new light on their reproductive ecology.

Keywords: Cirripedia; Acrothoracica; Cypris larva; Scanning electron microscopy; Larval dispersal; Morphology; Phylogeny; Reproductive ecology

1. Introduction

All species of the crustacean class Thecostraca have more or less sessile adults, which are highly specialized either as parasites or as thoracopodal suspension feeders. The evolution into sessility has caused such changes to the thecostracan adults that their morphology cannot be used for reconstructing large-scale phylogeny. The adults of the subclass Facetotecta are completely unknown although suspected to be parasitic (Høeg and Kolbasov 2002). The subclass Ascothoracida and the cirripede order Rhizocephala are both composed of parasites, the latter specialized to the extent that the adults have lost virtually all morphological features of arthropods (Wagin 1976; Grygier 1983; Høeg and Kolbasov 2002; Grygier and Høeg 2005; Høeg, 1992a). The remaining cirripedes are suspension-feeders and either covered by calcareous plates (Thoracica) or lack such plates (Acrothoracica) and live as borers in calcareous substrata (Tomlinson 1969; Kolbasov et al. 1999).

Due to the differences in adult biology and morphology, larval development becomes the unifying theme for the Crustacea Thecostraca. In the ground pattern development comprises a number of naupliar instars and the terminal cypridiform instar, which is specialized to carry out settlement (Høeg and Møller 2006). Høeg et al. (2003) reviewed the morphology and homology of the cypridiform larvae of all Thecostraca. In their view, the name cyprid should be reserved for the very specialized type of instar found in the Cirripedia (Acrothoracica, Rhizocephala, Thoracica), while the homologous instars in other Thecostraca should be called ''y-cyprid'' (Facetotecta) and ''a-cyprid'' (Ascothoracida).

In the Cirripedia what appears to be structurally very similar cyprids can settle on very different types of substrata and metamorphose into highly diverse adult forms (Høeg and Møller 2006). Recent ultrastructural studies have revealed that cyprids, despite their superficial similarity, exhibit interesting variations, and these characters are becoming increasingly important components in morphology-based matrices for phylogenetic analysis of the Thecostraca. In addition, many Rhizocephala and most Acrothoracica hatch as cyprids, which greatly impedes the use of naupliar characters for phylogenetic analysis at this level.

Acrothoracicans deviate considerably from other barnacles in both morphology and ecology, and they have featured prominently in phylogenetic speculations concerning both the Cirripedia and the Thecostraca in general (Newman 1971, 1974, 1987; Turquier 1972; Glenner et al. 1995). The initial application of molecular data to the Thecostraca indicated a close relationship between the Acrothoracica and Ascothoracida (Spears et al. 1994), which challenged the basic monophyly of the Cirripedia. More recent molecular investigations and data from cypris morphology supported the monophyly of the Cirripedia (Pérez-Losada et al. 2002; Høeg and Kolbasov 2002), but with the Acrothoracica in a basal position, again highlighting their importance in analyzing the phylogeny of all Thecostraca. In addition, the reproductive biology of the Acrothoracica is interesting, because they have separate sexes as in the Rhizocephala, while most species of the Thoracica are hermaphroditic.

Detailed knowledge of the microanatomy of the acrothoracican cypris larvae is important in discussions about both phylogeny and ecology, but unfortunately most previous accounts lack details, because they have used light microscopy only (Berndt 1907; Kühnert 1934; Batham and Tomlinson 1965; Wells and Tomlinson, 1966; Tomlinson 1969; Turquier 1967, 1970, 1971, 1985a, b). The general morphology of acrothoracican cyprids has only been examined with SEM in two species of *Armatoglyptes*, two species of *Trypetesa* and, in part, one species of *Kochlorine* (Kolbasov et al. 1999; Kolbasov and Høeg 2001; Kolbasov 2002), which is in contrast to the considerable number of recent studies that have used SEM to describe thoracican and rhizocephalan cyprids (e.g., Glenner et al. 1989; Walker 1992; Jensen et al. 1994a; Elfimov 1995; Moyse et al. 1995; Høeg et al. 2003).

We therefore decided to use SEM to examine the cypris larvae in a range of species representing all acrothoracican families and the majority of the genera.

2. Materials and methods

Our systematics follows Tomlinson (1969) as revised by Kolbasov and Newman (2005). Only few species of the Acrothoracica possess free-swimming nauplii, viz., *Lithoglyptes indicus* Aurivillius, *Bendtia purpurea* Utinomi,

Trypetesa lampas (Hancock) and *Trypetesa nassarioides* Turquier. Most acrothoracicans have brooded nauplii, where this phase is passed within the egg coat and only the cyprids are released (Batham and Tomlinson 1965; Tomlinson 1969; Turquier 1985a; Kolbasov et al. 1999). For these species, the cypris stage can often be sampled directly from preserved specimens in museum collections.

The main part of the material was found during examination of the collections of mollusc shells and corals stored in the Zoological Institute Russian Academy of Sciences (RAS), St.-Petersburg and the Zoological Museum of Moscow State University. We also investigated the acrothoracicans deposited by J.T. Tomlinson in the Zoological Institute RAS. The cypris larvae of *Trypetesa lampas* were reared at the Kristineberg Marine Research Station. In other cases we sampled cypris larvae from the mantle cavity of the acrothoracican females (Fig. 3A). We also studied larvae, which had settled on females as prospective dwarf males and still retained the cypris morphology. The material studied came from the following locations:

Family Lithoglyptidae: *Weltneria spinosa* Berndt, 1907. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. South Africa, False Bay, one female with 21 cypris larvae inside the mantle cavity (Fig. 3A), from gastropod *Turbo sarmaticus*.

Weltneria reticulata Tomlinson, 1969. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. South-China Sea, Philippines, Palavan I., several exuviae of cypris larvae, on the coral *Acropora digitifera*.

Armatoglyptes habei (Tomlinson), 1963. Aden Gulf, 13°59′5″N, 48°24′7″E, depth 3 m, coral-reef, one specimen of female with one cyprid inside, in *Turbo argirostomum*; Seychelles, Silhouette I., 4°36′S, 56°48′E, subtidal zone, six specimens of females and one free-swimming cyprid in *Mancinella mancinella*; South-China Sea, Vietnam, 12°N, 109°E; depth 1.5 m, three female specimens (one female with a cyprid inside) in *Mancinella mancinella*; depth 2 m, two specimens of females and one free-swimming cyprid in *Coralliophilla deformis*; 2–4 m, five female specimens (one female with a cyprid inside) in *Drupa morum*.

Armatoglyptes mitis Tomlinson, 1969. Maldives; Feartu I., 3°48′N, 73°05′E, tidal zone, coral-reef, eight female specimens (one female with a cyprid inside); Genego I., 3°49′N, 73°06′E, tidal and subtidal zones, coral-reef, two female specimens and one cyprid with stretched antennules in *Trochus pyramis*, 17 female specimens (two females with a cypris inside) in *Mancinella alauina*, eight female vodka-preserved specimens (one female with a cyprid inside) in *Latirolagena smaragdula*, three female specimens (one female with a cyprid inside) in *Morula cavernosa*, two female specimens (one female with a cyprid inside) in *Hipponix* sp.

Kochlorine grebelnii Kolbasov, 2002. Islands Cape Verde, Santiago I., Orotawa (app. 15°N, 23°6′W), just settled cypris larva from coral *Prionastrea* sp.

Family Trypetesidae: *Trypetesa lampas* Hancock, 1949. The Kristineberg Marine Research Station (Sweden), 59°15.79′N, 11°27.79′E, 5–10 m, more than 10 reared cypris larvae from buccinid gastropod shells, occupied by hermit-crab *Pagurus bernhardus*.

Trypetesa lateralis Tomlinson, 1953. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. California, Monterey Bay, Monterey County, Point Pinos, tidal zone, a female with just settled cypris larvae of dwarf male, in gastropod shell of *Tegula* sp., occupied by hermit-crabs.

Family Cryptophialidae: *Australophialus melampygos* (Berndt), 1907. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. New Zealand, North I., Auckland two females with approximately 10 cypris larvae inside, and about 15 cyprids in sample (free), in lamellibranch *Perna canaliculus*.

Australophialus turbonis (Barnard), 1925. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. South Africa, False Bay, a female with three cypris larvae inside, in gastropod *Turbo sarmaticus*.

Cryptophialus gantsevichi Kolbasov, 2004. South-China Sea, Vietnam, Suandai Bay, 3–4 m, a female with five cypris larvae and about five free larvae in sample, in fragments of gastropod shells, occupied by hermit-crabs.

Cryptophialus heterodontus Tomlinson, 1969. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS in Awamori. Micronesia, Bikini Atoll, Namu I., four free cypris larvae, on gastropod *Turbo setosus*.

Cryptophialus hoegi Kolbasov, 2000. Aden Gulf, Sikha I., app. 12°11′N, 44°16′E, subtidal zone, two free cypris larvae, and a female with three cypris larvae inside, in gastropod *Purpura persica*.

Cryptophialus wainwrighti Tomlinson, 1969. Material was deposited by Dr. J.T. Tomlinson to the collection of the Zoological Institute RAS. Mexico, Sonora, Soldado Bay, Guayamas, a female with just settled cypris larvae of dwarf males, in gastropod *Thais triseriallis*.

Regardless of initial fixation/preservation (generally unknown), cyprids were postfixed in 2% OsO_4 for 2 h, dehydrated in acetone and critically point dried from CO_2. Dried specimens were sputter-coated with platinum-gold or gold and examined in a HITACHI S405A scanning electron microscope operated at 15 kV at the University of Moscow. Resulting photographs were touched up using CorelDraw X3 Graphics Suite. Several specimens caused severe difficulty in SEM photography owing to their state of preservation, but are included because they do yield important information. Some line drawings and SEM micrographs have been reused in edited form from

Kolbasov et al. (1999); Kolbasov and Høeg (2001) and Kolbasov (2002).

3. Results

3.1. General morphology of the Cyprids

Cypris larvae of the Acrothoracica differ both in their general shape and in the detailed morphology of the locomotory and sensory organs.

3.1.1. Lithoglyptidae and Trypetesidae

In these families the cypris head shield (carapace) covers the body completely and has a spindle or elongated oval shape with an anterior rounded end and a narrower, truncated posterior end (Figs. 1A,B and 3B,C,E). The cypris body is strongly compressed laterally, being about 450–700 μm long (Fig. 2). The dorsal margin is only slightly curved in cyprids of *Armatoglyptes* and *Kochlorine* (Figs. 1A,B and 3C,D), but distinctly curved in those of *Weltneria* and *Trypetesa lateralis* (Fig. 3B and E). This difference is reflected in the length/height ratio of the head shield which is 3/1 for *Armatoglyptes* and 4/1 for *Kochlorine*, but only ca. 2.5/1 for the more rounded cyprids of *Weltneria* and *T. lateralis*. *T. lampas* cyprids have a more elongated carapace (L/H 3:1) (Kolbasov et al., 1999; Kolbasov and Høeg 2001). The shield valves are completely fused along the entire dorsal margin without any conspicuous posterior slit. The ventral margin of the head shield is practically straight. In some specimens the antennules and the thoracopods were partially extended outside the mantle cavity (Figs. 1B and 3C). Occasionally we found specimens where the thin cuticle of the mantle cavity has been everted, so both antennules and the thorax are fully exposed. This situation is probably not natural but rather an artefact of preservation (Fig. 3D).

3.1.2. Cryptophialidae

The cyprids differ in several important respects from those of the Lithoglyptidae and Trypetesidae (Figs. 1C–H and 3F–I). The reduction of the thorax described below results in a small body, only 300–400 μm long, dorso-ventrally compressed (Fig. 3F). Dorsally, the body is widest close to the rounded posterior end and narrows gradually towards the blunt anterior end (Figs. 1C and 3H). Cyprids of *Australophialus* (Figs. 1C and 3H) are wider (ca. 200 μm wide, 400 μm long) than those of *Cryptophialus* (Fig. 1H) and look very plump in dorsal aspect. The shield encloses only the dorsal half of the body, while the thin mantle cuticle covering the ventral part of the body is freely exposed (Fig. 3F and I). In addition, there is a distinct slit at the posterior end of the dorsal margin of the head shield (Figs. 1C,D, 3H, and 4F). The shape of the head shield means that the antennules cannot be fully retracted into the mantle cavity but must always remain extended at the anterior end. Posteriorly, the ventral margins of the mantle are closely apposed with only the thoracopodal rudiments and the furcal rami extending freely (Figs. 1C,F and 3F,I).

3.1.3. Internal structures

We did not perform sections, but some internal organs were clearly visible with the light microscope. The big, loboform cement glands, have a brown color (in alcohol) and lie at the base of the first antennular segments. The paired compound eyes, associated with frontal filaments, are situated in front of the cement glands (Fig. 1A and C). The unpaired nauplius eye lies near the dorsal margin, one-third of the body length from the anterior end (Fig. 1A). The extrinsic muscles of the antennules and the thorax (Fig. 1A) and the adductor muscle (Fig. 1C) lie in the anterior and middle parts of the cypris body and attach to the dorso-medial and lateral sides of the head shield. The undifferentiated oral (buccal) cone and the thorax (rudimentary in the Cryptophialidae) lie within the posterior part of the larval body (Figs. 1A,B,E and 9). The postcephalic region is described below.

3.2. Head shield (carapace) structures

In the Lithoglyptidae and Trypetesidae the head shield has a rather smooth surface even at high magnifications (Fig. 4A–D). The ornamentation consists merely of a system of furrows at the anterior end (Fig. 4A and B), a few minute pits or pores 0.5–0.6 μm in diameter (Fig. 4A) and very small setae sparsely distributed over the entireshield. The ca. 0.7 μm long setae are located single or paired in shallow, 1 μm wide depressions (Fig. 4A–C). Single setae predominate on the anterior and lateral surfaces, whereas the pairs lie in a longitudinal row extending from the anterior end along the dorsal midline of the head shield (Fig. 4C). In the Cryptophialidae the shield is prominently ornamented by cellular ridges and furrows in a hexagonal pattern or pockmarked with conspicuous, 1–2 μm wide pits or pores on the entire surface (Figs. 1D and 4E,F). In addition the shield often carries very long (20–100 μm), simple setae (Figs. 1E–H and 4E).

3.3. Fronto-lateral pores

Cyprids of the Lithoglyptidae and Trypetesidae have a pair of fronto-lateral pores situated near the anterioventral margin, about 80–100 μm from the anterior end (Figs. 3B,D and 4D). They are oval or rounded and 4–5 μm in diameter in *Armatoglyptes*, *Kochlorine* and *Trypetesa* (Fig. 4H–J) but reaching 25 μm in diameter in

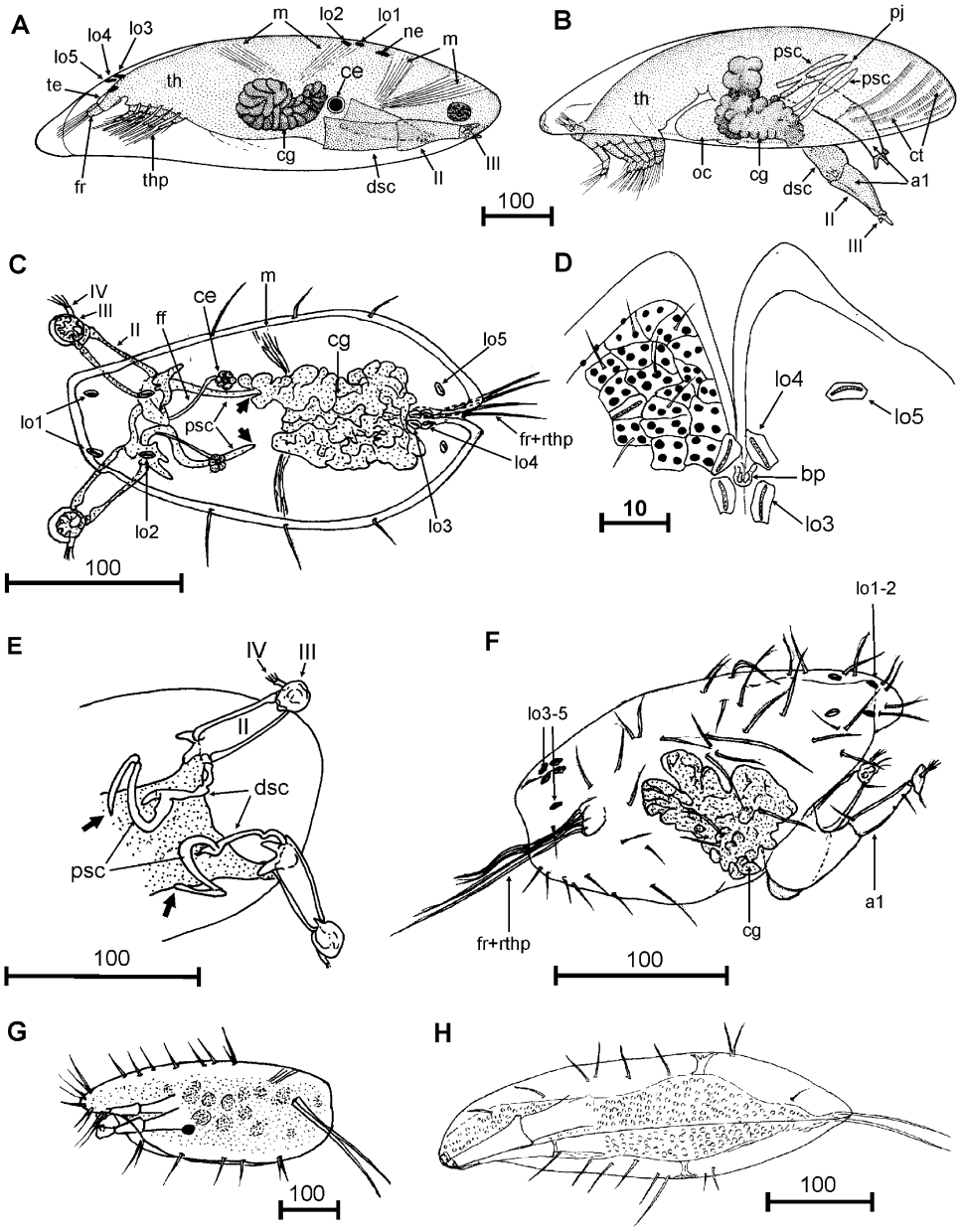

Fig. 1. Cypris larvae of Acrothoracica. General morphology: (A, B) *Armatoglyptes habei* lateral views; (C–E) *Australophialus melampygos*, dorsal view (C), posterior end in dorsal view (D), anterior end in ventral view (E); (F) *Cryptophialus heterodontus* dorso-lateral view; (G) *C. gantsevichi*, lateral view; (H) *C. hoegi,* ventral view. In (B) the proximal sclerites (psc) of the first antennular segments articulate in a pendulary point (pj) with their counterpart in the other antennule; in C and E they end freely (thick arrows) without articulating. I–IV = antennular segments 1–4; a1 = antennules; ce = compound eye; cg = cement gland; ct = rows of ctenes inside mantle cavity; dsc = distal sclerite of first antennular segment; ff = frontal filaments; fr = furcal rami; fr + rthp = furcal rami and rudiments of thoracopods; lcp = large central pore; lo1-5 = lattice organs; m = muscles; ne = nauplius eye; oc = oral cone; pj = pendulary joint; psc = proximal sclerite of first antennular segment; te = telson; th = thorax; thp = thoracopods. Scale bars in μm.

Weltneria (Fig. 4G). A simple, 1.3 μm high cuticular ridge surrounds the pores. In the Cryptophialidae we could not with certainty identify any fronto-lateral pores. In *Australophialus turbonis* we found a structure resembling such pores (Fig. 4K), but it lies on the exposed mantle cuticle rather than on the head shield proper.

3.4. Lattice organs

All acrothoracican cyprids possess five pairs of lattice organs (LO) on the dorsal surface of the head shield. They are arranged as two anterior (LO1–2) and three posterior (LO3–5) pairs (Figs. 1A, C and F). The posterior-most pair (LO5) is situated more laterally than

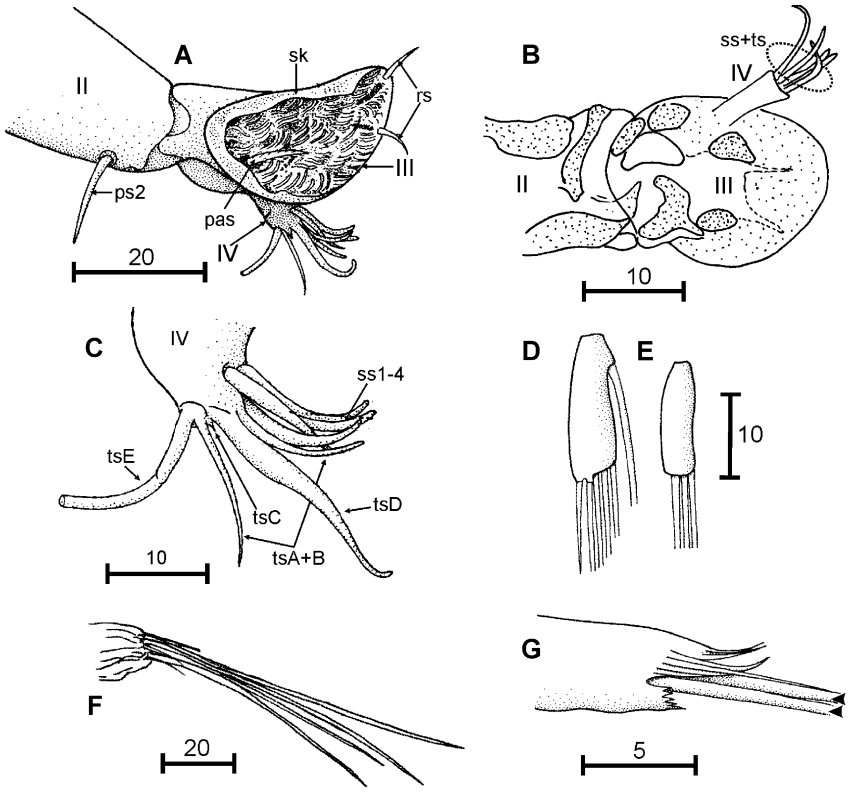

Fig. 2. Cypris larvae of Acrothoracica. Appendage structure: (A) *Armatoglyptes habei*, terminal part of antennule; (B) Cryptophialidae, terminal part of antennule; (C) *Armatoglyptes habei*, setation on fourth antennular segment; (D–E) Lithoglyptidae and Trypetesidae, thoracopodal setation on terminal (second) segment of exopod (D) and terminal (third) segment of endopod (E); (F) Cryptophialidae, posterior part of thorax with rudiments of limbs and furca; and (G) Lithoglyptidae and Trypetesidae, terminal end of furcal ramus with two setae (arrowheads). II–IV = Antennular segments 1–4; pas = postaxial sensory organ; ps2 = postaxial seta 2; rs = radial setae; sk = skirt encircling attachment disk; ss1–4 = subterminal setae; ss + ts = subterminal and terminal setae of fourth antennular segment grouped together; tsA–E = terminal setae of fourth antennular segment. Scales bars in μm.

the other ones (Figs. 4F, 5E,F, and 6G). Within this common pattern the specific morphology of the organs differs significantly between the families.

In the Lithoglyptidae and the Trypetesidae the lattice organs are elongate and narrow depressions (7–18 μm by 0.8–1 μm) perforated by numerous very small rounded pores (Fig. 5D, G, I, and H). The depression is normally traversed by a median crest, which can be very distinct (Fig. 5C, D, and I). All lattice organs have a distinct, large terminal pore, situated anteriorly in LO2 but posteriorly in LO1 and LO3–5 (Fig. 5A–D, G, H, and I). LO1–2 are arranged around a large, central "pore" in the dorsal midline of the carapace, whilst LO3–5 lie around a similar, posteriorly situated "pore" (Fig. 5A and G).

In the Cryptophialidae the structure of the individual lattice organs differ from that seen in the Lithoglyptidae and Trypetesidae (Figs. 1D and 6). None of them carry large terminal pores, and they look like thick penta- or hexagonal plates, which stand out by lacking the numerous pits or pores ornamenting the general carapace cuticle. This makes them easily discernible even with the light microscope (Fig. 1C, D, and F). A conspicuous, wide and smooth ridge surrounds a central, elongated area perforated by small pores, while a rather narrow furrow again separates the ridge from the surrounding carapace cuticle (Fig. 6I–L). There is never any median ridge and the densely clustered pores in the central field differ from those in the Lithoglyptidae and Trypetesidae by having an elongated, irregular shape. LO3 and LO4 lie around a small cuticle area ornamented by minute perforations (Fig. 6G and H), and by position we surmise this to be homologous with the central pore or pit seen in cyprids of the two other families.

3.5. Mantle and mantle cavity

In the Lithoglyptidae and the Trypetesidae the inner surface of the mantle carries up to five 3–5 μm high folds running parallel to the ventral mantle edge (Figs. 1B and 7A,B). The free ends of these folds are fringed, i.e., they consist of a row of cuticular "hairs" unfused throughout their length (Fig. 7C). In the cyprids investigated here, the presence of such fringed folds in

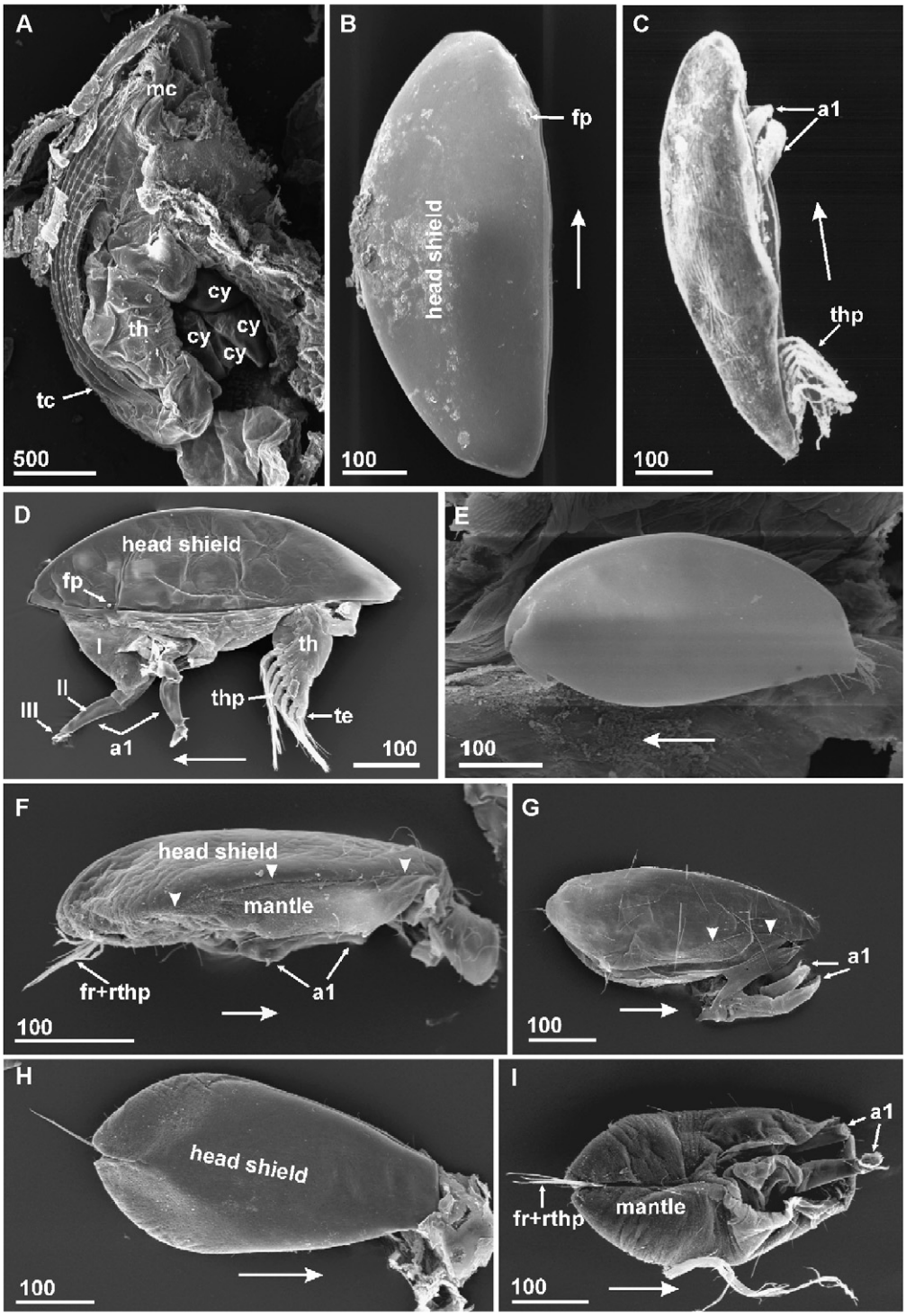

Fig. 3. Cypris larvae of Acrothoracica, SEM, general morphology: (A–D, Lithoglyptidae; E,Trypetesidae; F–I, Cryptophialidae), long arrows = anterior direction, arrowheads = border line between head shield and mantle: (A) *Weltneria spinosa,* adult female with cyprid larvae brooded in the mantle cavity, lateral view; (B) *W. reticulata*, cyprid, lateral view; (C) *Armatoglyptes habei*, cyprid, lateral view; (D) *Kochlorine grebelnii*, cyprid, lateral view, both antennules and thorax extended from mantle cavity; (E) *Trypetesa lateralis*, cyprid, lateral view; (F) *Australophialus turbonis*, cyprid, lateral view; (G) *Cryptophialus heterodontus,* cypris, lateral view; (H-I) *A. melampygos*, cyprid, dorsal and ventral views. I–III = antennular segments 1–III; a1 = antennules; cy = cyprid, fp = frontolateral pore; fr + rthp = setae of furcal rami and thoracopodal rudiments; mc = mouth cone with mouth cirri, tc = terminal cirri; te = telson; th = thorax; thp = thoracopods. Scale bars in μm.

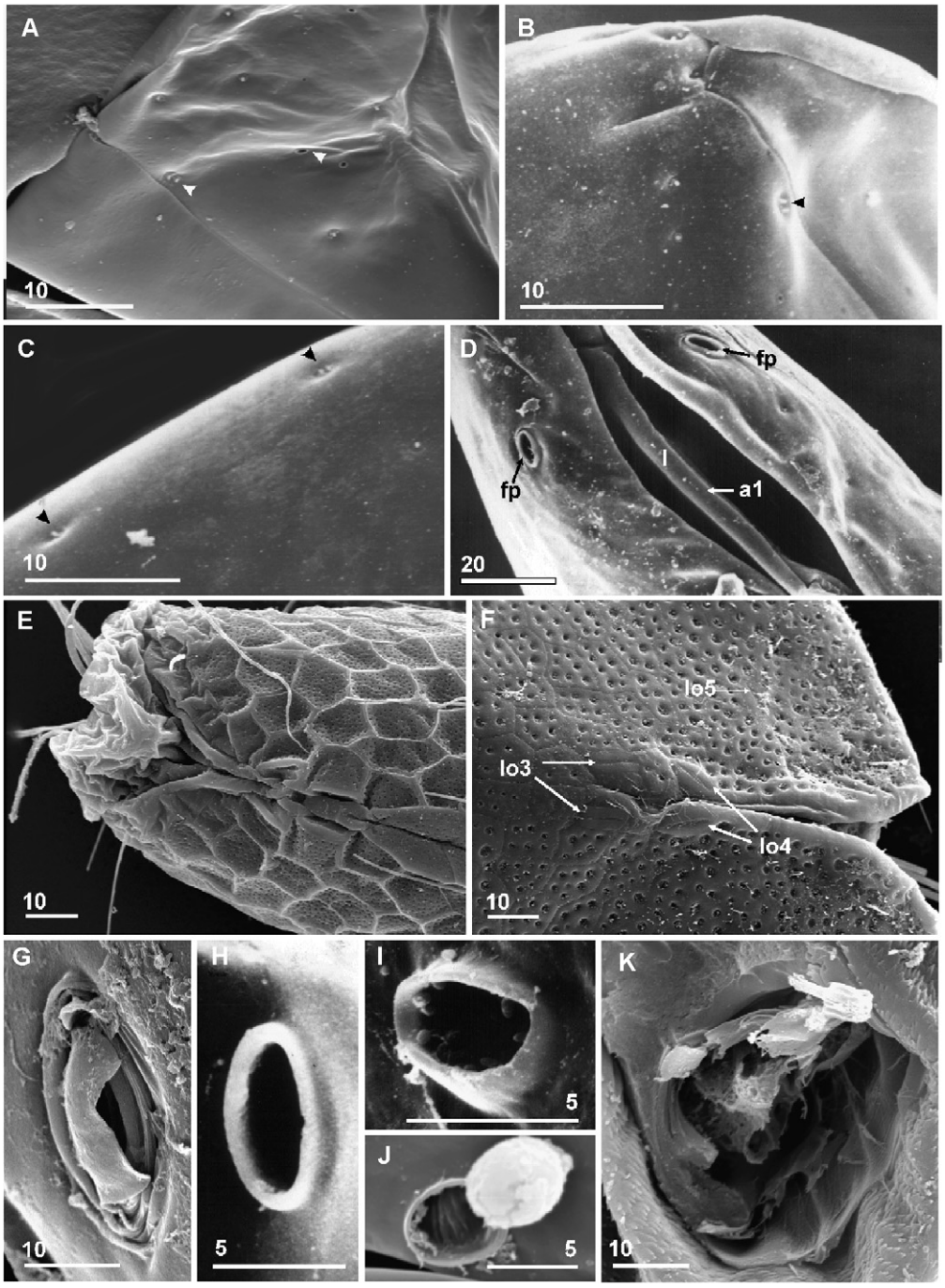

Fig. 4. Head shield of cypris larvae, SEM (A–D, G, I, J Lithoglyptidae; H Trypetesidae; E, F, K Cryptophialidae): (A) *Kochlorine grebelnii*, anterior end, lateral view, double setae and small pore arrowed; (B) *Armatoglyptes habei*, anterior end, top view, double setae arrowed; (C) *A. habei*, double setae (arrowed) along dorsal margin of head shield; (D) *Armatoglyptes mitis*, anterior end, ventral view, frontolateral pores and entrance to mantle cavity with antennule; (E) *Cryptophialus heterodontus*, posterior end, dorsal view; (F) *Australophialus melampygos*, posterior end, dorsal view; (G-J) frontolateral pores of *Weltneria reticulata* (G), *Trypetesa lampas* (H), *A. habei* (I) and *K. grebelnii* (J); (K) *A. turbonis*, mantle, anterior end, below head shield. I = antennular segment 1; a1 = antennules; fp = frontolateral pores; lo3–5 = posterior pairs (3–5) of lattice organs. Scale bars in μm.

the posterior part of mantle cavity is still unclear, but a-cyprids (ascothoracid larvae) have them along the whole length of the ventral margin (unpublished). We have also found similar rows of fringes in cyprids of the Thoracica (unpublished).

In the Cryptophialidae, the head shield can only in part cover the exterior surface of the cypris body. Soft mantle cuticle is therefore exposed both in the mantle cavity and on the more ventral parts of the exterior surface of the body. The ventral edge of the mantle carries fringes as in

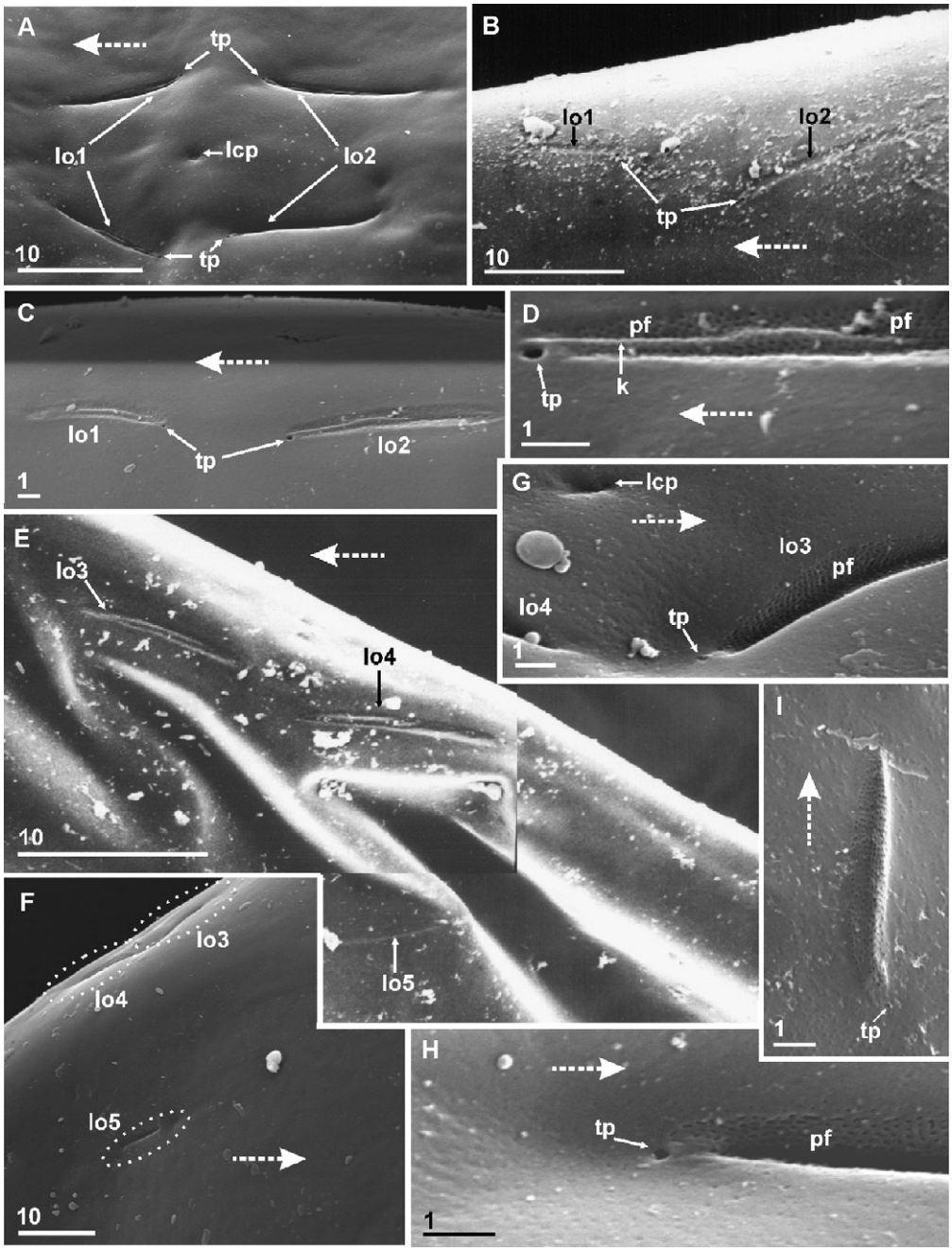

Fig. 5. Lattice organs of cypris larvae (A, B, E, F–I Lithoglyptidae; C, D Trypetesidae); note the distinct median crest in the organs in C–E; dotted arrows indicate anterior direction: (A) *Weltneria spinosa*, anterior lattice organs, dorsal view; (B) *Armatoglyptes mitis*, anterior lattice organs, lateral view of one side; (C) *Trypetesa lateralis*, anterior lattice organs, lateral view of one side; (D) *T. lateralis*, lattice organ 2, lateral view; (E) *A. mitis*, posterior lattice organs, lateral view; (F) *Weltneria spinosa*, posterior lattice organs, lateral view; (G–I) *W. spinosa*, lattice organs 3 (G), 4 (H) and 5 (I) lateral views. *k* = median keel; lcp = large, central, lo1–5 = lattice organs 1–5; pf = pore field of lattice organ; tp = terminal pore of lattice organ. Scale bars in μm.

the two other families (Fig. 7D). The exteriorly exposed part the mantle is covered by a dense mass of pointed, 0.3–1 μm long denticles (Fig. 7D and E) with the tips most often oriented posteriorly. In addition, the mantle carries many smooth setae, which are conspicuously long (20–60 μm) relative to the cypris body.

3.6. Antennules

The antennules are four-segmented and have the same general morphology as seen in cyprids of other Cirripedia (Nott and Foster 1969; Lagersson and Høeg 2002; Lagersson et al. 2003). The first segment is

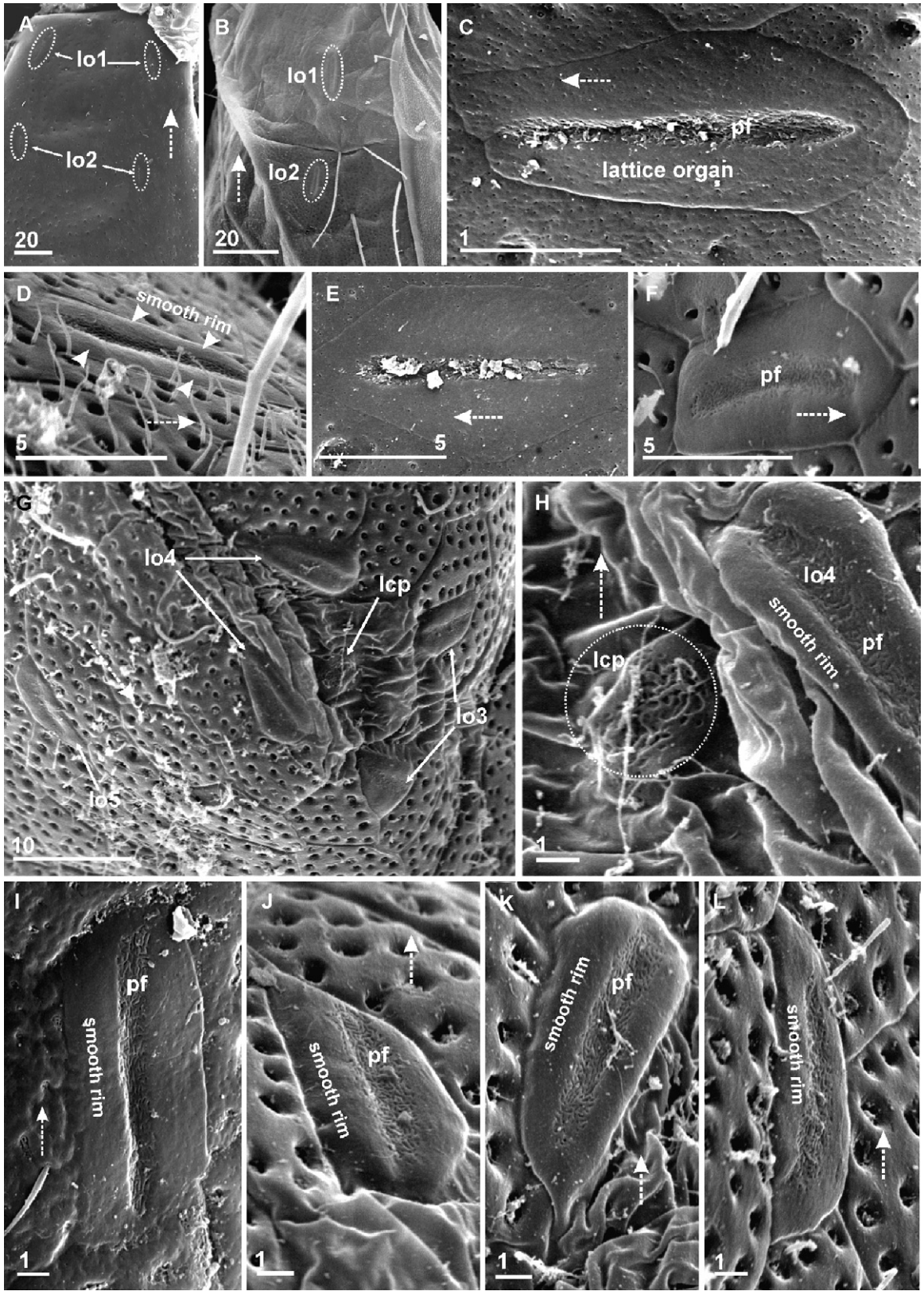

Fig. 6. Lattice organs of cypris larvae (Cryptophialidae), dotted arrows indicate anterior direction: (A) *Australophialus melampygos*, anterior end, dorsal view; (B) *Cryptophialus wainwrighti*, anterio-lateral view; (C) *A. melampygos*, lattice organ 1; (D) *C. wainwrighti*, lattice organ 1; (E) *A. melampygos*, lattice organ 2; (F) *C. wainwrighti*, lattice organ 2; (G) *C. wainwrighti*, posterior lattice organs (3–5), dorsal view; (H) *C. wainwrighti*, large central pore in posterior midline between lattice organs; (I) *A. melampygos*, lattice organ 3; and (J–L) *C. wainwrighti*, lattice organs 3 (J), 4 (K) and 5 (L). Lcp = large central pore; lo1–5 = lattice organs 1–5; pf = pore field of lattice organ. Scale bars in μm.

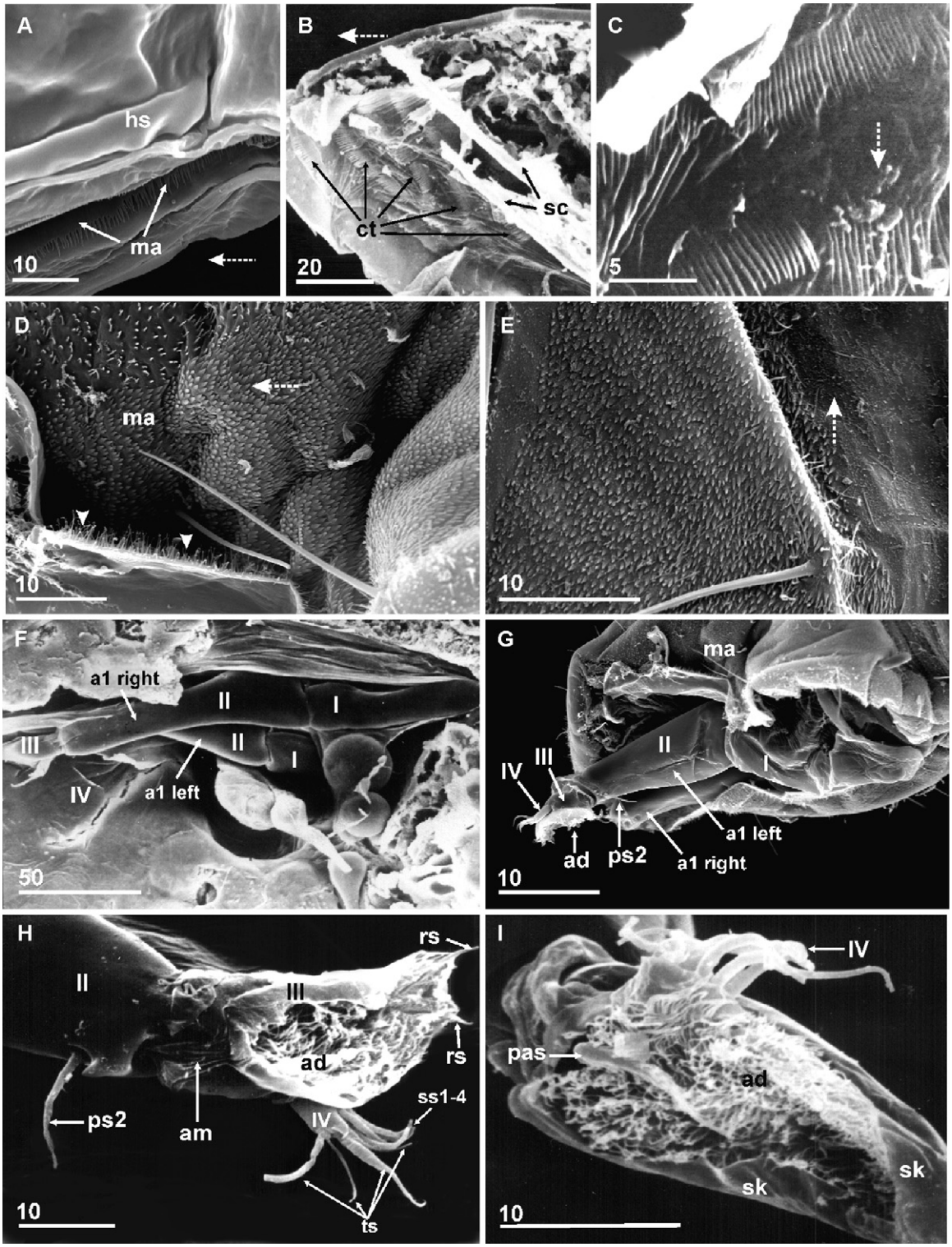

Fig. 7. Cypris larvae, mantle and antennules (A–C, H, I Lithoglyptidae; F Trypetesidae; D, E, G Cryptophialidae), dotted arrows indicate anterior direction: (A) *Weltneria spinosa*, entrance to mantle cavity between ventral margins of head shield; (B) *Armatoglyptes habei*, anterior end, left side of shield (carapace) removed to expose inner side of mantle with rows of cuticular ctenes; (C) *A. habei*, inner side of mantle, anterior end, with rows of cuticular ctenes; (D) *Australophialus melampygos*, anterior part of mantle, mantle border marked with arrowheads; (E) *Cryptophialus heterodontus*, posterior part of mantle; (F) *Trypetesa lampas*, antennules inside mantle cavity, lateral view; (G) *A. melampygos*, antennules, ventral view; (H) *A. habei*, distal part of antennule; and (I) *Armatoglyptes mitis*, oblique ventral view of third antennular segment with attachment disk. I–IV = antennular segments 1–4; a1 = antennules; ad = attachment disk; am arthrodial membrane (between 2 and 3 segments); ct = rows of cuticular ctenes; hs = head shield (carapace); ma = mantle; pas = postaxial sensory organ; ps2 = postaxial seta 2; rs = radial setae; sc = proximal sclerite of first antennular segment; sk = cuticular skirt encircling attachment disk; ss1–4 = subterminal setae on fourth antennular segment; ts = terminal setae on fourth antennular segment. Scale bars in μm.

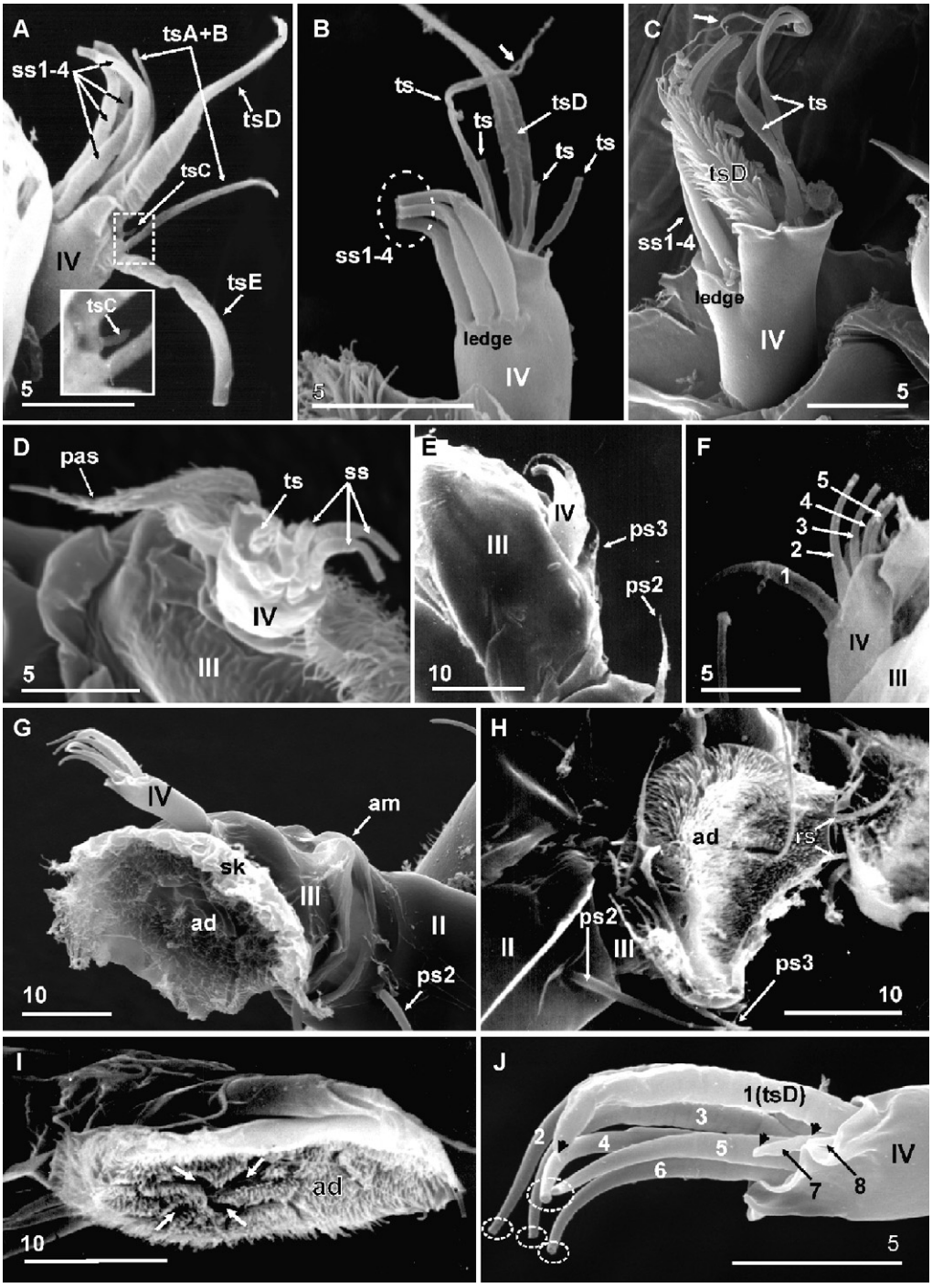

Fig. 8. Cypris antennules (A, C–E Lithoglyptidae; B Trypetesidae; F–J Cryptophialidae): (A) *Armatoglyptes habei*, distal end of fourth antennular segment, inset shows the minute terminal seta C; (B) *Trypetesa lampas*, fourth segment, one terminal seta is bifurcated (arrowhead), terminal seta D not shown in full length; (C) *Weltneria spinosa*, fourth segment, at least one terminal seta is bifurcated (arrowhead), terminal seta D with complex setulated morphology; (D) *Kochlorine grebelnii*, third and fourth segments; (E) *A. habei*, third segment, dorso-lateral view showing position of fourth segment; (F) *Cryptophialus gantsevichi,* fourth segment, seta 1 may represent terminal seta D (tsD); (G) *Australophialus melampygos*, oblique ventral view, distal part of antennule with attachment disk; (H) *C. gantsevichi*, distal part of antennule; (I) *C. gantsevichi*, third segment, oblique lateral view showing furrows (arrows) in the attachment disc; (J) *A. melampygos*, fourth segment, lateral view, setae 2–6 have terminal pores (circles) while 1, 7 and 8 lack pores (arrowheads). II–IV = second–fourth antennular segments; ad = attachment disk on III; am = arthropodial membrane; pas = postaxial sensory organ; ps2 = postaxial seta 2; ps3 = postaxial seta 3; rs = radial setae; sk = cuticular skirt encircling attachment disk; ss1–4 = subterminal setae on fourth segment; ts (A–E) = terminal setae on fourth segment. Scale bars in μm.

particularly complex and consists of two articulating sclerites, a proximal and a distal. The second segment has an elongate, cylindrical shape. The third segment is hoof shaped and carries the attachment disk, while the fourth segment is cylindrical and attached on the lateral side of the third.

3.6.1. The first segment

The first segment Carries no setae. In lateral view it has a conical (Lithoglyptidae and Trypetesidae) or triangular (Cryptophialidae) shape, 80–100 μm long and 40–60 μm wide. The shape and articulation of the proximal sclerite differs between the families. In the Lithoglyptidae and Trypetesidae it is straight and equipped with two anteriorly projecting rods, homologous with the medial and lateral Y-rods *sensu* Høeg (1985). The tips of the medial rods from either antennule articulate with each other in a pendulary joint in the roof of the mantle cavity (Fig. 1B). Cyprids of the Cryptophialidae have an "S-shaped" proximal sclerite, which unlike the situation in all other cirripedes, does not articulate with its counterpart from the other antennule (Fig. 1C and E).

In preserved larvae of the Lithoglyptidae and Trypetesidae, the first segment is normally retracted into the mantle cavity, but in a few specimens it may project outside as during exploratory walking on the substratum (Fig. 3D).

3.6.2. The second segment

The second segment is 70–100 μm long and articulates proximally with the distal sclerite of the first segment in a joint that can flex in the vertical plane over a wide angle (Figs. 1A–C,E,F and 7F,G). Its width decreases from 35 to 40 μm proximally to 12–20 μm at the distal end. A single, conspicuous, postaxial seta 2 (number 13 in the classification of Nott and Foster 1969) inserts ventro-distally (Figs. 7G,H and 8G,H).

3.6.3. The third segment

The third segment is hoof-shaped, 30–40 μm long by 15–20 μm wide and articulates with the second segment (Figs. 2A,B, 3D, and 7G). A well-developed cuticular skirt (*sensu* Moyse et al. 1995) encircles the distal (morphologically ventral) attachment disk, which is covered by a dense mass of cuticular villi (Figs. 7H,I and 8G–I). Several grooves devoid of such villi often form a radial pattern at the center of the disk (Fig. 8I). All setae on the third segment sit on or just around the attachment disk. We did not find an axial sense organ (seta) in any of the investigated cyprids. A well-developed postaxial sensory organ (pas) inserts at the postaxial margin of the segment between the skirt and the cuticular villi (Figs. 2A, 7I and 8D). Two radial setae sit at the distal, preaxial rim of the attachment disc (Figs. 2A and 7H). We did not find any additional radial setae along the rim, but they could be obscured in the mass of villi. A small, indistinct seta located on the lateral surface near the base of the fourth segment (Fig. 8E and H) is interpreted as a rudimentary postaxial seta 3 (ps3) (see Kolbasov et al. 1999).

3.6.4. The fourth segment

The fourth segment is small, cylindrical and inserts laterally on the third segment (Figs. 2A, 7H, and 8G). It ranges in length from 5 μm in *Armatoglyptes*, *Kochlorine* and *Trypetesa* to 10–12 μm in *Weltneria*, *Australophialus*, and *Cryptophialus*.

In the Lithoglyptidae and Trypetesidae this segment carries a subterminal and a terminal cluster of setae (Fig. 2A and C) and in our terminology of these we follow Clare and Nott (1994), Glenner and Høeg (1995), Kolbasov et al. (1999) and Blomsterberg et al. (2004). *Weltneria*, *Armatoglyptes* and *Trypetesa* all have four subterminal setae. In *Kochlorine* the setae were damaged, so we could only establish the presence of a subterminal and a terminal group but not the exact setal number (Fig. 8D). The subterminal setae sit close together on a distinct ledge on the side of the segment (Fig. 8B and C). They are morphologically identical and approximately equal in length, measuring 16 μm (*Weltneria*), 9 μm (*Armatoglyptes*) and 5 μm (*Trypetesa*). The proximal part of these setae is swollen as a flask but continues with an apically slender part that bends away from the segment and terminates in a pore. The terminal setae sit on the apex, surrounded by a low cuticular skirt (Figs. 8B,C, and 12). There are five in *Armatoglyptes* (Fig. 8A) and *Trypetesa* (Fig. 8B), but only three in *Weltneria* (Fig. 8C). All terminal setae are smooth in *Armatoglyptes* and *Trypetesa*. In *Armatoglyptes* (Fig. 8A) seta A and B are equally long and both simple and rather thin. Seta D is the longest (13 μm) and rather thick, but somewhat laterally compressed in its basal half, while more distally it decreases gradually in diameter towards the tip. Seta E is stout, isodiametrical throughout, slightly curved and with a large pore at the tip. Seta C is tiny. In *Trypetesa* (Fig. 8B) only seta D is easily identifiable, being 13 μm long, ribbon-like and tapering towards the tip. The second longest seta is thin, 8 μm long and bifurcated near the tip. The three remaining setae are equally long, more or less isodiametrical and at least two of them terminate in a distinct pore.

In *Weltneria* seta D is 13 μm long, 3 μm wide at the base and very conspicuous by being densely armed with foliated setules throughout its length. The two other terminal setae are longer, with flat and wide proximal halves and thin, whip-like distal parts, which in one of them forks into two branches (Fig. 8C).

In the Cryptophialidae there is no ledge carrying subterminal setae, whence the whole segment assumes a more slender shape than in the other species examined

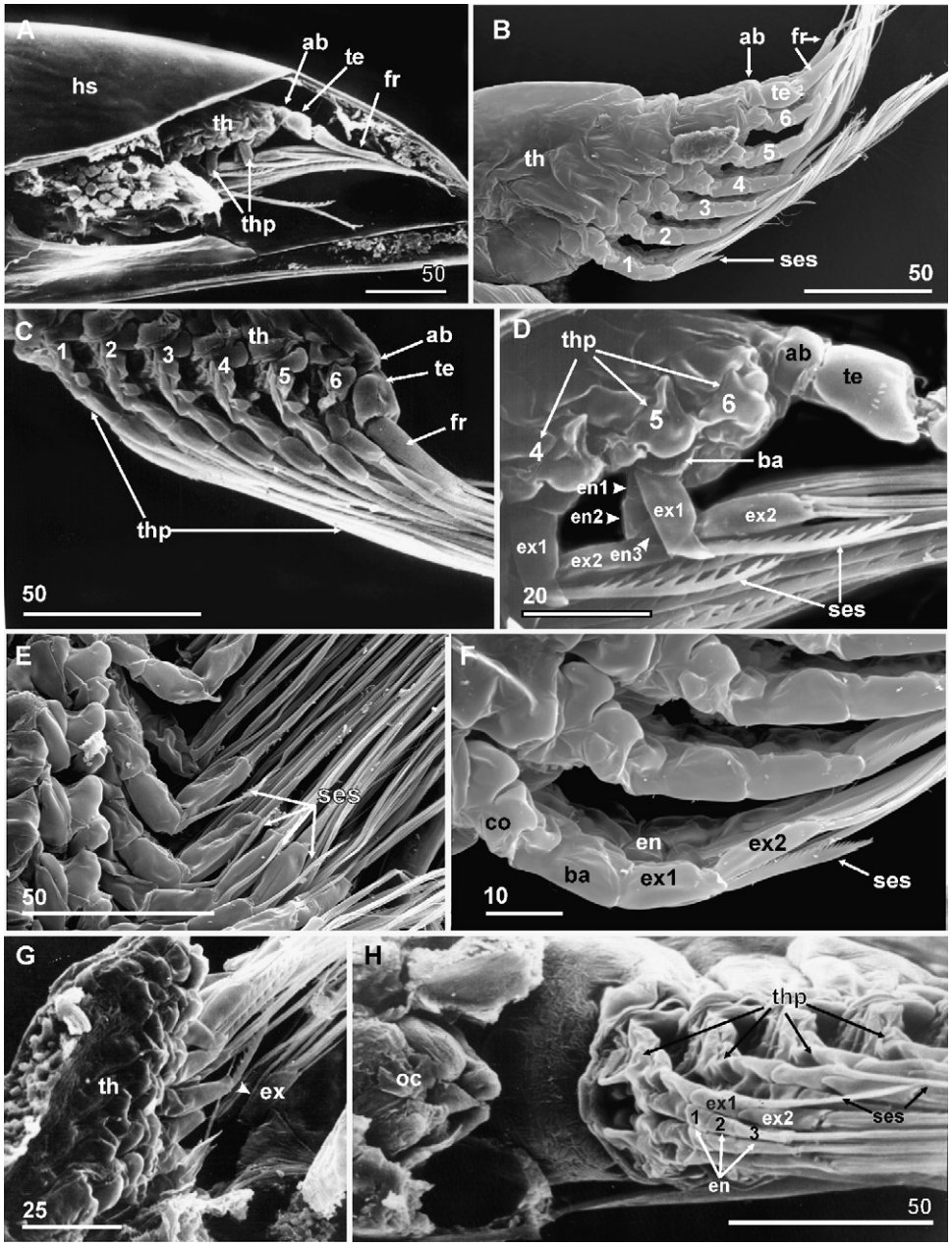

Fig. 9. Cypris thorax and thoracopods (A, B, D–G Lithoglyptidae; C, H Trypetesidae): (A) *Armatoglyptes habei*, lateral view, posterior part of thorax and abdomen, part of left head shield removed; (B) *Kochlorine grebelnii*, lateral view, thorax with thoracopods (numbered), abdomen with telson and furcal rami; (C) *Trypetesa lampas*, lateral view, thoracopods (numbered), abdomen and telson with furcal rami; (D) *A. habei*, detail of 'A' showing last three thoracic segments (th4–6) and exopods 5 and 6 (numbered); (E) *Weltneria spinosa*, lateral view of thoracopods; (F) *K. grebelnii*, lateral view of thoracopods 1–3; (G) *A. habei*, thorax, dorsolateral view (arrowhead indicates basal seta on terminal segment of exopod); (H) *T. lampas*, vestigial oral cone, thoracopods 1–4, oblique ventral view. 1–6 = thoracopods 1–6; ab = abdomen; ba = basis of thoracopod; co = coxa of thoracopod; en = endopod; en1–3 = endopod segments 1–3; ex = exopod; ex1–2 = exopod segments 1–2; fr = furcal ramus; hs = head shield (carapace); oc = vestigial oral cone; ses = serrated seta on exopod segment 1; te = telson; th1–6 = thoracic segments 1–6; thp1–6 = thoracopods 1–6. Scale bars in μm.

(Figs. 2B and 8F,G,J). All fourth segmental setae (eight in *Australophialus*, five in *Cryptophialus*) are smooth and sit close together on the obliquely sloping apical surface. In *Australophialus* seta 1 (numbering as in Fig. 8J) has the same length as setae 2–6, but it differs in being conspicuously thicker, having a more irregularly shaped surface and lacking a terminal pore (Fig. 8J). Five of the remaining setae (2–6) are equal in length (10 μm) and structure, being curved apically and tapering gradually towards a conspicuous terminal pore (Figs. 8J and 2–6)

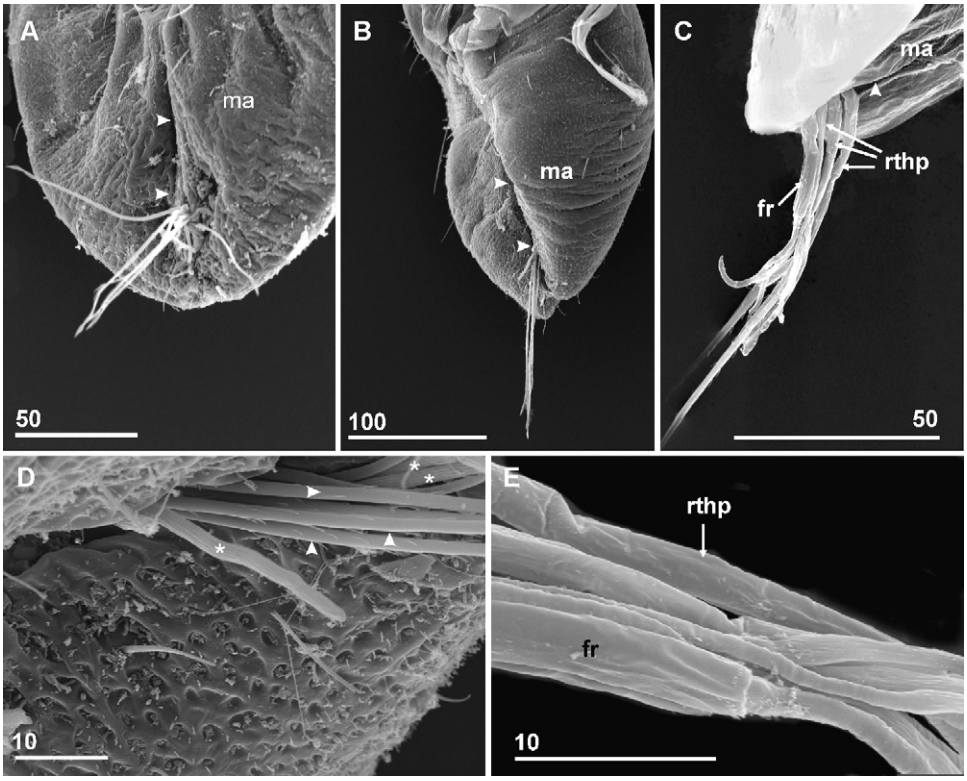

Fig. 10. Cyprids of the Cryptophialidae; thoracopodal rudiments and furcal rami: (A) *Australophialus turbonis*, posterior end, ventral view, arrowheads indicate entrance to mantle cavity; (B) *A. melampygos*, posterior end, oblique lateral view, arrowheads indicate entrance to mantle cavity; (C) *Cryptophialus heterodontus*, posterior end, lateral view, arrowheads indicate entrance to mantle cavity; (D) *A. melampygos*, setae of thoracopodal rudiments and furcal rami, setae with setules marked with arrowheads, unsetulated setae with asterisks; and (E) *C. heterodontus*, setae of thoracopodal rudiments and furcal rami. fr = furcal ramus; ma = mantle; rthp = setae of thoracopodal rudiments. Scale bars in μm.

very much like the subterminal setae seen in e.g. *Armatoglyptes* (Fig. 8A). The two remaining setae (7, 8) are small and rudimentary, measuring 3 and 1 μm, respectively. The whole apex is partially enclosed by a low skirt of thin cuticle. In *Cryptophialus* the lowermost seta (1) is also longer (8–11 μm) and thicker than the rest (Fig. 8F). The remaining four are of similar length (4–5 μm) and with a structure identical to setae 2–6 in *Australophialus*, but we cannot wholly exclude that rudimentary setae remained hidden and unobserved.

3.7. Thorax and thoracopods

All investigated cyprids of the Lithoglyptidae and Trypetesidae possess a well-developed thorax with six pairs of natatory limbs (Figs. 1A,B, 3C,D and 9), whereas both the thorax and the thoracopods are rudimentary in the Cryptophialidae and cannot serve in swimming (Figs. 1C,E, 2F and 10C).

In the Lithoglyptidae and Trypetesidae the thorax is 100–120 μm long and forms the posterior third of the larval body (Figs. 1A,B and 9A). It consists of six segments, each bearing a pair of biramous natatory thoracopods. We searched in vain for any unpaired, medio-ventral process between sixth and seventh trunk segments such as observed in a few species of the Rhizocephala (Walossek et al. 1996).

The thoracopods of the Lithoglyptidae and Trypetesidae consist of a protopod (coxa + basis) carrying a two-segmented exopod and three-segmented endopod (Fig. 9D,F, and H). More basally, a complex array of pseudo-quadrangular sclerites covers the limb insertion area (Fig. 9C–E). All thoracopods can bend at two joints, one situated between the basis and the first ramal segment and the other between ramal segments. In the exopod the joint is situated between first and second ramal segments, whilst it lies between the second and third segments in the endopod. No movement seems to be possible between the first and second segments of the endopod (Fig. 9D). The first exopod segment carries a single, stout seta (*ses*). It sits latero-distally, extends beyond the tip of the ramus (Fig. 9B–F and H) and has a distinct serration. This serrated seta is 35–40 μm long

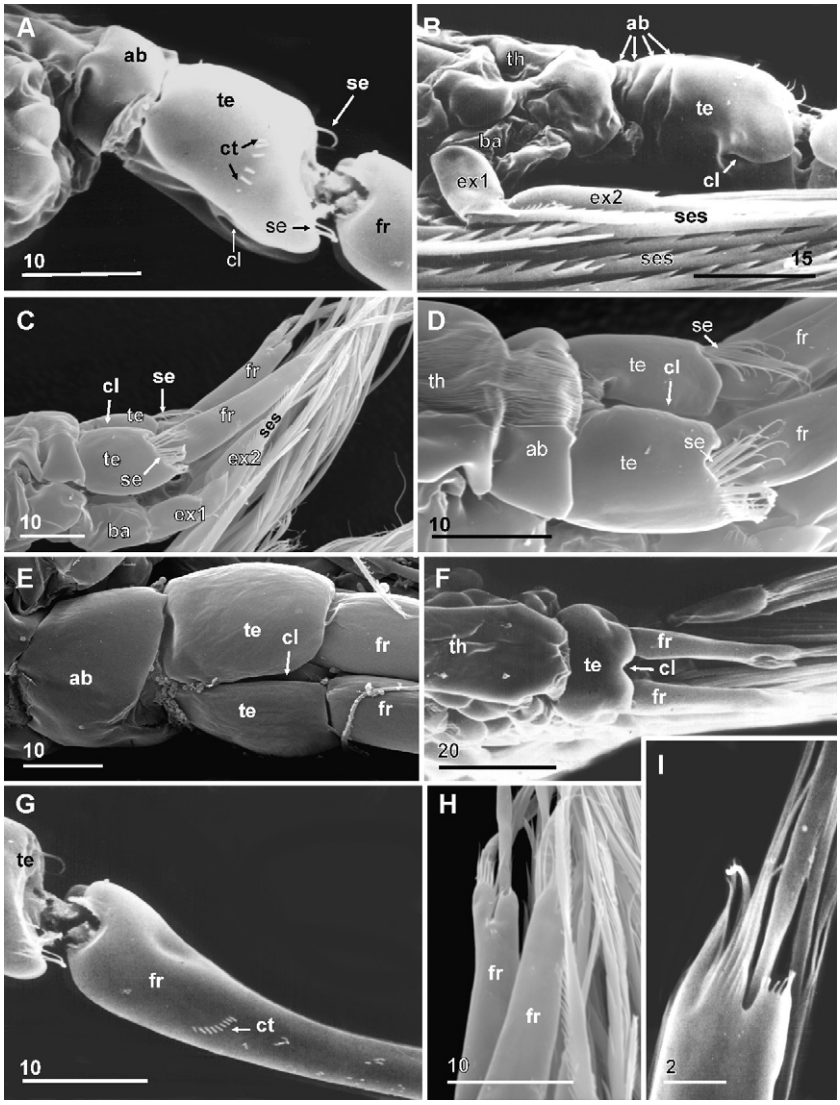

Fig. 11. Cypris abdomen, telson and furcal rami (A–E, G–I Lithoglyptidae; F Trypetesidae). In (C–E) the deep cleft (cl) in the telson reaches almost to the base: (A) *Armatoglyptes habei*, abdomen, left lateral view, telson and proximal part of left furcal ramus; (B) *A. habei*, oblique ventral view, posteriormost part of thorax, exopod segments of thoracopod six numbered, abdomen with furrows indicating four fused, rudimentary segments and telson; (C) *Kochlorine grebelnii*, lateral view, posteriormost part of thorax, telson and furcal rami (segments of thoracopod six numbered); (D) *K. grebelnii*, dorso-lateral view, posteriormost part of thorax, abdomen, telson and proximal parts of furcal rami; (E) *Weltneria spinosa*, abdomen, telson and proximal parts of furcal rami, dorsolateral view; (F) *Trypetesa lateralis*, dorsal view, posteriormost part of thorax, telson and furcal rami; (G) *A. habei*, proximal-middle part of furcal ramus, lateral view, distal end is down; (H) *K. grebelnii*, distal ends of furcal rami; and (I) *A. habei*, distal end of furcal rami, lateral view. ab = abdomen; ba = basis of thoracopods; cl = cleft; ct = ctene; ex1–2 = exopod segments 1–2; fr = furcal ramus; se = setae of telson; ses = serrated seta on exopod segment 1; te = telson; th = thorax. Scale bars in μm.

in *Armatoglyptes* and *Trypetesa,* the spines being largest in *Armatoglyptes*, while it measures only 20–25 μm and has smaller spines in *Weltneria* and *Kochlorine* (Fig. 9). The second exopod segment bears five simple setae at the apex and a single, simple seta at the base (Figs. 2D and 9).

The endopods are slightly shorter than the exopods (Fig. 9D and H). Details of their setation is partially obscured by the exopods, but the second endopod segment appears to carry a single, simple latero-distal placed seta, while the third carries three simple, terminal setae (Figs. 2E and 9).

In the Cryptophialidae both the thorax and the thoracopods are rudimentary, and the larvae are therefore unable to swim. Several long setae emerge posteriorly between the mantle valves (Fig. 10). Four are omniserrate setae and may belong to the hidden or reduced furcal rami rather than the thorax itself. More abundant setae with a longitudinal striation but lacking setules altogether seem to belong to the rudimentary

thoracopods, but morphological details in the latter could not be traced (Fig. 10D and E).

3.8. Abdomen, telson and furcal rami

Cyprids of the Lithoglyptidae and Trypetesidae possess a rudimentary, but distinct abdomen and a well-developed telson, equipped with furcal rami (Figs. 9A–D and 11). In the Cryptophialidae only the furcal rami remain (Fig. 10C and E).

The Lithoglyptidae and Trypetesidae have a short, cylindrical abdomen (Figs. 9A–D and 11A–E) with smooth dorsal and lateral surfaces but four transverse furrows on the ventral side (Fig. 11B). In the Lithoglyptidae the lateral surface of the telson may carry a row of separate denticles (Fig. 11A). The latero-distal margins of the telson can carry a row of small setae, which are dense in *Kochlorine* (Fig. 11C and D), sparse in *Armatoglyptes* (Fig. 11A) and completely absent in *Weltneria* and *Trypetesa* (Figs. 9C and 11E). A distinct, medial cleft originates posteriorly and partially divides the telson into two equal parts. The cleft is shallow in *Trypetesa* (Fig. 11F) but half the length of the telson in *Armatoglyptes* (Fig. 11A and B) while in *Weltneria* and *Kochlorine* it almost cleaves the telson so the two halves are connected only at the base (Fig. 11D and E). The furcal rami are unsegmented (Figs. 9 and 11), but the telsonic cleft effects that the halves can masquerade as basal segments in "two segmented" rami (Fig. 11E).

The furcal rami are ca. three times longer (30–44 μm) than the telson and distally constricted. A single row of spines can ornament the lateral surface (Fig. 11G). The distal end of the ramus is divided by a notch, deepest in *Kochlorine* and *Trypetesa* (Figs. 2G and 11F,H,I), and carries a pair of long and simple setae surrounded by a collar of cuticular villi of different sizes (Figs. 2G and 11H,I). In the Cryptophialidae the furcal rami are unsegmented and tube-shaped, without any sculpture and each with a pair of distal setae (Fig. 10C and E).

4. Discussion

This is the first study to survey cypris characters in representatives from all three families of the Acrothoracica. Previously, cypris morphology based on broad taxon sampling and ultrastructural methods existed only for the Thoracica and Rhizocephala, so this study is also the first time cypris morphology can be compared across all three ingroups of the Cirripedia.

In most features the acrothoracican cyprids comply with the morphology for cirripede cyprids set down by Høeg et al. (2003), but we have found several interesting variations in this pattern. Since the cyprid is a key player in the cirripede life-cycle by initiating the sessile phase it becomes very interesting to analyze in what features its morphology and function are stereotyped within the Cirripedia and in which it exhibits variations that may have evolved in response to the highly divergent substrata and lifestyles found in the order (Høeg and Møller 2006).

Obviously all characters treated here should eventually be part of an across-the-board cladistic analysis of all Thecostraca, but taxon sampling and character analysis is still too limited to allow this and we therefore preliminarily resort to a by-hand establishment of ground patterns. The intrinsic phylogeny of the Acrothoracica is almost unknown, since the existing taxonomy is based on precladistic methods. Recently, the family Lithglyptidae was reviewed with cladistic methods to establish the relations between the species of the genus *Lithoglyptes s.l.* Tomlinson 1969 (Kolbasov and Newman 2005). Three genera, viz., *Lithoglyptes* s.s., *Auritoglyptes* Kolbasov and Newman 2005, and *Armatoglyptes* Kolbasov and Newman 2005 were proposed, but only the characters of adult females and males were explored in this study. To establish a ground pattern for cypris morphology in the Acrothoracica we will therefore compare the acrothoracican larvae examined here with those from the remaining Cirripedia and use the presently accepted phylogeny for the Thecostraca (Fig. 13. In this the Acrothoracica is sistergroup to a clade comprising the Rhizocephala and the Thoracica. More distant outgroups are the Ascothoracida (sistergroup to the Cirripedia) and the Facetotecta (sistergroup to the Cirripedia + Ascothoracida) (Høeg and Kolbasov 2002; Pérez-Losada et al. 2002, 2004). The Rhizocephala and Thoracica therefore become the relevant outgroups for polarizing character evolution.

4.1. General shape and carapace

A head shield, or carapace, that is U-shaped in cross-section and completely covers the larval body is found without exception in cyprids of all other Cirripedia and also in the Ascothoracida. Compared to other cirripedes, the cyprids of *Armatoglyptes* and *Trypetesa* are extraordinarily narrow, which may relate to peculiarities of settlement within the narrow confines of the calcareous substrate (Kolbasov et al. 1999).

The incomplete shield found in the Cryptophialidae, exposing large parts of the body is unique in cirripedes and must represent an autapomorphy. In these non-swimming cyprids, relaxation of the need for a fusiform body shape may explain both the peculiar carapace and the plump body shape. The reduction of the thorax and the thoracopods was also observed by Batham and Tomlinson (1965) and Turquier (1985a) and represents autapomorphies for these totally benthic cyprids. The retention of some thoracopodal setae indicates that they

still serve a role either as sensilla and/or perhaps assisting as a posteriorly projecting ''third leg'' during exploratory walking in a manner similar to the furcal rami in other cirripede cyprids.

No acrothoracican or rhizocephalan cyprids have a dorsal hinge line (Jensen et al. 1994a, this paper). Within the Cirripedia a dorsal hinge line exists only in cyprids from a few thoracican species, such as those of the Lepadidae and the scalpellid genera *Pollicipes* and *Capitulum*. The presence of a distinct hinge line in a-cyprids of the Ascothoracida indicates that this feature might be part of the cirripede ground pattern. The presence of a hinge bears no strong correlation to size, since lepadid cyprids are generally very large while those of *Capitulum* are much smaller (Jensen et al. 1994a). Even without a hinge, the two sides of the shield can still be apposed by action of the adductor muscle, while reopening is effected by the elastic properties of the shield cuticle (Høeg 1985).

Considerable information now exists on the ornamentation of the head shield in cypridiform larvae (Itô and Grygier 1990; Jensen et al. 1994a, b; Elfimov 1995; Walossek et al. 1996; Kolbasov et al. 1999; Høeg and Kolbasov 2002), but no clear ground pattern can yet be perceived. In the Acrothoracica the smooth surfaced head shield seen in the Lithoglyptidae and Trypetesidae differs from the conspicuous, hexagonal, cellular ridges characteristic for the Cryptophialidae. The presence of a similar pattern in facetotectan y-cyprids (Schram 1970; Itô and Takenaka 1988; Kolbasov and Høeg 2003), ascothoracidan a-cyprids (Itô and Grygier 1990) and in some thoracican cyprids such as certain Lepadidae (Jensen et al. 1994a) could signify a ground pattern feature, but we believe that such honeycomb patterns in the cuticle would be very prone to adaptive evolution.

Almost all cypridiform larvae bear setae on the head shield. They are normally fairly short and apparently randomly distributed, but on closer analysis their pattern can be surprisingly fixed and confer important phylogenetic information (Jensen et al. 1994b). The row of setal pairs along the dorsal midline in trypetesids and lithoglyptids could represent such a case. The exceptionally long setae in cyprids of the Cryptophialidae represent a clear deviation from both the cirripede and the general thecostracan ground pattern. The only similar case seems to be the few, but exceptionally long setae found in the exceedingly small cyprids of the rhizocephalan family Chthamalophilidae. Interestingly, both cryptophialid and chthamalophilid cyprids lack natatory thoracopods, indicating that a large number of moderately sized setae on the shield may be coupled to swimming.

The presence of a distinct, although small abdomen with rudimentary segmentation indicated by the ventral furrows is a clear plesiomorphy compared to the Rhizocephala and Thoracica (Kolbasov et al. 1999) and is matched by a similarly plesiomorphic expression of Hox genes (Gibert et al. 2000)

4.2. Frontolateral pores

The frontolateral pores in cyprids develop from those situated at the tip of the frontolateral horns of cirripede nauplii. In the Facetotecta and Ascothoracida neither nauplii nor cyprids have such horns and pores, whence they represent an autapomorphic ground pattern feature for the Cirripedia. (Høeg 1992a, b; Walker 1992; Anderson 1994; Høeg and Møller 2006).The presence of these pores in the acrothoracican species with brooded cyprids studied here indicates that they must also have a function when naupliar stages are absent. Their absence in some acrothoracican cyprids is obviously due to secondary loss but convergent with a similar condition in many rhizocephalan species (Glenner et al. 1989). Within the Cryptophialidae, only *Australophialus turbonis* cyprids have a structure resembling a frontolateral pore, and its unusual position on the soft mantle could be explained by the reduced size of the sclerotized part of the cuticle characteristic for this family.

4.3. Lattice organs

Lattice organs are specialized chemoreceptors that develop from setae in the naupliar head shield (Rybakov et al. 2003). In the first detailed account of the organs, Jensen et al. (1994a, b) distinguished two distinct varieties. The ''crest-in-a-trough'' type consists of a crest reminiscent of a reclined seta, which traverses an elongated depression without pores. The ''porefield type'' consists of a depression without any crest but with the flat floor perforated by numerous closely spaced pores. Common to both types is a large, terminal pore situated at one end of the organ. The porefield type is normally considered a synapomorphy for the Rhizocephala and Thoracica, but our discovery of small pores in acrothoracican lattice organs that also have a more or less distinct crest complicates the distinction between the two varieties. The TEM analysis of Høeg et al. (1998) showed that the pores in the ''porefield type'' of the Rhizocephala and Thoracica are actually deep pits that extend down to the cuticular sensory chamber and are separated from it only by a thin epicuticle in the bottom. TEM revealed that the crest-in-trough organs in the acrothoracican *T. lampas* also have small shallow ''pores'', but these concerned only the epicuticle, not the exocuticle, and they did not extend down through the underlying layers to the sensory chamber. Outgroup comparison to the Ascothoracida and Facetotecta sets the absence of pores other than the terminal one and

presence of a crest as the plesiomorphic condition. The morphology of the acrothoracican lattice organs therefore represents an intermediary state, where both the crest and small pores (pits) can be more or less conspicuous and it accords well with their phylogenetic position as the sistergroup to the remaining Cirripedia (Fig. 13).

There is little doubt that both the small acrothoracican pores and the deeper ones in the other cirripedes serve to facilitate the passage of the sensory stimulus to the outer dendritic segments (ciliary derivatives) located in the cuticular chamber. The lattice organs in the Facetotecta and Ascothoracida have no pores other than the large terminal one, which therefore remains the only passageway for the chemical stimulus. In the Cirripedia, the small pores or pits above the organ have largely taken over this role by facilitating the passage of chemical stimuli to the outer dendritic segments (''cilia'') located in the underlying sensory chamber (Høeg et al. 1998). The end of this trend is seen in lattice organs of the Rhizocephala Akentrogonida and of the Cryptophialidae described here, where the terminal pore is absent altogether. Without the morphologically intermediate types or ontogenetic data, there would be little if any basis for postulating a homology between these advanced types of sensory organs and the normal chemosensory seta.

The irregularly elongate pores found in the Cryptophialidae have no equivalent elsewhere, and is yet another autapomorphy for the family. To this list also adds the remarkable plate-like shape of their lattice organs, which enabled Berndt (1907) to depict the anterior pairs in his figure of *Cryptophialus* (*Australophialus*), although he did not specifically describe them. In truth the smooth circumferential cuticle area should perhaps not be considered as a part of the organ proper inasmuch as the sensory chamber probably extends only beneath the pore field.

The large, central pores associated with the anterior (LO1–2) and posterior (LO3–4) pairs of lattice organs seem to be a ground pattern feature for thecostracan cypridiform larvae and are internally associated with a special gland of as yet unknown function (Høeg et al. 1998; Høeg and Kolbasov 2002).

4.4. Antennules

Except for the Cryptophialidae, the overall morphology of the acrothoracican antennules resembles that seen in cyprids of the Rhizocephala and Thoracica (Walker et al. 1987; Høeg et al. 2003; Høeg and Møller 2006).

The presence of a postaxial seta distally on the second segment (ps2) and proximally on the third segment (ps3) is a cirripede ground pattern feature (Fig. 8H). Most cirripedes have a long ps2 as seen here in *Armatoglyptes* and *Australophialus* (Fig. 7G and H), but both Moyse et al. (1995) and we found it to be very short in *Trypetesa lampas* and a similar size variation is found for this seta in rhizocephalan cyprids (Walker 1985; Glenner et al. 1989). A decision on the ground pattern condition for the postaxial seta 3 (ps3) is more problematic. It is always very prominent in cyprids of the Thoracica but, where at all present, always minute in the Acrothoracica (Fig. 8E and H). In the Rhizocephala it either has the form of a large aesthetasc or has been secondarily lost (Walker 1985; Glenner et al. 1989; Moyse et al. 1995; Blomsterberg et al. 2004). The failure to find an axial sensory organ in our SEM pictures is hardly significant. The cuticular villi can easily obscure setae on the attachment disc and the TEM picture of Moyse et al. (1995, Plate 1C) clearly reveals the presence of an axial sense organ in *Trypetesa lampas* and thereby, by outgroup comparison, also in the acrothoracican ground pattern. The attachment disc of acrothoracican cyprids does not exhibit any particular specializations. The grooves in the disc (Fig. 8I) may well be passageways for cement flowing from the exit pore during settlement and a similar pattern has been observed elsewhere in cirripedes (Glenner et al. 1989; Moyse et al. 1995).

4.5. Fourth antennular segment

On the fourth segment we found considerable variation in the number, position and morphology of setae. *Armatoglyptes* has exactly the same number and arrangement and approximately the same morphology of the individual setae as seen in the Cirripedia Thoracica (Nott and Foster 1969; Clare and Nott 1994; Blomsterberg et al. 2004). Four identical, rather short setae, each with a distinct pore at the apex, are sited close together on a distinct subterminal ledge. There are five terminal setae (A–E). Two (A,B) are very similar, normally long and thin and always without a terminal pore; they are setulated in the Thoracica but naked in the Acrothoracica. Seta C is always diminutive. Seta E is stout, isodiametrical throughout its length and has a distinct apical pore. Seta D is normally the longest, being rather broad, somewhat ''baggy'' and always without a terminal pore.

Both *Trypetesa* and *Weltneria* deviate from this ground pattern (Fig. 12). In *Trypetesa* we can only reliably identify the four subterminal setae and the characteristic, terminal seta D. The presence of five terminal setae indicates that they are the same as found in *Armatoglyptes* and thoracican cirripedes, but, if so, seta C must be longer than ever seen in these taxa.

In *Weltneria* there is no short terminal seta, so seta C seems to be lost. The setulated one we identify as seta D

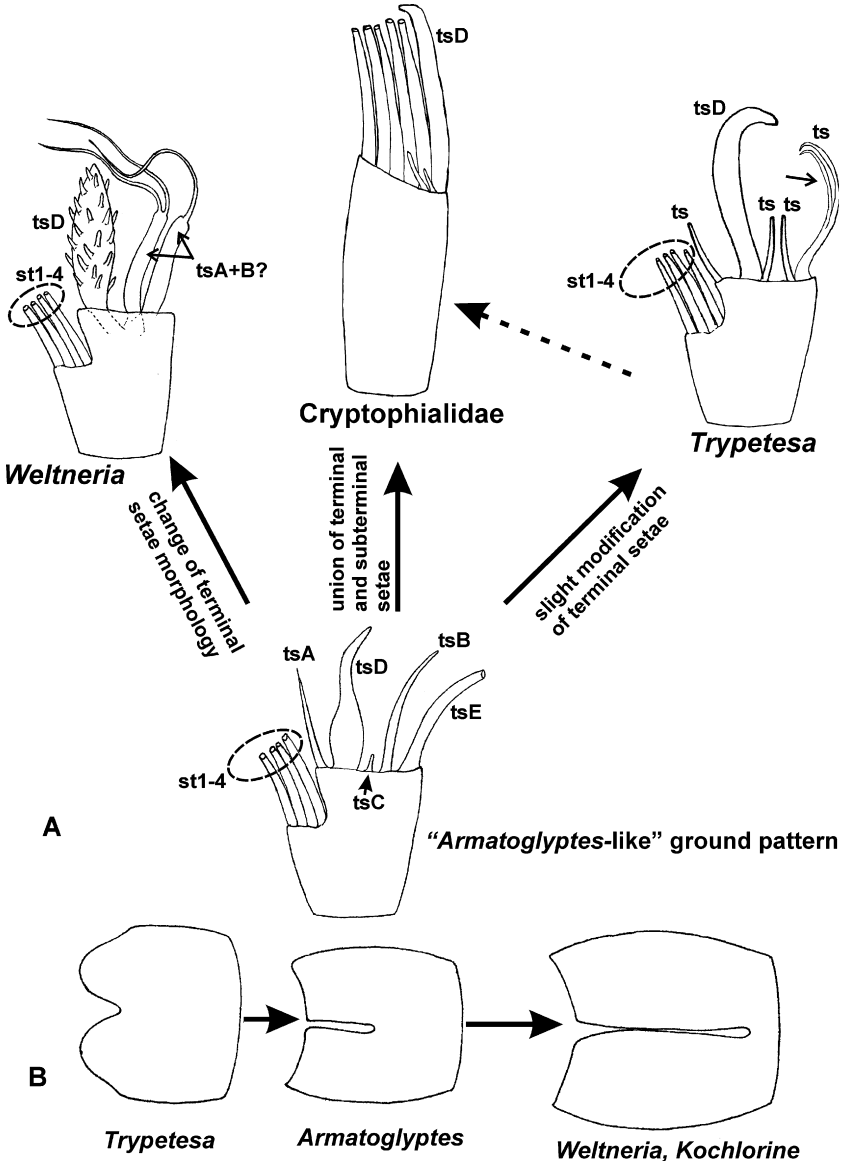

Fig. 12. Variation in morphology and possible evolutionary changes in the fourth antennular segment (A) and cleavage of the telson (B) in cypris larvae of the Acrothoracica. Antennular setation in *Armatoglyptes* resembles that in the outgroup Thoracica. *Weltneria* has fewer, but very specialized terminal setae. In *Trypetesa* the terminal setae other than tsD have lost some of their distinctiveness, but one have become bifurcated (arrow). In the Cryptophialidae, the subterminal and terminal setae are grouped together making homologizations difficult (except for tsD). All drawn from SEM micrographs. Further explanation in text.

is unlike anything seen elsewhere in cirripedes, and it probably represents an apomorphy correlated to a specialized function. Høeg and Rybakov (1996) argued that seta D is homologous to the aesthetasc found on the fourth segment of most rhizocephalan cyprids (Walker 1985; Glenner et al. 1989; Pasternak et al. 2004). If true, the presence of an aesthetasc on the fourth antennular segment becomes a ground pattern feature for the Cirripedia. For *Weltneria* it would be particularly interesting to know whether the branching ciliary projections characteristic for aesthetascs are present internally and perhaps associated with the setules (Pasternak et al. 2004). The two remaining terminal setae in *Weltneria* might be setae A and B, because they are rather similar and deviate from seta C in being long and from seta E in lacking a terminal pore. Both *Weltneria* and *Trypetesa* have a terminal seta which is bifurcated near the tip, but it is doubtful whether this indicates any homology. Such bifurcations could indicate an origin by partial fusion of two setae such as was shown to be the case with TEM by Høeg and Rybakov (1996) in the single quadri-furcated, terminal seta on the 4th antennular segment in cyprids of *Mycetomorpha*.

4.6. The antennules of the Cryptophialidae

The antennules of the Cryptophialidae exhibit many remarkable specializations. In all other cirripedes, the proximal sclerites of the two antennules articulate in a pendulary point which is a key part of the extensive envelope of motions possible by these appendages during exploratory walking on the substratum (Lagersson and Høeg 2002). In the Cryptophialidae these sclerites end freely without a pendulary joint, but only a study of live larvae can tell whether this and the peculiar shape of the sclerites confer some special advantage during surface exploration, or merely indicates that these cyprids need only to traverse very short distances.

On the 4th segment all setae are sited in a terminal group, but both their number and morphology reveal that this condition has evolved by grouping together of the originally terminal and subterminal setae (Fig. 12). A somewhat comparable process has also occurred in some Rhizocephala (Glenner et al. 1989; Høeg and Rybakov 1996). We suggest that the lowermost seta (1) corresponds to seta D, because it is large, baggy and without a pore (Fig. 8F and J). It is also probable that one of the two rudimentary setae in *Australophialus* (7 or 8) corresponds to seta C. In *Australophialus* this leaves five setae (2–6 in Fig. 8J), which all terminate in pores and all resemble the subterminal setae in the cirripede ground pattern. At least four of them must correspond to the subterminal ones, while the supernumerary seta could either be an autapomorphic addition or correspond to seta E, which also sports a distinct terminal pore (Cp. Figs. 8B and J). In this interpretation, *Australophialus* retains the four originally subterminal setae, terminal setae C–E and 1 seta of uncertain identity. In Figs. 8J and 12 we have conservatively identified seta D only.

4.7. Evolution of antennular setation

The variation in antennular setation presently revealed for cyprids of the Acrothoracica resembles in many ways the condition found in the Rhizocephala. In both taxa, the original pattern is subjected to variation that involves rearrangements, loss of setae and extreme specialization of others (Fig. 12). Like the parasitic Rhizocephala acrothoracicans are mostly epibiotic, and the demands this poses on locating the right substratum may possibly have caused a variation in the sensory setae of their cyprids, especially on the 4th segment, that goes beyond what is seen in any thoracicans.

4.8. Larval dispersal and reproduction

Most Acrothoracica (families Lithoglyptidae and Trypetesidae) are normally found singly or only a few together on their hosts. In contrast, the adults of the Cryptophialidae form dense settlements with hundreds or more individuals inhabiting a single host (Batham and Tomlinson 1965; Tomlinson 1969; Kolbasov 2000) and this special ecology is also reflected in their larvae. As a highly unusual specialization their cyprids cannot swim but disperse by walking using the antennules (Batham and Tomlinson 1965; Turquier 1985a; this study). In highly gregarious thoracican barnacles, such as *Semibalanus balanoides*, limitations in the amount of antennular adhesive dictate that their cyprids can walk only about 100 cm when exploring surfaces for settlement (Crisp 1976). It follows that the much smaller cyprids of the Cryptophialidae are limited to even smaller dispersal distances and may explain why the members of this family are always found in isolated but very dense populations. This ecology may also explain why their cyprids can function with a somewhat simplified sensory apparatus compared to species with pelagic cyprids.

In cirripedes the prevailing reproductive strategy is a "high risk" one, where the larvae (nauplii and cyprids) can disperse over long distances, but is offset against a high mortality and the cyprid having little chance of finding a suitable settlement site. Some limitation in dispersal is normal for the Acrothoracica, since most species hatch as cyprids and this entails a very limited duration in the plankton. But a total absence of pelagic larvae as in the Cryptophialidae has only one other parallel in the Cirripedia. Cyprids of the rhizocephalan family Chthamalophilidae similarly lack thoracopods and the adults, which infest other barnacles, are in accordance found in small, isolated populations (Bocquet-Védrine 1972; Høeg et al. 1990). The cryptophialid–chthamalophilid system can obviously only work in habitats where the chance of finding a suitable settlement site by walking alone is quite high and where competition for space is low. Even though both chthamalophilids and cryptophialids have a diecious reproductive system the male cyprids are similarly limited in dispersal. It would therefore be extremely interesting to study whether these specialized species have a higher level of inbreeding compared to species with pelagic larvae.

4.9. Cypris size and brood size

As a side effect of the present study we obtained a semi-quantitative measure of brood size in the Acrothoracica. *Trypetesa lampas* and *T. nassarioides* have nauplii and fairly large brood sizes (Kühnert 1934; Turquier 1970; pers. observation). Among the several species with brooded cyprids studied by us, the largest clutch size was 21 in a female of *Weltneria spinosa* (see Materials and methods). All other females

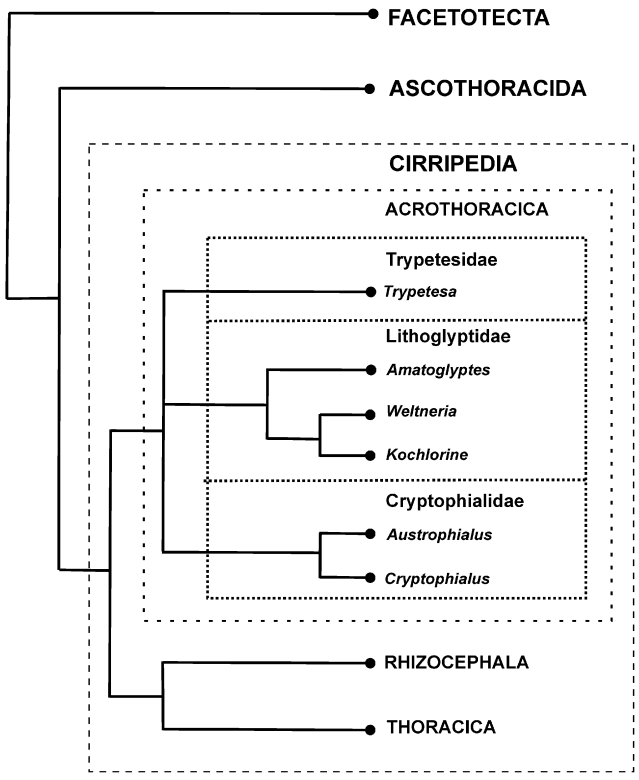

Fig. 13. Tentative phylogeny of the acrothoracican genera studied in this paper and put into a phylogeny of all Crustacea Thecostraca. Neither cyprid nor adult characters can at present resolve the trichotomy between the three acrothoracican families. Branching pattern extrinsic to Acrothoracica from Høeg and Kolbasov (2002) and Pérez-Losada et al. (2002); topology inside Acrothoracica estimated from cyprid characters. Further explanation is found in the text.

from a variety of species had very low clutch sizes, ranging from 1 to 3 larvae. In several species the clutch size is effectively limited by the female being very small compared to the cypris larva (Fig. 3A). This system differs from all other cirripedes, which release hundreds or thousands of larvae and the low reproductive output in these "K-selection" acrothoracicans must have drastic but unknown consequences for their ecology. Rhizocephalan cirripedes resemble acrothoracicans in having non-feeding larvae, but in these parasites the trend is towards very large broods of very small larvae, even in species that release cyprids (Høeg and Lützen 1995). Even the aforementioned Chthamalophilidae have clutch sizes at hundreds of larvae. The difference may be that acrothoracican cyprids have a fairly good chance of finding a suitable substratum, whereas rhizocephalan cyprids must attach to a host animal that often invokes very effective countermeasures against settlement (Ritchie and Høeg 1981; Høeg et al. 1992a, b) resulting in very high mortalities even when the substratum has been found.

4.10. Cypris morphology and phylogeny

The last comprehensive revision of the Acrothoracica was by Tomlinson (1969) and based on traditional, non-cladistic methods. This study is the first time cypris morphology has been examined in a range of acrothoracican species representing all families. Although the database is still limited, we will make a preliminary attempt to use larval characters in the analysis of acrothoracican phylogeny. Based on the large-scale phylogeny of the Thecostraca by Billoud et al. (2000), Høeg and Kolbasov (2002) and Perez-Losada et al. (2002, 2004) we use the Thoracica and Rhizocephala as outgroups and use the ground pattern established for cirripede cyprids by Høeg et al. (2003) to trace characters on the tree (Figs. 12 and 13).

4.10.1. Carapace shape

The much reduced carapace of cryptophialid cyprids is clearly an apomorphy. The remaining species investigated by us have a well-developed carapace which is either elongated (*Armatoglyptes*, *Kochlorine*) or more rounded (*Weltneria*, *Trypetesa*), but we cannot establish the plesiomorphic condition, because carapace shape also varies considerably within the two outgroups.

4.10.2. Lattice organs

The lattice organs of the Cryptophialidae have several autapomorphic features compared to the conventionally shaped ones in the other acrothoracican cyprids studied by us, Jensen et al. (1994a) and Kolbasov et al. (1999). The similarities between the organs in cyprids of the Cryptophialidae and the Rhizocephala Akentrogonida must be considered as homoplasies.

4.10.3. Telson

The telsonic cleft is shallow in *Trypetesa*, of intermediate depth in *Armatoglyptes*, while it almost cleaves the telson in cyprids of *Weltneria* and *Kochlorine*. Rhizocephalan cyprids have a shallow telsonic cleft (Walossek et al. 1996; Rybakov et al. 2002), but, where investigated, the telson is almost completely cleaved in the Thoracica (Glenner and Høeg 1995; Kolbasov et al. 1999). The cypridiform larvae of the Ascothoracida (a-cyprids) and Facetotecta (y-cyprids) have no telsonic cleft so a shallow cleft is here considered as the plesiomorphic condition. The reduced hindbody makes it impossible to score cyprids of the Cryptophialidae for this character.

4.10.4. Antennules

We found interesting variation, especially in the morphology of the fourth segment. In both shape and number of setae the fourth segment in *Armatoglyptes* seems to be very close to the putative ground pattern for

the Cirripedia (Høeg et al. 2003; Blomsterberg et al. 2004). *Weltneria* deviate from the ground pattern in several features (Fig. 12A). The pronounced specialization of seta D into a large, setulated shape, is not present elsewhere in Cirripedia and we consider this as an apomorphy. *Trypetesa* also deviates from the ground pattern, but mostly in having a less distinct specialization-differentiation of the terminal setae. In the Cryptophialidae, the close grouping of the subterminal and terminal setae is an obvious autapomorphy, but no antennular characters indicate any specific relationship to the other acrothoracican genera.

4.10.5. Phylogeny

The cyprids of the Trypetesidae and Lithoglyptidae are in most characters fairly close to the putative ground pattern, while those of the Cryptophialidae are remarkably specialized. The elongated carapace shape might be a synapomorphy for *Armatoglyptes* and *Kochlorine*, but we leave this point moot. An increased degree of telsonic cleavage is a potential synapomorphy for *Armatoglyptes*, *Weltneria* and *Kochlorine*, and within that clade, a cleavage almost to the base may be an additional synapomorphy for *Weltneria* and *Kochlorine* (Fig. 12B). If true, the cleaved telson in at least some thoracicans represent a homoplasy. The reduced carapace, thorax and abdomen-telson, the missing articulation between the proximal antennular sclerites and the joint grouping of all setae on the fourth antennular segments are all clear synapomorphies for *Australophialus* and *Cryptophialus* (Cryptophialidae), but none of these larval characters indicate any particular sistergroup relationship between this monophyletic family and other Acrothoracica. Our tentative scheme in Fig. 13 does not conform to the traditional (non-cladistically based) systematics of the Acrothoracica, which recognizes two suborders: Pygophora (Lithoglyptidae and Cryptophialidae) and Apygophora (Trypetesidae). The Apygophora (= Trypetesidae) was characterized by several clear apomorphies in adult morphology, but adults of the Lithoglyptidae and Cryptophialidae share only symplesiomorphies, whence the Pygophora most likely represent a paraphyletic assemblage. With the few larval characters available, we are therefore left with three apparently monophyletic families in an unresolved trichotomy at the base (Fig. 13).

As is in the Cirripedia Rhizocephala, cypris morphology in the small taxon Acrothoracica exhibits considerable variation compared to the generally more uniform cyprids of the speciose taxon Thoracica. The acrothoracicans also have separate sexes, but it remains to be studied whether their cyprids are sexually dimorphic as in the Rhizocephala (Walker 1985; Glenner et al. 1989; Høeg 1991; Walker and Lester, 1998). The Acrothoracica are important because, as sistergroup to all remaining barnacles, they may confer information on the early evolution of the Cirripedia. We have shown that larval characters can add important information on acrothoracican phylogeny, and this is welcome, since live adults for molecular analysis are very difficult to obtain on a large scale, while brooded larvae can often be easily harvested from the mantle cavity of museum specimens.

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