

External morphology of the two cypridiform ascothoracid-larva instars of *Dendrogaster*: The evolutionary significance of the two-step metamorphosis and comparison of lattice organs between larvae and adult males (Crustacea, Thecostraca, Ascothoracida)

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Abstract

We describe the external morphology of the two cypridiform larval instars (first and second ascothoracid-larvae, or “a-cyprids”) of the ascothoracidan genus *Dendrogaster*. Ascothoracid-larvae of five species were studied with light and scanning electron microscopy, including both ascothoracid-larval instars in *Dendrogaster orientalis* Wagin. The first and second instars of the ascothoracid-larvae differ in almost all external features. The carapace of instar 1 has a smooth surface and lacks pores, setae, and lattice organs, while instar 2 has all these structures. The antennules of the first instar have only a rudimentary armament, the labrum does not encircle the maxillae, thoracopods 2–3 are not armed with a plumose coxal seta, and the abdomen is four-segmented (versus five-segmented in instar 2). Thus, the first ascothoracid-larva of *Dendrogaster* represents a transitional, generally brooded stage between the naupliar stages and the dispersive and fully functional second ascothoracid-larva that accomplishes settlement. The presence of two instars of ascothoracid-larvae (a-cyprids) in members of the order Dendrogastrida differs from the single cypridiform instar found in the Cirripedia (cyprid) and Facetotecta (y-cyprid), and we discuss the evolutionary significance of these ontogenies. We found lattice organs in both the second ascothoracid-larvae and in adult males of *Dendrogaster*. We could not observe both ascothoracid-larvae and males in any single species, but our data suggests that the lattice organs change significantly at the molt between these two instars. The lattice organs of second ascothoracid-larvae have no distinct keel and are situated in wide, shallow pits, whereas they have the ground pattern “crest-in-a-trough” morphology in adult males of two additional species examined for comparison. The positions of the terminal pores of lattice organs 1 and 2 also seem to change during maturation. These findings show that comparative data on lattice organ morphology for phylogenetic purposes must derive from strictly homologous instars, viz., the second

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ascothoracid-larva (a-cyprid) of the Ascothoracida, the y-cyprid of the Facetotecta, and the cyprid of Cirripedia. The ascothoracid-larvae of *Dendrogaster* and those of the family Ascothoracidae have four pairs of lattice organs, which suggests that this genus and family form a monophylum, to the exclusion of *Ulophysema*, which then brings into question the monophyly of the Dendrogastridae. *Ulophysema* is currently placed in the Dendrogastridae, but its second ascothoracid-larva has lattice organs of different and more plesiomorphic number and morphology. We briefly review lattice organ morphology across the Thecostraca. These organs are normally considered structures of the cypridiform larva and their presence in adult (males) Ascothoracida is unique in the Thecostraca. The continued morphological modification of these sensory structures in males compared to ascothoracid-larvae may suggest that they originated in adult thecostracans, but have come to be functional in the cypridiform larvae as well.

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1. Introduction

Recent studies have revealed the importance of larval morphology in reconstructing the phylogeny of the Thecostraca, and the cypridiform larva becomes especially important in understanding how thecostracans first became sessile and diversified into the impressive range of morphologies and modes of life seen in extant forms (Grygier 1983b, 1987d; Itô and Grygier 1990; Jensen et al. 1994a; Kolbasov et al. 1999; Høeg and Kolbasov 2002; Rybakov et al. 2003; Høeg and Møller 2006; Kolbasov and Høeg 2007).

Within the Thecostraca, the subclass Ascothoracida has adopted a parasitic way of life with echinoderms and anthozoans as their hosts. The approximately 100 described species are classified in two orders, Laurida and Dendrogastrida (Grygier 1987b). In the ground pattern of the Thecostraca larval development comprises six instars of pelagic nauplii and a terminal cypridiform larva adapted for attachment (Grygier 1987d; Høeg et al. 2004). Some Ascothoracida retain this scheme and may even have planktotrophic nauplii, but the majority of the species either release lecithotrophic nauplii or brood their offspring inside the mantle cavity until their release as ascothoracid-larvae (Itô and Grygier 1990). The cypridiform larvae of the Thecostraca share a number of putative synapomorphic similarities such as a large head shield (carapace) with five pairs of lattice organs, a pair of prehensile antennules, six pairs of specialized, biramous and natatory thoracopods, and a pair of frontal filaments associated with the compound eyes (Grygier 1987d; Høeg et al. 2004). In the Ascothoracida, the cypridiform stage is traditionally called the “ascothoracid-larva” but was renamed “a-cyprid” by Høeg et al. (2004) to emphasize the homology with the facetotectan y-cyprid (see Itô 1985) and the true cirripede cyprid (see Glenner 1998). Here we use “ascothoracid-larva” whenever we mean “a-cyprid” and employ “ascothoracidan” as an adjective of the taxon. We use the term “head shield” for

the “carapace” of the ascothoracid-larva to emphasize its development as an enlargement of the naupliar head shield (Walossek et al. 1996).

Unlike all other Thecostraca, the species of the order Dendrogastrida (families Dendrogastridae, Ascothoracidae and Ctenosculidae) possess two consecutive cypridiform instars, called first and second ascothoracid-larvae. The first is normally retained within the mantle cavity with only the second being eventually released into the plankton to locate a new host or mate (Brattström 1948; Wagin 1976; Grygier and Fratt 1984; Grygier 1987c; Grygier and Høeg 2005), but one species has been inferred to also have a free first ascothoracid-larva (Grygier 1991a). Species of the Laurida have, as far as is known, only one ascothoracid-larva, called “Tessmann’s larva” in the Lauridae. No one has cultured the larvae through both ascothoracid-larval instars, so the time of development remains unknown.

Sexes are separate in the Ascothoracida, except for the hermaphroditic Petrarciidae (Grygier 1987a, b), and dwarf males, little or just moderately modified compared to the ascothoracid-larvae, are known from most taxa with modified females. Ascothoracidans whose adult females resemble ascothoracid-larvae are probably close to the ground pattern, but in many species the adult females show hypertrophy of the head shield (or mantle) and reduction of segmentation in the antennules, thoracopods, thorax, and abdomen.

The chemosensory lattice organs are highly modified setae and an autapomorphy of the class Thecostraca (Jensen et al. 1994a, b; Høeg et al. 1998; Kolbasov et al. 1999; Høeg and Kolbasov 2002; Rybakov et al. 2003). In the ground pattern, found in the Facetotecta and some Ascothoracida, they occur with five pairs on the head shield of the cypridiform larva, with each individual organ having the form of a crest-like structure (the modified seta) traversing a shallow depression and equipped with a posteriorly situated terminal pore. Within the Ascothoracida there are numerous variations both in the number of lattice

organs and in the position of the terminal pore. Also adult Ascothoracida can possess these organs, whereas in the Cirripedia they disappear completely, when the cyprid metamorphoses into a juvenile (Itô and Grygier 1990; Grygier 1991a; Grygier and Itô 1995; Grygier and Ohtsuka 1995). This shows that lattice organs have been prone to evolutionary modification both within the Cirripedia (Jensen et al. 1994a, b) and within the Ascothoracida, and it begs the question of whether they first evolved to function in larval or adult thecostracans.

Dendrogaster Knipowitsch, 1890 (Dendrogastrida, Dendrogastridae) is the largest genus of the Ascothoracida, with about 30 species, all of which are parasitic in various species of Asteroidea. Normally, the offspring are retained within the brood chamber until released as ascothoracid-larvae, and the dwarf males live there as well. A few species possess free-swimming nauplii (Okada 1925; Wagin 1948, 1954, 1976), but none of those was studied here. Knipowitsch (1890, 1891, 1892) described *Dendrogaster astericola* Knipowitsch, 1890, the type species of the genus, from the White Sea. His thorough study of the second ascothoracid-larva (Knipowitsch 1892) became the first description of the cypridiform larva of the Ascothoracida. The comprehensive studies by Wagin (1948, 1950, 1954, 1957, 1976) provided descriptions or redescriptions of 12 species of *Dendrogaster* and investigations of both instars of the ascothoracid-larvae as well as the dwarf males. Males show little change from the second ascothoracid-larvae, except that the inner face and visceral contents of the head shield valves develop by hypertrophy into a pair of usually elongate and cylindrical sacs, each containing a gut diverticulum and testes. The morphology of the first ascothoracid-larva is less well documented for *Dendrogaster* than that of the second. Wagin (1976) wrote that the first instar has a slightly “infantile” appearance and represents a transitional link between the last metanauplius and the invasive second ascothoracid-larva.

In this study we investigate ascothoracid-larvae in a range of species of *Dendrogaster* using SEM. We put particular emphasis on comparing the two instars of ascothoracid-larvae and on the morphology of lattice organs in both ascothoracid-larvae (a-cyprids) and adult males. The variation in lattice organ morphology is compared with previously investigated ascothoracidans and other Thecostraca.

2. Materials and methods

We examined the ascothoracid-larvae and males of various species of *Dendrogaster* from the vast Wagin collection of Ascothoracida deposited in the Zoological Institute of the Russian Academy of Sciences in

St.-Petersburg; for an inventory of the collection, see Grygier (1991b). Most of the examined larvae had been extracted already by Wagin from the female mantle cavity and stored separately.

All materials were preserved in 70% alcohol. For each species, we investigated with SEM up to about 20 ascothoracid-larvae (minimum of five individuals per available instar of five species) and one male each of two additional species. G.A. Kolbasov (GAK) also mounted some ascothoracid-larvae of various species and a male of *D. astropectinis* on glass slides in glycerine for light microscopy. The material for SEM investigation was dehydrated in acetone and critical-point-dried in CO₂. Dried specimens were sputter-coated with platinum or gold and examined at 15 kV accelerating voltage with a HITACHI S405A or CAMSCAN—S2 SEM (in Moscow), and with a JEOL JSM-35CF SEM (in Vienna). The head shield valves of some larvae were removed to reveal the body proper.

The material studied by GAK in Moscow came from the following localities:

Dendrogaster astericola Knipowitsch, 1890: White Sea, Solovets (Solovetskiy) Islands, app. 65°N, 36°E, more than 20 second ascothoracid-larvae accompanying lectotype female from *Henricia skorikovi* Djakonov, ZIN 2/19632.

Dendrogaster astropectinis (Yosii, 1931): Kamchatka Peninsula, Petropavlovsk-Kamchatskiy, 52°34.4'N, 159°39.1'E, 1500–2000 m, three dwarf males in female, from *Psilaster pectinatus* Fisher, ZIN 1/23383.

Dendrogaster dichotoma Wagin, 1950: Sea of Okhotsk, Terpeniya Cape, 49°01.1'N, 144°37.8'E, two dwarf males in female from *Crossaster papposus* (Linnaeus), ZIN 1/23366.

Dendrogaster elegans Wagin, 1950: Bering Sea, Anadyr Gulf (?), Natalia Bay, app. 61°N, 171°E (the collection data are confused, for this bay is not located in Anadyr Gulf, and the station coordinates doubtfully inferred in Grygier's (1991b) paper, 63°34.4'N, 179°49'W, do not correspond to those of Natalia Bay), depth 170 m, about 10 second ascothoracid-larvae in female from *Leptasterias polaris* (Müller et Troschel), ZIN 3/23381.

Dendrogaster leptasteriae Wagin, 1950: Sea of Okhotsk, 49°01.0'N, 144°48.5'E, depth 127 m, 13 first ascothoracid-larvae accompanying syntypes of *Leptasterias fisheri* Djakonov, ZIN 2/23374.

Dendrogaster murmanensis Wagin, 1950: Sea of Japan, Tatar Strait, 47°10.0'N, 141°48.0'E, depth 165 m, about 18 first ascothoracid-larvae in female from *Crossaster papposus* (Linnaeus), ZIN 1/23368.

Dendrogaster orientalis Wagin, 1950: Sea of Okhotsk, 47°32.0'N, 143°38.2'E, depth 128 m, five first ascothoracid-larvae (exuviae) and 10 second ascothoracid-larvae in female from *Leptasterias orientalis* Djakonov, ZIN 1/23376.

From the same lots, M.J. Grygier (MJG) examined in Vienna two second ascothoracid-larvae of *D. astericola* and three first ascothoracid-larvae each of *D. leptasteriae* and *D. murmanensis*. For comparison, J.T. Høeg (JTH) provided SEM pictures of thecostracan larvae originating from Jensen et al. (1994a, b) and Høeg and Kolbasov (2002), and also some previously unpublished pictures of rhizocephalan cyprids taken by himself and A.V. Rybakov. General findings by MJG and W. Klepal (WK) on lattice organ structure and cuticular ornamentation in ascothoracidans, based on an SEM survey of many genera conducted in Vienna in 1994–95 but hitherto only reported at meetings, are cited as necessary, as unpublished data. Unpublished observations of lattice organs in species of the family Ascothoracidae by GAK are implicitly included in such citations.

In describing the cuticular microstructures or ornaments of the inner surface of the head shield and various other body surfaces, we use the term “fringe” sensu Klepal and Kastner (1980) to mean a single, long and thin, non-setal cuticular structure that appears to be flexible, but we include under this term also some shorter elements. Our “fringes” appear to correspond to “setules” sensu Garm (2004), who uses this term also for some microcuticular features not situated on the shaft of setae.

3. Results

3.1. Head shield

3.1.1. First ascothoracid-larvae

The bivalved head shield (carapace) with inflated valves does not fully enclose the body proper (Figs. 1A, E, 5A, B). It measures 640–700 μm long by 350–480 μm high (L:H ratio \approx 4:3). Not varying much among species, the valves have rounded, not sharp edges, with the ventral margin slightly convex in outline. The dorsal hinge line extends for about 1/3–1/2 of the total length, with conspicuous and wide gaps between the two valves occupying 1/4–1/3 of the anterior and posterior ends of the dorsal side. The shield has a smooth external surface, lacking any structures such as setae, pores, or lattice organs (Fig. 5A, B).

3.1.2. Second ascothoracid-larvae

This larva has a bivalved, oval head shield with a slightly truncated dorso-posterior edge. Size varies even among specimens of a single species (540–900 μm long by 300–550 μm high, L:H ratio \approx 2:1). The valves can enclose the entire body when the posterior part of the trunk is fully flexed (Fig. 5I), but in preserved specimens the trunk is usually bent ventrally so it extends well

beyond the valve margin (Fig. 5C, D). The small, dark, anterior spot shown in Fig. 3(A, G) may be the naupliar eye found in some ascothoracidans. A distinct dorsal hinge occupies about 2/3 of the total length, with conspicuous narrow gaps anteriorly and posteriorly of it and a weak “umbo” in the middle of the dorsal margin or slightly displaced posteriorly. The valves of the shield are low-convex with sharp edges and with rounded anterior and posterior ends. The entire surface of the shield is decorated with a weak pattern of grooves forming elongate polygonal (normally hexa- and pentagonal) cells (Fig. 6A–C, F). Small, single setae 10–15 μm long are situated along the dorsal hinge (Fig. 6A–C). Similar setae and minute pores (no more than 1 μm in diameter) are sparsely distributed over the entire head shield, with rare tiny setae (3–5 μm long) in pits, as well as shallow, obscure pits, also being scattered on the surface (Fig. 6H).

3.2. Lattice organs

3.2.1. Ascothoracid-larvae (Fig. 6)

We describe only lattice organs from the head shield of the second ascothoracid-larva of *D. astericola*, since we could not find them in second ascothoracid-larvae of *D. elegans* and *D. orientalis* owing to bad fixation.

The ascothoracid-larva has four pairs of lattice organs (*lo*) of similar morphology. They are arranged as two anterior and two posterior pairs (Fig. 6A, F), but sometimes the organs of *lo1* or *lo2* lie in staggered positions rather than strictly pairwise.

All the lattice organs are wide, oval and shallow depressions, 5–7 μm long and 3.6–4.6 μm wide. They have a weak or completely reduced medial crest and no pore-field (Fig. 6D, E, G, H). The first pair (*lo1*) lies approximately 1/4 of the way from the anterior end and 20 μm from the dorsal hinge line, converging posteriorly (Fig. 6B). The pit is about 6 μm long and 3.6 μm wide, with the terminal pore sub-central but displaced toward the anterior end and situated on the weak medial keel (Fig. 6D). *Lo2* are situated 110 μm behind *lo1* and 23 μm from the dorsal hinge line, converging anteriorly (Fig. 6C). The pit is about 7 μm long and 4.6 μm wide. The terminal pore lies almost centrally, situated on the posterior end of the small (3 μm long and 1.5 μm wide) medial crest (Fig. 6E). The posterior pairs (labelled as *lo3* and *lo4* for convenience; but see Section 4.5.3 below concerning their true identities) lie closer to one another (about 3 μm apart) and parallel to the dorsal hinge line, 1/4 of the way from the posterior end of the head shield and 19 μm from the dorsal hinge (Fig. 6F). The pits are 5–6 μm long and 4 μm wide, with a reduced medial crest; the tiny terminal pore of each is displaced to the posterior end (Fig. 6G, H).

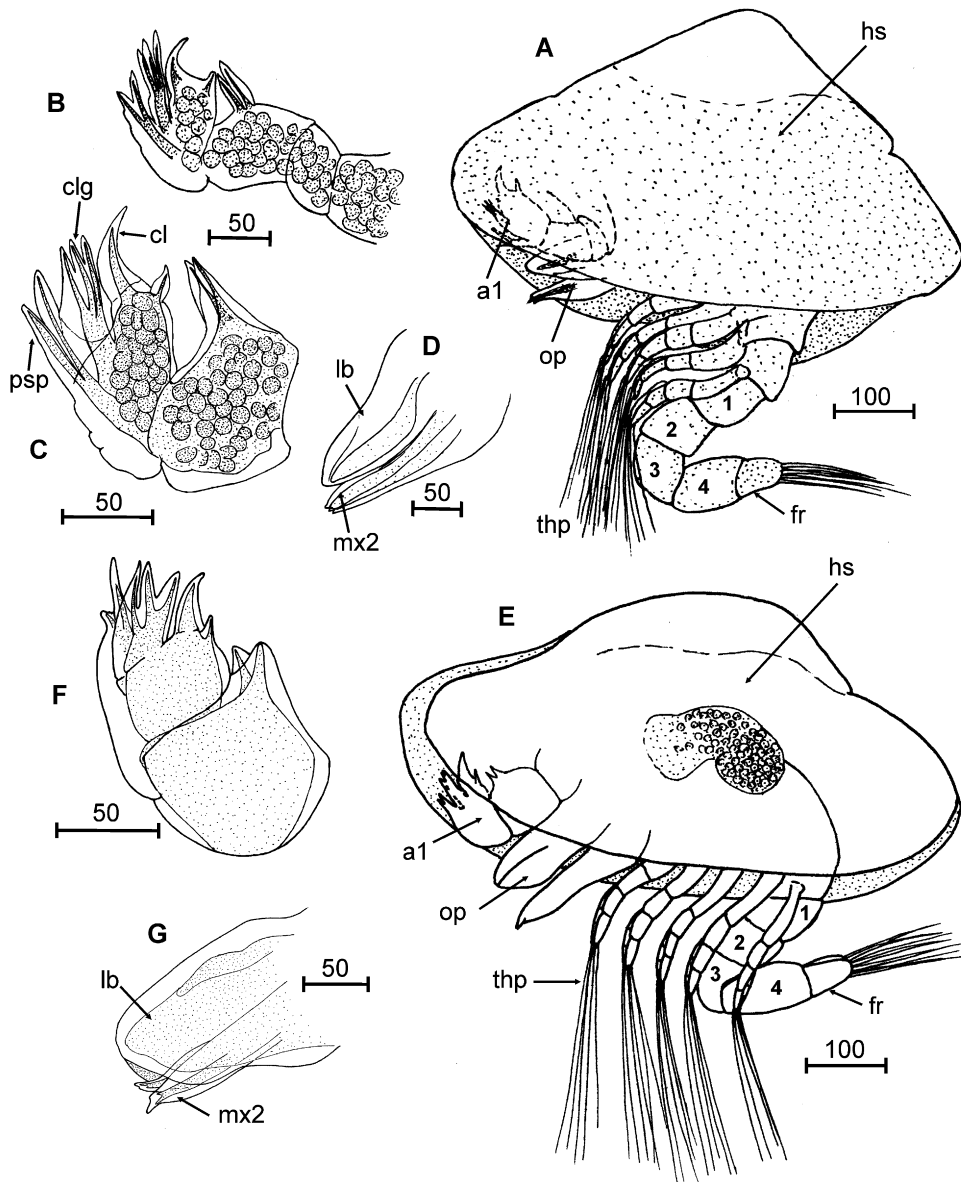


Fig. 1. First ascothoracid-larvae of *Dendrogaster* (A–D) *D. murmanensis*; (E–G) *D. leptasteriae*. (A) Larva, lateral view. (B) Antennule. (C) Distal segments (III–IV) of antennule. (D) Oral pyramid, lateral view. (E) Larva, lateral view. (F) Distal segments (III–IV) of antennule. (G) Oral pyramid, lateral view. *Al* = antennule, *cl* = claw, *clg* = claw guard, *fr* = furcal ramus, *hs* = head shield (carapace), *lb* = labrum, *mx2* = maxillae, *op* = oral pyramid, *psp* = proximal sensory process, *thp* = thoracopods, *I–IV* = antennular segments, *1–4* = abdominal segments. Scale bars in μm .

3.2.2. Males (Fig. 7)

The males of the two examined species also have four pairs of lattice organs. We did not have material to study lattice organs in both larvae and males of any single species, but the morphology seen in males of *D. dichotoma* and *D. astropectinis* differs significantly from that just described for the ascothoracid-larvae of *D. astericola* (Fig. 7A–F). All individual lattice organs, 5–6 μm long and 2–3 μm wide, have a typical “crest-in-a-trough” form with the conspicuous median crest lying within a deep, narrow trough without a pore-field. By SEM we could not clearly see whether the crests are truly attached lengthwise to the

floor of the trough as in the lattice organs of *Ulophysema oeresundense* Brattström, 1936 (see Høeg et al. 1998) or represent free, recumbent tubes.

Lo1 lie 1/5–1/4 of the way from the anterior end and 30 μm from the dorsal hinge line, converging posteriorly (Fig. 7A). In *D. dichotoma* (Fig. 7B) they have a distinct crest with a posterior terminal pore, within a trough 6 μm long and 2 μm wide. The lattice organs in *D. astropectinis* have a similar but larger form, 8 μm long and 2.5 μm wide.

Lo2 lie 90–100 μm behind *lo1* in *D. dichotoma* (170 μm in *D. astropectinis*) and 26 μm from the dorsal hinge in

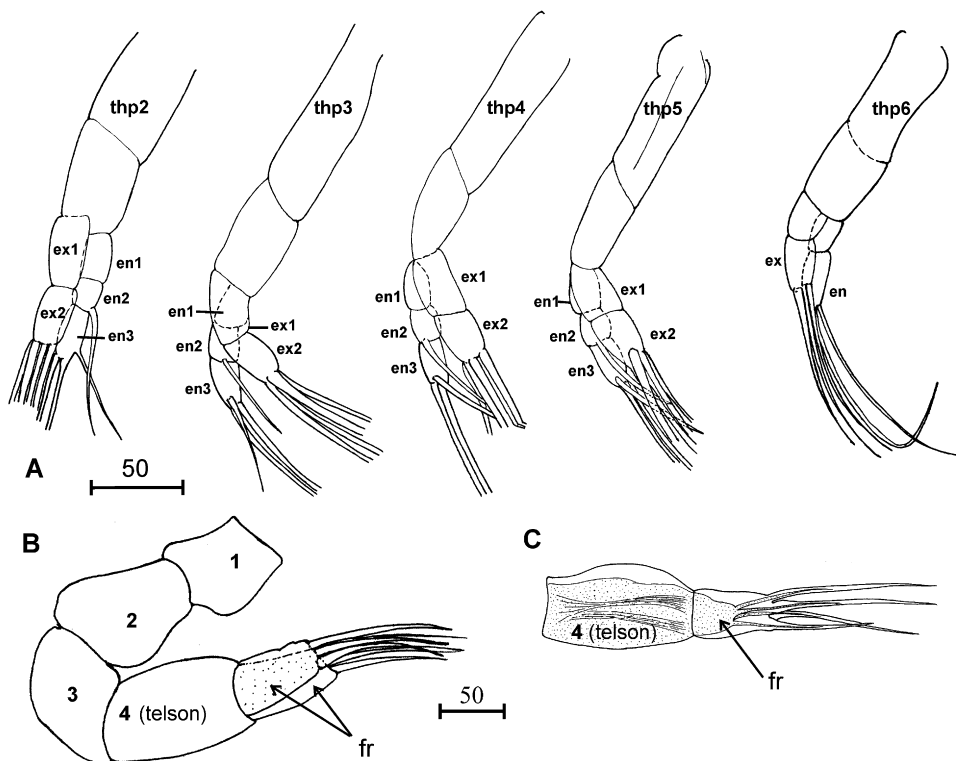


Fig. 2. First ascothoracid-larvae of *Dendrogaster*. (A) *D. orientalis*, thoracopods 2–6. (B) *D. murmanensis*, abdomen with furcal rami, lateral view. (C) *D. leptasteriae*, telson (“abdominal segment 4”) with furcal ramus, lateral view. *En1–3* = endopodal segments 1–3, *ex1–2* = exopodal segments 1–2, *fr* = furcal rami, *thp2–6* = thoracopods, 1–4 = abdominal segments. Scale bars in μm .

both species, converging posteriorly (Fig. 7A). In *D. dichotoma*, the distinct crest is $5.5\mu\text{m}$ long, with an anterior terminal pore and becoming gradually more developed posteriorly (Fig. 7C). In *D. astropectinis* the trough is $9\mu\text{m}$ long and $2.5\mu\text{m}$ wide, but the crest is not as developed posteriorly.

The two posterior pairs of lattice organs lie close to one another at the top of the posterior gap between the head shield valves, $30\mu\text{m}$ apart in *D. dichotoma* (Fig. 7D), $20\mu\text{m}$ in *D. astropectinis*. *D. astropectinis* has straight, $9\text{--}10\mu\text{m}$ long posterior lattice organs, lying parallel to the dorsal hinge. In *D. dichotoma* the third pair (*lo3*) deviate by lying almost perpendicular to the dorsal hinge line (Fig. 7D) and by their $5\mu\text{m}$ by $1\text{--}2\mu\text{m}$ and cone-shaped crest having a terminal pore that we consider as posterior, due to the posteriorly converging orientation of this pair (Fig. 7E). The fourth pair (*lo4*) in *D. dichotoma* has an irregular crescentic shape, $5\mu\text{m}$ long and $1\text{--}2\mu\text{m}$ wide, with a posterior terminal pore (Fig. 7D, F).

3.3. Mantle cavity ornamentation

The inner surface of the head shield valves (i.e., the cuticle of the mantle cavity, or briefly, the mantle) has an armament of cuticular ornaments. We have informally classified most of the ornaments into eight types

of fringe arrays based on such distinctions as fringe length, presence of evident “roots”, spacing within a row or comb, row or comb length and shape, and degree of development as ridges or scales. In the arrays described below, the fringes generally point centripetally, toward the free margin of the mantle (Fig. 9).

3.3.1. First ascothoracid-larvae (Fig. 9A–E). *D. leptasteriae* and *D. murmanensis*

Three types of arrays are present, composed of simple, unbranched fringes in single rows. *Type 1*: linear arrays of non-tapering, $5\text{--}10\mu\text{m}$ long fringes arising close to but independently of each other; forming several rows parallel to the anterior and antero-ventral margins of the head shield (Fig. 9A). *Type 2*: short and curved arrays (“pseudoscales”) with the component fringes/denticles spaced farther apart from each other and much shorter ($0.6\text{--}1.5\mu\text{m}$) than in type 1; located well away from the valve margin anteriorly (Fig. 9A, arrowheads). *Type 3*: well-defined, obliquely arising combs formed of $2\text{--}6\mu\text{m}$ long, basally fused fringes and lining the edges of discrete, flat, and slightly undercut “scales”; found posteriorly and postero-ventrally, more or less parallel to the valve margin (Fig. 9B, C).

D. murmanensis. *Type 4*: linear arrays on the posterior mantle surface (Fig. 9D), composed of short ($3\text{--}6\mu\text{m}$), obliquely arising, usually pointed fringes, these being

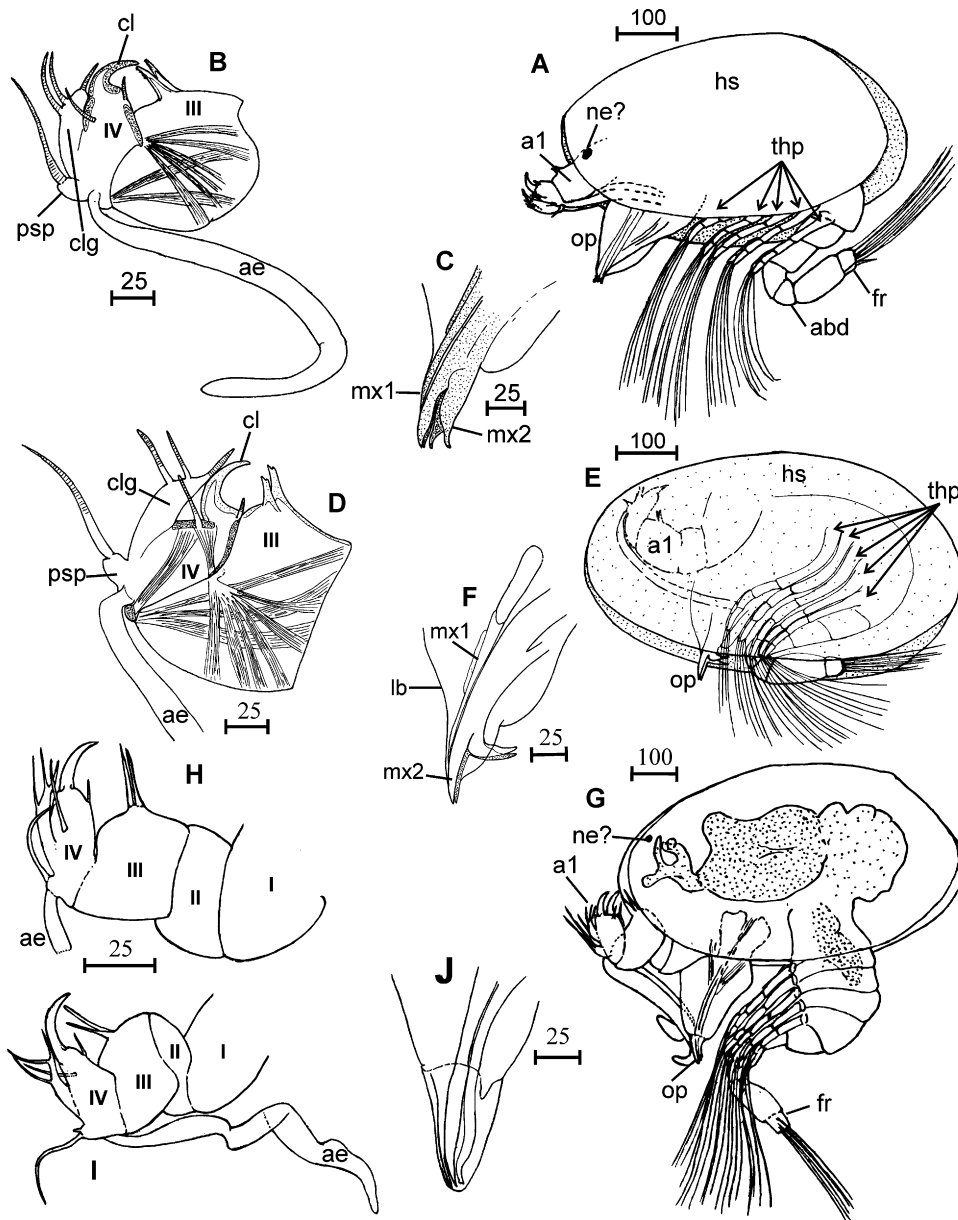


Fig. 3. Second ascothoracid-larvae of *Dendrogaster* (A–C) *D. orientalis*; (D–F) *D. elegans*; (G–J) *D. astericola*. (A) Larva, lateral view. (B) Distal segments (III and IV) of antennule. (C) Oral pyramid. (D) Distal segments of antennule. (E) Larva, lateral view. (F) Oral pyramid. (G) Larva, lateral view. (H, I) Antennules. (J) Oral pyramid. *A1* = antennule, *abd* = abdomen, *ae* = aesthetasc, *cl* = claw, *clg* = claw guard, *fr* = furcal rami, *hs* = head shield, *lb* = labrum, *md* = mandible, *mx1* = maxillule, *mx2* = maxilla, *ne?* = putative nauplius eye, *op* = oral pyramid, *psp* = proximal sensory process, *thp* = thoracopods, *I–IV* = antennular segments 1–4. Scale bars in μm .

adjacent or slightly separated, varying up to twofold in length within a row, and displaying distinct, sometimes very long “roots”, i.e. ridges perpendicular to the array but continuous with the proximal end of each fringe (Fig. 9E).

3.3.2. Second ascothoracid-larvae (Fig. 9F–H).

D. astericola and *D. elegans*

This larva carries three types of fringe arrays that are somewhat differently developed and better consolidated

than in first ascothoracid-larvae, as well as strong, widely spaced denticles 2–5 μm long in two to three rows just inside the valve margin (Fig. 9G). *Type 5*: comb-like arrays, often curved into “pseudoscales”, composed of variable-length fringes with parallel “roots”; found near the valve margin anteriorly and in the postero-ventral to postero-dorsal sector (Fig. 9F). *Type 6*: a continuous, nearly recumbent, membrane-like ridge or fold about 4.6 μm broad with a distinct inner boundary, running along the mantle margin in the same regions as type 5,

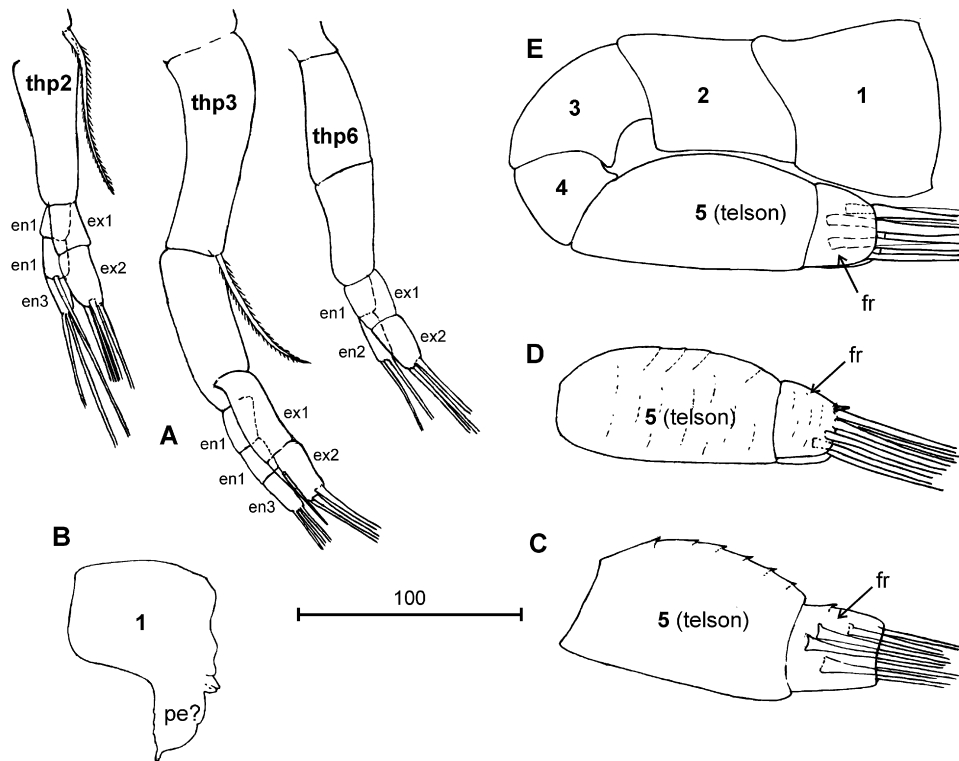


Fig. 4. Second ascothoracid-larvae of *Dendrogaster*. ((A–C) *D. astericola*). (A) Thoracopods 2, 3, and 6. (B) first abdominal segment. (C) telson (abdominal segment 5) with furcal rami, lateral view. (D) *D. orientalis*. Telson (abdominal segment 5) with furcal rami, lateral view. (E) *D. elegans*. Abdomen with furcal rami, lateral view. *En1–3* = endopodal segments 1–3 in thoracopods, *ex1–2* = exopodal segments 1–2 in thoracopods, *fr* = furcal rami, *pe?* = probable penis rudiment, *thp2,3,6* = thoracopods, *1–5* = abdominal segments. Scale bar in μm .

with closely spaced, minute ($0.5\text{--}1\mu\text{m}$) denticles or fringes along its outer edge (Fig. 9F, arrowheads; 9G), and with occasional gaps exposing underlying “knobs” (Fig. 9G, arrowhead) and sometimes also associated with tiny pores (Fig. 9G, arrows). *Type 7*: straight and continuous comb-like arrays similar to but more pleat-like than the type-6 structure, with longer ($0.8\text{--}3\mu\text{m}$), denticle-like fringes forming the combs; up to two anterior and four posterior arrays present, parallel to and inwards from the type-6 structure; not illustrated for *D. astericola* but also observed in the second ascothoracid-larva of *D. elegans* (Fig. 9H).

D. elegans. Type 8: short arrays, about $20\mu\text{m}$ long and curved to form “pseudoscales”, each showing a transition along its length from small, separated fringes/denticles into an organized comb; especially well developed away from the margin in the posterior region (Fig. 9H, asterisks).

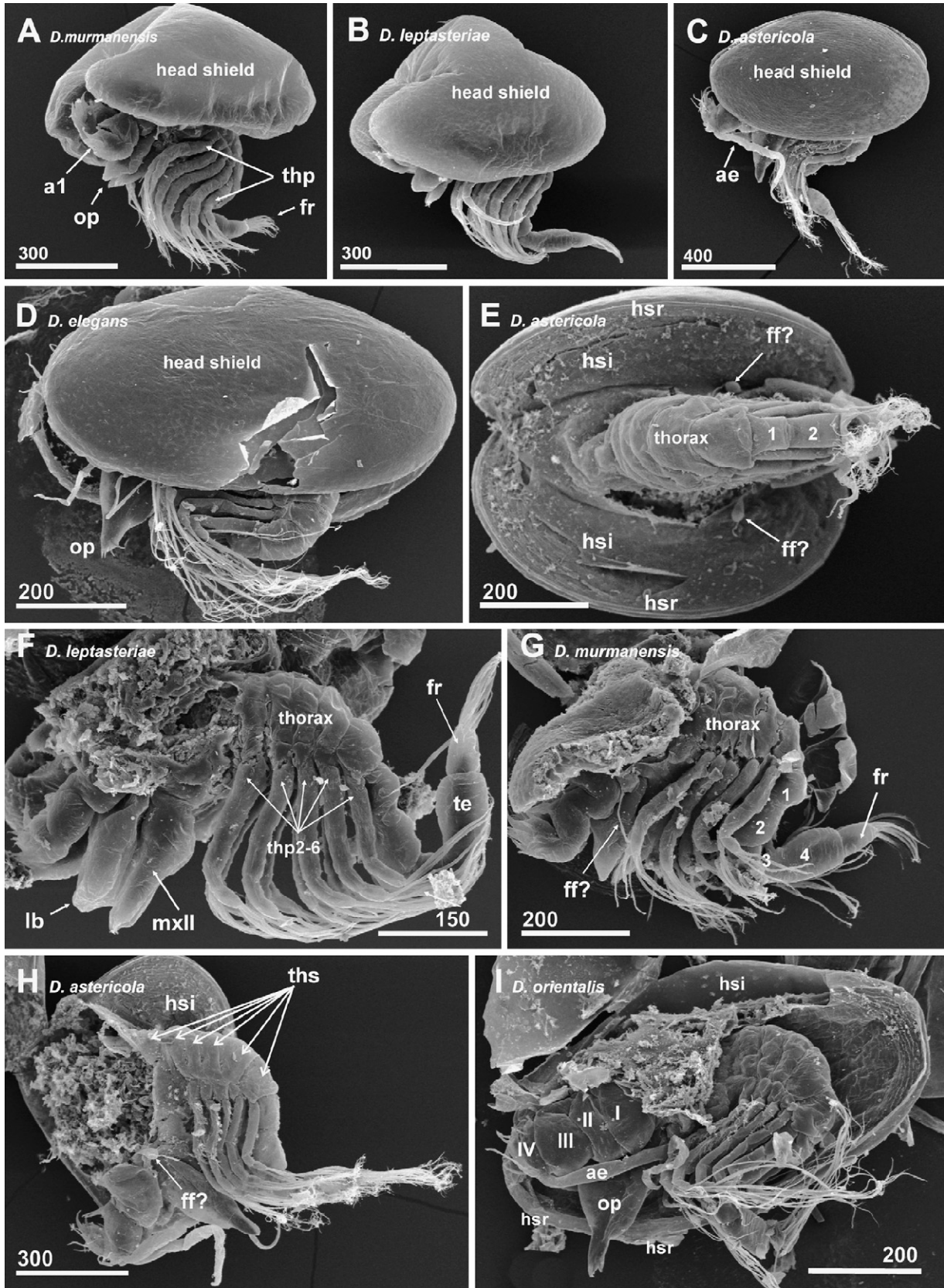
3.4. Antennules

Both instars of ascothoracid-larvae have four-segmented antennules, which assume a W-shape when retracted into the mantle cavity (Figs. 5G–I, 10A, C).

3.4.1. First ascothoracid-larvae

The antennules appear to be not yet fully functional. The cuticle is partly exfoliated, only loosely investing the appendage, with indistinct segment boundaries and carrying rudimentary armament and ornamentation (Fig. 1B, C, F). Internally, the appendage has no clear muscle fibers, only a “cellular pattern” (Fig. 1B, C). The first segment is somewhat trapezoidal and short. The second segment is rhombic or rectangular (Figs. 1B, 10A). The third segment, the biggest, is irregularly pentagonal with a pair of preaxial/dorsal spines that are $25\text{--}50\mu\text{m}$

Fig. 5. First and second ascothoracid-larvae of *Dendrogaster*, SEM. (A, G) *D. murmanensis*. (B, F) *D. leptasteriae*. (C, E, H) *D. astericola*. (D) *D. elegans*. (I) *D. orientalis*. (A, B) First instar, lateral view. (C, D) Second instar, lateral view. (E) Second instar, ventral view. (F, G) body proper of first instar (valves of head shield removed), lateral view; (H, I) Body proper of second instar (left valve of head shield removed), lateral view. *Al* = antennules, *ae* = aesthetasc, *ff?* = putative frontal filament complex, *fr* = furcal rami, *hsi* = inner surface of head shield, *hsr* = free rim of head shield, *lb* = labrum, *mxII* = maxillae, *op* = oral pyramid, *te* = telson, *thp* = thoracopods, *ths* = thoracic segments, *I–IV* = antennular segments, *1–4* = abdominal segments. Scale bars in μm .



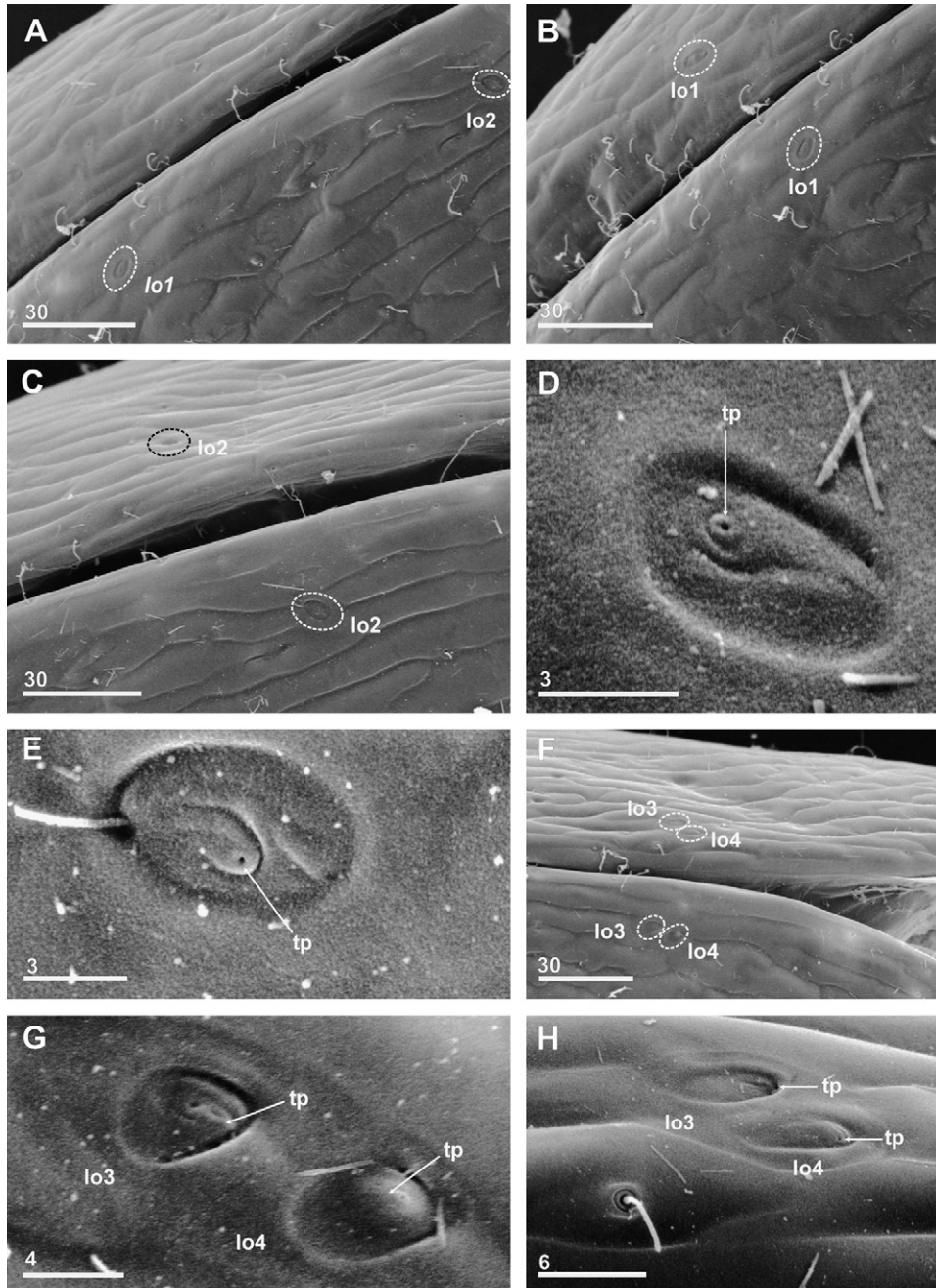


Fig. 6. Lattice organs of second ascothoracid-larva of *Dendrogaster astericola*, anterior end left in all figures. (A) Anterior lattice organs. (B) First pair of lattice organs. (C) Second pair of lattice organs. (D) Lattice organ 1. (E) Lattice organ 2 (seta-like artifact at anterior end). (F) Posterior two pairs of lattice organs. (G, H) Lattice organs 3, 4. *lo1-4* = lattice organs, *tp* = terminal pore. Scale bars in μm .

long and quite thick due to accumulations of exfoliated cuticle (Figs. 1B, C, F, 10A). There is no oblique suture at the preaxial margin of the segment. The terminal, fourth segment bears the proximal sensory process, the claw guard, the claw and setae (Figs. 1C, F, 10B). The proximal sensory process carries two short, thick setae. The proximal one, obviously corresponding to the aesthetasc in the second ascothoracid-larva, is 8–30 μm long and may be either roughly equal to, or shorter than,

the 30–50 μm long distal seta. The claw guard bears three short (10–25 μm long), blade-like, terminal setae. The massive terminal claw is 30–40 μm long, with three blade-like setal rudiments at its base, one on the segment's margin and one on each side (Fig. 10B).

3.4.2. Second ascothoracid-larva

Segments 2–4 bear short rows of minute fringes/denticles similar to the type-2 arrays described above

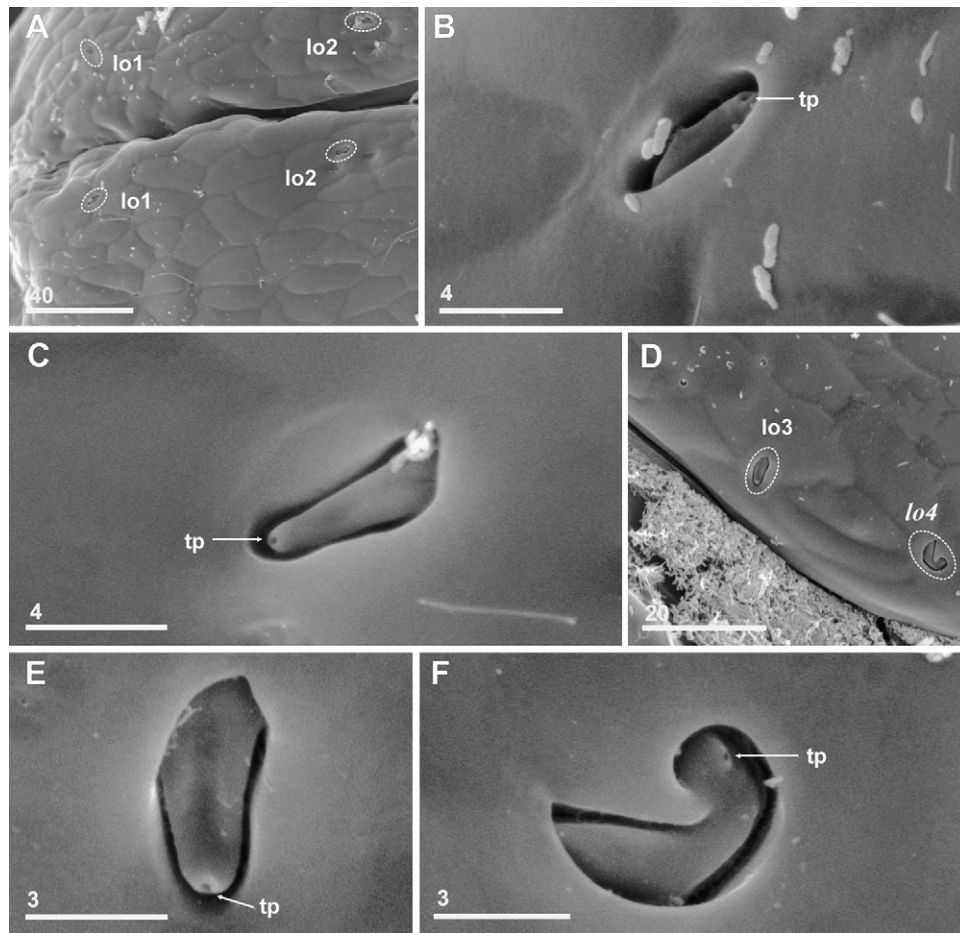


Fig. 7. Lattice organs of males of *Dendrogaster dichotoma*. (A) Anterior lattice organs 1, 2. (B) Lattice organ 1 (anterior end left). (C) Lattice organ 2 (anterior end left). (D) Posterior lattice organs 3, 4 (anterior end in left upper angle). (E) Lattice organ 3 (anterior end left). (F) Lattice organ 4 (anterior end left). *lo1-4* = lattice organs; *tp* = terminal pore. Scale bars in μm .

from the mantle (Fig. 10D, E, G, H). Distinct muscles in the form of extensors, flexors, and retractors are now clearly seen within the segments (Fig. 3B, D). The trapezoidal first segment is the biggest. The second segment has a rhombic, rectangular, or irregular form (Figs. 3H, I, 10C). The third segment (Figs. 3B, D, H, I, 10C, D, F, H) is irregularly quadrangular, and now has a distinct, oblique suture at the preaxial margin, corresponding to the border line between two fused segments of an ancestral form (Wagin, 1950, 1954, 1976). The preaxial margin has a pair of sharp, 20–70 μm long spines in the middle (Figs. 3B, D, H, I, 10C–G). The form and size of these spines vary among species of *Dendrogaster*. They are needle-shaped and longest (50–70 μm) in *D. astericola* (Figs. 3H, I, 10F), shorter (25–30 μm) in *D. elegans* (Figs. 3D, 10E), and shortest (18–30 μm) with a bifid tip in *D. orientalis* (Figs. 3B, 10D).

The fourth segment carries a very long (300–400 μm), ribbon-shaped aesthetasc at its base (Figs. 3B, D, H, I, 5I), almost separated from the remainder of the proximal sensory process, which bears a simple and finely annulated

seta (70–90 μm long) on its distal end (Fig. 10D, E). The proximal sensory process is situated near the base of the elongated claw guard, which bears three annulated setae with small barbs (Figs. 3B, D, 10D–G). All setae are shifted toward the distal end of the claw guard, but there is some variation in their distribution. One seta is always found on the distal end of the claw guard, and a proximal seta 2/3 of the way from the base of the postaxial/free side. The intermediate seta is grouped with the proximal one in *D. orientalis* (Fig. 3B), displaced close to the distal one in *D. astericola* (Fig. 3H, I), or set halfway between them in *D. elegans* (Fig. 3D). The conspicuous claw is about 30–40 μm long in *D. orientalis* (Figs. 3B, 10D), 40–50 μm in *D. elegans* (Figs. 3D, 10E), and 70–80 μm in *D. astericola* (Figs. 3H, I, 10F, G) and has a smooth surface, lacking small denticles.

3.5. Frontal filament complex

Both instars carry structures, which we assume are frontal filament complexes (Figs. 5E, G, H, 10A, I).

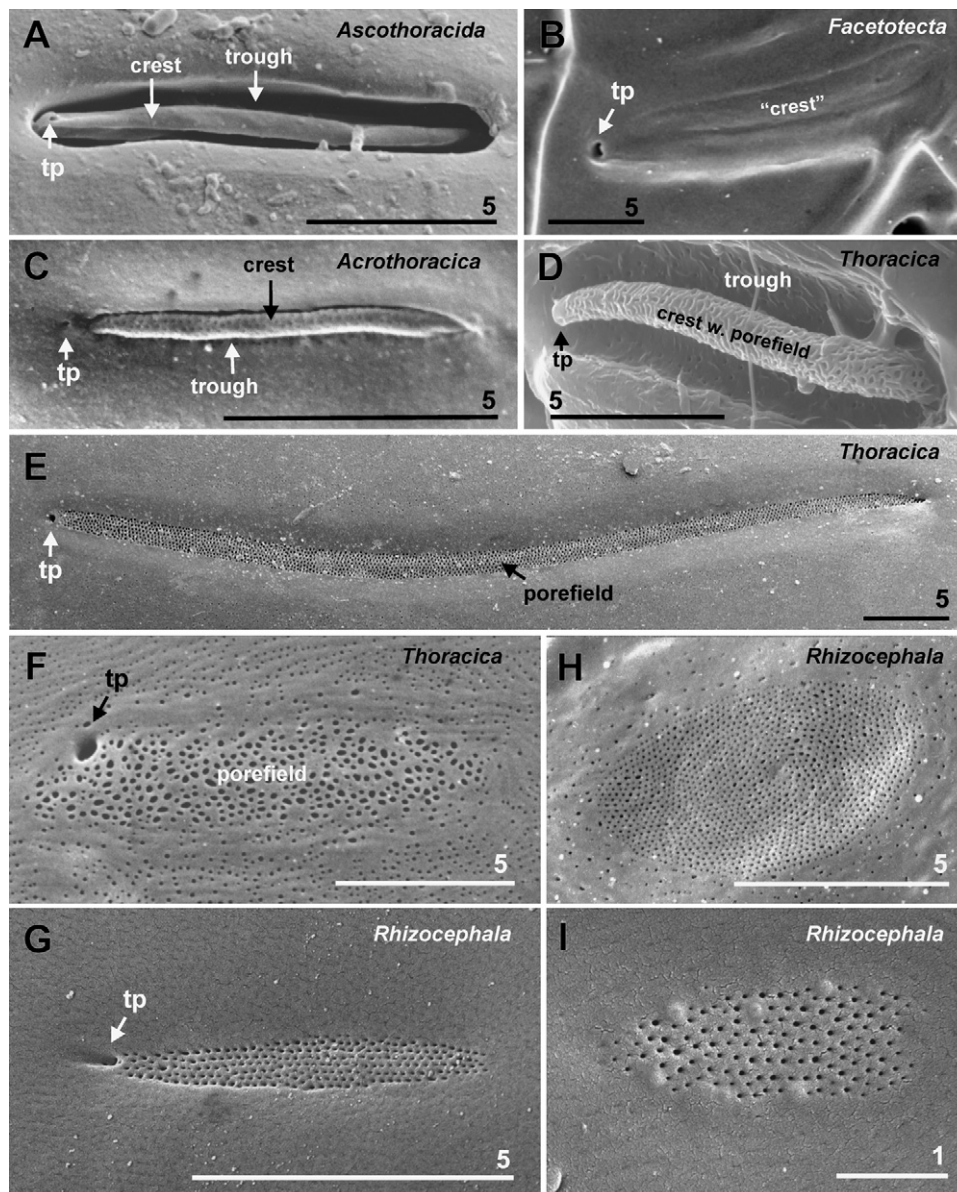


Fig. 8. Lattice organ morphology in cypridiform larvae of the Thecostraca. For comparison, all lattice organs oriented with the terminal pore to left. See also Fig. 6 and text. (A) Ascothoracida, *Ulophysema oeresundense*, second ascothoracid-larva, typical “crest-in-a-trough” type. (B) Facetotecta, *Hansenocaris itoi*, cypris-y, “crest-in-a-trough” type with subdued crest. (C) Acrothoracida, *Trypetesa lampas*, cyprid, crest-in-a-trough with minute pores on crest that do not reach sensory chamber beneath. (D) Thoracica, *Capitulum mitella*, cyprid, intermediate type with numerous deep pores on crest-in-a-trough. (E) Thoracica, *Lepas australis*, cyprid, elongated pore-field type. (F) Thoracica, *Balanus improvisus*, cyprid, typical pore-field type. (G) Rhizocephala, *Sacculina confragosa*, cyprid, typical pore-field type. (H) Rhizocephala, *Clistosaccus paguri*, cyprid, oval-circular pore-field without terminal pore. (I) Rhizocephala, *Loxothylacus panopaei*, cyprid, *lo5*, oval pore-field without terminal pore, *lo1* and *lo2* in this species are typical elongated pore-field types with terminal pores. *tp* = terminal pore. Scale bars in μm .

They are paired and situated laterally to the mouthparts just behind the first segment of each antennule. The morphology is similar in both instars and consists of a rounded or drop-like basal part, about 40–60 μm long, which bears the slender and ca. 100 μm long distal part, the filament proper (Fig. 10A, I).

3.6. Mouthparts

Ascothoracid-larvae have large and prominent mouthparts, situated behind and between the bases of the antennules and comprising principally the labrum and the maxillae (Figs. 1A, D, E, G, 3A, C, E–G, J,

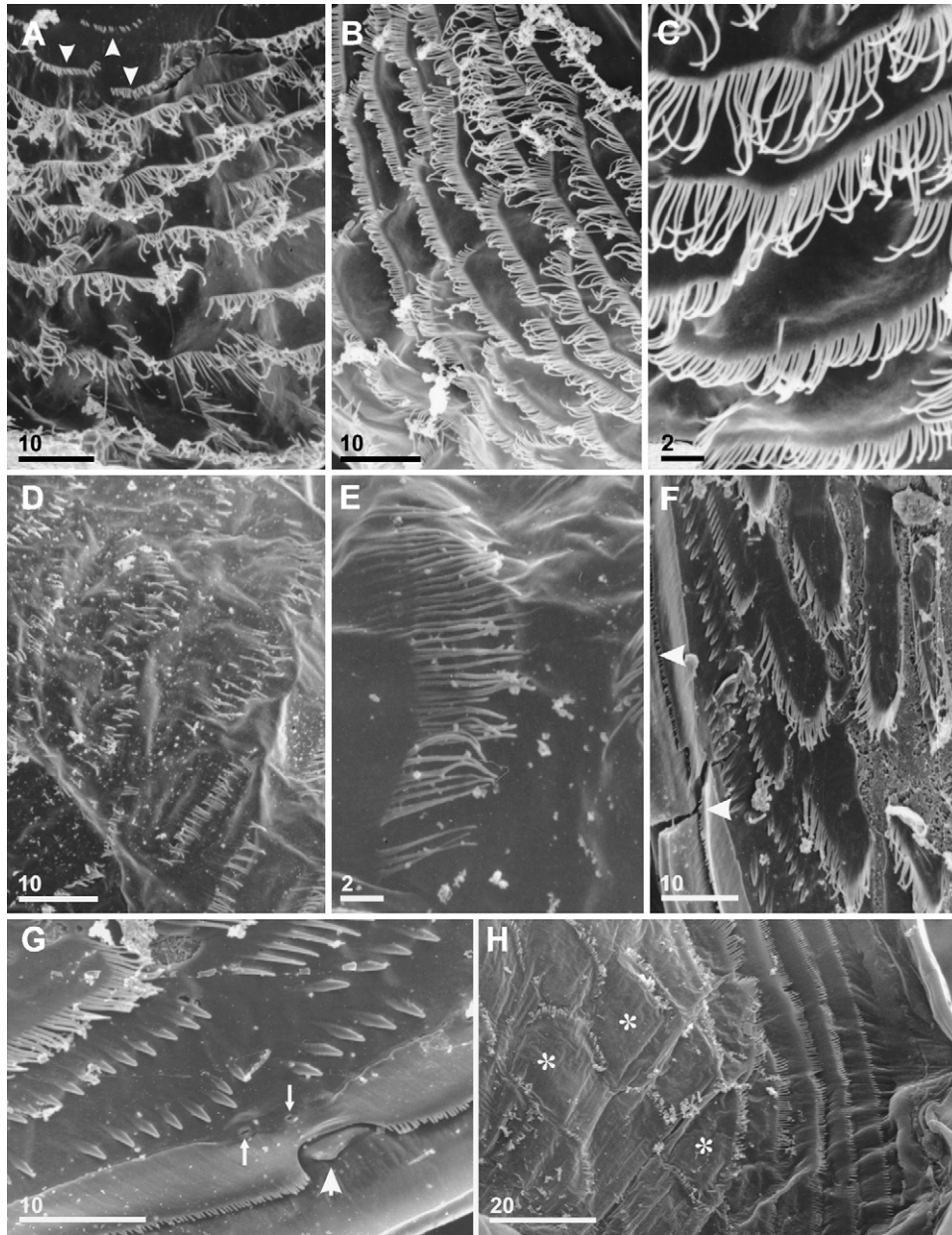


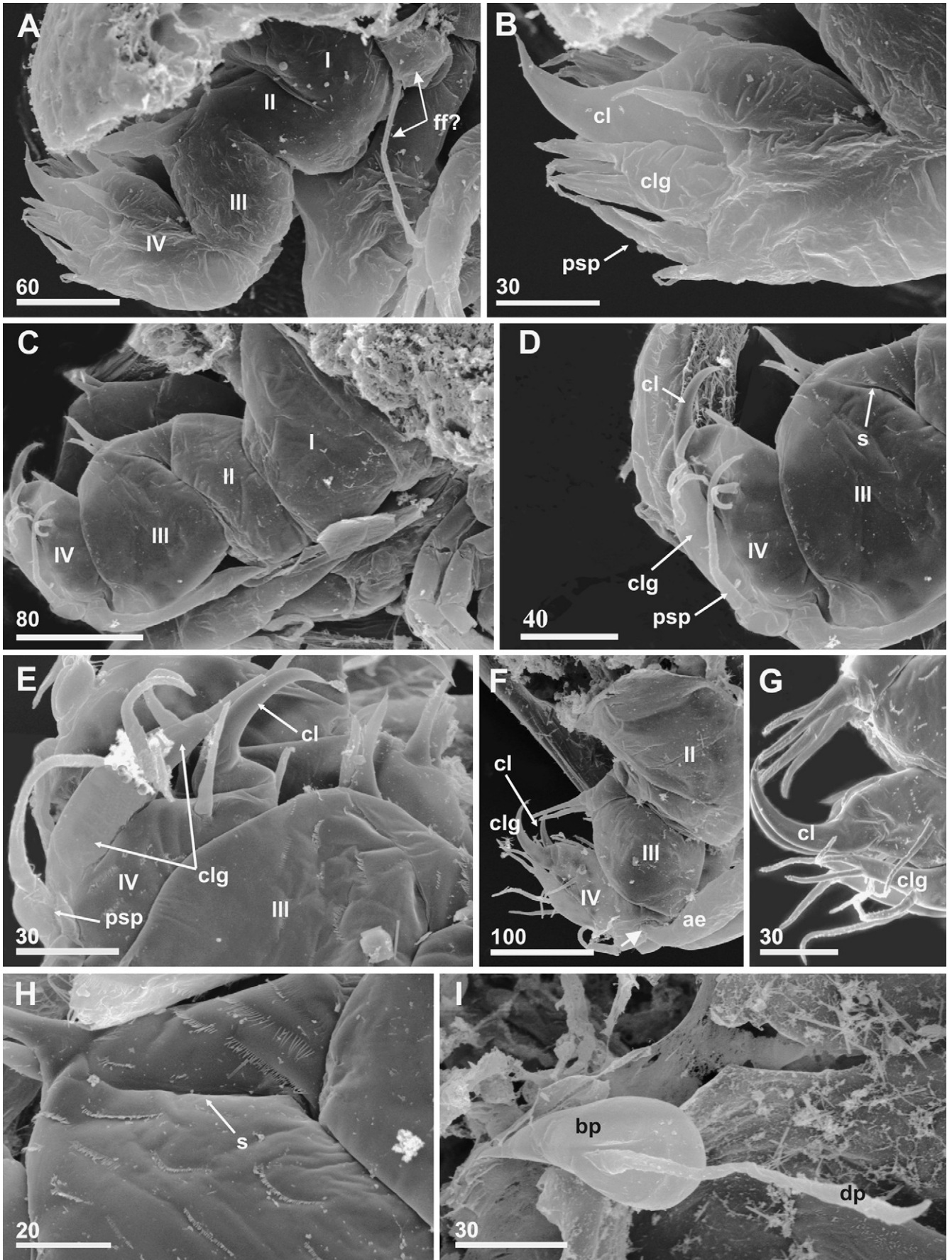
Fig. 9. Types of ultrastructure of mantle lining (inner surface of head shield = carapace) of ascothoracid-larvae of *Dendrogaster*. (A–C) *D. leptasteriae*, first instar; (D, E) *D. murmanensis*, first instar; (F, G) *D. astericola*, second instar; (H) *D. elegans*, second instar). (A) Rows of medium-long fringes (Type 1) and “pseudoscales” (Type 2: arrowheads) of short fringes/denticles, anterior and anterio-ventral margins. (B, C) Combs of short to medium-sized fringes (Type 3), posterior and postero-ventral margins. (D) Short, pointed fringes (Type 4), posterior part. (E) Comb of short, pointed fringes, posterior part. (F) Obliquely arising, comb-like arrays of fringes (Type 5) and submarginal membrane (Type 6: arrowheads), posteroventral margin. (G) Tooth-like denticles and gap in submarginal membrane (Type 6), with knob (arrowhead) and pair of tiny pores (arrows), posterior margin. (H) Comb-like rows of fringes (Type 7) and short “pseudoscales” (Type 8: asterisks), posterior part. Scale bars in μm .

5F–I; 11A–D). Their structure differs between the first and second instars and in the latter they jointly form an oral pyramid.

3.6.1. First ascothoracid-larvae

The mouthparts are about 200–230 μm long, consisting of a tongue-shaped labrum and long,

rod-shaped maxillae (Figs. 1D, G, 5F, 11A). The labrum does not encircle the maxillae, and may only partially shield them laterally. The tips of the maxillae of different species are often bifid, with small and almost straight terminal prongs (Fig. 1G). First ascothoracid-larvae seem to lack rudiments of both mandibles and maxillules.



3.6.2. Second ascothoracid-larvae

The oral pyramid is ca. 250–300 µm long and consists of a bulbous proximal part and an elongated distal part (Fig. 5H, I). The labrum encircles the mouthparts completely, with only the tips of the maxillae being free at the distal end (Figs. 3C, F, J, 11B, C). The maxillae have a typical piercing shape, but their tips differ among species. In *D. elegans* and *D. orientalis* they have harpoon-like, bifid tips (Fig. 3C, F). In *D. elegans*, the posterior prong is strongly deflected and perpendicular to the anterior one (Figs. 3F, 11B), whilst the prongs are almost parallel to each other in *D. orientalis* (Figs. 3C, 11C). The form of the tip corresponds to that described for the respective adult females (Wagin 1950), but, being movable, the position of the posterior prong should not be considered strictly as a species-specific character. In *D. astericola* we did not, contrary to Knipowitsch (1892), observe clearly bifid tips in the maxillae (Fig. 3J), but they may have been completely hidden by the labrum. Thin, stylet-shaped structures appear to adjoin the maxillae in this species (Fig. 3C, F), but without dissecting we cannot be sure whether they represent vestiges of the mandibles and maxillules, or tube-like endoskeletal elements.

3.7. Thorax and thoracopods

The thorax, 260–300 µm long in the first ascothoracid-larva and 350–400 µm in the second, is arched and lies in the posterior half of the mantle cavity (Fig. 5F–I). As in other thecostracans, it consists of six segments if the penis-bearing segment (see below) is excluded from the count. It carries five pairs of biramous thoracopods on segments 2–6, which we number as thoracopods 2–6 to conform to the thoracomere number and take into account the fact that most thecostracan larvae and adults have a pair of thoracopods on thoracomere 1 as well. The first thoracic segment lacks thoracopods, having only a pair of small hillocks, which may be rudiments of paired limbs or precursors of the gonopore papillae of the adult female (Fig. 11D). There are no dorsal horns on the anterior thoracic segments, nor any filamentary appendages laterally on the first segment. The sixth segment has small, smooth-surfaced, lateral

epaulets at the insertions of the thoracopods (Fig. 11E). Segmentally arranged pairs of rectangular sclerites fill the pleural area between the tergites and the thoracopods (Figs. 5F–I, 11D, E). On the side of the thorax there are, at least in second ascothoracid-larvae of *D. astericola*, dorso-ventrally aligned and sometimes curved rows or narrow bands of short fringes (Fig. 11H).

All thoracopods have long protopods, but their morphology differs between first and second ascothoracid-larvae. In the first instar of *D. orientalis*, *D. murmanensis* and *D. leptasteriae*, the protopods have a smooth surface without any cuticular ornaments and an oblique suture divides them into coxa and basis (Fig. 5F, G). In thoracopods 2–5 the coxae are twice as long as the bases, whereas in thoracopod 6 they have about the same length. The exopods consist of two segments, with the distal one of thoracopods 2–5 bearing four simple terminal setae (Figs. 2A, 11A), but only three on thoracopod 6. Thoracopods 2–5 have three-segmented endopods, the medial segment bearing a single simple seta and the distal segment three terminal setae. Thoracopod 6 has a two-segmented endopod with two terminal setae on the distal segment (Fig. 2A).

The second ascothoracid-larvae have a single row of strap-like structures (interpreted as compound fringes) on the outer margins of the coxae in thoracopods 2–3 and, at least in *D. astericola*, on the most proximal part of thoracopod 4 (Fig. 11D–F, I). These straps bear along both edges fine side branches that represent the distal parts of the component fringes. In thoracopods 2 and 3, a conspicuous, 60–85 µm long, plumose setae with long setules sits at the postero-distal angle of the coxa (Figs. 4A, 11D–G; for *D. orientalis* we only have information about the coxal seta of thoracopod 3). In all the thoracopods, rows of short fringes/denticles lie parallel to the outer margin of the coxa (Fig. 11F, I). Proximally, the coxa of thoracopod 6 has a break or secondary articulation, close to the epaulet (Fig. 11E). In *D. astericola*, the two-segmented exopods have three long setae terminally on the distal segment (Figs. 4A, 11E) In thoracopods 2–5, the three-segmented endopods all carry a single seta on the middle segment and three terminal setae on the distal segment, whereas

Fig. 10. Antennules and frontal filament complex of ascothoracid-larvae of *Dendrogaster*. (A, B) *D. murmanensis*, first instar. (C, D, H) *D. orientalis*, second instar. (E) *D. elegans*, second instar. (F, G, I) *D. astericola*, second instar. (A) Antennule and frontal filament complex, lateral view. (B) Distal (4th) segment of antennule with claw and claw guard. (C) Antennule, lateral view. (D, E) Distal segments (III, IV) of antennule. (F) Antennule showing origin of aesthetasc (arrowhead), lateral view. (G) Dorsal (preaxial) parts of segments III and IV. (H) Third (penultimate) antennular segment, lateral view. (I) Frontal filament complex with basal bulbous and distal filamentous parts. *ae* = aesthetasc, *bp* = basal part of putative frontal filament, *cl* = claw, *clg* = claw guard, *dp* = distal part of putative frontal filament, *ff?* = putative frontal filament complex, *psp* = proximal sensory process, *s* = suture, corresponding to border of two fused segments, *I–IV* = antennular segments. Scale bars in µm.

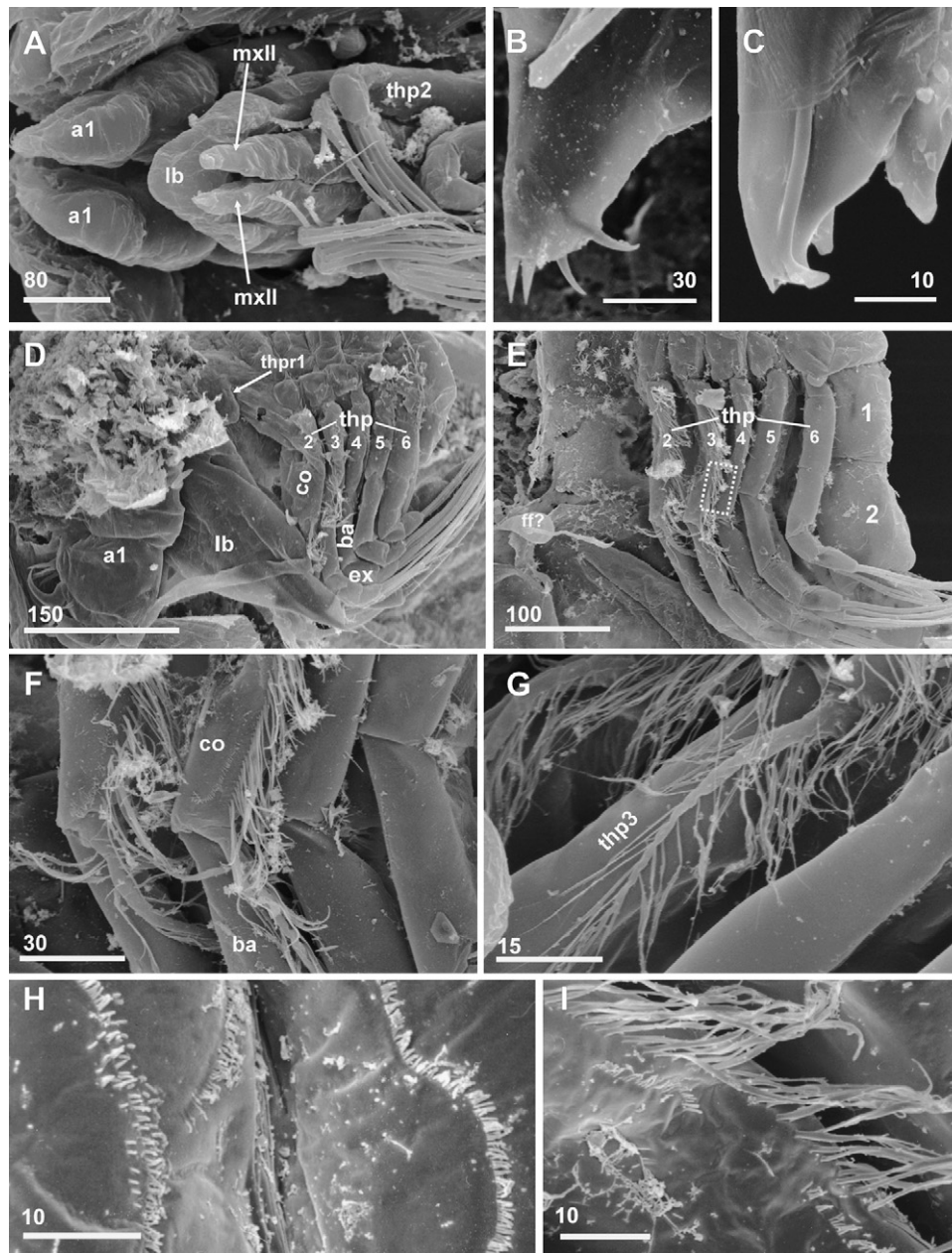


Fig. 11. Oral pyramid and thoracopods of first instar (A) and second instar (B–I) ascothoracid-larvae of *Dendrogaster*. (A) *D. leptasteriae*. (B, D) *D. elegans*. (C, G) *D. orientalis*. (E, F, H, I) *D. astericola*. (A) Anterior part of body proper, ventral view. (B, C) Distal parts of oral pyramid, lateral view. (D, E) Thoracopods, lateral view. (F) Protopods of thoracopods 2–5. (G) Coxal setae on thoracopod 3. (H) Lateral ctenae of short fringes on thoracic tergites 3 (left) and 4 (right). (I) Short denticles/fringes and strap-like fringes on coxae of thoracopod 3 (area of dotted rectangle in E). *a1* = antennules, *ba* = basis, *co* = coxa, *ex* = exopod, *ff?* = putative frontal filaments, *lb* = labrum, *mxII* = maxillae, *thpr1* = rudiment of thoracopod 1, *thp* = thoracopod(s), *1, 2* = abdominal segments. Scale bars in μm .

in thoracopod 6, the two-segmented endopod carries two terminal setae on the distal segment (Fig. 4A).

3.8. Abdomen and furcal rami

The abdomen is here understood as starting with the first limbless segment following those bearing the thoracopods.

3.8.1. First ascothoracid-larvae

The abdomen consists of four segments, including the terminal telson (Figs. 1A, E, 2B, 5F, G). Segments 1–2 are widest posteriorly, while segment 3 is quadrangular. The telson is elongated with a slightly arched dorsal margin and bears a pair of unbranched, one-segmented furcal rami (Figs. 2B, 12A). We found no ventral process, often identified as a penis rudiment, on the first

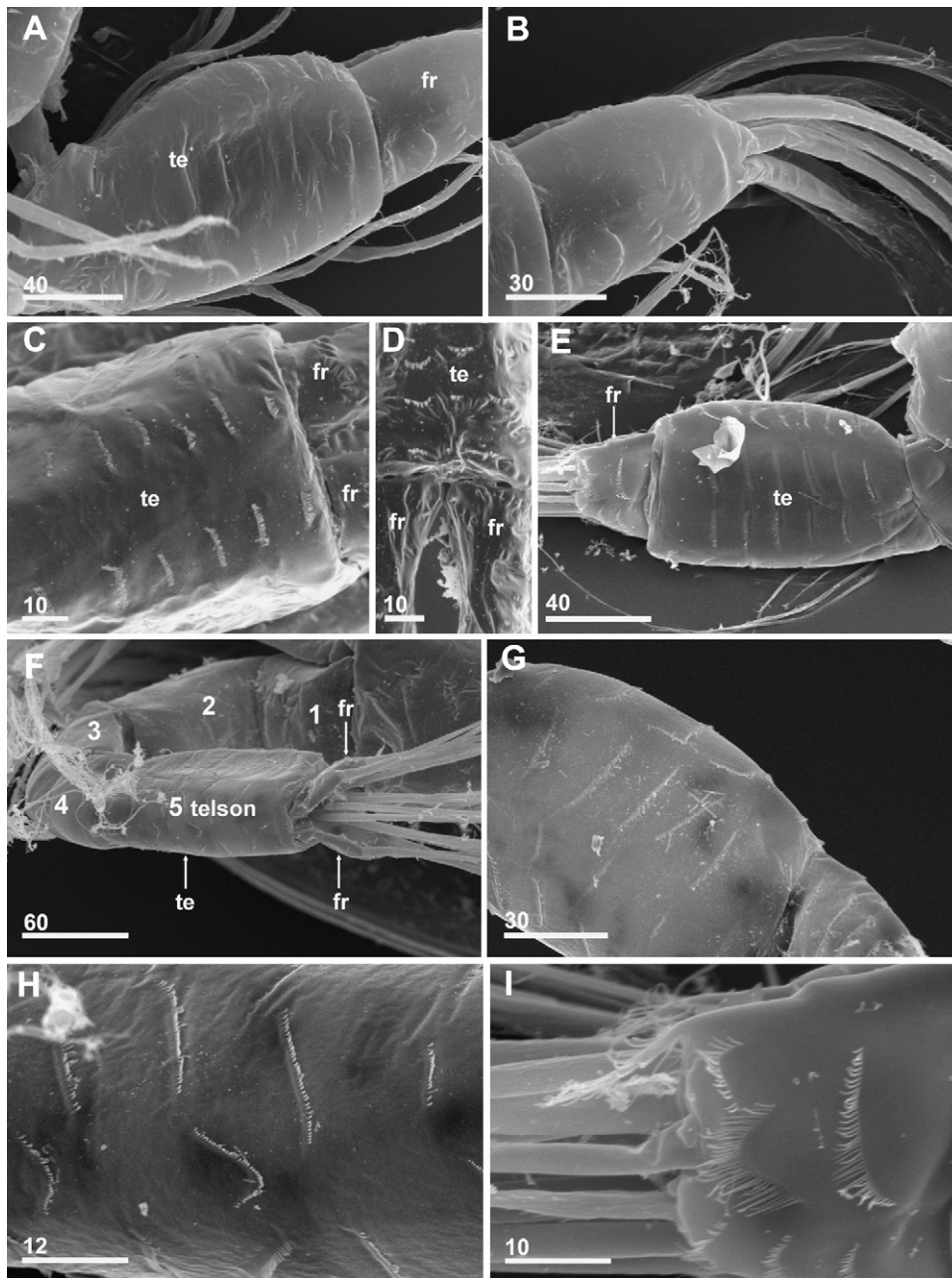


Fig. 12. Telson and furcal rami of ascothoracid larvae of *Dendrogaster*, (A–D) first instar, (E–I) second instar. (A–C) *D. murmanensis*. (D) *D. leptasteriae*. (E, I) *D. orientalis*. (F–H) *D. astericola*. (A) Telson with proximal part of one furcal ramus, lateral view. (B) Furcal ramus with setae, lateral view. (C) Telson and bases of the two furcal rami, ventral view. (D) Furcal rami and posterior part of telson, ventral view. (E) Telson with furcal rami, lateral view. (F) Abdomen, telson, and furcal rami, latero-ventral view. (G) Lateral face of telson. (H) Ventral face of telson. (I) Distal parts of furcal rami with setae, lateral view. *fr* = furcal ramus, *te* = telson or segment 5, 1–5 = abdominal segments. Scale bars in μm .

abdominal segment. The cuticle of segments 1–3 lacks setae, denticles, and fringes. In *D. murmanensis*, the telson has two ventral rows of transverse arrays (10 μm wide) of short fringes (Fig. 12C), whilst *D. leptasteriae* has three rows of similar arrays and other rows on the ventral and lateral sides of the furcal rami (Fig. 12D). The furcal rami are twice as long (70 μm) as high and covered by smooth cuticle. Each carries four setae

arising from the medial face and four terminal setae, all relatively short and with tiny, scarcely visible setules (Figs. 2B, C, 12B).

3.8.2. Second ascothoracid-larvae

The abdomen is five-segmented (Figs. 3A, G, 4E, 12F). Segments 1–3 are irregularly rectangular and decrease in size posteriorly. Segment 4, not yet separated

from the telson in the first ascothoracid-larva, is much smaller than segments 1–3 and almost triangular. On the first abdominal segment, one specimen of *D. astericola* carried a ventral process, presumably the penis (Fig. 4B); this part of the body is hard to observe by SEM, being hidden by thoracopods, so we cannot state whether this “penis” is omnipresent in *D. astericola* or present in any other species. The telson is elongate, with an arched dorsum and a straight ventral margin (Fig. 12E). Combs of short fringes similar to type-5 arrays on the mantle are evenly distributed over its surface (Fig. 12E–H), and each array is 10–20 µm long. Seen under the compound microscope in optical section, some combs may be mistaken for dorsal denticles (Figs. 4C, D, 12G). The furcal rami are as long as wide and flattened laterally, resting closer together dorsally than ventrally (Figs. 4C–E, 12E–F). Fringe arrays similar to types 2 and 5 of the mantle lining are present proximally on the lateral faces of the furcal rami (Fig. 12E, I). The dorso-distal corner of each furcal ramus bears a small, triangular, feathered spine ca. 15 µm long (Figs. 4D, 12I). Each ramus has four long, terminal setae with tiny, sparse setules, three medial setae arising in a dorso-ventral proximal row, and a fourth medial seta inserted more posteriorly (clearly shown in Fig. 12F, only approximately in Fig. 4C, E).

4. Discussion

4.1. First and second ascothoracid-larvae

Both our study and previous ones (Brattström 1948; Wagin 1976; Grygier and Fratt 1984; Grygier 1991a) found a large number of significant morphological differences between the first and second instars of the ascothoracid-larvae of various members of the order Dendrogastrida. Here we summarize those valid for *Dendrogaster*.

In instar 1 the head shield, antennules, and mouthparts look inflated. The shield has a smooth outer face without pores, setae and lattice organs, features otherwise characteristic of thecostracan cypridiform larvae, whereas these structures are all present on the oval head shield of instar 2 larvae. The antennules of instar 1 have a rudimentary appearance, lacking fully formed setae and a differentiated aesthetasc, and they represent an intermediate state between the naupliar antennules, used only for sensing, and the prehensile, fully functional ones of the second ascothoracid-larva. The labrum of instar 1 does not encircle the maxillae, which have only small terminal prongs, while instar 2 larvae have a fully developed oral pyramid and harpoon-like maxillae. In instar 1 the thoracopods have relatively short and simple terminal setae, whilst those in instar 2 have long and

finely setulated terminal setae. Thoracopods 2–3 of instar 1 lack a plumose seta on the coxa that is present in instar 2. Judging from the present material, the thoracopodal exopods of instar 1 have a larger number of terminal setae than seen in instar 2, but, as discussed below, this may not be universal. The abdomen of instar 1 is four-segmented (including the telson), but it becomes five-segmented in instar 2 due to a proximal splitting of the telson, and the first instar has smoother abdominal cuticle.

Wagin (1954) described and illustrated the ascothoracid-larva of *Dendrogaster murmanensis*, but without stating what stage. Judging from the clarity of the trunk segmentation, the form of the antennule, and other traits, he seems to have studied the second ascothoracid-larva, but the mouthparts are those of a first-instar larva. We found only first ascothoracid-larvae of this species in Wagin’s collection. His description of the thoracopodal setation in *D. murmanensis* differs in several respects from ours based on first-instar larvae of *D. orientalis*: three (*murmanensis*) versus four (*orientalis*) distal setae on the exopod of thoracopods 2–5, absence of a seta on the second endopodal segment of these limbs (*murmanensis*), and three (*murmanensis*) versus two (*orientalis*) distal setae on the endopod of thoracopod 6.

First ascothoracid-larvae have been described for species of several other genera of the order Dendrogastrida, such as *Parascothorax synagogoides* Wagin, 1964 (see Grygier 1991a), *Ascothorax gigas* Wagin, 1968 (see Grygier and Fratt 1984), *Gongylophysema aetosum* Grygier, 1987 (see Grygier 1987c), and *U. oeresundense* (see Brattström 1948). A description by Wagin (1947) of what appears to be this stage in *Ascothorax ophioctenis* Djakonov, 1914 is too vague with regard to the thoracopods to be useful here. In all these descriptions the exopods of thoracopods 2–5 carry four distal setae, while the exopod of thoracopod 6 carries only three. Differences between the species concern the presence or absence of setae on the middle endopodal article in thoracopods 2–5 (present in *G. aetosum*), and the presence of two versus three distal endopodal setae in these limbs (three in *P. synagogoides*) and one versus two distal setae on this ramus in thoracopod 6 (one in *A. gigas*).

The apparent reduction in the number of exopodal setae in the second versus the first ascothoracid-larva in *D. orientalis* is, if correct, unusual for the order Dendrogastrida. *U. oeresundense*, *A. gigas* and *P. synagogoides* all have four terminal exopodal setae on thoracopods 2–5 in both instars (Brattström 1948; Grygier and Fratt 1984; Grygier 1991a), and there are also four such setae in the (presumably second) ascothoracid-larva of *Bifurgaster freyellae* Stone and Moyses, 1985 (q.v.). In *Dendrogaster* our data from *D. orientalis* are the only available information on thoracopodal setation for both instars. There are few comparative data for second ascothoracid-larvae in this

genus at all, but males are essentially similar to the second instar, and both three and four exopodal setae have been recorded for these legs in males of different species (and also two versus three apical endopodal setae). Therefore, it seems rather unlikely that the setal ontogeny pattern noted in the present study applies to all species of *Dendrogaster*.

4.2. Function and evolution of ascothoracid-larvae

Morphologically, the first ascothoracid-larva of *Dendrogaster* represents a transitional stage between the naupliar instars and the more truly cypridiform second ascothoracid-larva (a-cyprid). Grygier (1991a) supposed, based on an abundance of material containing brooded larvae only up to the late nauplius stage, that the first ascothoracid-larva is the first non-brooded instar in *P. synagogoides*. But for many species of *Dendrogaster* (those that do not possess free-swimming nauplii) the second ascothoracid-larva is probably the first non-brooded instar, because both stages of ascothoracid-larva may be found inside the mantle cavity of a female (Knipowitsch 1892; Wagin 1950, 1954, 1976). All the morphological differences found here in the locomotory appendages and the sensory structures are similarly consistent with only the second ascothoracid-larva in this genus being fully functional and pelagic, while the first instar is retained in the brood chamber until it molts.

In the thecostracan ground pattern, larval development begins with pelagic nauplii and terminates with the cypridiform stage, which can both swim using the thoracopods and attach to a substratum by the antennules. The presence of two cypridiform instars is unique for the Ascothoracida (Grygier 1984; Boxshall and Huys 1989; Itô 1989; Høeg et al. 2004; Kolbasov and Høeg 2003), while the two other subclasses have only a single such instar, the y-cyprid in the Facetotecta and the true cyprid in the Cirripedia. This raises the question of the functional and evolutionary significance of the developmental scheme seen in the Ascothoracida.

The available information seems to indicate that the presence of two instars of the ascothoracid-larvae phase is coupled to a development with brooded larvae and no free nauplii. Most available descriptions of first ascothoracid-larvae (from *Ascothorax*, *Gongylophysema*, *Ulophysema*, and *Dendrogaster*, all belonging to the order Dendrogastrida) derive from species with brooded larvae, not from laboratory-rearing studies of nauplii that molt into the cypridiform stage while in the plankton. *P. synagogoides* is the only apparent exception, and even it broods all the naupliar stages. As far as is known, all species within the other order of the Ascothoracida, the Laurida, release their larvae as nauplii, whether planktotrophic or lecithotrophic, and

this is followed by a single cypridiform instar, the so-called Tessmann's larva (Itô and Grygier 1990). It has not yet been confirmed whether species of *Dendrogaster* with free-swimming, lecithotrophic nauplii, such as *D. okadai*, *D. ludwigi* and *D. astropectinis*, have two ascothoracid-larval instars like their congeners or only a single one.

Available information does not provide a clear functional explanation for the presence of an extra, intermediate stage in the transition from metanauplius to ascothoracid-larva in late-brooding ascothoracidans. Some free-swimming metanauplii have relatively longer, more clearly segmented antennules than brooded nauplii, making a direct transformation to a fully prehensile or subchelate antennule easier, but no ascothoracidan nauplius at all has external thoracopodal rudiments, apart from rows of bumps that represent the setae. The situation is similar in cirripedes and facetotectans, the cyprid and y-cyprid of which each appears in a single molt from the last nauplius instar (see Walossek et al. 1996). Brooding alone probably cannot explain the presence of two ascothoracid-larval instars. An abbreviated development, in which there are no pelagic nauplii and the embryos hatch as cypridiform larvae, is a derived state that also occurs in various cirripedes (Kolbasov and Høeg 2007; Høeg and Møller 2006; Høeg 1995). Accordingly, there seems to be no ontogenetic problem associated with hatching directly as the fully functional, cypridiform settlement stage.

Whether or not the presence of two cypridiform instars belongs to the ground pattern of the Ascothoracida, and ultimately also that of the Thecostraca, it now seems reasonable to consider the second ascothoracid-larva as homologous to the y-cyprid (Facetotecta) and the cyprid (Cirripedia) instars. These are all terminal larval stages and all are equipped with the requisite sensory and antennular apparatus for locating and attaching to a suitable substrate. An alternative hypothesis, in which the first ascothoracid-larva is considered homologous to the y-cyprid and the cirriped cyprid, would allow instead for the female first kentrogon and male trichogon larvae of kentrogonidan rhizocephalans (Glennner and Høeg 1994) to correspond to the second ascothoracid-larva.

4.3. Cuticular ornamentation

4.3.1. Shield ornamentation

In general, the types and distribution of setae and pores on the head shield of ascothoracid-larvae fall within the range of variation seen in cirripede cyprids (Moyse et al. 1995). A reticular groove/ridge pattern as found here on the head shield of the second ascothoracid-larva of *Dendrogaster* is also characteristic for ascothoracid-larvae of some other species (Grygier 1988,

1991a; Itô and Grygier 1990), but the sculpturing observed in the species studied by us is distinctly less pronounced than in the Lauridae (Tessmann's larva) and is reminiscent of that noted for *U. oeresundense* (Jensen et al. 1994a). Elfimov (1995) attempted a phylogeny-oriented survey of shield ornamentation in cirripede cyprids, but no clear pattern appeared. Nevertheless, a reticular ornamentation of the cypridiform larva's head shield (carapace) may be plesiomorphic for the Thecostraca, because this feature is found both in the Facetotecta and in some Ascothoracida and Cirripedia and without having any correlation to the size of the larvae.

4.3.2. Fringe-type ornaments

Structures similar to many of the cuticular ornamentations described herein, such as the fringe arrays of types 1–8 on the head shield and others on various body surfaces, have been found both in other ascothoracid-larvae or cypridiform males of ascothoracidans (Grygier 1982, 1988, 1991a; Itô and Grygier 1990; Grygier and Ohtsuka 1995) and on the mantle of many cirriped cypris larvae (Kolbasov et al. 1999). These represent only part of the morphological spectrum of fringe and fringe-array morphologies found in our SEM survey of various body surfaces of assorted species of adult and larval ascothoracidans (unpublished data). Some parts of this spectrum may form a continuous gradation, but in this paper we show that the fringes themselves and their arrays are sufficiently diverse to allow the scoring of many independent features for cladistic analysis. Klepal and Kastner (1980) and Klepal (1983) have already provided a practical categorization of the non-setal cuticular structures of crustaceans and suggestions of the routes of morphological differentiation among them, and to our knowledge, only Klepal and Nemeschkal (1995) have tried to use microcuticular elements in a cladistic analysis. But more precision is required than just presence and absence of any broad category of such structures in a taxon; precise categorization, as we have attempted here, along with attention to occurrence on specified parts of the body in specified life stages, is probably required for useful results.

In agreement with Garm's (2004) truly innovative attempt to distinguish setae from other, non-setal types of cuticular ornamentation, we emphasize that fringes are not setae. Consequently, the fringe arrays found on the present ascothoracid-larvae cannot have any sensory function. They might be involved in grooming the appendages when these are extended or retracted from the mantle cavity, but it is impossible at present to say what subtle differences in function the impressive morphological diversity of fringe arrays may reflect.

In our SEM photographs (Fig. 9), suggestions of fringe fusion are sometimes apparent. In arrays of types 1, 2 and 4 in first ascothoracid-larvae, the adjacent

fringes are clearly independent of each other (Fig. 9A, E), but in type-3 arrays they appear to be conjoined at their bases to form the slightly protruding lip of each "scale" (Fig. 9C, narrow, light-coloured zone). As for the membrane-like type-6 array in second ascothoracid-larvae, comparison with the similarly positioned "palisade" in male *Synagoga millipalus* Grygier et Ohtsuka, 1995 (*q.v.*), located just inward from the margins of the head shield valves, suggests that both structures are compound in nature. The palisade is clearly composed of spines fused in their proximal 10.3–13.8 μm , somewhat in the manner of a picket fence. Along the ventral part of the valves, the free ends of the component spines protrude no more than the denticles or fringes that line the type-6 array do [compare Grygier and Ohtsuka (1995, Fig. 5) with Fig. 9G herein]; furthermore, both the palisade and the type-6 array have a discrete inner (basal) margin. Parallel striations that mark the spine borders in the palisade are absent from the type-6 array, but the other resemblances suggest an origin of the latter as well by fusion among adjacent fringes or spines, and that both structures may be homologous.

4.4. Frontal filaments

The structures that we provisionally refer to as the frontal filament complex (see Grygier 1987d) were described first by Knipowitsch (1892) in the second ascothoracid-larva of *D. astericola*. He labelled them as "X" organs of indefinite nature. Similar projections were found in other ascothoracid-larvae of *Dendrogaster* (Yosii 1931; Okada 1938; Grygier 1982), and in the male of e.g., *D. tasmaniensis* Hickman, 1959 (*q.v.*), where they were erroneously described as segmented [second] antennae. Knipowitsch (1892) stated that frontal filaments originate at the borderline of the body proper and the head shield valves and are covered by a thin cuticle. Our study confirms that they are associated with the mantle (Figs. 5E, 10I, 11E). In cirripede nauplii and cyprids, Walker (1973) and Høeg (1985) used TEM to study the assumedly homologous structures, which are sensory organs containing profusely branched ciliary extensions and appear to be related to organs of Bellonci (Chaigneau 1978). As in the ascothoracid-larvae studied here, the cirripede frontal filaments consist of a basal, bulbous part and a filamentous extension. In species with cyprids that have compound eyes, the base of the filament originates in association with these structures.

4.5. Lattice organs

4.5.1. General features

Lattice organs are found in all Ascothoracida, Facetotecta and Cirripedia and represent an autapomorphy of the class Thecostraca (Høeg and

Kolbasov 2002). These specialized chemoreceptors of the cypridiform larva develop from distinct setae in the naupliar head shield, and they are situated pair-wise along the dorsal margin of the cypridoid shield (Jensen et al. 1994a, b; Høeg and Kolbasov 2002; Rybakov et al. 2003). A condition with two anterior and three posterior pairs is found in species from all three subclasses and represents the ground pattern for the Thecostraca (Høeg and Kolbasov 2002), but secondary absence of one or several pairs occurs throughout the class. The external morphology of the individual organ varies considerably and is surveyed in Fig. 8. The only external feature common to almost all varieties is the presence of a large pore situated at one end of the organ. The position of this terminal pore (anterior or posterior) can vary both between the individual pairs in a single species and between taxa. In the Facetotecta the pore is situated posteriorly in all five pairs in all species studied until now, and Høeg and Kolbasov (2002) claimed that this condition represents the thecostracan ground pattern. Irrespective of the variation in external morphology, the TEM level structure of lattice organs is very similar throughout the class and is clearly indicative of both their overall homology and chemoreceptive function (Høeg et al. 1998).

4.5.2. Variation within the Thecostraca

According to Høeg and Kolbasov (2002), the most plesiomorphic morphology of a lattice organ is a crest-like structure traversing an elongated depression (“crest-in-a-trough”, Fig. 8A), just as we describe here for males of *Dendrogaster* (Figs. 7). Organs with a low and rather indistinct crest occur in ascothoracid-larvae of *Dendrogaster* and in some facetotectan y-cyprids (Fig. 8B).

An advanced form of lattice organ, “the pore-field type”, characterizes the Cirripedia Thoracica and Rhizocephala (Fig. 8E–G). It has no crest at all, but consists of an elongated area that is slightly depressed relative to the surrounding cuticle and perforated by numerous small pores. The only external resemblance to other lattice organs is the presence of the large terminal pore. Cyprids of a few thoracican cirripedes (*Capitulum*, *Pollicipes*) have a morphological intermediate between the “crest-in-a-trough” and the “pore-field” types, in which a distinct central crest, traversing an elongated depression, is perforated by numerous small pores (Fig. 8D). An advanced variety of the pore-field type, in which the whole area is nearly circular and lacks a terminal pore (Fig. 8H, I) occurs in some rhizocephalan and acrothoracican cirripedes (Jensen et al. 1994b; Kolbasov and Høeg 2007).

In the Ascothoracida, lattice organs are present not only in the cypridiform (ascothoracid-) larvae but also in adult males and females of some species (Itô and Grygier 1990; Jensen et al. 1994a; Grygier and Itô 1995;

Grygier and Ohtsuka 1995; present study). Until now, studies on lattice organs have mostly focussed on variation within the Cirripedia. Our paper represents one of the few SEM-based studies of lattice organs in the Ascothoracida and reveals a hitherto largely unrecognized variation within this subclass as well, indicating that the use of these structures in phylogenetic analysis is likely to be more complicated than first believed. Other SEM-based surveys by us of lattice organs in a much wider assortment of adult and larval ascothoracidans (unpublished data) have confirmed the existence of even more hitherto unrecognized lattice organ variability in this group. The present discussion, therefore, can only give a preliminary evaluation of the significance of the variation here reported, while a fuller discussion must await separate publication of the rest of the relevant evidence.

4.5.3. Lattice organs in ascothoracid-larvae and males

In the laurid *Bacculaureus falsiramus* Itô et Grygier, 1990, the lattice organs of the ascothoracid-larva (so-called “Tessmann’s larva”) have a morphology and disposition as in the putative thecostracan ground pattern, viz., two anterior and three posterior pairs of the “crest-in-a-trough” type with posteriorly situated terminal pores (Itô and Grygier 1990). An ascothoracid (Tessmann’s) larva of an unidentified species, but evidently closely allied to *B. falsiramus*, has six lattice organs (two anteriorly, four posteriorly) on one valve (Grygier 1992), but this should perhaps be considered as an abnormality. An SEM study of the second ascothoracid-larva of *U. oeresundense* revealed five pairs of lattice organs having the same morphology and disposition as those of *B. falsiramus* (Jensen et al. 1994a). Other second ascothoracid-larvae of the order Dendrogastrida (family Ascothoracidae), investigated under a light microscope, appeared to have only four pairs of lattice organs (two anterior and two posterior) of unknown ultrastructure (Grygier and Fratt 1984; Grygier 1991a); we have since confirmed this using SEM (unpublished data).

Analysis of the relative positions of lattice organs in species with five pairs versus those with four might allow a determination of which posterior pair is absent in the latter species. On the other hand, the spacing between the anterior two pairs, which all species have, does vary. In second ascothoracid-larvae, *lo1* and *lo2* of *D. astericola* are separated by 110 µm (present study), those of *U. oeresundense* by 70 µm (Jensen et al. 1994a, b), and those of *P. synagogoides* by only 13–18 µm (unpublished data). Similar variation in the spacing of the posterior lattice organs might mask the identity of a missing pair. A more complete analysis of this matter must await the publication of our additional findings from ascothoracid-larvae and males of

Ascothorax and *Parascothorax*, and adults of certain other genera.

Orientation of lattice organs has been considered similarly important to their number. The cypridiform male of *Synagoga millipalus* has five pairs of lattice organs of the “crest-in-a-trough” type, but, unlike the ascothoracid-larvae of the above-mentioned species, *lo1* and *lo3* have anteriorly situated terminal pores. Grygier and Ohtsuka (1995) argued that this fact weakens the utility of terminal pore position in reconstructing thecostracan phylogeny, because the anterior position of the pore in *lo1* is an alleged synapomorphy of the Cirripedia Thoracica and Rhizocephala [Jensen et al. (1994a); see also Kolbasov et al. (1999) and Høeg and Kolbasov (2002) for detailed discussions of this point]. The data for *S. millipalus* concern an adult male, not an ascothoracid-larva, but Grygier and Ohtsuka (1995) suggested that “probably” very little morphological change takes place during the ontogeny of the species. The second ascothoracid-larva of *D. astericola* studied here is the first documented ascothoracid-larva with an anterior position of the terminal pore in *lo1*. This may be judged convergent with the position of the *lo1* pore in cyprids of the Rhizocephala and Thoracica if the Facetotecta are regarded as retaining the putative ground-pattern condition, with a posterior pore position in all five pairs of lattice organs in all forms reported to date (Høeg and Kolbasov 2002).

We were unable to study lattice organs in both ascothoracid-larvae and males of any single species of *Dendrogaster*. Comparison between lattice organs in different species of *Dendrogaster* nonetheless raises the possibility that the morphology may change significantly during maturation. In second ascothoracid-larvae of *D. astericola* the lattice organs lack a distinct keel and are situated in wide, shallow pits, whereas they are of the “crest-in-a-trough” type in males of *D. dichotoma* and *D. astropectinis*. In addition, the pore sits anteriorly in *lo1* and posteriorly in *lo2* in second ascothoracid-larvae of *D. astericola*, while the reverse is found in males of the two species studied by us. If a similar shift occurs during the molt from the second ascothoracid-larva to the male in a single species, it means that characters from lattice organs must be scored separately for ascothoracid-larvae and males, adding additional characters for cladistic analysis of the intrinsic phylogeny of the Ascothoracida. Until this problem is settled and the database increased, we consider it inadvisable to use lattice organ characters from ascothoracidan males as a proxy for larval characters in such a phylogenetic analysis.

4.5.4. Lattice organs and ascothoracidan taxonomy

Dendrogaster is currently united with *Ulophysema* in the family Dendrogastridae (Fig. 13A; Grygier 1987b). In the ascothoracid-larvae, *Ulophysema* still presents the

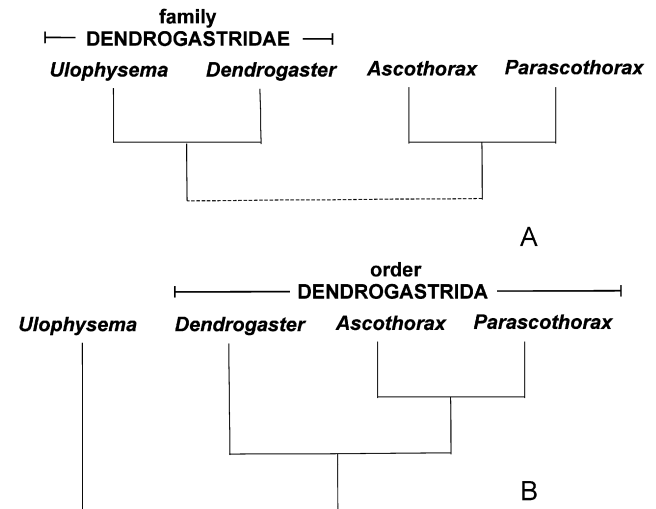


Fig. 13. Conflicting phylogenies and taxonomy of the genera *Ulophysema*, *Dendrogaster*, *Ascothorax*, and *Parascothorax*. In (B) *Dendrogaster*, *Ascothorax*, and *Parascothorax* are united into a monophyletic order Dendrogastrida, a solution that receives support in putative synapomorphies involving, e.g., the lattice organs, but this cannot be reconciled with the current concept of the family Dendrogastridae shown in (A). The dotted line in (A) indicates an uncertain relationship; the Ctenosculidae are excluded from both trees owing to lack of knowledge of lattice organs in this family. For further explanation see the text.

putative thecostracan ground pattern with five pairs of lattice organs, all of the “crest-in-a-trough” type and with posterior terminal pores. In contrast, the examined species of *Dendrogaster* and also *Ascothorax* and *Parascothorax* (family Ascothoracidae) have just four pairs of lattice organs in the ascothoracid-larvae (Grygier and Fratt 1984; Grygier 1991a; unpublished data). If the missing pair is the same in all three genera, this deviation from the ground pattern therefore becomes a potential synapomorphy for a monophylum (Dendrogastrida) comprising *Dendrogaster*, *Ascothorax* and *Parascothorax* to the exclusion of *Ulophysema*, and therefore in conflict with the concept of a monophyletic Dendrogastridae (Fig. 13B). The two dendrogastrid genera also differ in the morphology of the adult females. Those of *Ulophysema* have poorly segmented antennules and lack maxillae but have a developed thorax and abdomen, whereas those of *Dendrogaster* have distinctly segmented antennules and well developed maxillae but a reduced trunk. In fact, *Ulophysema* was originally approximated to the Lauridae (Brattström 1937), and only later was this genus formally assigned to the Dendrogastridae (e.g., Krüger 1940). Grygier (1987b) provided an elaborate taxon-character matrix for the Ascothoracida, but it has never been updated with new characters (mainly larval) compiled since then, and a formal cladistic analysis of the subclass has not yet been performed.

4.5.5. Evolution of lattice organs

Most previous accounts have dealt with lattice organs specifically in the cypridiform larvae of the Thecostraca (Elfimov 1986a,b; Itô and Grygier 1990; Jensen et al. 1994a,b; Kolbasov et al. 1999; Høeg and Kolbasov 2002). In the Cirripedia, lattice organs disappear at the metamorphosis of the cyprid, but they are retained in adults of some Ascothoracida. This study and Grygier and Ohtsuka (1995) found them in ascothoracidan adult males, while Grygier and Itô (1995) found them in females of *Waginella*. In all these cases the adult male or female retains a bivalved head shield. Furthermore, an ontogeny involving little morphological change from ascothoracid-larva to adult may well be plesiomorphic within the Ascothoracida. According to all published reports, adult ascothoracidans have well-developed lattice organs of the “crest-in-a-trough” type with terminal pores (although our SEM data show that recumbent “tube-in-a-trough” lattice organs also exist), and the lattice organs in males of *Dendrogaster* are even more morphologically differentiated than those of the ascothoracid-larvae. All this suggests that the organs are not just passively taken over, but functional also in the adults, where they might assist in finding a mate or a suitable host. Unlike cirripedes, which are all irreversibly sessile after metamorphosis, adults of the most plesiomorphic genera of Ascothoracida may be able to change substrate location. This could call for functional lattice organs and suggest that these sensory structures initially evolved to serve the adults and were only later transferred to the cypridiform larvae. We therefore conclude that the Ascothoracida offer a glimpse of the early thecostracan evolution and may cast some light on how sessility evolved in this taxon.

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