Lattice organs in y-cyprids of the Facetotecta and their significance in the phylogeny of the Crustacea Thecostraca

J. T. Høeg and G. A. Kolbasov[1]

Department of Zoomorphology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; [1]Moscow State University, Faculty of Biology, Department of Invertebrate Zoology, 119899 Moscow, Russia

Abstract

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Scanning and transmission electron microscopy (SEM and TEM) were used to study lattice organs in facetotectan y-cyprids from the White Sea and from Norwegian and Bahamian waters. The larvae represent at least four and possibly five different species of Facetotecta. Y-cyprids have five pairs of lattice organs in the head shield (carapace) organized into two anterior pairs and three posterior pairs. Both groups of lattice organs are arranged around a large central pore. The facetotectan lattice organs are elongate areas with a longitudinal keel, just as in the Ascothoracida and some Cirripedia Acrothoracica. The terminal pore of the organs is situated posteriorly in all five pairs. TEM confirms that the organs have the same general morphology as in the Cirripedia and Ascothoracida, namely, a cuticular chamber into which project ciliary segments from the chemosensory cells. Unlike Cirripedia the cuticular roof of the chamber lacks any pores. We conclude that five pairs of lattice organs represent an autapomorphy for the Thecostraca, which supports the monophyly of this taxon. In the ground pattern the terminal pore is posterior in all five pairs. The anterior position of the pore in lattice organ pair 2 is apomorphic for the Cirripedia, while within this taxon an anterior position also in pair 1 is apomorphic for a monophylum comprising the Thoracica and the Rhizocephala. Minute pores in the roof of the organs is another apomorphy of the Cirripedia, but its elaboration into pores visible with SEM may have been subject to some homoplasy. Since lattice organs are omnipresent in the settling instar of the Thecostraca they probably serve a critical role for the function of these cypris or cypris-like larvae.

Dr J.T. Høeg, Department of Zoomorphology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. E-mail: jthoeg@zi.ku.dk

Introduction

Grygier (1984, 1985) created the taxon Facetotecta to comprise the enigmatic, marine larvae of type 'y' (y-nauplii and y-cyprids). Grygier (1987) also redefined the taxon Thecostraca as a monophylum comprising the Ascothoracida, the Cirripedia and the Facetotecta. The Thecostraca are unique among the Crustacea because, where known, the adults are permanently and irreversibly sessile and live either as parasites or as filter feeders. Reconstruction of the phylogeny of the Thecostraca is a prerequisite to explain how the sessile cirripedes evolved from a maxillopodan ancestor, and why the two other thecostracan taxa, the Facetotecta and the

Ascothoracida, have remained very small in terms of species number (Høeg 1995a,b; Kolbasov 1996). Adult thecostracan features are a difficult data source for phylogenetic analysis. Those of the Facetotecta are unknown, while those of the Ascothoracida and the Cirripedia Rhizocephala are so specialized to parasitism that they have lost many or almost all traits characteristic of Crustacea. This highlights the importance of alternative character sets, such as larval morphology and molecular sequence data, in the discussion of thecostracan phylogeny (see papers in Schram and Høeg 1995).

All Thecostraca have pelagic larvae. The terminal pelagic instar has prehensile antennules and is specialized for locating and attaching to the substrate of the adult organism. Lattice

organs are chemosensory structures in the head shield (carapace) of this settling stage. Until now they have been found in cypris larvae of all three ingroup taxa of the Cirripedia (Acrothoracica, Thoracica, Rhizocephala) and in the ascothoracid larvae of the Ascothoracida (Elfimov 1986; Itô and Grygier 1990; Jensen *et al*. 1994a,b; Høeg *et al*. 1998).

Lattice organs occur in five pairs, organized as two anterior pairs and three posterior pairs and variations in their morphology seem to contain important phylogenetic information. In the Ascothoracida the individual organs have the shape of a more or less pronounced keel situated in an elongated depression. We name this the 'keel in a trough' type (Itô and Grygier 1990; Jensen *et al*. 1994a; Grygier and Itô 1995). The lattice organs in the Cirripedia Acrothoracica have a rather similar morphology, but the keel is sometimes rather indistinct (Jensen *et al*. 1994a; Kolbasov *et al*. 1999). The Cirripedia Thoracica and Rhizocephala invariably have lattice organs of the 'pore field' type, where the elongate area organ is perforated by numerous pores clearly visible with scanning electron microscopy (SEM; Jensen *et al*. 1994a,b; Høeg *et al*. 1998).

Each individual lattice organ has a large terminal pore situated at one end of the elongate area. The position of this pore varies both between individual pairs of lattice organs and between the higher taxa of the Thecostraca.

The Facetotecta is the most enigmatic group within the Thecostraca. They were described more than a hundred years ago by Hansen (1899), but until now we know them only as so-called y-nauplii and y-cyprids (Bresciani 1965; Schram 1970; Grygier 1987, 1991a, 1996), and apomorphies with the remaining Thecostraca are but few. The prehensile antennules and the hooked labrum of the y-cyprids indicate that they become parasitic, but at the time of publication the adults remain entirely unknown. Facetotectan larvae seem to occur in all oceans and the last 15 years have seen a surge of interest in their morphology (Grygier 1991b; Itô 1984, 1985, 1986a,b,c, 1987a,b,c; Itô and Ohtsuka 1984). A few studies have employed SEM or even transmission electron microscopy (TEM; Itô and Takenaka 1988; Itô 1989, 1990), but despite these efforts the phylogenetic position of the Facetotecta within the Thecostraca has remained unsolved.

The presence of lattice organs in all studied species of the Ascothoracida and the Cirripedia prompted us to search for these structures also in the y-cyprids of the Facetotecta. Absence or presence of lattice organs and, if present, their specific morphology, can yield important information with respect to the phylogenetic position of the Facetotecta and bring us closer to understanding the morphology of the last common ancestor to all Thecostraca.

Materials and Methods

We studied y-cyprids from three different geographical areas. A complete y-cypris, referred to here as the Bergen specimen, originates from a plankton sample taken off the west coast of Norway and was collected on 20 June 1981 by Dr K. F. Wiborg. It was originally fixed in formaldehyde. Three loose head shields originate from the material of Schram (1970) and were collected in April and May 1967 in Bahamian waters. The three larvae were originally fixed in formaldehyde, dyed with lignin pink in lactic acid, and whole animals and dissected parts were studied by light microscopy. Only three of the original four head shields were available for the present study since the fourth was embedded in polyvinyl lactophenol. The transfer through lactic acid effected a suboptimal quality of the SEM images from the Bahamian specimens but we include them to document the presence of lattice organs. A large sample of y-cyprids representing a new species was sampled as nauplii at the White Sea Biological Station of the Moscow University and cultured until they moulted into y-cyprids (Kolbasov and Høeg, submitted for publication).

Larvae of the thoracican cirripede *Scalpellum scalpellum* (Linnaeus, 1767) were cultured at the Kristineberg Marine Station on the west coast of Sweden until they moulted into cyprids. Ascothoracid larvae of *Ulophysema oeresundense* Brattström, 1936 were obtained from the mantle cavities of adult parasites. The latter were obtained by dredging the host, the heart urchin *Echinocardium cordatum* (Pennant 1777) from the Sound near the Marine Biological Laboratory of the University of Copenhagen.

For SEM the y-cyprids were fixed in osmium tetroxide, dehydrated through acetone, and critical point dried in CO_2. Examination took place with a Jeol 840 SEM equipped with the Semaphore digital image storage system.

For TEM, y-cyprids were fixed in either glutaraldehyde in cacodylate buffer or in trialdehyde (Lake 1973), osmificated, dehydrated with dimethoxypropane or acetone and embedded in TAAB 812 resin.

Results

The head shield of y-cyprids

The head shield of y-cyprids has a deep posterior excavation and is not folded down laterally, large parts of the body are therefore exposed. There is no dorsomedial hingeline. The cuticle is sculptured, with longitudinal ridges forming the most conspicuous feature.

The Bergen y-cyprid

The simple, roof-shaped head shield (carapace) is unhinged, *c*. 490 μm long from the anterior end to the tip of the posterolateral extensions, with a maximal width of *c*. 205 μm. The cuticle sculpture consists of low ridges dividing the head shield into more or less rectangular fields, the individual fields having a totally smooth surface (Fig. 1). The ridges are very indistinct on the mid-dorsal side but become more
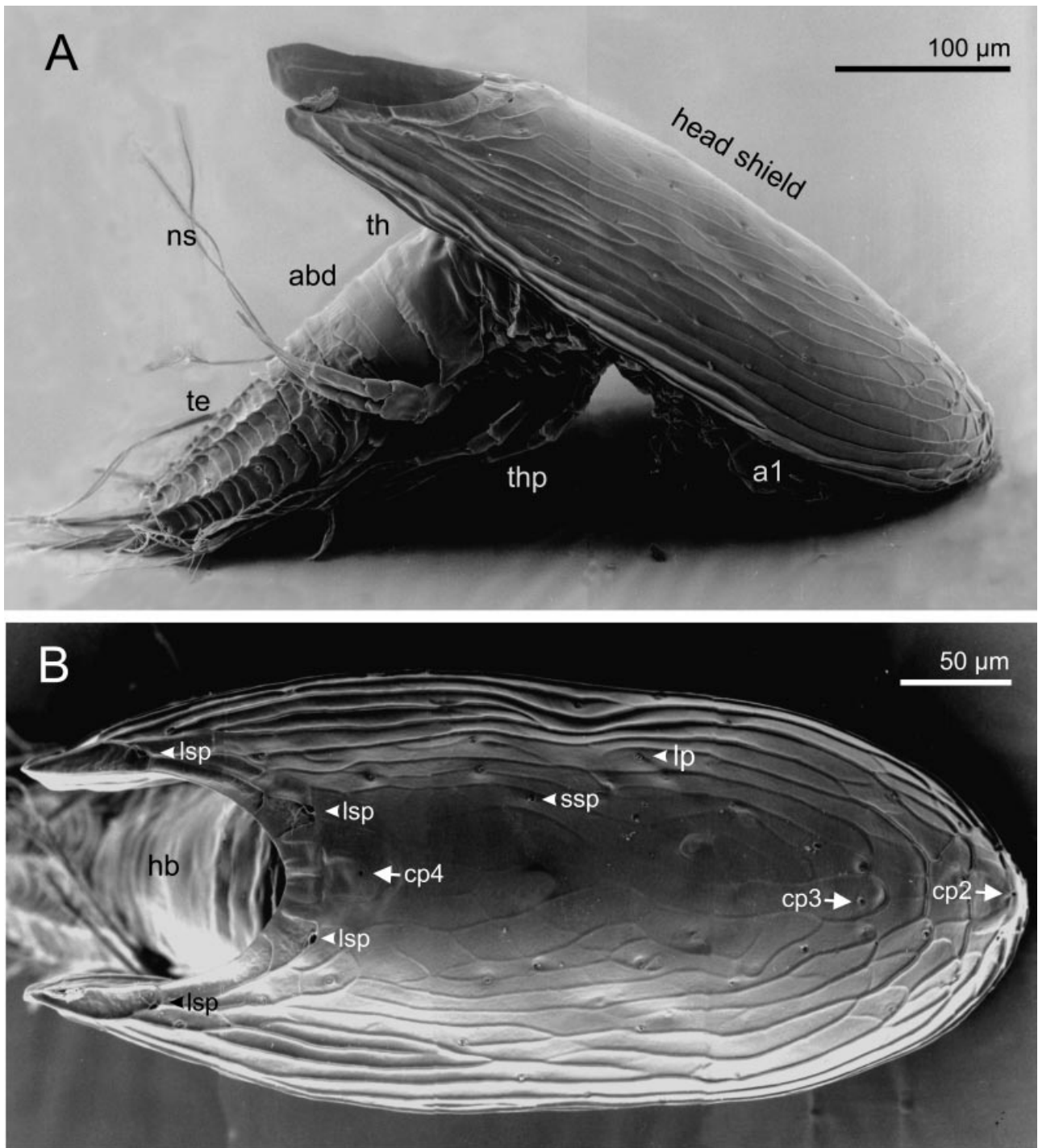
Fig. 1—Bergen specimen. —**A**. Whole y-cyprid in lateral view, electronically fused composite of three different SEM pictures. —**B**. Dorsal view of head shield (carapace), electronically fused composite of three SEM pictures, the lattice organs, grouped around central pores 2 and 3 (cp2, cp3), are detailed in Fig. 2(A,B). A1, antennule; abd, abdomen; cp1–4, central pores 1–4; hb, hindbody; lp, lentoid pore; lsp, large setated pore; ssp, small setated pore; ns, natatory setae; te, telson; th, thorax; thp, thoracopods.

pronounced towards the lateral margin of the shield (Fig. 1B). The lateral fields have a more oblong shape than the dorsal ones, while anteriorly some are almost square.

Four distinct central and unpaired pores lie in the midline of the shield (cp1–4). The first lies near the anterior margin of the shield within a weak depression. The second is between lattice organ 1 (lo1) and lo2 (Fig. 2B), the third lies *c*. 80 μm behind the second one (Fig. 1B) and the fourth is between lo3 and lo4 (Figs 1B and 2A). The cp1 has a raised margin but cp2–4 are all simple pores. A limited number of smaller pores of different types are also distributed over the head shield.

The head shield carries five pairs of lattice organs (lo) situated near the dorsal midline and grouped as two anterior and three posterior pairs. The anterior pairs (lo1 and lo2) lie around the second, central and unpaired pore (cp2) in the anterior end of the shield, where bending is most pronounced (Fig. 2B). Both the lo1 and the lo2 organs converge anteriorly using the terminology of Jensen *et al.* (1994a). The cuticle area surrounded by these lattice organs lacks the normal sculpture described above.

The three posterior pairs (lo3–lo5) lie one after another near the midline of the shield, with the posterior end of lo5 almost reaching the posterior margin of the shield (Fig. 2A); lo3 and lo4 are located around cp4. The third pair (lo3) converges strongly anteriorly. The fourth pair (lo4) lies almost parallel to the midline, while the fifth pair (lo5) converges weakly posteriorly.

The individual lattice organs are *c*. 12–15 μm long and 1–2 μm wide and are demarcated from the general cuticle by a weak depression from which the organ rises slightly into a keel reaching the same level as the general cuticle (Fig. 2B). The organ is broad anteriorly (especially lo1 and lo3) and tapers weakly towards the posterior end (Fig. 2B). All lattice organs have a large terminal pore situated at the posterior end (Figs 2B–F and 5B), but they completely lack the small pores found in most cirripede cyprids (Fig. 5A). The large terminal pores of lo1 and lo2 are wider than those of lo3–lo5.

The head shield carries both small (*c*. 5 μm) setae and large (10–15 μm) setae, both originating within distinct pores or depressions (Figs 1, 2). The number of these setae is small and they are arranged in a very distinct pattern which will be described elsewhere.

The White Sea y-cyprids

Scanning electron microscopy The head shield carries five pairs of lattice organs grouped into two anterior and three posterior pairs. The cuticle sculpture and the morphology of the organs resemble the condition in the Bergen specimen. The terminal pores lie posteriorly in all five pairs (Fig. 2G–L). The anterior pairs (lo1–2) and the posterior pairs (lo3–5) are arranged around large central pores corresponding to the cp2 and cp4 of the Bergen specimen. Despite some general similarity to the Bergen specimen we

also noted differences. In the Bergen specimen the lo3 organs are broad anteriorly but taper towards their posterior ends (Fig. 2A). In the White Sea specimens the lo3 organs have almost the same width throughout but exhibit a distinct curvature (Fig. 2G,J). A complete SEM-based account of the morphology of the cypris-y from the White Sea will be given elsewhere.

Transmission electron microscopy Sagittal sections reveal that the lattice organs have a morphology very similar to that described from the Cirripedia by Høeg *et al.* (1998). Ciliary segments from the sensory cells pass through a canal into a chamber in the head shield cuticle (Fig. 3A). The terminal pore is situated at the opposite end of the chamber and seems to be open to the exterior except for a plug of very fuzzy material (Fig. 3C).

The head shield cuticle is layered but shows no distinct separation into an exocuticle and an endocuticle. The cuticle above the chamber is only 0.2 μm thick and totally devoid of pores (Fig. 3D). It has neither the minute, epicuticular pores seen in the Acrothoracica nor the larger, pit-shaped pores found in the Thoracica and the Rhizocephala (cp. Figures 3D and 5C). The fixation did not allow us to study details of the ciliary elements inside the cuticular chamber, but the ciliary microtubules traversing through the canal could be distinguished (Fig. 3A, inset).

The Bahamian y-cyprids

The condition of these specimens was not optimal for SEM but was still sufficient to document the presence of lattice organs. We identify the head shield in Fig. 4(A) as specimen no. 2 of Schram (1970). It is undamaged but rather dirty. The cuticle is heavily sculptured with symmetrically arranged, longitudinal ridges. The surface in the elongate or rectangular fields between ridges is also sculptured, but less so (Fig. 4A). One of the longitudinal ribs forms the midline of the shield. Two large pores are situated anteriorly and posteriorly to this midrib and we assume that they correspond to the cp2 and cp4 of the Bergen specimen (Fig. 4B,C). Two pairs of lattice organs (lo1, lo2) lie in the vicinity of cp2 (Fig. 4B). The lo1 organs of this specimen differ slightly from those of the Bergen specimen, since they lie in a more median position and converge anteriorly to a greater extent; lo3–lo5 lie in the vicinity of cp4 (Fig. 4C) and are arranged in the same manner as in the Bergen specimen; lo5 lies more isolated and nearer the posterior margin of the head shield. The individual lattice organs are more strongly demarcated from the surrounding shield cuticle than in the Bergen specimen, and the central keel is more pronounced just as in the Ascothoracida (Fig. 5B). We tentatively identified large terminal pores for some of the lattice organs and they always lie posteriorly.

We identified the head shield in Fig. 4(D) as specimen no. 3 of Schram (1970). It is slightly damaged and with an
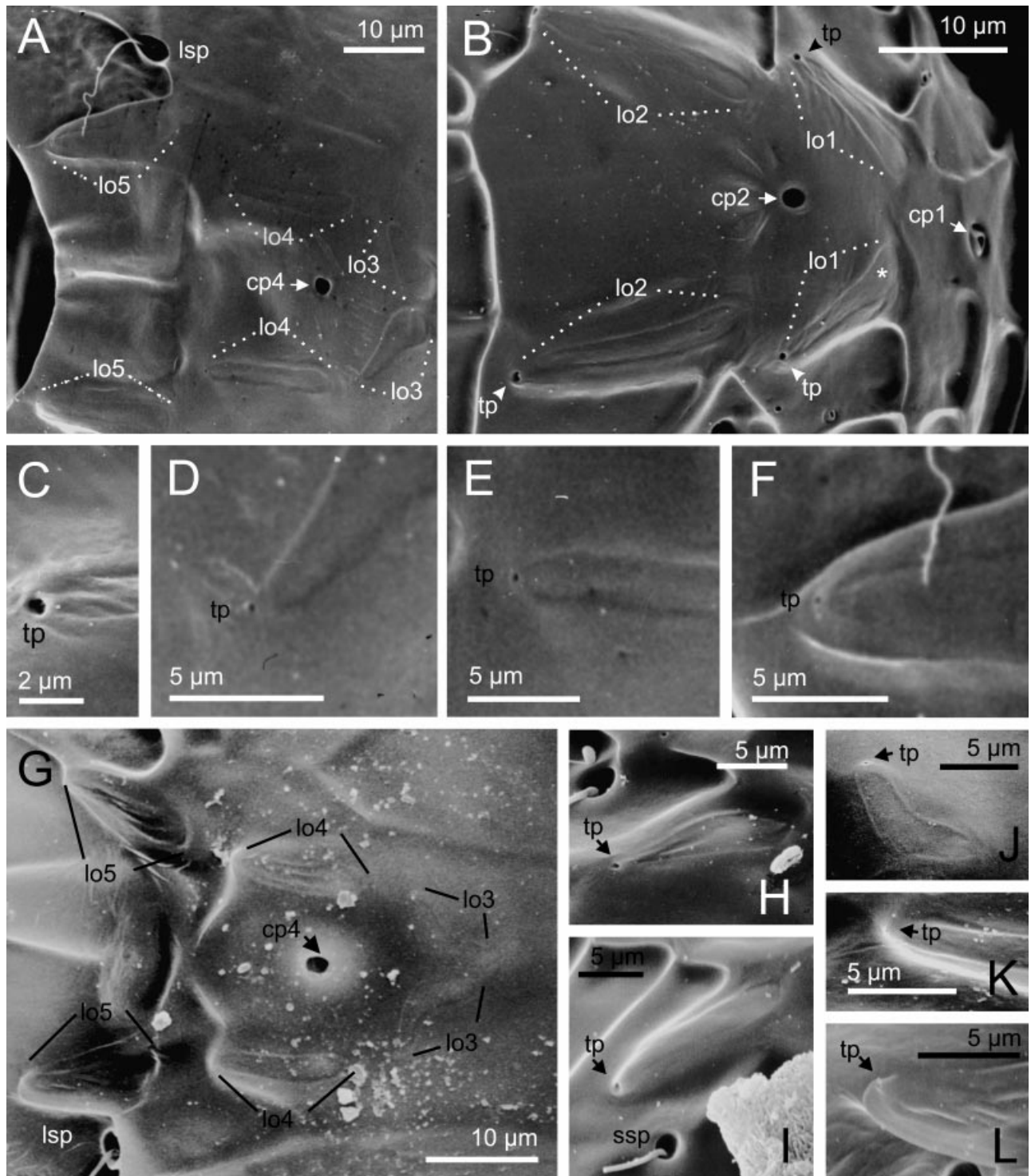
Fig. 2—Lattice organs (lo) in the Bergen specimen (**A–F**) and the specimens from the White Sea (**G–L**); anterior is right in all figures; note that the terminal pore (tp) is situated posteriorly in all lattice organ of both specimens. —**A**. Detail of Fig. 1(B), posterior part of head shield with the three posterior pairs of lattice organs (lo3–lo5) around central pore 3 (cp3). —**B**. Detail of Fig. 1(B), anterior part of head shield with the two anterior pairs of lattice organs (lo1, lo2) around central pore 2 —(cp2); note the raised rim in the more anteriorly situated cp1. —**C**. lo1. —**D**. lo2. —**E**. lo3. —**F**. lo5. —**G**. White Sea specimens, posterior part of head shield with the posterior lattice organs (lo3–lo5) around central pore (cp4). —**H**. lo1. —**I**. lo2. —**J**. lo3. —**K**. lo4. —**L**. lo5. Cp1–4 central pores 1–4, lo1–5 lattice organs pairs 1–5, lsp large setated pore, tp terminal pore.
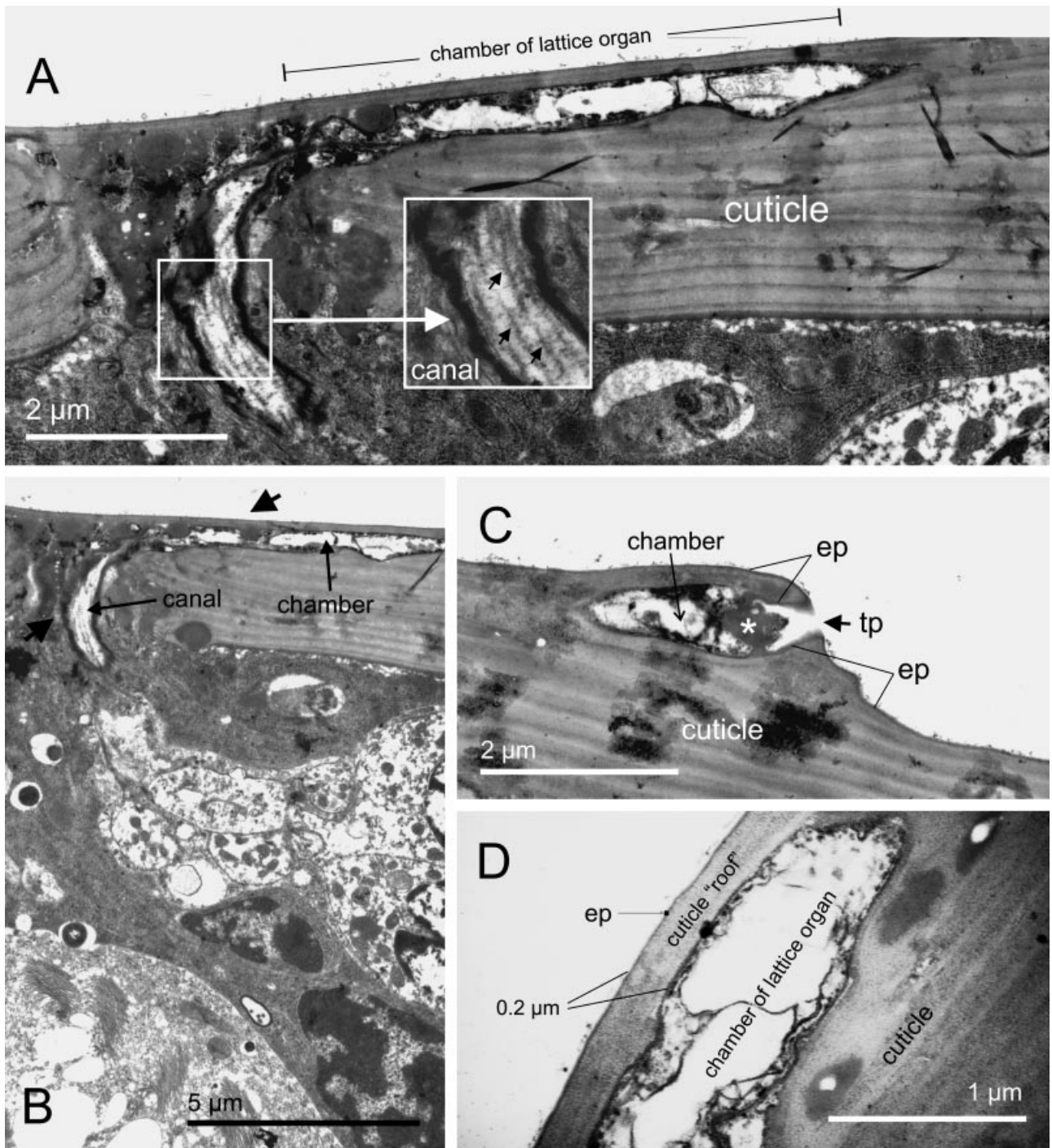
Fig. 3—TEM of lattice organs in the White Sea specimens. —**A**. Sagittal section through head shield cuticle and lattice organ; the cuticular chamber of the organ communicates through a canal with the interior of the y-cyprid; the cuticle lacks any division into endo- and exocuticle; the enlarged rectangle shows microtubules of the ciliary segments of the sensory cells. —**B**. Overview of lattice organ in **A** (large pair of arrowheads indicate the sectional plane of Fig. 5F). —**C**. Other section from same series showing the terminal pore (tp) and a plug of fuzzy material (*) separating the exterior from the chamber. —**D**. The cuticular roof of the lattice organ is only 0.2 μm across; both epicuticle (ep) and the subjacent general cuticle of the roof are without any pores. Ep epicuticle, tp terminal pore.

identical but less distinct sculpture compared to specimen no. 1. All lattice organs, cp2, and cp4 seem to occupy the same positions as in specimen 1 although only lo1 could be seen with certainty. The anteriormost organs (lo1) are very broad anteriorly where the tips of the pair almost meet in the midline (Fig. 4E), but they soon taper and curve laterally towards their posterior, diverging ends. The demarcation of the lattice organ from the general head shield cuticle is just as weak as in the Bergen specimen.

The third head shield (Fig. 4F) is heavily damaged and lacks the right posterolateral extension. We therefore identify it as specimen no. 1 of Schram (1970). The cuticle sculpture differs from the two other Bahamian specimens. It has less distinct longitudinal ridges and no distinct sculpture of the rectangular fields. The anterior end of the shield has a number of deep, roundish pits not seen in any of the other y-cyprids studied by us (Fig. 4F,G). We could identify cp2, lo1 and lo2 (Fig. 4G), but not lo3–lo5 and cp4 because of the damage to the head shield.

Ascothoracida and Thoracica

In their TEM-based description of lattice organs Høeg *et al.* (1998) studied only cyprids of the Cirripedia Acrothoracica and Rhizocephala. To compare these results with those from the present paper we give a brief account on the TEM ultrastructure of the lattice organs in the ascothoracidan *Ulophysema oeresundense* and in the thoracican *Scalpellum scalpellum*.

Scalpellum scalpellum *(Cirripedia Thoracica)* The large terminal pore lies at the posterior end of the median keel (Fig. 5B). The chamber of the lattice organ is situated in the exocuticle, which is almost twice as thick as outside the lattice organ (Fig. 5C,D). The cuticle roofing the chamber is *c.* 1 µm thick and has numerous distinct pores of the type also found in the Rhizocephala. These pores penetrate almost into the chamber, apparently separated only by a thin layer of epicuticle. Balls of electron-dense material are situated in the chamber outside the sheath encircling the ciliary segments. The chamber communicates with the interior of the cyprid via a long canal passing down through the thick endocuticle (Fig. 5D). Cross-sections revealed that four ciliary segments originate from two sensory cells beneath the cuticle and pass through the canal and into the chamber (Fig. 5E). Sometimes lattice organs from different pairs appear in the same cross-section as in Fig. 5(D), which shows the canal of one organ and the near terminal end of the chamber of an adjacent lattice organ.

Ulophysema oeresundense *(Ascothoracida)* The cross-section of the lattice organ in Fig. 5(F) is cut as indicated by arrows in Fig. 5(B), i.e. near the anterior end where the canal passes from the chamber into the interior of the larva. Due to the curvature of the canal and an oblique angle of section

the micrograph shows both chamber and canal of the same organ (arrowheads in Fig. 3B serve to indicate the approximate sectional plane). The chamber lies inside the keel-shaped protuberance of the cuticle situated in a deep trough. The surrounding cuticle lacks any clear separation into exo- and endocuticle. The chamber fills almost all the interior of the keel (Fig. 5F). It is surrounded by a rather electron-lucent, *c.* 0.2 µm thick cuticle and an outermost, electron-dense epicuticle, but there are no cuticular pores of any type in the wall of the chamber.
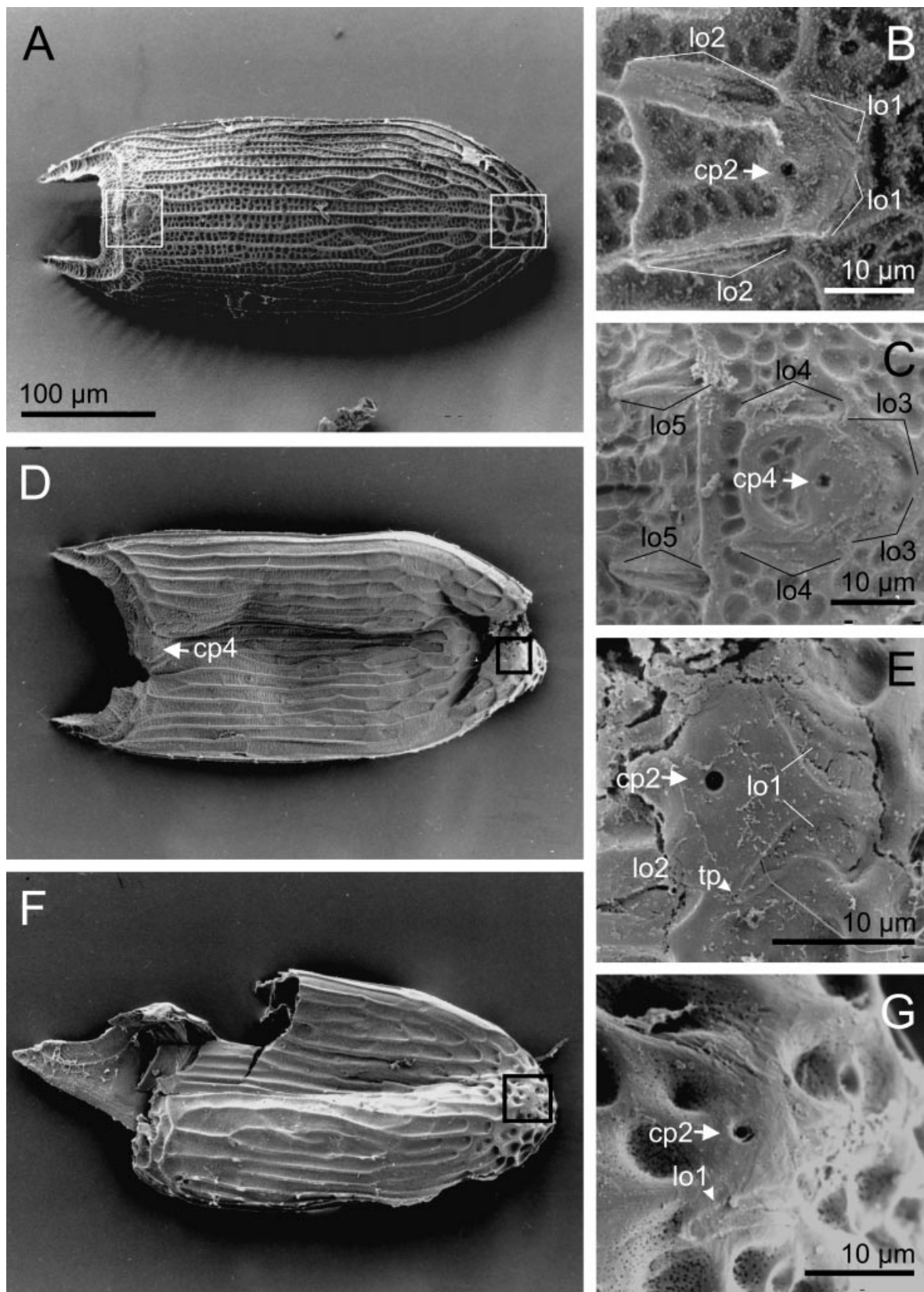
Discussion

Homology of lattice organs

This is the first report of lattice organs from the Facetotecta. We found these structures in all the examined y-cyprids, which probably represent four if not five different species. This suggests that they are omnipresent in the taxon. With our report lattice organs have been found in all three taxa of the Thecostraca (Elfimov 1986; Itô and Grygier 1990; Jensen *et al.* 1994a,b; Grygier and Itô 1995; Kolbasov *et al.* 1999). They occur in the head shield (carapace) of cyprids or cypris-like larvae arranged as two anterior and three posterior pairs. The external morphology varies extensively from the 'keel in a trough' type (Fig. 5A) to the 'pore field' type (Fig. 5B), but TEM reveals an underlying close similarity. The individual lattice organ consists of two sensory cells equipped with two cilia (outer dendritic segments, ciliary segments). The ciliary segments extend through a channel and into a chamber in the head shield cuticle, where they branch extensively. The chamber communicates or pseudo-communicates with the exterior through a terminal pore or pit. In the Facetotecta we produced only sagittal sections and could therefore verify the presence of ciliary segments but not the exact number of sensory cells.

The presence of five pairs of lattice organs (lo1–lo5) organized into two groups and the similar TEM level morphology leaves no doubt that these structures are homologous throughout the Thecostraca. The presence in the Facetotecta of a large central pore between lo1 and lo2 and between lo3 and lo4 (Figs 1, 2) corresponds to the situation in many cirripede cyprids and supports homology (Jensen *et al.* 1994a; Høeg *et al.* 1998).

Lattice organs have not been found outside the Thecostraca. They are most notably lacking in the the Tantulocarida and in the Upper Cambrian 'Orsten' fossil *Bredocaris admirabilis* Müller 1983, which in the phylogeny of Walossek & Müller (1998) are the two closest relatives to the Thecostraca (Fig. 6A). We therefore conclude that lattice organs represent an autapomorphy (Fig. 7, character 1) of the Thecostraca *sensu* Grygier (1987) and that the Facetotecta belong within this group. The absence of lattice organs outside the Thecostraca does not preclude that they ultimately correspond to some of the dorsal organs identified in other Crustacea

(Walossek 1993), but a discussion of this aspect goes beyond our present scope.

Character evolution

Several traits in the morphology of lattice organs vary in a phylogenetically interesting manner (Jensen *et al.* 1994a), but they have not previously been used in a cladistic analysis of all Thecostraca. The variation concerns principally the shape of the individual organ and the position of the terminal pore in all five pairs.

In Fig. 7 we map the character states of lattice organs onto a phylogeny based on the hypotheses in Grygier (1987), Høeg (1992, 1995a,b), Spears *et al.* (1994), Glenner *et al.* (1995) and Høeg *et al.* (1999). The presence of lattice organs is an autapomorphy of the Thecostraca. The Cirripedia forms a monophylum characterized by the autapomorphic possession of special nauplii with frontolateral horns and a multitude of characters in the cypris larva. Within the Cirripedia, the sister-group relationship between Thoracica and Rhizocephala is based on the molecular evidence in Spears *et al.* (1994) and is confirmed by later studies (Mizrahi *et al.* 1998; Mouchel-Viehl *et al.* 1998; Perl-Treves *et al.* 2000; Harris *et al.* 2000).

Grygier (1987) could not resolve the basal trichotomy between the Ascothoracida, the Facetotecta and the Cirripedia. Information from lattice organs is also compatible with all three hypotheses in Fig. 6(B)–(D), but the morphology of the head shield in y-cyprids provides additional information. Unlike the ascothoracid larvae and some cirripede cyprids, the head shield of y-cyprids lacks a dorso-medial hinge line and is not folded down laterally, so large parts of the body are exposed. Posteriorly it has a deep and somewhat angular excavation. In these features it resembles *Bredocaris admirabilis* and to some extent also the tantulus larva of the Tantulocarida. From this outgroup comparison we favour the cladogram in Fig. 6(A) and consider the down-folded head shield and the more cypris-like morphology as synapomorphic for the Ascothoracida and Cirripedia.

Terminal pore position

We emphasize that the position of the terminal pore varies between the individual pairs of lattice organs. In a future character analysis it must therefore be scored as a separate character for each of the five pairs.

The terminal pore lies posteriorly in all five pairs of lattice organs in the Facetotecta and in the ascothoracidan species *Ulophysema oeresundense* Brattström, 1936, and we therefore consider this as the plesiomorphic condition present in the ground pattern (= stem species) of the Thecostraca (Jensen *et al.* 1994a). In the stem line to the Cirripedia the position of the pore changed to anterior in the 2nd pair of lattice organs (Fig. 7, character 2). In the stem line to the Rhizocephala and the Thoracica the pore position changed to anterior also in the first pair of lattice organs (Fig. 7 character 3). The Acrothoracica therefore display the apomorphic, anterior pore position in lo2 but retain the plesiomorphic, posterior position in lo1.

The Rhizocephala Akentrogonida lack terminal pores altogether (Jensen *et al.* 1994b), and this could question the phylogenetic position of this enigmatic suborder.

For the 2nd pair of lattice organs (lo2) the changes in pore position could be more complicated than would appear from the cladogram in Fig. 7. This is because characters cannot reliably be optimized on a consensus tree but only on the fully resolved trees from which they derive. Our interpretation in Fig. 7 about the plesiomorphic pore position in lo2 holds true in trees where either the Ascothoracida or the Facetotecta is the sister group to the Cirripedia (Fig. 6B,C). Both trees have two consecutive outgroups to the Cirripedia with a posterior pore position in lo2. Outgroup comparison (Maddison *et al.* 1984) will therefore unambiguously set 'posterior' as the plesiomorphic state for the Cirripedia. In the tree in Fig. 6(D) it is equally parsimonious that the plesiomorphic condition in lo2 was an anterior position, as now found in all Cirripedia. In this case a posterior position in lo2 would map as a synapomorphy for the clade comprising the Ascothoracida and the Facetotecta. We find this unlikely for two reasons. First, lattice organs are serially homologous structures and we therefore expect that the pore positions were originally identical in all five pairs. Secondly, Grygier (1987) argued that the tree in Fig. 6(D) has somewhat less character support than those in Fig. 6(B,C); we agree and argued above from head shield data that we favour the one in Fig. 6(B).

Pore field lattice organs

The Facetotecta, the Ascothoracida and Acrothoracica have a 'keel in a trough' morphology of the lattice organ and we consider this as the condition already present in the

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Fig. 4—Head shield of three different y-cyprids from Bahamian waters. —**A**. Specimen no. 2 of Schram (1970); anterior and posterior lattice organs (within rectangles) detailed in **B** and **C**, the mid-dorsal area is heavily sculptured compared to the Bergen specimen in Fig. 1(B). —**B**. Anterior lattice organs (lo1, lo2) in **A** situated around central pore (cp2), anteriorly converging ends of lo1 organs almost meet in the midline. —**C**. Posterior lattice organs (lo3–lo5) in **A** situated around central pore (cp4), anterior ends of lo3 almost meet in the midline. —**D**. Specimen no. 3 of Schram (1970); somewhat damaged, anterior lattice organs within rectangle detailed in **E**; scale as in **A**. —**E**. Rectangle in **D**, note the curved shape and wide anterior ends of lo1. —**F**. Specimen no. 1 of Schram (1970); very damaged posteriorly; note the large pits anteriorly on the head shield, anterior lattice organs (within rectangle) detailed in **G**; scale as in **A**. —**G**. Rectangle from **F** with central pore and lo1.
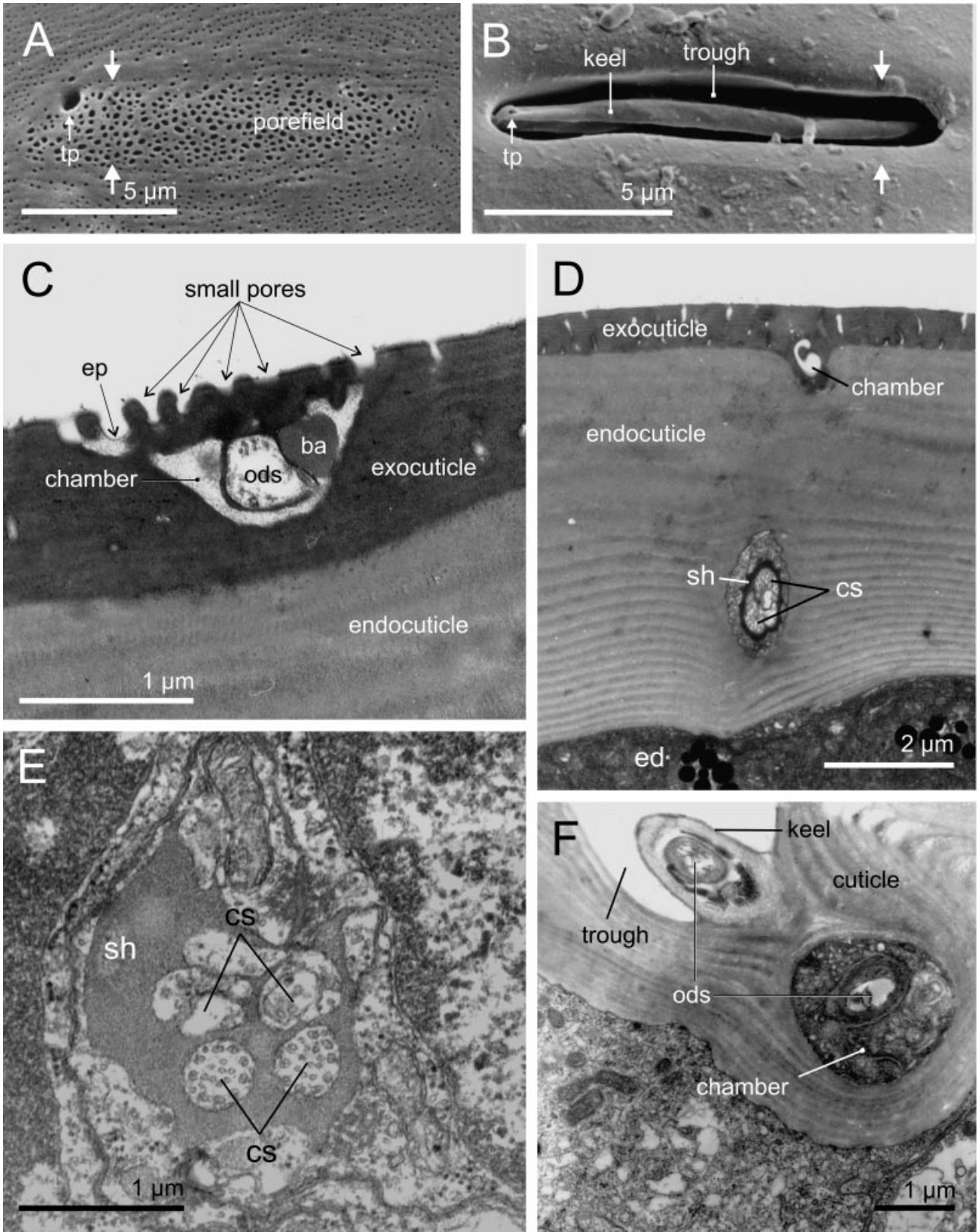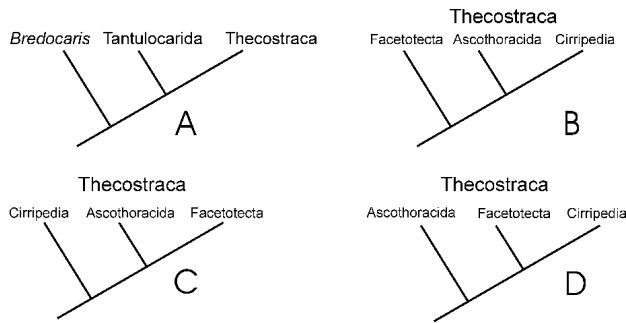
Fig. 6—**A**. The closest relatives of the Thecostraca (from the phylogeny in Walossek and Müller 1998). —**B**–**D**. Three possible phylogenies of the Thecostraca. Lattice organ morphology is compatible with all three cladograms, but the shape of the head shield in y-cyprids favours the one in **B** (see text).

ground pattern of the Thecostraca. The Thoracica and Rhizocephala share the apomorphic possession of a 'pore field' lattice organ with deep pits visible on SEM (Jensen *et al.* 1994a).

In the Acrothoracica, the lattice organs of *Trypetesa lampas* (Hancock, 1849) have no pits when viewed with SEM, but a TEM study reveals minute pores in the epicuticle above the chamber (Høeg *et al.* 1998). Our TEM results demonstrate that neither the Facetotecta nor the Ascothoracida possess such epicuticular pores. If the minute pores in the Acrothoracica correspond to the larger, pit-like pores in the Thoracica and the Rhizocephala, the possession of pores in the roof of lattice organs becomes an autapomorphy for all Cirripedia. The evolution of this feature could make it easier for chemicals to reach the sensory elements in the chamber and thus increase the efficiency of the organ.
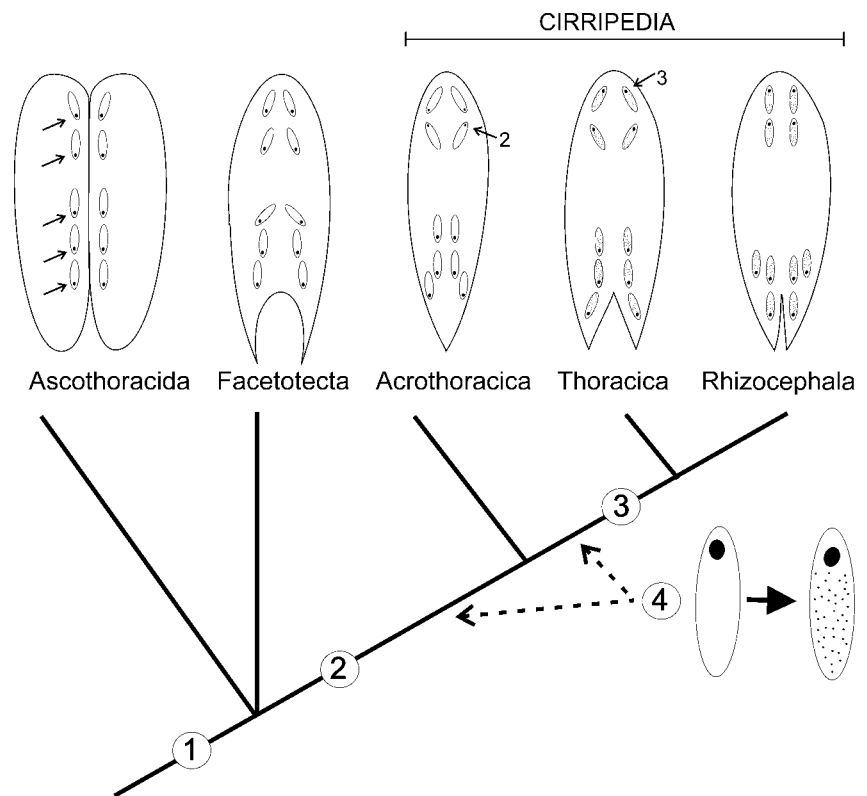
Fig. 7—Consensus phylogeny of the Crustacea Thecostraca and the possible evolution of the lattice organs; small arrows indicate the position of the terminal pore; (1) origin of lattice organs, the terminal pore situated posteriorly in all five pairs; (2) terminal pore shifts to anterior position in second pair; (3) terminal pore shifts to anterior position in first pair; (4) origin of pore field type lattice organ. The pore field type is omnipresent in the Thoracica and Rhizocephala; it also occurs in some Acrothoracica, but never in the Ascothoracida or the Facetotecta.

Fig. 5—Lattice organs in the Ascothoracida and the Cirripedia Thoracica. —**A**. SEM of 'pore field' type of lattice organ from the thoracican *Scalpellum scalpellum*. —**B**. SEM of 'keel in a trough' type of lattice organ from the ascothoracidan *Ulophysema oeresundense*. —**C**. *Scalpellum scalpellum* TEM, cross-section where indicated by arrows in **A**; chamber of lattice organ lies in the exocuticle and the roof is penetrated by numerous small pores only separated from the chamber by a very thin layer of cuticle (pore at left). —**D**. *Scalpellum scalpellum* TEM, cross-section showing canal of one lattice organ within endocuticle and terminal part of chamber from another lattice organ within exocuticle. —**E**. *Scalpellum scalpellum* TEM, lattice organ beneath the cuticle, four ciliary segments with microtubules enveloped by sheath. —**F**. *Ulophysema oeresundense* TEM, cross-section where indicated by arrows in **B**; chamber of lattice organ within 'keel', no pores in cuticle roofing the organ; both canal and chamber visible in cross-section due to oblique sectional plane (see arrowheads in Fig. 3B). Ba, ball-shaped body; cs, ciliary segment; ed, epidermis; ep, epicuticle; ods, outer dendritic segment; sh, sheath; ta, talisker; tp, terminal pore.

Origin and function of lattice organs

The TEM structure of the lattice organs displays all the characteristics of a chemoreceptor (Høeg *et al.* 1998). In the Ascothoracida and in the Facetotecta the terminal pore is the only pathway through which chemical compounds can reach the ciliary extensions in the cuticular chamber. Within the Cirripedia, the Acrothoracica have minute epicuticular pores that would most likely facilitate the diffusion of substances into the chamber throughout its length. In the Thoracica and Rhizocephala there is only a thin layer of epicuticle between the bottom of the pit-shaped pores and the chamber of the lattice organ. It therefore seems that the terminal pore becomes less important in the Cirripedia and this may also explain why species such as the akentrogonid rhizocephalans can lose it altogether.

Walossek *et al.* (1996) argued that lattice organs have setal precursors in the nauplius instars, and the 'keel in trough morphology' have some resemblance to a reclined seta (Fig. 5B). If lattice organs evolved from setae, the 'pore field' variety found in the Cirripedia would represent one of the most highly modified setae known from Crustacea. We hypothesize that the presence of lattice organs in all investigated Thecostraca is linked to the role of their terminal larval instar (cypris-y, ascothoracid, cypris) in seeking out a specific substratum, settling, and initiating a sessile adult life.

Acknowledgements

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