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The Chemoreceptive Lattice Organs in Cypris Larvae Develop from Naupliar Setae (Thecostraca: Cirripedia, Ascothoracida and Facetotecta)

Alexey V. RYBAKOV[1], Jens T. HØEG[2], Peter Gram JENSEN[2] and Gregory A. KOLBASOV[3]

[1]Department of Chorology, Institute of Marine Biology, Far East Division, Russian Academy of Sciences, Vladivostok, Russia
[2]Department of Zoomorphology, Zoological Institute, University of Copenhagen, Denmark
[3]Department of Invertebrate Zoology, Moscow State University, Russia

Abstract. Lattice organs are peculiar chemoreceptors found only in the Crustacea Thecostraca (Facetotecta, Ascothoracida, Cirripedia). In these taxa, five pairs occur in the head shield (carapace) of the terminal larval instar (y-cyprid, ascothoracid larva, cyprid), which is the settlement stage. Lattice organs represent an autapomorphy for the Thecostraca but their evolutionary origin and possible homologues in other Crustacea remain obscure. We have used scanning electron microscopy to describe the setation pattern of the head shield in late nauplii of one species of Ascothoracida, one species of Facetotecta and several species of the Cirripedia Thoracica, Acrothoracica, and Rhizocephala. The naupliar head shield always carries two pairs setae situated anteriorly near the midline. Each of these setae carry a single pore, and positional, structural and ontogenetic evidence show that these setae are homologous in all the examined species and that they represent precursors of the two anterior pairs of lattice organs of the succeeding larval stage, viz., the ascothoracid larva (Ascothoracida), y-cyprid (Facetotecta), and cyprid (Cirripedia). This leads us to infer that lattice organs are among the most highly modified sensilla in all Crustacea and they have in most cases lost all external resemblance to a seta. The nauplii of the Rhizocephala carry an additional three pairs of setae situated more posteriorly on the head shield and they could be precursors of the three posterior pairs of lattice organs. All other species examined lack these posterior setae, except the Facetotecta which have one posteriorly situated pair.

Key words. Nauplius, cyprid, SEM, morphology, development, homology, seta.

1. INTRODUCTION

Lattice organs are peculiar sensory structures that have been described from cyprids (cypris larvae) or their homologues in all groups of the Crustacea Thecostraca. They occur in the ascothoracid larvae of the Ascothoracida, in the y-cyprids of the Facetotecta (EL'FIMOV 1986; ITÓ & GRYGIER 1990; GRYGIER 1991, 1992; JENSEN et al. 1994a; KOLBASOV et al. 1999; HØEG & KOLBASOV 2002), and in cyprids from all three orders of the Cirripedia (Thoracica, Acrothoracica, Rhizocephala). All these larvae have five pairs of lattice organs located near the dorsal midline of the head shield (carapace), grouped as two anteriorly and three posteriorly situated pairs. Transmission electron microscopy (TEM) shows that each lattice organ consists of an elongate chamber within the head shield cuticle containing ciliary branches from two sensory cells wrapped in a sheath cell. The chamber communicates with the exterior through a large pore at one end of the chamber and sometimes also by numerous much smaller pores in the cuticular roof (HØEG et al. 1998). The only external manifestation of the organ is these pores and sometimes also a crestshaped elevation. The ultrastructure identifies the lattice organs as chemoreceptors, but their peculiar morphology ensures that their homology to structures in other Crustacea has remained obscure (HØEG et al. 1998). This is unfortunate because the presence of lattice organs is an autapomorphy for the Thecostraca and identification of homologous structures in other taxa could shed light both on the evolution of specialized sense organs and

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on the phylogenetic relationships within the Crustacea Maxillopoda (WALOSSEK & MÜLLER 1998). One approach to these questions is to study the ontogeny of lattice organs during larval development.

Although the nauplius and the succeeding settlement stage (the cypris larva or cyprid) differ in form and function they still share a number of common morphological features (WALLEY 1969). The shape of the cypris carapace is already foreshadowed in the late naupliar head shield (WALOSSEK et al. 1996). Some other naupliar structures, such as the bicellular glands of the frontolateral horns, the frontal filaments, and the nauplius eye are retained and function in the cyprid (cypris larva), although their morphology and position may have changed somewhat (WALKER 1992; GLENNER 1999). Other structures are functional only in the cyprid but develop earlier as anlagen and can be visible externally through the late naupliar cuticle. Examples are the paired compound eyes, the thoracopods and the antennular attachment organ (NOTT & FOSTER 1969; MOYSE 1987; WALLEY 1969; WALKER 1992; WALOSSEK et al. 1996). Therefore, a search for lattice organs or their possible precursors on the dorsal surface of late nauplius stages seems warranted. With this purpose the present study describes the head shield of the last nauplius instar from one species of Ascothoracida, one species of Facetotecta and several species of Cirripedia belonging to all three orders (Thoracica, Acrothoracica, and Rhizocephala).

2. MATERIAL AND METHODS

The origin of the examined species is given in Tab. 1. The nauplii of *Scalpellum scalpellum*, *Trypetesa lampas*, and *Balanus amphitrite* and all species of Rhizocephala discussed below were laboratory reared to the last nauplius stage and fixed. The nauplii of *Ulophysema oeresundense* were dissected from live female parasites and identified to instar using the drawings of BRATTSTRÖM (1948). The nauplii

Tab. 1. List of species larvae examined.

Species	Stage	Origin	Remarks
Ulophysema oeresundense	nauplius IV[1]	The Sound, Denmark	Dissected from live female
Trypetesa lampas	nauplii I–IV[2]	Gullmar Fjord, Sweden	Laboratory reared[4]
Hansenocaris itoi	late nauplii	White Sea, Russia	Plankton haul
Lepas pectinata	nauplius VI	Sargasso Sea	Plankton haul[5]
Scalpellum scalpellum	nauplius VI	Gullmar Fjord, Sweden	Laboratory reared[4]
Balanus amphitrite	nauplius VI and cyprid	Beaufort, USA	Laboratory reared [6]
Briarosaccus tenellus	nauplii II–VI[3] and cyprid	Alaska, USA	Laboratory reared[7]
Peltogasterella gracilis	nauplii I–V and cyprid	Nakhodka, Russia	Laboratory reared[8]
Peltogasterella sulcata	nauplii I–V and cyprid	Gulmar Fjord, Sweden	Laboratory reared[4]
Peltogaster paguri	nauplii I–V and cyprid	Gulmar Fjord, Sweden	Laboratory reared[4]
Peltogaster reticulatus	nauplii I–V and cyprid	Nakhodka, Russia	Laboratory reared[8]
Septosaccus rodriguezi	nauplius V	Mediterranean	Laboratory reared[9]
Lernaeodiscus porcellanae	nauplius V	Southern California, U.S.A.	Laboratory reared[4]
Heterosaccus californicus	nauplii II–V and cyprid	Southern California, USA	Laboratory reared[10]
Sacculina carcini	nauplii I, II and V and cyprid	Roscoff, France	Laboratory reared[4]
Sacculina pilosella	nauplii I–V and cyprid	Nakhodka, Russia	Laboratory reared[8]
Sacculina polygenea	nauplii I–V and cyprid	Nakhodka, Russia	Laboratory reared[8]

[1] Last naupliar stage of *Ulophysema oeresundense.*
[2] Last naupliar stage of *Trypetesa lampas*
[3] This species probably has 6 naupliar instars, unlike other examined rhizocephalans that have only 5 instars (see RYBAKOV et al. 2001)
[4] By J. T. HØEG.
[5] See CONWAY et al. 1990)
[6] By Henrik GLENNER
[7] By T. SHIRLEY (see WALOSSEK et al. 1996)
[8] by O. M. KORN and A.V. RYBAKOV
[9] by J. LÜTZEN
[10] by the Prof. Armand Kuris laboratory.
Species from the Gulmar Fjord, west coast of Sweden were reared at the Kristineberg Marine Research Station; those from Nakhodka, Russia, at the Vostok Marine Station.

of *Lepas pectinata* and *Hansenocaris itoi* were obtained from plankton samples; the former have been identified according to MOYSE (1987). The lecitotrophic nauplii of *S. scalpellum*, *T. lampas* and most Rhizocephala were reared as in HØEG (1984); those of *Peltogasterella socialis*, *Peltogaster reticulatus*, *Sacculina pilosella* and *S. polygenea* as in RYBAKOV et al. (2002); those of *Briarosaccus tenellus* as in HAWKES et al. (1985). The planktotrophic larvae of *Balanus amphitrite* were reared as in RITTSCHOF et al. (1984). The larvae were fixed in either formalin or glutaraldehyde and stored in the fixative until further processing.

For SEM some samples were first postfixed in OsO_4 but omitting this procedure produced comparable results. They were thereafter dehydrated through an acetone series, critical point dried in CO_2, and studied on a JEOL-840 scanning electron microscope in the Zoological Museum of the University of Copenhagen, Denmark. Some pictures were recorded using a Semaphore© system; the remaining ones were digitized by scanning photographic prints. For the Cirripedia we do not show pictures of cyprids since the lattice organs of that stage have been studied by JENSEN et al. (1994a, b), KOLBASOV et al. (1999) and KOLBASOV & HØEG (2001).

In naming shield and body features such as spines, we do not follow conventional cirripede terms (ANDERSON 1994) but use the strict terminology of WALOSSEK (1993) and WALOSSEK et al. (1996) to reflect the true position on the body and supposed homologies throughout Crustacea. In nauplii we refer to the entire postcephalic region as as hindbody, which incorporates both thorax and abdomen. The latter remains vestigial in all Cirripedia. To facilitate comparison with nauplii we also use the term “head shield” for the cypris “carapace”. Our dorsal shield spine is a true head shield (cephalic) feature, while the dorsal thoracic spine originates dorsally on the hindbody. The paired furcal spines sit on the true telson even if the latter is rudimentary, and in the cyprid they come to sit on true furcal rami articulated to the telson at the end of the hindbody, just as in the ground plan of the Maxillopoda (WALOSSEK et al. 1996; KOLBASOV et al. 1999).

The settlement stage of the thecostracan taxa has often been called cyprid or cypris larva. Due to numerous specializations we prefer to reserve the name “cyprid” for the Cirripedia. The homologous larva in other Thecostraca is called y-cyprid (Facetotecta) and ascothoracid larva (Ascothoracida).

3. RESULTS

3.1. Ascothoracida

We examined the last nauplius instar (nauplius IV) of *Ulophysema oeresundense* Brattström, 1936. The anterior margin the head shield bears a weak demarcation of the two valves of the succeeding ascothoracid larva (Figs. 1A–B). The surface lacks almost any ornamentation except for folds caused by specimen processing.

The anterior half of the head shield carries two pairs of setae (Figs. 1A, 1C). The distance between the first and second pairs is about 60 µm. All four setae are directed posteriorly. Each of them inserts in a pronounced depression and is simple, blunt, ca. 10 µm long and tapers toward the distal end where there seems to be a terminal pore (Fig. 1D).

These two pairs of setae also occur in all other examined species and we consider them homologous throughout (see Discussion). For this reason we henceforward designate the anteriormost pair of setae (which usually are shorter) as setae 1 (S1) and the second pair (which in most species are longer) as setae 2 (S2).

3.2. Facetotecta

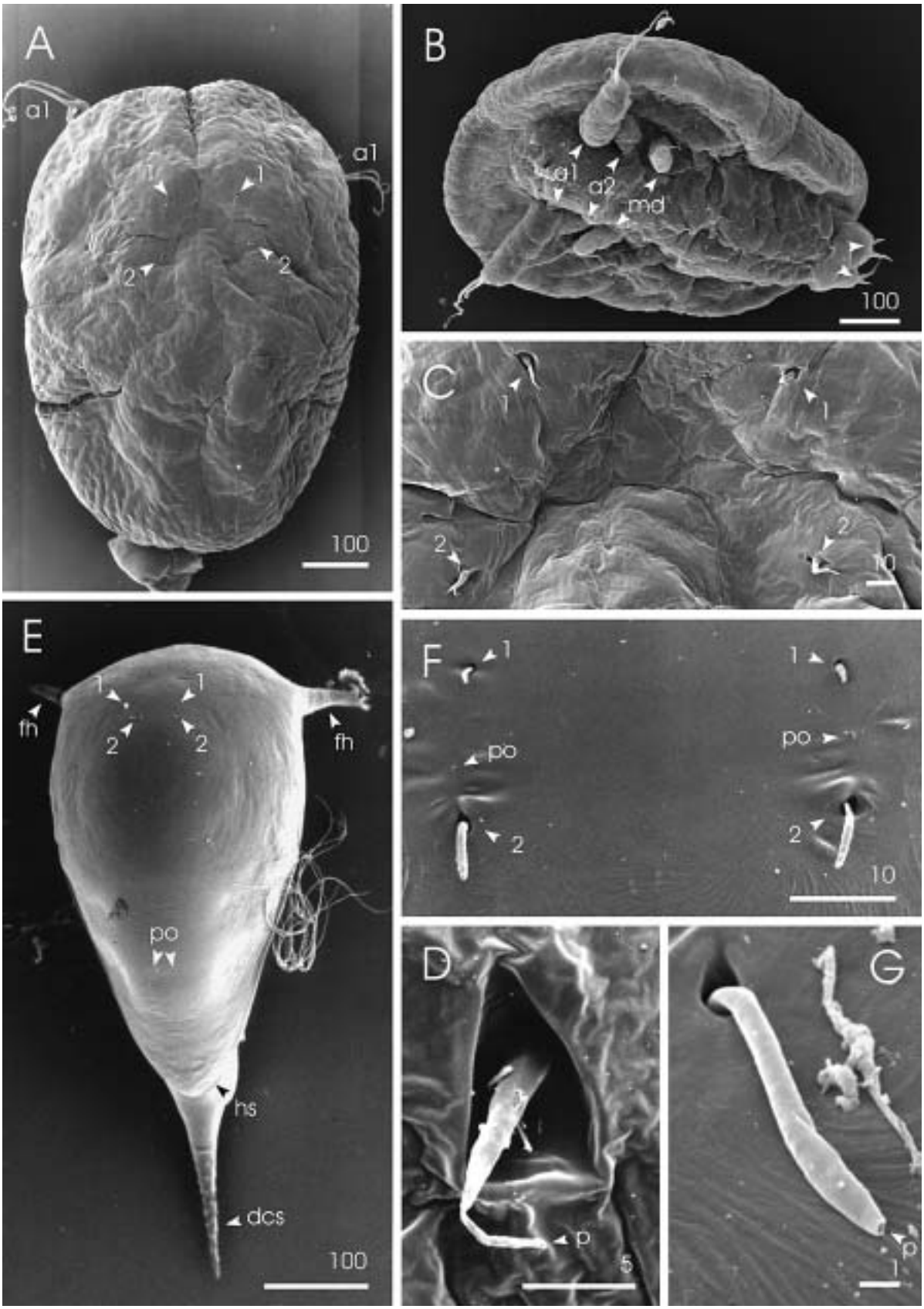
We examined the late nauplii and y-cyprids of *Hansenocaris itoi* Kolbasov et Høeg, collected in the White Sea (HØEG & KOLBASOV 2002). The nauplius has an oval head shield with an abruptly truncated posterior margin (Figs. 2A–B). It bears four pairs of setae, three pairs in the anterior portion of the head shield and one pair in the posterior part. All these setae have terminal pores (Figs. 2D–E). The anteriormost pair corresponds to the S1 setae of other species (Fig. 2C). The setae of the second pair are somewhat larger, located behind the S1 setae and more closely to each other. The position and relative size identify them as the S2 setae. The setae of the third pair are located laterally of the S2 setae and may be somewhat shifted either forwards (Fig. 2A) or backwards (Fig. 2B). They have no homologues in nauplii of the Ascothoracida, Acrothoracica, and Thoracica, but judging from their position they may correspond to the S2a setae of rhizocephalan larvae (see below).

The fourth pair of setae sits close to the posterior margin of the head shield (Figs. 2A–B). They are almost as long as the S2, and judging from position and size they could correspond to the S5 setae of the Rhizocephala.

The y-cyprid has an oblong, oval head shield (Fig. 2F) and carries five pairs of lattice organs as in all other Thecostraca (HØEG & KOLBASOV 2002). The two anterior pairs (LO1, LO2) are arranged around a large pore near the anterior end of the body (Fig. 2G) while the remaning three pairs (LO3–5) are found in the posteriormost part of the shield. All the lattice organs are crest-shaped, lack pore fields and have a large and posteriorly situated terminal pore (HØEG & KOLBASOV 2002).

3.3. Cirripedia Acrothoracica

We examined nauplii of *Trypetesa lampas* (Hancock, 1849). The head shield is broadest somewhat behind the level of frontolateral horns and has an elongated triangular shape. Very characteristically for this species, the last stage (nauplius IV) has a very well demarcated posterior margin of the shield.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Two pairs of setae are found near the dorsal midline at the level of frontolateral horns (Fig. 1E). The anterior, S1 setae arise in nauplius III but the S2 setae are already present in stage II. In nauplius IV the setae of both pairs are separated by ca. 15 µm and each individual seta is simple, more or less cylindrical in shape, and with a distal pore (Fig. 1G). The S2 setae are distinctly longer (ca. 8 µm) and stouter than those of S1 (ca. 5 µm).
The cuticle between these four setae is completely smooth except for a single pair of pores located halfway between the two pairs (Fig. 1F). The pores often exude a secretion product and seem to be gland exits. Another pair of large pores, also often with secretion coming out, is located more posteriorly (Fig. 1E)

3.4. Cirripedia Thoracica

We examined nauplii of *Lepas pectinata* Spengler, 1793; *Scalpellum scalpellum* Linnaeus, 1767; and *Balanus amphitrite* Darwin, 1854. In all three species the head shield of the late nauplius bears two centrally located pairs of setae (S1 and S2).
L. pectinata nauplii have an oblong hexagonal head shield with huge frontolateral horns at the anterolateral margins, and large and medium sized spines alternating along the lateral margins. Mid-dorsally the nauplius carries a small but distinct spine and a distinct hump protrudes between this and the anterior margin of the shield (Fig. 3B). Furrowed conical spines cover the entire surface of the head shield including the hump (Fig. 3C). The setae of the S1 pair are distinctly thinner and smaller (ca. 13 µm) than those of S2 (ca. 18 µm) and are situated closer to the midline (Fig. 3C). All four setae are slightly tapering, distinctly furrowed and with a distal pore (Fig. 3D–E). Each S2 seta is situated in a distinct depression (Fig. 3E) and a large simple pore is located between the pair (Fig. 3C).
Scalpellum scalpellum nauplii have a relatively short and broad shield, with strongly curved lateral margins, an almost straight anterior margin, and distinct frontolateral horns (Fig. 4A). The general surface appears smooth at low magnification but a network of tiny "ridges" is revealed at high magnifications (Fig. 4B). All four head shield setae (S1, S2) are simple, less than 10 µm long, more or less isodiametric, tapering only at the distal end, which terminates in a distal pore (Fig. 4C). Those of the posterior, S2, pair are only slightly longer and stouter than the S1 pair. Each of the four setae is situated in a narrow depression (Figs. 4B–C).
B. amphitrite nauplii have a more oblong head shield than in the other thoracican species studied, with slightly curved anterior and lateral margins and conspicuous frontolateral horns. The posterior margin sports two prominent spines (Fig. 4D). The general surface is smooth with a mesh of very fine ridges that are smaller than those of *S. scalpellum* (Fig. 4E). The two pairs of setae (S1, S2) are situated near the midline of the head shield and slightly posteriorly to the frontolateral horns (Fig. 4D). The S1 setae are more widely separated than the S2 and between them is a pair of large simple pores (Fig. 4E). The S2 setae are slightly larger and stouter than the S1. All four setae are simple, less than 10 µm long, weakly tapering, point posteriorly and carry a large distal pore (Fig. 4F). Each is situated in a narrow depression (Fig. 4E), which is occasionally elaborated into an oblong groove running for the entire length of the somewhat reclined seta (Fig. 4F).
One among several examined larvae of *B. amphitrite* had a different appearance (Fig. 4G). It lacked both the posterior dorsal thoracic spine, the dorsocaudal spine and the two posterolateral spines of the head shield (cf. Figs 4D and G). It also had reduced frontolateral horns and a large number of scattered depressions on the shield, each with a single short seta. In the precisely same area where normal nauplii carry the two pairs of head shield setae (Fig. 4H) this "monster" specimen had two pairs of true lattice organs with a morphology identical to lattice organ pairs 1 (LO1) and 2 (LO2) of the cyprid as described from balanid thoracicans by JENSEN et al. (1994a). The additional three pairs of lattice organs were found in the posterior end of the head shield of this specimen, in a relative position comparable to that of LO3–LO5 of the cyprid.

Fig. 1. A–D. Ascothoracida, *Ulophysema oeresundense* metanauplius. **A.** Dorsal view of whole nauplius. **B.** Oblique ventrolateral view of whole nauplius. **C.** Detail of A showing the two pairs of head shield setae. **D.** Dorsal view of the right anterior seta (1) of another specimen. **E–G.** Cirripedia Acrothoracica, *Trypetesa lampas* nauplius IV. **E.** Oblique dorsal view of whole nauplius. **F.** Detail of E with the two pairs of head shield setae and a pair of pores. **G.** Dorsal view of left posterior seta (2). 1–2 = pairs of head shield setae with pores, a1 = antennule, a2 = antenna, dcs = dorsocaudal spine, fs = furcal spine, fh = frontolateral horns, hs = posterior margin of head shield; md = mandibles, p = distal pore on seta, po = simple pore in shield cuticle.

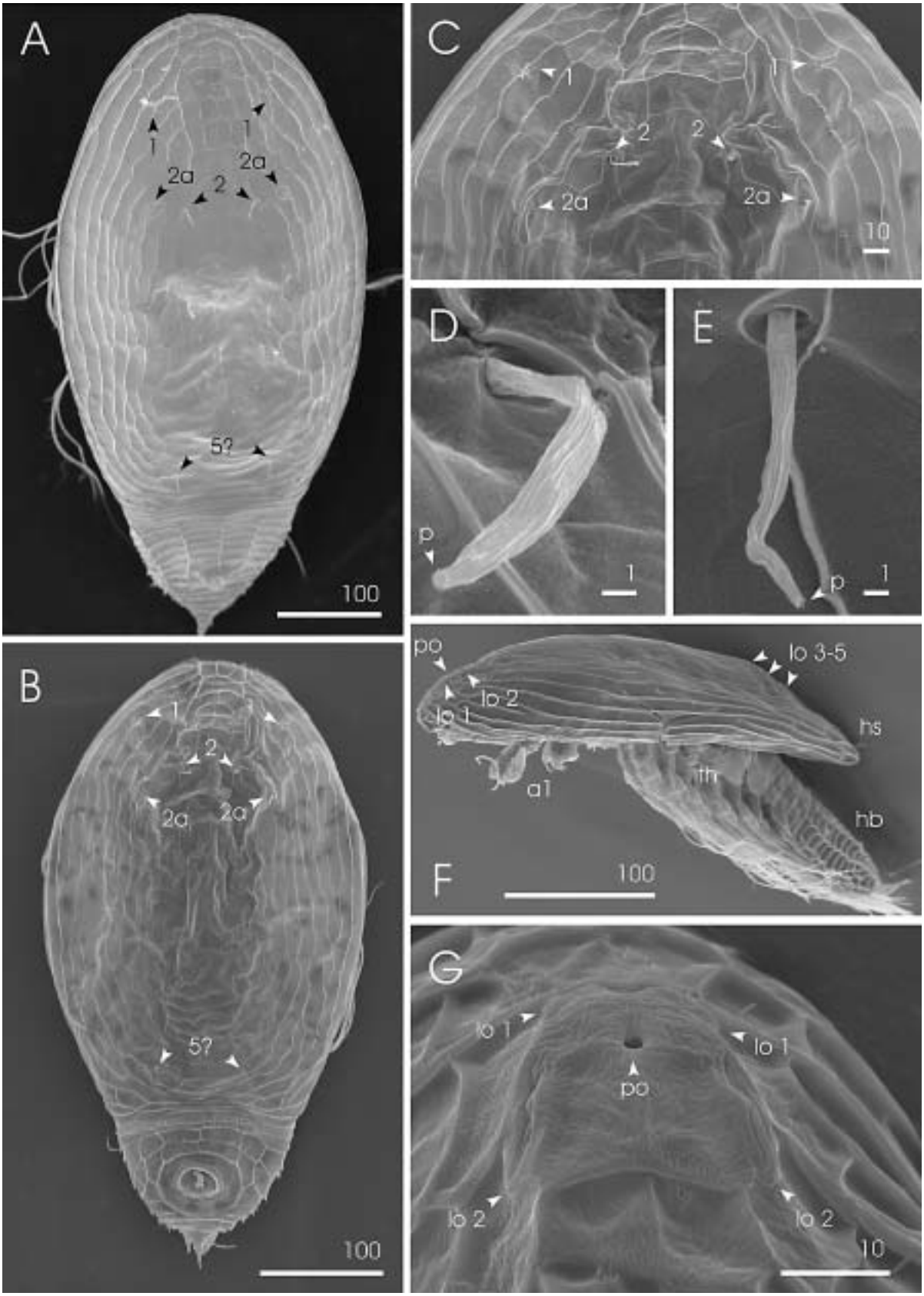
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Fig. 2.

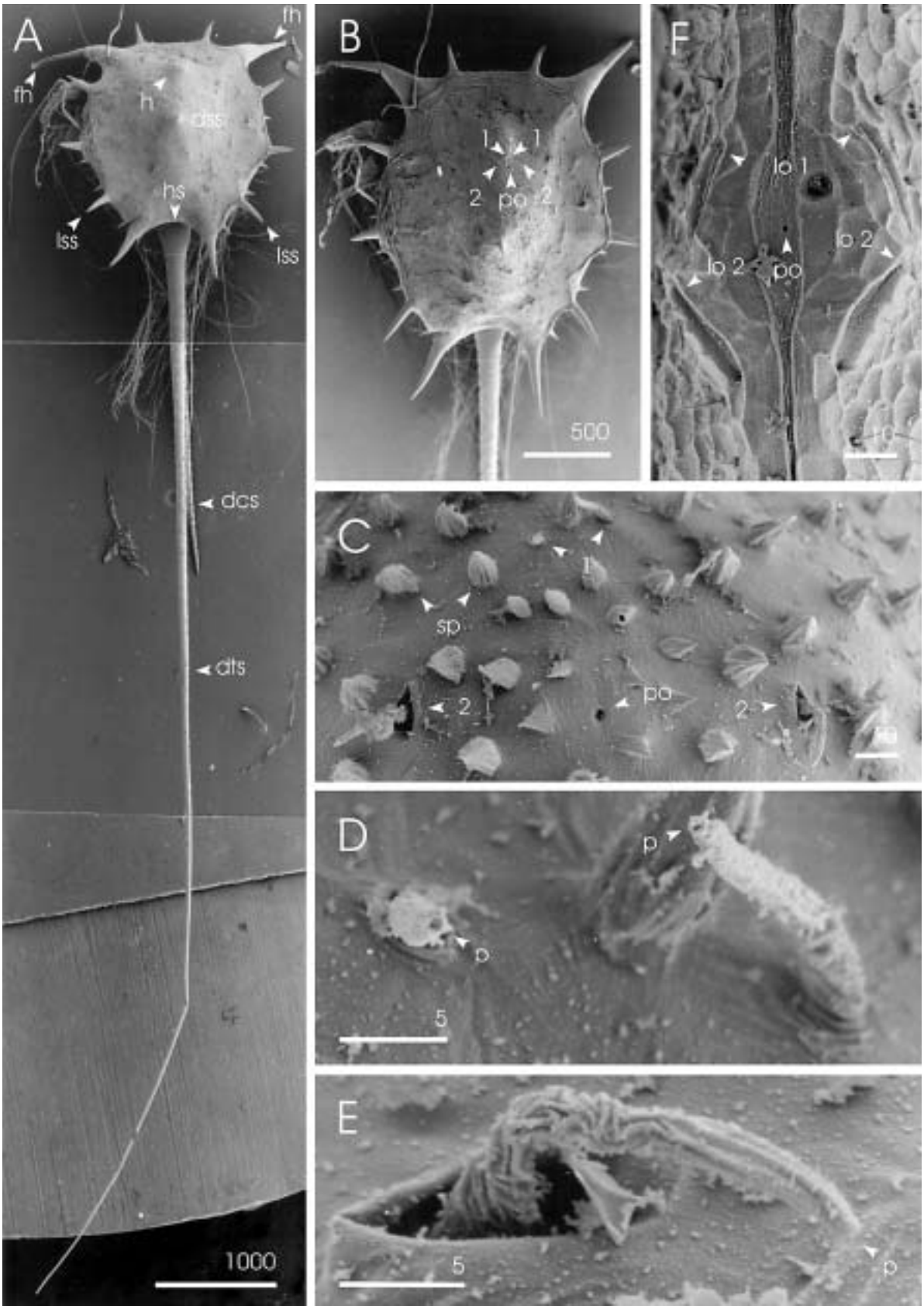
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Fig. 3.

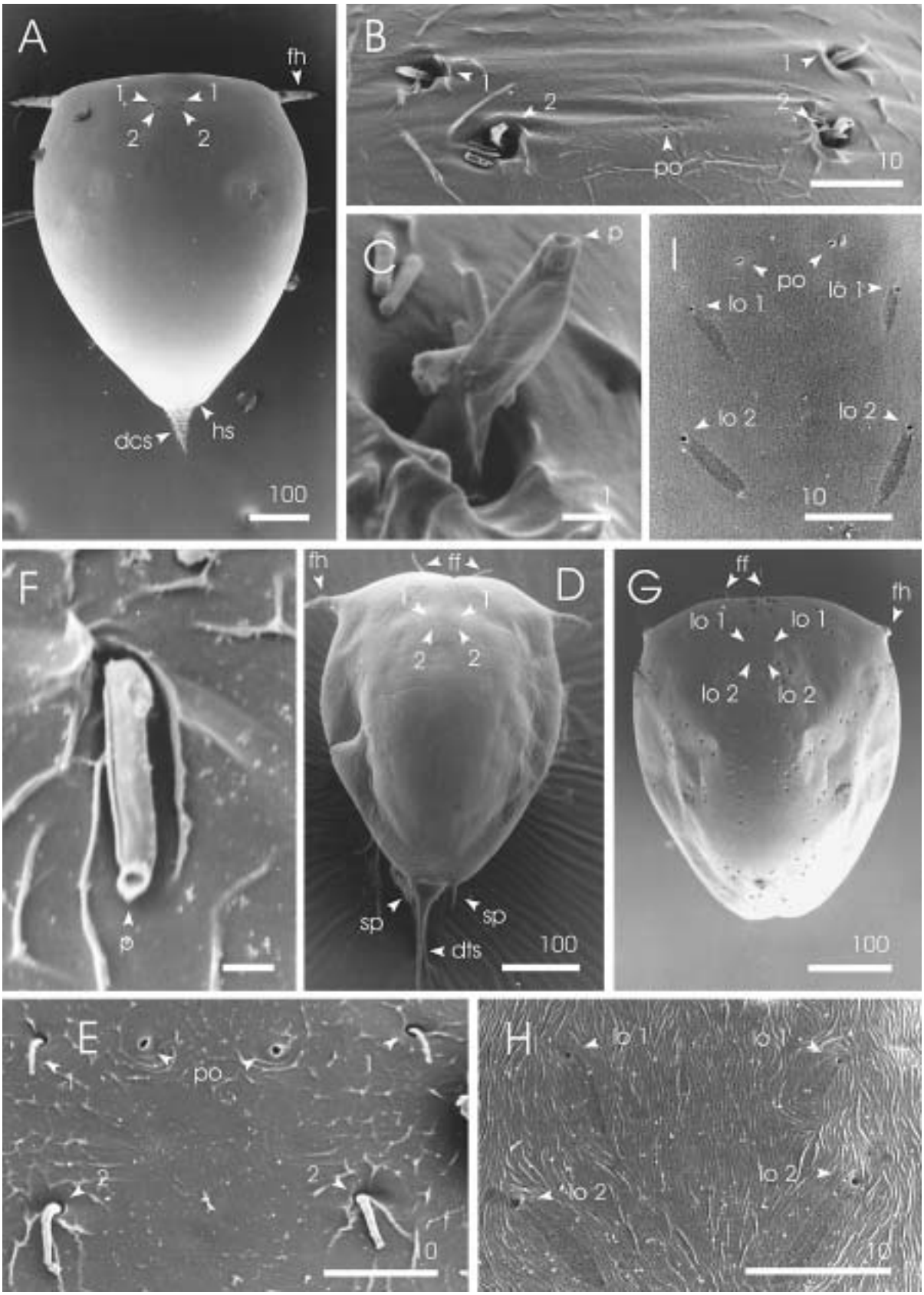
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Fig. 4.

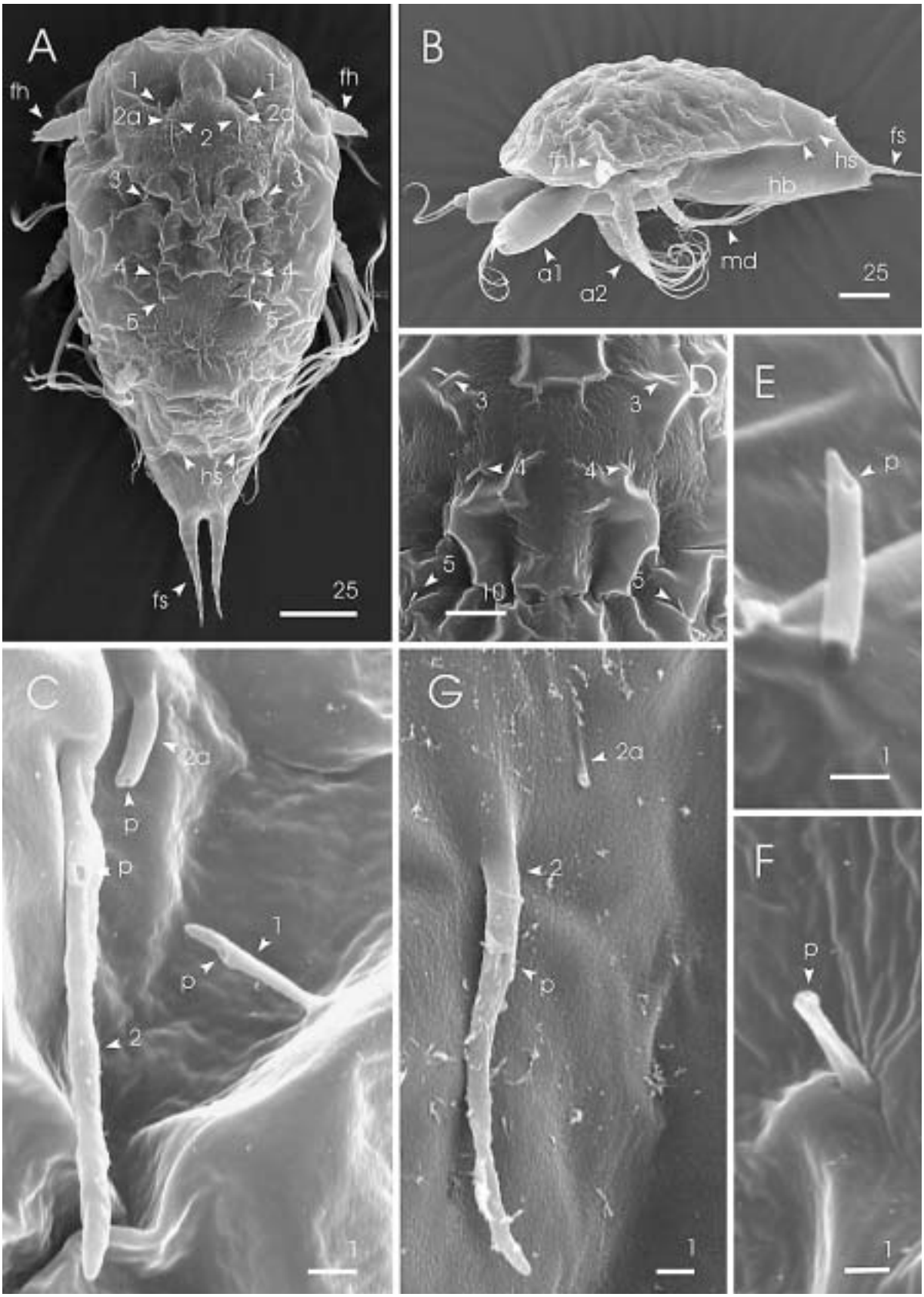
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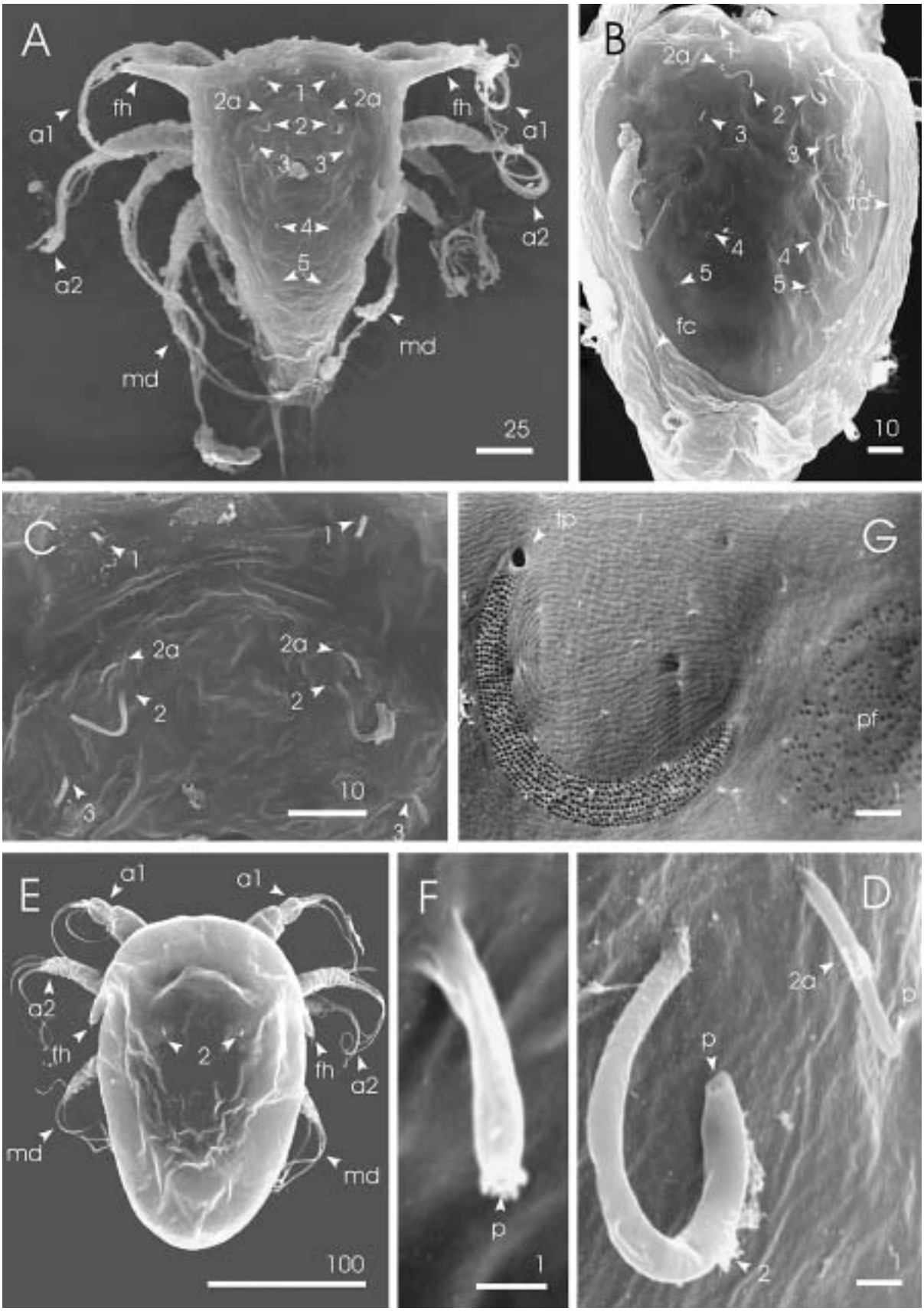
Fig. 5.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(Fig. 2–5, see p. 6–9)

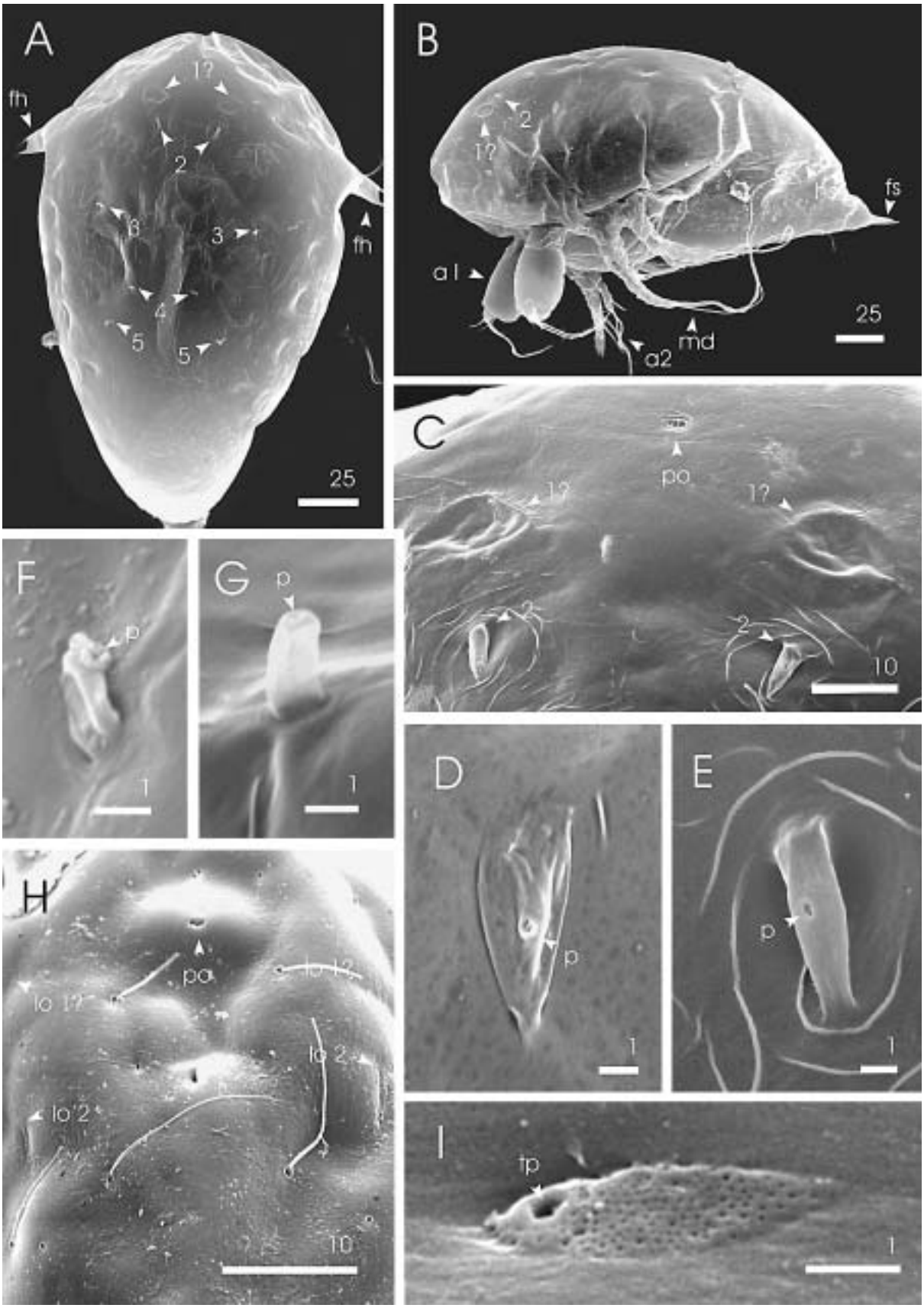
Fig. 2. Facetotecta, *Hansenocaris itoi*. **A, B.** Late nauplii, dorsal view, showing locations of the head shield setae with pores. **C.** Detail of anterior end in B. **D, E.** Late nauplius, two different head shield setae, both with terminal pore. **F.** Y-cyprid in lateral view, positions of lattice organs (lo 1–5) indicated. **G.** Y-cyprid in dorsal view of anterior part of head shield with lattice organ pairs 1–2 and large median pore. 1–5 = pairs of setae with pores, a1 = antennule, a2 = antenna, fs = furcal spine, fh = frontolateral horns, hb = hindbody, hs = posterior margin of head shield, lo1–5 = lattice organs, md = mandible, p = distal pore of seta, po = simple pore in shield cuticle, th = thorax.

Fig. 3. Cirripedia Thoracica, *Lepas pectinata*, nauplius 6. **A.** Dorsal view, showing dorsal shield spine, dorsothoracic spine and dorsocaudal spine. **B.** Detail of head shield in A. **C.** Detail of B, dorsal hump with setae pairs S1 and S2 and central pore. **D**. The pair of S1 setae (1) in C. **E.** Oblique lateral view of the right posterior seta (2) in C. **F.** Cyprid, anterior part of the head shield with two anterior pairs of lattice organs. 1–2 = pairs of head shield setae with pores, dcs = dorsocaudal spine, dss = dorsal shield spine, dts = dorsothoracic spine, fh = frontolateral horn, h = hump, hs = posterior margin of head shield, lo1, lo2 = lattice organs, lss = lateral shield spines, p = pore on seta, po = pore in shield cuticle, sp = spine on head shield.

Fig. 4. Cirripedia Thoracica. **A–C.** *Scalpellum scalpellum*, nauplius VI. **A.** Dorsal view of whole nauplius, arrowheads show seta pairs 1 and 2. **B.** Detail of A, posterodorsal view setae pairs 1 and 2. **C.** Right seta of second pair (2), a few bacteria at its base. **D–I.** *Balanus amphitrite*, nauplius IV **D.** Dorsal view of whole nauplius, arrowheads show seta pairs 1 and 2. **E.** Detail of D, region with setae pairs 1 and 2 and two pores in shield cuticle. **F.** Right seta of second pair (2), appearance reminiscent of lattice organs in ascothoracid larve of *Ulophysema oeresundens* (see text). **G–I.** *Balanus amphitrite*, newly molted cyprid or naupliar monster (see text). **G.** Dorsal view of whole larva, note naupliar shape of head shield, cp. to D, but minute frontolateral horns (fh), arrowheads point to lattice organs. **H.** Detail of G, region with lo1 and lo2, possibly derived from setae 1 and 2 in E. **I.** *Balanus amphitrite*, cyprid, dorsal view of lo1 and lo2, all of pore field morphology with anteriorly situated terminal pores (at arrowheads) and two separate anterior pores in shield cuticle. 1, 2 = pairs of head shield setae with pores, dcs = dorsocaudal spine, dts = dorsothoracic spine, ff = frontal filaments, fh = frontolateral horns, hs = posterior margin of the head shield, lo1, lo 2 = lattice organs, p = distal pore of seta, po = pore in shield cuticle.

Fig. 5. Cirripedia Rhizocephala Sacculinidae, last nauplius. **A–F.** *Heterosaccus californicus.* **A.** Whole nauplius, dorsal view. **B.** Lateral view, cypris morphology heralded in distally distended antennules (prospective attachment organ) and in hindbody projecting below and behind large headshield (cf. to Fig. 2F of y-cyprid). **C.** Detail from anterior part of head shield with right setae of pairs 1, 2, and 2a. **D.** Detail from posterior part of head shield, seta pairs 3–5. **E.** Seta from pair 3 with subterminal pore. **F.** Seta from pair 4 with terminal pore. **G.** *Sacculina carcini*, detail of anterior head shield, long seta 2 with proximally situated pore, satellite seta 2a fused with surface of head shield throughout most of its length. 1–5 = pairs of head shield setae with pores, a1 = antennule, a2 = antanna, fh = frontolateral horns, fs = furcal spine, hb = hindbody, hs = posterior margin of head shield, md = mandible, p = pore of seta.

Fig. 6. Cirripedia Rhizocephala. **A.** *Lernaeodiscus porcellanae*, last nauplius, dorsal view (the flotation collar accidentally lost)**. B–D**. *Septosaccus rodriguezi*, last nauplius. **B.** Whole nauplius, dorsal view, note flotation collar (fc) encircling headshield. **C.** Anterior part of head shield with four pairs of setae (1, 2, 2a, and 3). **D**. Long U-shaped seta 2 with terminal pore and satellite seta 2a, anterior is up. **E–F.** *Peltogasterella gracilis*, nauplius I. **E**. Whole nauplius, dorsal view, seta pair 1 appears in nauplius II. **F.** Long seta 2 with terminal pore. **G.** *Briarosaccus tenellus* cyprid, u-shaped lattice organ (lo2) of pore field type (cf. to seta 2 in D) and associated pore field (pf) , anterior is left. 1–5 = pairs of head shield setae with pores, a1 = antennule, a2 = antanna, fc = flotation collar, fh = frontolateral horns, hs = posterior margin of the head shield, lo1,lo2 = lattice organs, md = mandible, p = pore of seta; tp = terminal pore in lattice organ, sc = scapa, tp = terminal pore in lattice organ.


A
fh
1?
2
8
3
4
5
5
fh
25
B
2
1?
fs
a1
md
a2
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C
po
1?
1?
2
10
F
p
1
G
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1
D
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E
p
1
H
po
lo 1?
lo 1?
lo 2
lo 2
10
I
tp
1

3.5. Cirripedia Rhizocephala

We examined larvae of the following species. Peltogastridae: *Briarosaccus tenellus* Boschma, 1970 (see WALOSSEK et al. 1996), *Peltogasterella gracilis* (Krüger, 1912), *P. sulcata* (Lilljeborg, 1859) (see RYBAKOV et al. 2002), *Peltogaster paguri* Rathke, 1842, *P. reticulatus* Shino, 1943, and *Septosaccus rodriguezi* (Fraisse, 1877); Lernaeodiscidae: *Lernaeodiscus porcellanae* Müller, 1862; Sacculinidae: *Heterosaccus californicus* Boschma, 1933, *Sacculina carcini* Thompson, 1836, *S. pilosella,* and *S. polygenea* Lützen & Takahashi, 1997.

The instar I nauplius has an oviform head shield (Fig. 6E) that becomes rounded-triangular in the later stages (Figs. 5A–B, 6A–B, 7A–B). The head shield of the late nauplii of rhizocephalans usually comprises a set of 6 pairs of setae.

3.5.1. Anterior setae. The S1 setae appear in nauplius II (Figs. 5A, 6A). They insert in front of the S2 setae and point either forward or laterally. Each seta has a large terminal pore or a subterminal pore opening at the base of a narrow finger-like extremity (Fig. 5C).

The S2 setae appear already in nauplius I (Fig. 6E) and are situated at the level of or somewhat posterior to the frontolateral horns (Figs. 5A, 6A). They are much longer and are set more closely together than the S1 pair. They have a slender shape with a large pore that is subterminal (Sacculinidae, Fig. 5C) or terminal (Peltogastridae, Lernaeodiscidae, Fig. 6F). The S2 setae are directed backward, but in species of the Peltogastridae and Lernaeodiscidae (*B. tenellus, L. porcellanae*, *S. rodriguezi*) they are U-shaped so the apex points forward (Figs. 6C–D). Exactly the same curvature and orientation characterizes the second pair of lattice organs (LO2) in the cyprids of these two families (Fig. 6G). In later nauplii the S2 setae increase markedly in length. In the Peltogastridae and Lernaeodiscidae the large pore retains its terminal or slightly subterminal position (Fig. 6D), but in the Sacculinidae the pore has a much more proximal position in nauplii III–V (Fig. 5C, G).

The setae of the third pair, here called S2a, appear in nauplius II or III. They are always associated with the long S2 setae, inserting a little more laterally (Figs. 5A, 6A). The S2a setae are short and directed backward. In some species (like *Heterosaccus californicus, Peltogasterella gracilis* and *P. sulcata*) they are rather well-developed, free, and provided with a terminal pore each (Fig. 5C, see also Fig. 10e in WALOSSEK et al. 1996 and Fig. 9B in RYBAKOV et al. 2002). In other species (like *Sacculina carcini*) the S2a setae are reduced and partially fused with cuticle of the head shield, so the bulk of the seta appears as a keel-like trace with only the distalmost portion protruding as a small tubercle (Fig. 5G). We found no pronounced, terminal pore. Finally, some species (like *Sacculina polygenea*) have no trace whatsoever of the S2a setae (Fig. 7C).

3.5.2. Posterior setae. From nauplius II the Sacculinidae carry three pairs of setae (S3–5) on the posterior half of the head shield (Fig. 5D). They insert behind each other but the S4 setae lie somewhat closer to the midline than the S3 and S5 pairs. The S3 setae are usually somewhat larger, but all three pairs resemble S1. The setae are short, cylindrical in shape, and have a large pore situated either terminally on a suddenly truncated tip or subterminally at the base of a tapering finger-like tip.

The nauplii of the Peltogastridae and the Lernaeodiscidae also have three pairs of setae in the posterior part of the head shield, but the putative S3 setae are shifted forwards, inserting just behind the large S2 setae in these species (Fig. 8E).

3.5.3. Cypris larvae. In all rhizocephalans examined here the cyprid has a pore field in the same position relative to LO2, as S2a relates to S2 in the nauplii (see Fig. 6D, G). The field has a broad, oval outline and lacks any terminal pore. The density of pores is much less than normal in lattice organs.

3.5.4. Sacculina polygenea larvae. In this species the setation pattern on the naupliar head shield differs somewhat from that seen in the other Rhizocephala although the gross morphology is comparable (Figs.

Fig. 7. Cirripedia Rhizocephala. *Sacculina polygenea*. **A–C.** Last nauplius. **A.** Dorsal view. **B.** Lateral view. **C.** Anterior part of head shield with modified setae 2 behind depressions (1?), which may be seta 1 derivatives, and large unpaired pore. **D.** Nauplius II, modified seta 2. **E.** Nauplius IV, modified seta 2. **F.** Seta 3 with subterminal pore. **G.** Seta 4 with terminal pore. **H–I.** Cyprid. **H.** Anterior part of head shield with second lattice organs (lo2), supposed derivatives of lo1, and large unpaired pore. **I.** Lo2, of porefield shape, anterior is left. 1–5 = pairs of head shield setae with pores, a1 = antennule, a2 = antenna, fh = frontolateral horns, fs = furcal spine, hs = posterior margin of head shield, lo1, lo2 = lattice organs, md = mandible, p = pore of seta; po, pore in head shield, tp = terminal pore in lattice organ.

7A–B). No setae were found in nauplius I. Nauplius II carries four pairs of setae.

There are no setae in the position of the S1 pair. The anteriormost pair inserts at the level of the frontolateral horns and we therefore consider them as S2 although no satellite S2a setae are found in *S. polygenea*. The S2 setae are short, very broad, with a somewhat triangular shape, and fused to the head shield cuticle throughout their length (Fig. 7D). In late nauplii each S2 seta resembles a keel and is sometimes located in an oval depression and provided with a conspicuous large pore situated dorsolaterally close to the middle of the keel (Figs. 7C, E).

Although we found no trace of S1 setae, a pair of of conspicuous depressions with a finely grained cuticle lies in their expected position. They are present in all the examined *S. polygena* larvae and therefore do not seem to be an artifact. A complex shaped pore lies in the body midline in front of these depressions. The arrangement of this pore, the pair of depressions, and the modified S2 setae is in the shape a regular pentagon. Cyprids of *S. polygenea* have a corresponding pentagon consisting of (Fig. 7H) a large unpaired pore of exactly the same structure as in the nauplii, two poorly developed pore fields lacking terminal pores, and the second pair of lattice organs (Fig. 7H). The said pore fields occupy exactly the same position as lattice organs LO1 of other cirripede cyprids. In *Sacculina polygenea* the LO2 organs are elongate, spindle-shaped, perforated by numerous small pores and have a posteriorly situated, large, terminal pore (Fig. 5H, I).

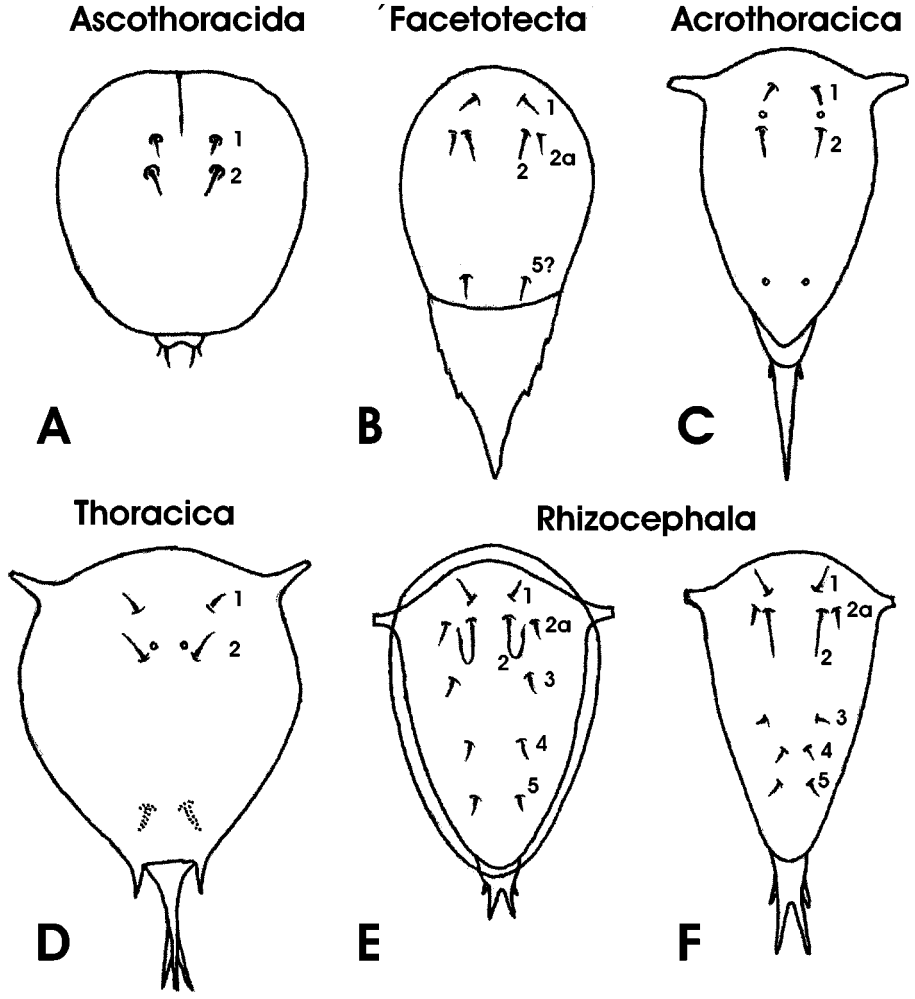

Fig. 8. Diagram of head shield setae with pores and pores on the head shield in late nauplii of the Crustacea Thecostraca. **A.** Ascothoracida (*Ulophysema oeresundense*). **B.** Facetotecta (*Hansenocaris itoi*). **C–F.** Cirripedia. **C.** Acrothoracica (*Trypetesa lampas*). **D.** Thoracica (*Balanus amphitrite*). **E.** Rhizocephala Peltogastridae and Lernaeodiscidae, note the U-shaped seta 2. **F.** Rhizocephala Sacculinidae. Seta pairs 1 and 2 are precursors for lattice organ pairs 1 and 2 in the cyprid. The three posterior pairs (3–5) are only present in the Rhizocephala and are probably precursors for lattice organ pairs 3–5. Satellite 2a setae are only present in the Rhizocephala and the Facetotecta.

The remaining three, posterior pairs of setae are considered as S3–5, because they have have a similar location and appearance to those of other rhizocephalan species (Figs. 7F–G).

4. DISCUSSION

We consider the five pairs of head shield setae (S1–5) found in thecostracan nauplii as homologous throughout the Facetotecta, Ascothoracida, and Cirripedia. We furthermore argue that they represent precursors for the five pairs of lattice organs (LO1–5) found in the carapace (head shield) of all cyprids and cypris-like larvae, proving that these very unusual sensory organs derive both ontogenetically and phylogenetically from sensory setae.

4.1. Homology of head shield setae

Unlike cypris larvae, the head shield of the nauplii in all species examined so far shows a surprising scarcity of setae or other ornamentation. All head shield setae share a common structural pattern and look like sensilla. Each is provided with a large, conspicuous pore that may occupy a terminal or subterminal position, or a more proximal portion on the seta (S2 setae).

We base our proposed homology of the S1–5 setae on their structural similarity and on their position relative to the frontolateral horns and to other setae and pores on the naupliar head shield. In non-rhizocephalan nauplii the situation is simple, since we found only two pairs of setae (S1, S2), differently sized and shaped and with distinct relative positions. In rhizocephalan nauplii the identification of the anterior two pairs as S1 and S2 is straight forward, since they occupy the same position as the corresponding setae in the other species and are generally far separated from the posterior three pairs (S3–5) found only in this taxon. In the rhizocephalan *Sacculina polygenea* the apparent absence of S1 setae complicates the pattern, but the identification of the anteriormost setae as S2 is supported by their location on the shield and by the position of their large pore.

In the *S. polygenea* cyprid we suggest that the pair of small porefields without terminal pores and sited anterior to the second pair of lattice organs (LO2) represents reduced or modified LO1s. The reduced state is in accord with the absence of setal precursors in the nauplii. The absence of a terminal pore is not unusual, since this is also lacking from all five pairs of lattice organs in cyprids of the Rhizocephala Akentrogonida (JENSEN et al. 1994b).

Most previous accounts of thecostracan nauplii have focussed on the appendages and other structures on the ventral surface but provided no details on the head shield except for a simple outline. Few studies have attempted to accurately describe the surface structures on the dorsal cuticle.

4.1.1. Ascothoracida. The nauplii possess up to four pairs of dorsal setae, but none of these has previously been described with SEM, so a detailed comparison is not possible (BOXSHALL & BÖTTGER-SCHNACK 1988; ITÓ & GRYGIER 1990; GRYGIER 1990, 1993). In *Baccalaureus falsiramus* Itô & Grygier, 1990 The two anterior pairs are already present in nauplius I and occupy a position comparable to the two anterior pairs found in all investigated species. We consider them as homologous to our S1 and S2 setae. The two posterior pairs in *B. falsiramus* appear later in ontogeny (ITÓ & GRYGIER 1990).

4.1.2. Facetotecta. Many facetotectan nauplii also possess up to four pairs of setae on the head shield (ITÓ 1986, 1987, 1990; GRYGIER 1987; SCHRAM 1970, 1972). In the larvae described by Itó, the two pairs of setae situated around the so-called ‘window’ are probably homologous to the S1 and S2 setae described here since they have a comparable position. The nauplii of *Hansenocaris itoi* studied here show a somewhat different situation by having three pairs of setae in the anterior part of the head shield and only one pair in its posterior part. We believe that two of the three anterior pairs correspond to the S1 and S2 setae, while the third pair may be homologous to the S2a found in rhizocephalan larvae. GRYGIER (1995) described exactly the same setation pattern in an unidentified facetotectan nauplius from Tanabe Bay, Japan.

4.1.3. Acrothoracica. Our results from *Trypetesa lampas* provide the only available detailed description.

4.1.4 Thoracica. Few of the many papers dealing with naupliar stages have given any attention to head shield setation, and this again highlights the inadequacy of the prevailing protocol for describing thoracican larvae. KADO (1982) and KADO & HØEG (1998) reported the presence of two pairs of setae on the head shield of some balanomorph and lepadomorph nauplii, and these setae again have a position comparable to S1 and S2 in our study. WALKER & LEE (1976) used SEM to study larvae of *Semibalanus balanoides* (Linnaeus, 1767) in one of the few detailed descriptions of the head shield for any thecostracan nauplius. Nauplius VI has a large number of simple pores but only two pairs of setae; they carry terminal pores and two pores are located on the head shield between anterior pair of setae. This pattern is very similar to that of *Balanus amphitrite* and we conclude that the four setae represent the S1 and S2 pairs.

It is pertinent to mention here the description of an unusual, unidentified barnacle nauplius, which seems to carry three pairs of setae on the head shield (GRYGIER 1995). Two pairs correspond to the S1 and S2 of other species, while the third pair may be comparable to the posterior pair of setae in *Hansenocaris itoi* or one of the posterior pairs seen in rhizocephalan nauplii. This paper also reveals how much information can actually be gleaned by careful use of the light microscope and should serve as a primer for all future studies.

4.1.5. Rhizocephala. The naupliar head shield has now been described with SEM from several species and may carry up to six pairs of setae (COLLIS & WALKER 1994; WALOSSEK et al. 1996; RYBAKOV et al. 2002; Present study). The two anterior pairs are obviously homologous to the S1 and S2 setae in other thecostracan nauplii. Three posterior pairs of setae have no homologues in representatives of the other cirripedes examined here, but one of them may correspond to the posterior pair of setae described in some ascothoracidan and facetotectan larvae (Fig. 8.) The pair of small satellite setae (S2a) in rhizocephalans seem to have no obvious homologues in other thecostracan taxa except perhaps the Facetotecta (Fig. 8B, E, F).

4.2. Homology of setae and lattice organs

No lattice organs in their final form are present in any thecostracan nauplii, but JENSEN et al. (1994A) suggested that they have evolved from sensory setae (sensilla). We find that both positional, structural and ontogenetic evidence indicates that the lattice organs (LO1–5) in cyprids, y-cyprids and ascothoracid larvae develop from the head shield setae with pores (S1–5) in thecostracan nauplii.

4.2.1. Position. In all species examined here the relative positions of the two anteriormost pairs of setae (S1–2) are the same as the two anteriormost pairs of lattice organs (LO1–2) in the succeeding settlement stage (cyprid, y-cyprid, ascothoracid larva). Within any single species the separation between the S1 and S2 setae is also about the same as between LO1 and LO2. There is a comparably large distance between S1 and S2 in the metanauplius of *Ulophysema oeresundense* (Fig. 1A) matching a comparable large separation between LO1 and LO2 in the ascothoracid larva (JENSEN et al. 1994A). The S1 and S2 setae in nauplii of *Lepas pectinata* sit on a conspicuous hump and around a central pore (Fig. 3), just as is the case for LO1 and LO2 in the cyprid (JENSEN et al. 1994a). In *Scalpellum scalpellum* both the S1 and S2 setae in nauplii and the LO1 and LO2 organs in the cyprid are similarly arranged around a central pore.
In nauplii of the Rhizocephala the three posterior pairs of setae have exactly the same positions as the three posterior pairs of lattice organs in the cyprids, so we conclude that the S3, S4 and S5 setae correspond to LO3, LO4, and LO5 respectively.
In the Ascothoracida and the Facetotecta it remains difficult to decide whether the one or two posterior pairs of setae in the nauplii correspond to any of the posterior pairs of lattice organs in the ascothoracids and y-cyprids.

4.2.2. Structure. The structural resemblance beween lattice organs and setae on the naupliar head shield is very striking in the Ascothoracida, where *Ulophysema oeresundense* has lattice organs that resemble an open ended seta lying prostrate in an oblong depression and partially fused with the headshield (JENSEN et al. 1994a; HØEG & KOLBASOV 2002). Some Facetotecta and some acrothoracican Cirripedia also retain such a morphology of the lattice organs. (JENSEN et al. 1994a). The remaining Cirripedia have pore field shaped lattice organs without any resemblance to a seta except that in our interpretation their terminal pore corresponds to the distal pore in the naupliar setae (HØEG & KOLBASOV 2002). The only exception is the thoracican *Capitulum mitella* (Linnaeus, 1767), where the cyprid has lattice organs shaped like a reclined seta as in the Ascothoracida but here provided with numerous small pores along its length in addition to the large terminal one (JENSEN et al. 1994a). In a simple character transformation series this would fit as an intermediate state between a seta shaped and a pore field shaped lattice organ. Judging from the accepted phylogenetic position of *C. mitella* rather high up in the thoracican tree (GLENNER et al. 1995) it is more likely that the form of its lattice organs represents a reversal, but even so the condition emphasizes the morphological similarity between lattice organs and setae.
Even though the lattice organs of pore field shape in cyprids of thoracican barnacles have lost any resemblance to a seta, it is interesting to observe the striking similarity between the S2 setae in nauplii of *Balanus amphitrite* and the lattice organs in the Ascothoracida as illustrated by JENSEN et al. (1994a) and HØEG & KOLBASOV (2002). Both structures lie prostrate in an antero-posteriorly oriented depression and have a terminal pore (Fig. 4F). The only real difference is that the "seta" in the ascothoracidan lattice organ is narrowly fused with the bottom of the depression throughout its length while the seta in the *B. amphitrite* nauplius is not, and we did observe partial fusion of naupliar head shield setae with the general shield cuticle in other cirripedes (Figs. 5G, 7D–E).

In all cirripede nauplii studied here, the S1 setae are slightly smaller than the S2 setae and this coincides with a similar size difference between LO1 and LO2 in the cyprids. (JENSEN et al. 1994A). In *Ulophysema oeresundense* there was no such size difference. Some rhizocephalan cyprids have peculiarly U-shaped LO2s (JENSEN et al. 1994a) and the same species have U-shaped S2 setae in the nauplii (cf. Figs. 6D, G). RYBAKOV et al. (2002) regard U-shaped LO2s as a synapomorphy for families Lernaeodiscidae and Peltogastridae and this also receives support from molecular evidence (GLENNER & SPEARS 2001). It seems that LO2 morphology is foreshadowed by the setal precursors in the nauplii.

4.2.3. Ontogeny. The characteristic head shield setae with pores observed in thecostracan nauplii seem to disappear at the moult to the settlement stage, and this agrees with their being precursors of lattice organs. The claim that lattice organs develop from naupliar setae also receives support from the larval "monster" we observed in *B. amphitrite*. This specimen might be either a nauplius with precociously developed lattice organs or a recently moulted and perhaps developmentally arrested cyprid that had not yet attained its final shape (a well known phenomenon, see e.g., ITÓ 1989). Whatever the explanation the specimen has a naupliar outline but carries fully formed lattice organs (LO1, LO2) in exactly the position where normal nauplii would carry the S1 and S2 setae, indicating that the former develop from the latter. Furthermore, WALKER & LEE (1976) documented that all pores observed in nauplius VI of *Semibalanus balanoides* were also present in the same relative positions in the cyprid. It is accordingly reasonable to assume that the pores situated between the anterior setae of the nauplius correspond to the pores situated between the anterior lattice organs of the cyprid, further indicating that these setae develop into lattice organs.

If we accept that lattice organs develop from naupliar setae, the results of ITÓ & GRYGIER (1990) and GRYGIER (1990) suggest the setal precursors of lattice organs may be present as early as nauplius I, at least in some ascothoracid and rhizocephalan larvae.

In conclusion, both the positional, morphological and ontogenetic observations indicate that lattice organs develop from setae in the nauplii. Outgroup comparison based on current ideas of thecostracan phylogeny indicates that the seta shaped morphology of lattice organs found in all Ascothoracida, all Facetotecta and some Acrothoracica is more plesiomorphic than the flat, pore field shaped organs found in the Rhizocephala and Thoracica (HØEG & KOLBASOV 2002). The same conclusion is reached by using the ontogenetic criterion for character polarity, since our observation indicate that lattice organs (also of the pore field type) develop from naupliar setae. The small pores in the pore field type of lattice organs are never seen in the naupliar precursor setae nor are they present in lattice organs of any of the cypris-like larvae outside the Cirripedia.

4.3. Ontogeny and terminal pore position

The position of the terminal pore in lattice organs seems to contain significant phylogenetic information (JENSEN et al. 1994a; KOLBASOV et al. 1999). In the thecostracan ground pattern the pore has a posterior position in all five pairs of lattice organs, and HØEG & KOLBASOV (2002) considered an anterior position of the terminal pore in LO2 as a synapomorphy for the Cirripedia and an anterior position in LO1 as a synapomorphy for the Rhizocephala and Thoracica. This agrees with the recently published phylogenies based on rRNA sequences (MIZRAHI et al. 2000; HARRIS et al. 2000). If lattice organs develop from head shield setae they must assume their final form and orientation during the moult from the last nauplius. The Ascothoracida seem to exemplify a plesiomorphic condition, where the lattice organs look like little more than a reclined seta that has partially fused with the headshield. Their S1 and S2 setae point posteriorly in the nauplius as do the terminal pores of LO1 and LO2 in the ascothoracid larva, so morphological changes during the moult to the ascothoracid larva may be minor.

In terms of shape, orientation and position of the pore the second pair of lattice organs is the more variable (JENSEN et al. 1994a, b; RYBAKOV et al. 2002) and it is especially interesting to review the situation within the Rhizocephala. Most rhizocephalans have the terminal pore situated anteriorly in LO2, but our new observations from nauplii could indicate that this situation can be achieved by different ontogenetic pathways. In the Sacculinidae the anterior position corresponds to the proximal end of the precursor seta (large seta S2), since the pore is displaced and located proximally on the large S2 seta in the late nauplius ("proximal pore"). In the Peltogastridae and Lernaeodiscidae, the anterior position of the pore in LO2 corresponds to the distal end of the precursor seta of the nauplius ("distal pore"). In these two families the S2 setae are U-shaped, so their distal ends terminating in a pore are directed anteriorly. It follows that the anterior end of LO2 in the Sacculinidae corresponds to the proximal end of the precursor seta, whereas it corresponds to its distal end in the Peltogastridae and Lernaeodiscidae.

To complicate the pattern a group of species in the Sacculinidae have the terminal pore situated posteriorly in LO2, viz., *Sacculina polygenea, Ptychascus barnwelli,*

P. glaber, and *Sesarmaxenos gedehensis*. The ontogeny of *S. polygenea* larvae reveals that this unusual position of the terminal pore is probably not a retained plesiomorphic condition. The pore position in the cyprid results from the premature fusion of the S2 seta with the head shield early in naupliar development. Unlike other Sacculinidae where the seta remains free, this prevents S2 from growing in length so the large pore cannot assume a pronounced proximal position. The unusual posterior pore position in LO2 of these sacculinids correlates with some morphological characteristics of the adult externa, viz., simplified colleteric glands that comprise a relatively small number of tubules and male receptacles situated in the mesentery, outside the visceral sac. Interestingly, Glenner and Lützen (pers. comm.) have used molecular data to show that *S. polygenea* (and two other species of *Sacculina*) do not belong within the Sacculinidae, but *Ptychascus* and *Sesarmaxenos* did not form part of their analysis.

Based on the terminal pore in LO2 of the cyprids, the Rhizocephala can therefore be divided into four informal groups: (1) The Peltogastridae and Lernaeodiscidae, where all studied species have a 'flipped' LO2 and the terminal pore ("distal pore") situated anteriorly; (2) Sacculinidae with the terminal pore ("proximal pore") situated anteriorly; (3) Sacculinidae with the terminal pore situated posteriorly; (4) the Akentrogonida, where the lattice organs lack terminal pores altogether. The Akentrogonida furthermore hatch as cyprids, so we cannot check how their peculiar lattice organs relate to naupliar structures. Whether (1) and (2) represent homoplasies or just different ontogenetic pathways to reach the same homologous character state is difficult to decide without a rigorous phylogenetic analysis of all Rhizocephala. In *Balanus amphitrite* the S1 and S2 setae and hence their terminal pores point posteriorly in the nauplius (Fig. 4E) whereas the terminal pore of LO1 and 2 is situated anteriorly in the cyprid,. Thus a dramatic shift in pore position can obviously occur without being heralded in the nauplius. At present we therefore prefer to regard conservatively an anterior pore position in LO2 as an apomorphy for all Cirripedia, and the condition in *S. polygenea*, *P. glaber*, *P. barnwelli*, and *S. gedehensis* as an apomorphy (reversal) developed within the Rhizocephala.

4.4. The number of lattice organs

We are uncertain how to interpret the obvious absence of setal precursors for the first pair of lattice organs (LO1) in the nauplii of *Sacculina polygenea*. In the cyprids of *S. polygenea* there are two pairs of pore fields located in front of LO2. One of them corresponds in position to the pair of peculiar depressions found in front of the S2 setae in the nauplii and may therefore represent LO1 lacking a terminal pore. If so, the said naupliar depressions may represent precursor setae that have precociously fused with the head shield cuticle. Another pair of pore fields, located more laterally, could be the vestige of a supposed sixth pair of lattice organs that in other species (see below) is associated with LO2, although the corresponding S2a setae are lacking entirely in *S. polygenea*.

It is also uncertain, how to interpret the presence of six pairs of setae with pores in some rhizocephalan nauplii, since their cyprids have only five pairs of lattice organs as in all other Thecostraca known so far. Our interpretation that the S1–2 setae correspond to LO1–2 and the S3–5 setae to LO3–5 leaves unanswered the question, whether the small, satellite S2a seta so characteristic of rhizocephalan nauplii, has a corresponding structure in the cyprid. The S2a setae are structurally similar to the remaining head shield setae in the nauplii and might correspond to the "satellite" pore field adjacent to LO2 in rhizocephalan cyprids (Figs. 6D,G). If so, these fields could represent a sixth pair of lattice organs, absent in all other Thecostraca but present in rudimentary form in the Rhizocephala. There are other pore fields in the head shields of cypris larvae, but these have never been accurately registered and only a TEM investigation can verify their true nature. The Facetotecta is the only group of Thecostraca that may share the presence of S2a setae with the Rhizocephala.

4.5. Evolution of lattice organs

Our observations support that lattice organs in the Thecostraca derive ontogenetically from naupliar setae. When looking outside the Thecostraca (e.g. in Copepoda) for structures potentially homologous to lattice organs and their precursor setae, an obvious candidate would therefore be setae with pores arranged in pairs along the midline of the naupliar head shield. Also relevant would be a comparison with the dorsal organ occurring on the anterodorsal surface of the carapace/head shield of many crustaceans (MARTIN & LAVERACK 1992; WALOSSEK 1993). Neither the Cambrian microfossil *Bredocaris admirabilis* Müller, 1983 nor the larvae of the Tantulocarida, both suspected close relatives to the Thecostraca, have anything resembling lattice organs (MÜLLER & WALOSSEK 1988; HØEG & KOLBASOV 2002). It may therefore well be that these sensory organs represent structures truly unique to the Thecostraca. Surprisingly, however, species of the extinct Thylacocephala have multiple pairs of elongated structures along the dorsal midline that could be homologous to lattice organs (LANGE & SCHRAM 2002).

5. CONCLUSIONS

Using SEM based evidence from nauplii and cyprids, we have shown that lattice organs in cyprids and cypris-like larvae of the Crustacea Thecostraca develop from setal precursors in the nauplii. Previous studies have established their nature as chemoreceptors so our study reveals them as being among the most highly modified sensory setae (sensilla) in all Crustacea. The observation that they have naupliar precursors in the form of (chemosensory?) setae with pores also indicates that lattice organs function during the pelagic larval phase.

Details of lattice organ morphology are shown to be considerably more complicated than first believed by JENSEN et al. (1994a). The anterior position of the terminal pore can be derived via different ontogenetic pathways. Moreover, our results might indicate the presence of an extra pair of lattice organs and their setal precursors adjacent to the original "second pair". Such variation is what one should expect when any complex character is studied in great detail in a variety of taxa and it adds to, rather than subtracts from, the phylogenetic information involved.

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Author's addresses: Jens T. HØEG (corresponding author) and Peter Gram JENSEN, Department of Zoomorphology, Zoological Institute, University of Copenhagen, 15 Universitetsparken, DK-2100, Copenhagen, Denmark; E-mail: jthoeg@zi.ku.dk.

Alexey V. RYBAKOV, Institute of Marine Biology, Russian Academy of Sciences, 17 Pal'chevskoga Str., 690041, Vladivostok, Russia; E-mail avr@eastnet.febras.ru

Gregory A. KOLBASOV, Moscow State University, Faculty of Biology, Department of Invertebrate Zoology, 119899, Moscow, Russia.

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