

External morphology of females in the burrowing barnacles *Lithoglyptes mitis* and *L. habei* (Lithoglyptidae) and the phylogenetic position of the Cirripedia Acrothoracica (Crustacea: Thecostraca)

Наружная морфология самок сверлящих усоногих *Lithoglyptes mitis* и *L. habei* (Lithoglyptidae) и филогенетическое положение Cirripedia Acrothoracica (Crustacea: Thecostraca)

G.A. Kolbasov* & J.T. Høeg**
Г.А. Колбасов*, Й.Т. Хёг**

* Department of Invertebrate Zoology, Pertsov White Sea Biological Station, Biological Faculty, Moscow State University, Moscow 119899 Russia.

** Institute of Zoology, University of Copenhagen, Universitetsparken 15, Copenhagen DK-2100 Denmark.

* Кафедра зоологии беспозвоночных, Беломорская Биологическая Станция, Биологический факультет МГУ, Москва 119899 Россия.

KEY WORDS: Cirripedia, Acrothoracica, morphology, organ, SEM, burrowing, phylogenetic relationships.

КЛЮЧЕВЫЕ СЛОВА: Cirripedia, Acrothoracica, морфология, органы, СЭМ, сверление, филогенетические связи.

ABSTRACT: We use scanning electron microscopy to study female morphology in *Lithoglyptes mitis* Tomlinson, 1969 and *L. habei* Tomlinson, 1963. All external features including opercular bars, lateral bars, comb collar, orificial knob, multifid scales, mantle teeth, calcareous plate, oral cone, thorax and terminal cirri are described in detail. We discuss the functional morphology and evolutionary status of these features and identify possible apomorphic features for the Acrothoracica. We conclude that available morphological and molecular data indicate that the Acrothoracica is the sister group to the Thoracica + Rhizocephala within a monophyletic Cirripedia.

РЕЗЮМЕ: Мы использовали сканирующую электронную микроскопию для изучения морфологии самок *Lithoglyptes mitis* Tomlinson, 1969 и *L. habei* Tomlinson, 1963. Такие наружные структуры как: оперкулярные утолщения, латеральные полосы, гребневидный воротничок, устьевой бугорок, чешуйки, мантийные зубы, известковая табличка, ротовой конус, торакс и терминальные усоножки – детально описаны. Обсуждается функциональная морфология и эволюционное значение этих образований, выделяются возможные апоморфные признаки для Acrothoracica. Мы считаем, что имеющиеся морфологические и молекулярные данные указывают на то, что Acrothoracica – сестринская группа для Thoracica и Rhizocephala в пределах монофилетических Cirripedia.

racica) and the parasitic barnacles (Rhizocephala) [Anderson, 1994; Schram & Høeg, 1995]. Like the Thoracica, the Acrothoracica are suspension feeders that live in self-excavated burrows in solid, calcareous as a rule, substrates, including gastropod shells. The Acrothoracica were discovered by Hancock [1849] and they have always occupied a prominent position in discussions on barnacle phylogeny [Grygier & Newman, 1985]. Novel data from 18S rDNA sequences [Spears et al., 1994] and selected features in cypris ultrastructure [Jensen et al., 1994; Kolbasov et al., 1999] indicate that the Acrothoracica diverged very early in cirripede evolution and made even the monophyly of the Cirripedia doubtful. On the other hand, adult acrothoracicans display many putative apomorphies with the Thoracica in being specialized for suspension feeding using thoracic cirri [Anderson, 1994].

Acrothoracican morphology is difficult to study due to their small size and only Smyth [1986], Tomlinson [1973], Turquier [1978], Kolbasov [1999] and Kolbasov et al. [1999] have used scanning electron microscopy. We use SEM to study all external features in two closely related species of *Lithoglyptes* Aurivillius, 1892 to provide a template for future studies of juvenile and adult Acrothoracica. We focus on possible autapomorphies of the Acrothoracica and whether there exist synapomorphies between the Acrothoracica and any group of extant Thoracica.

Material and Methods

In the collections of mollusc shells in the Zoological Museum of Moscow State University we examined 568 specimens of *Lithoglyptes mitis* Tomlinson, 1969, 87 specimens of *L. habei* Tomlinson, 1963 and 46 speci-

Introduction

The Cirripedia consists of the stalked and sessile barnacles (Thoracica), the boring barnacles (Acrotho-

mens sharing the characters of both species. Most specimens were collected from the Maldives, the Seychelles, the Red Sea, and the Gulf of Aden. Some additional specimens came from Vietnam and the Persian Gulf.

The specimens for light and scanning electron microscopical study come from the following stations: *L. mitis*: The Red Sea, Isl. Shumma, arch. Dahlak, 15°05.7'N, 41°41'E, depth 2 m, 3 females in *Trochus pyramis*; Maldives, Isl. Feartu, 3°48'N, 73°05'E, tidal zone, 7 females in *Trochus virgatus*, depth 1.5–3 m, 3 females in *Turbo argirostoma*; Isl. Genego, 3°49'N, 73°06'E, tidal and subtidal zones, approximately 20 females in *Mancinella alauina*, *Latirolagena smaragdula*, *Morula cavernosa* and *Hipponix* sp.

L. habei: Seychelles, Isl. Silhouette, 4°36'S, 56°48'E, subtidal zone, 6 females in *Mancinella mancinella*; Maldives, Isl. Genego, 3°49'N, 73°06'E, tidal zone, coral-reef, 1 female in *Hipponix* sp.; Aden Gulf, 13°59'5"N, 48°24'7"E, tidal zone, 10 females in *Turbo* sp.; South-China Sea, Bay Maxfield, depth 80 m, 4 females in *Xenophora* sp.; atoll Kosmoledo, Isl. Wizard, 10°30'S, 47°30'E, subtidal zone, 1 female in *Latirus polygonus*.

All material was originally preserved in 70% alcohol. The margins of the burrow containing a barnacle were treated in 2% HCl, or the burrow was mechanically destroyed to remove the animal. This method preserves the calcareous plates characterizing some lithoglyptid species. For light microscopy we used KOH-treated material transferred to glycerine [Tomlinson, 1969]. Five adult and 5 juvenile stages of each species were post-fixed in 2% OsO₄ for 2 hr., dehydrated in acetone, and critical point dried in CO₂. Dried specimens were sputter coated with platinum-palladium or gold, and examined in a HITACHI S405A scanning microscope at 15 kV accelerating voltage in Moscow and in a JEOL JSM-840 in Copenhagen (15 kV).

Taxonomy of *Lithoglyptes habei* and *L. mitis*

Tomlinson [1969] considered *Lithoglyptes habei* (Fig. 1) and *L. mitis* (Fig. 2) as distinct species based on differences in the armament of the conical process of the mantle aperture and in the degree of development of the lateral bar. The author noted that he had insufficient material of *L. mitis* at his disposal. We have examined numerous individuals of both species from different regions. We found that the lateral bars of both species are feebly developed and that their variations are similar. Therefore, the principal remaining difference between the two species concerns the armament of the conical opercular process. In *L. habei* the process terminates anteriorly at or near a strong spur-like spine, which is absent in *L. mitis* [Tomlinson, 1969]. Both species, studied by us, exhibit a full range of spine development (Figs. 2D–G), and very often one conical process bears a clear spine, whereas the other process of the same specimen bears only a bifid tooth. We informally call such intermediate forms "*L. habei-mitis*". Specimens of the two "species" and "*L. habei-mitis*" forms can coexist in similar areas and depths and may even inhabit the same host-shell. Tomlinson [1969] also wrote that *L. mitis* might represent immature forms of *Lithoglyptes spinatus* (= *L. bicornis*, Aurivillius). Although *L. mitis* and *L. bicornis* may sometimes inhabit the same shell, we find Tomlinson's statement very unlikely. Our unpublished data show that juvenile females of both species already possess the species specific characters of

the adults even at the ultrastructural level. In accordance with this, we also found mature females of *L. mitis* and *L. habei* with eggs, nauplii or cypris larvae.

In our investigation *Lithoglyptes mitis* and *L. habei* have the same colour, size, and structure of mouth parts, cirri, caudal appendages, orificial knob, and lateral bars; both species have the mantle apertures armed with a pair of conical processes, and they have very similar dwarf males. We conclude that *L. habei* and *L. mitis* are very closely related, with "*L. habei-mitis*" specimens representing hybrid forms, or perhaps more likely, that all forms represent variation within a single species.

Results

As in other cirripedes, the acrothoracican body is suspended in a sac-like mantle cavity, acting as a brood sac and communicating with the exterior through an aperture that can be closed. Some structures of the mantle exterior were described in the Kolbasov paper [1999], therefore we prefer to describe it shortly and concentrate on the body proper.

The mantle (Figs. 1A, 2A,B, 3A–C). The mantle consists of several distinct parts. The aperture, surrounded by the opercular bars and the comb collar lies in the distal part (Figs. 1A, 2A, 3F). The opercular area occupies the upper fourth of the mantle sac in adults (Figs. 1A, 2A, 3A,B) and the upper third in juveniles (Fig. 2B). This area has a smooth mantle cuticle and contains the lateral bars and rows of multifid scales (Figs. 1A, 2A, 3F,G). The orificial knob lies anteriorly "under" the ends of the opercular bars (Figs. 1A, 2A, 3H). The exuviae of the cypris antennules used for initial attachment may be seen between the orificial knob and the attachment disk (Fig. 2B). The attachment disk area occupies the lower half of the anterior side of the mantle and is covered by a calcareous, so-called "rostral" plate (Figs. 2,G, 3,B). Dwarf males may attach to the female mantle by the rudiments of the cypris antennules near the margins of the calcareous plate (Fig. 3B).

The lower part of the mantle sac has a wrinkled cuticle, with transverse and longitudinal striations. It is armed with numerous teeth which are more frequent and larger in the middle part of the mantle sac (Figs. 3A, 4F). The longitudinal striations probably reflect the longitudinal muscles of the mantle.

Opercular bars (Figs. 1A, 2G, 3D, F). Opercular bars are sculptured by small granulations and carry a row of evenly spaced, bifid teeth, whose tips are often broken off. Conspicuous setae insert between the bifid teeth and just under the opercular bars (Fig. 3D). At the posterior ('carinal') end each bar extends into a peculiar conical process covered by teeth, spines, and dense long setae (Figs. 1A, 2A, 3F, 4B,C). The conical process of *L. habei* specimens terminates in a long curved thorn (Figs. 1A, 3A,F) or carries a long spine near the tip (Figs. 4C).

Comb collar (Figs. 3E–G, 4E). The comb collar forms the posteroventral margin of the mantle aperture. It consists of a complex membranous velum, which on each

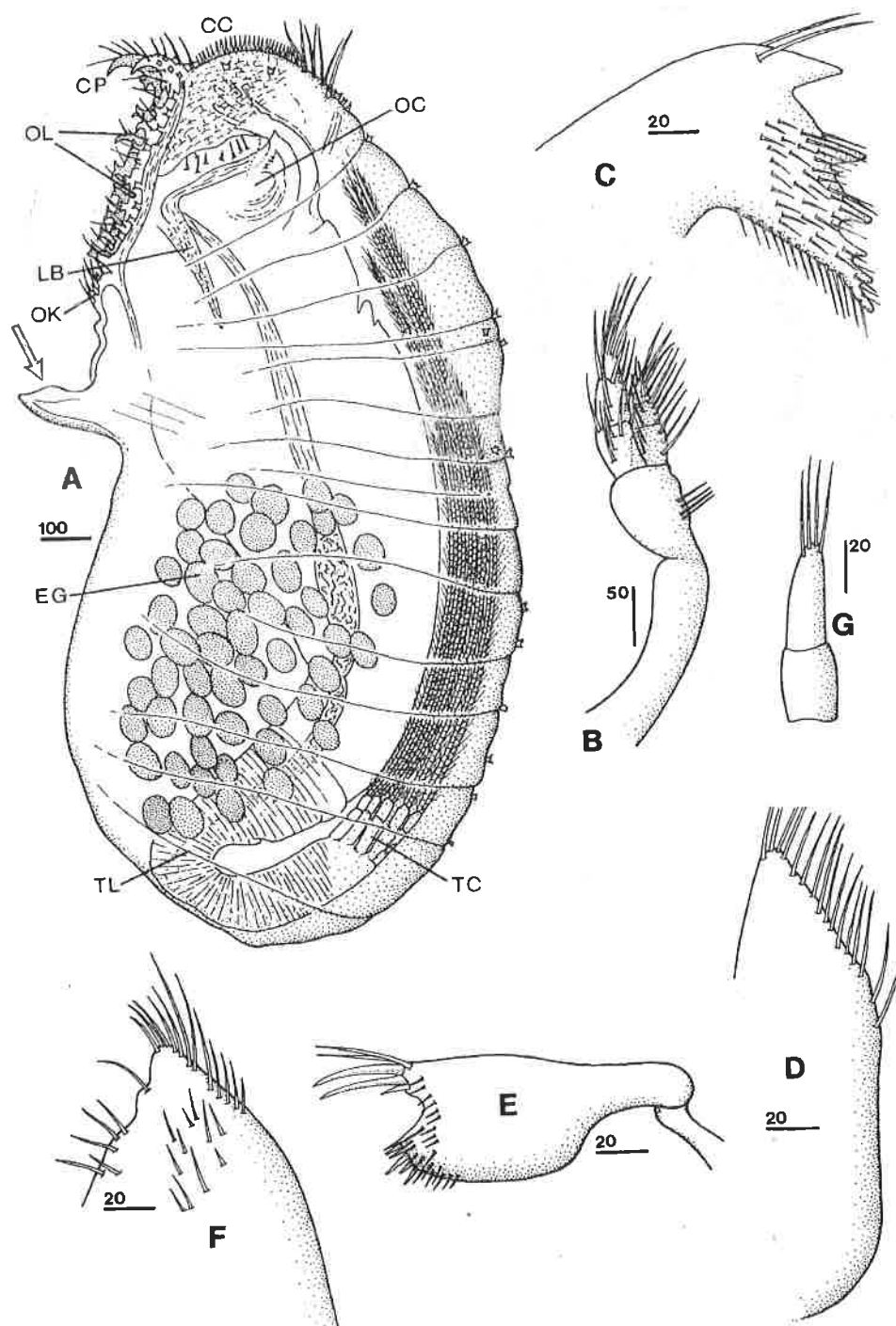


Fig. 1. *Lithoglyptes habei* Tomlinson: A — female, lateral view; arrow indicates sharp process above attachment disk; B — mouth cirrus (cirrus I), anterior is left; C — mandible; D — mandibular palp; E — maxilla I; F — maxilla II; G — caudal appendages. Abbreviations: CC — comb collar; CP — cone process; EG — eggs; LB — lateral bar; OC — oral cone; OK — orificial knob; OL — opercular bars; TC — terminal cirri; TL — thoracic lappets. Scales in μm . All parts belong to specimen A.

Рис. 1. *Lithoglyptes habei* Tomlinson: A — самка сбоку; стрелка указывает заостренный вырост над прикрепительным диском; B — ротовая усложка (усложка I), передняя сторона слева; C — мандибула; D — мандибулярный щупик; E — максилла I; F — максилла II; G — каудальные придатки. Обозначения: CC — гребневидный воротничок; CP — конический вырост; EG — яйца; LB — боковое утолщение; OC — ротовой конус; OK — устьевой бугорок; OL — оперкулярные утолщения; TC — терминальные усложки; TL — торакальные складки. Масштаб в мкм. Все части принадлежат особи A.

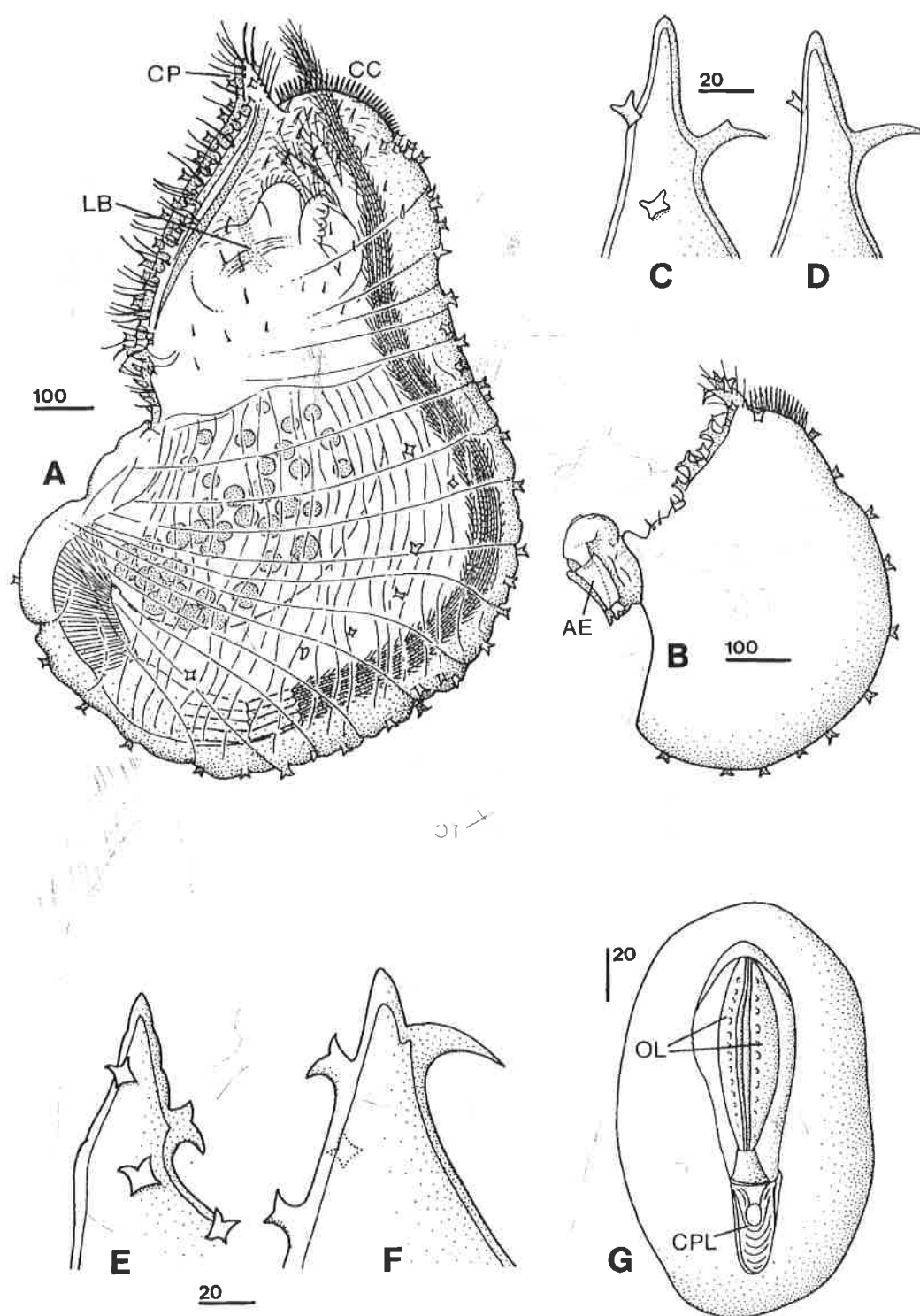


Fig. 2. A — *Lithoglyptes mitis* Tomlinson, female, lateral view; B — *L. habei*, juvenile female with antennular exuviae (AE) in attachment area; C,D — left and right opercular spines of "*L. habei-mitis*" specimen; E,F — left and right opercular spines of "*L. habei-mitis*" specimen; G — burrow, with barnacle, top view. Abbreviations: AE — antennular exuviae; CC — comb collar; CP — cone process; CPL — calcareous plate; LB — lateral bar; OL — opercular bars. Scales in μm .

Рис. 2. А — *Lithoglyptes mitis* Tomlinson, самка сбоку; В — *L. habei*, самка, ювениль с экзuviaми антеннул (АЕ) у прикрепительной области; С, D — левый и правый оперкулярные шипы особи "*L. habei-mitis*"; Е, F — левый и правый оперкулярные шипы особи "*L. habei-mitis*"; G — норка с усонгим, вид сверху. Обозначения: АЕ — экзувий антеннул; СС — гребневидный воротничок; СР — конический вырост; СРL — известковая табличка; LB — боковое утолщение; OL — оперкулярные утолщения. Масштаб в мкм.

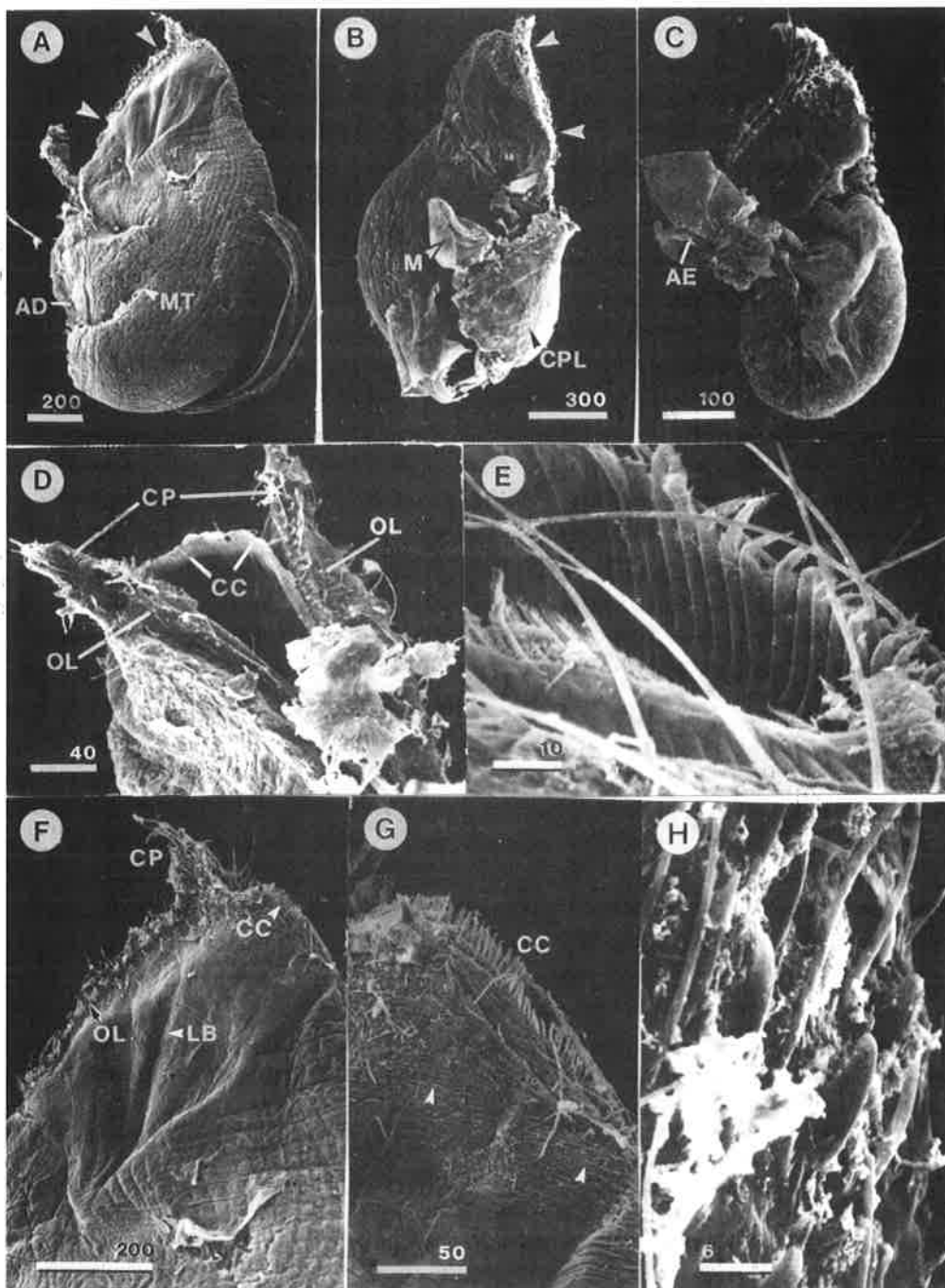


Fig. 3. A–C — females, lateral view, arrowheads indicate operculum, B — with dwarf male (M) and calcareous plate (CPL), cuticle of attachment disk removed, in situ, C — juvenile female with exuvium, including antennular rudiments; D — aperture of mantle cavity bordered by opercular bars (OL) cone processes (CP) and comb collar (CC); E — close up of comb collar, palisade of setae with only distalmost ends free; F — detail of A, lateral view of opercular area; G — detail of F, posteroventral part of aperture with comb collar (CC) and rows of massive multifid scales (arrowheads); H — surface of orificial knob (A,C,F,G — *L. habei*, B,D,E,H — *L. mitis*). Abbreviations: AD — attachment disk; CC — comb collar; CP — cone process; CPL — calcareous plate; LB — lateral bar; M — dwarf male; MT — mantle teeth; OL — opercular bars. Scales in μm .

Рис. 3. A–C — самки сбоку, оперкулум указан стрелками, B — с карликовым самцом (M) и известковой табличкой (CPL), кутикула прикрепительного диска удалена; C — ювенильная самка с экзuviем, включающим рудименты антеннул; D — отверстие мантийной полости, ограниченное оперкулярными утолщениями (OL), коническими выростами (CP) и гребневидным воротничком (CC); E — гребневидный воротничок, ряд щетинок (видны только дистальные концы); F — оперкулярная область сбоку (особь A); G — заднецентральный участок отверстия с гребневидным воротничком (CC) и рядами массивных чешуек, отмеченных стрелками (деталь рис. 3 F); H — поверхность устьевых бугорков (A,C,F,G — *L. habei*, B,D,E,H — *L. mitis*). Обозначения: AD — прикрепительный диск; CC — гребневидный воротничок; CP — конический вырост; CPL — известковая табличка; LB — боковое утолщение; M — карликовый самец; MT — мантийный зуб; OL — оперкулярные утолщения. Масштаб в мкм.

side joins the internal margins of the opercular bars near the conical processes (Fig. 3D). In *L. mitis* and *L. habei* the comb collar is well developed in both juveniles and adults. With SEM, it appears as a palisade row of closely spaced cuticular projections, presumably of setal nature (Figs. 3D,E; 4E). The 20–30 µm long projections are united for most of their length, but have free apical ends with numerous villi on the lateral margins (Figs. 3E, 4E). This is common comb collar ultrastructure for all acrothoracicans [Kolbasov, 1999; Smyth, 1986].

Orificial knob (Figs. 1A, 3H, 4D). The orificial knob is characteristic for some lithoglyptid species and looks like a hillock on the anterior ('rostral') side of the mantle sac below the opercular bars. The knob carries simple and curved teeth and long setae in adult specimens (Fig. 3H). In juveniles it also bears bifid and even trifid teeth, and the lower surface is covered by multifid scales (Fig. 4D). The simple teeth of adult specimens probably originate from the bifid ones visible on juveniles by means of the reduction of one tip in the course of the moults.

Antennular exuviae (Fig. 2B). The cyprid antennules of the acrothoracicans attach to the host substrate outside the future burrow [Turquier, 1970]. However, after complete burrow dissolution by HCL, juveniles often retain their rudiments, as exuviae, on their antero-ventral side, and they indicate the point of first attachment to the host. The sharp process above the attachment disk (arrow in Fig. 1A) corresponds to this point in the adults [Kolbasov, 1999].

Attachment disk (Figs. 3A, 4G, H). The attachment disk is characteristic for the Acrothoracica. In the investigated species it occupies the lower half of the anterior side and has an oval form. Its cuticle lacks muscles, bears distinct transverse furrows, and covers a calcareous plate (Fig. 4H). The furrows, probably, reflect growth lines of a calcareous plate and may correspond to moults in a manner analogous to the ecdysial rings encircling the stalk of rhizocephalan barnacles [Høeg & Lützen, 1995]. In both juveniles and adults, the cuticle of disk also bears transverse rows of small cuticular papillae-like structures (Fig. 4G, H), which may secrete a cement for attachment to the host [Kolbasov, 1999]. We have found similar papillae on the cuticle of the attachment disks of *Kochlorine bocqueti*, *Kochlorine* sp., *Kochlorine hamata*, *L. bicornis*, *L. viatrix*, and undescribed two species of *Weltneria* and *Lithoglyptes* [Kolbasov, 1999, own data].

Calcareous plate (Figs. 2G, 3B, 4A). A calcareous plate was described in deep-water species of *Weltneria* and *Lithoglyptes* [Newman, 1971, 1974; Grygier & Newman, 1985]. Recently, it was described for the shallow-water species *L. mitis* and *L. habei* [Kolbasov, 1999]. It protects or reinforces the anterior (basal) area and is covered by the cuticle of the attachment disk. The plate has drop-like form, is thin and semitransparent, and adorned with fine growth lines.

Multifid scales (Figs. 3G, 4B,C, 5A–G). Smyth [1986] firstly classified the different types of multifid scales, which were so far observed in all acrothoracican genera studied with SEM, i.e., *Trypetesa* Norman, 1903, *Kochlorine* Noll, 1872 [Turquier, 1978], *Cryptophialus* Dar-

win, 1854 (Smyth, 1986), *Lithoglyptes* Aurivillius, 1892, *Kochlorine*, *Cryptophialus* [Kolbasov, 1999], *Weltneria*, Berndt, 1907 and *Trypetesa* (own data). They are represented by different types of denticles (in Watling, 1989 and Høeg et al., 1994 terminology).

Lithoglyptes habei and *L. mitis* have two general types of multifid scales: the massive and feeble ones [Kolbasov, 1999]. The massive multifids are 8–15 µm long, 2–2.5 µm high and consist of 20–40 sharp and strong denticles to be similar to small fan denticles fused together, leaving only the apical one third of the length free (Figs. 5A–C). The feeble multifids (Figs. 5D–F) are 6–15 µm long and 4 µm high, and consist of 7–20 thin variable denticles grouped together at their bases, leaving most of the length free. In both scale types the sharp end point upwards towards the mantle aperture.

In *L. habei* and *L. mitis* the form and number of multifid scales differ between the various areas of the mantle sac, and they are most frequent on and near the opercular area and the ventral surface. The structure and arrangement of scales is completely identical in juveniles and adults. Massive multifids are considerably more frequent than the feeble scales and numerous transverse rows occur in the opercular area (Figs. 3F,G, 4B,C, 5A–C). Feeble multifids occur in the ventral area under the opercular region approximately to the middle of the mantle sac (Figs. 5D–F).

The lower posterior half of the mantle sac is occupied by rows of separate variable denticles, whose tips point in different directions, probably, due to shrinkage, and hardly form clear scales (Fig. 5G). In addition, setae are distributed singly or in small groups on the whole mantle under the opercular area.

Mantle teeth (Figs. 3A, 4F). The different mantle teeth occur on the whole surface of the mantle sac, but they are most numerous on the posterior surface and on the lateral sides of the lower third part. The largest mantle teeth occur in the area near the attachment disk. Mantle teeth are bifid, trifid, or tetrafid, and 8–12 µm in height. The tooth has a round, 20–30 µm diameter base covered by a smooth, chitinous cuticle. The body of the tooth originates from the centre of this base (Fig. 4F) and is also completely chitinous without any calcareous formations. SEM failed to reveal pores of duct-like structures in the mantle teeth. Therefore, the acrothoracican mantle teeth differ in all these characters from the spicules found by Dineen [1988] in the thoracican *Lithotrya dorsalis*.

Lateral bars (Figs. 1A, 2A, 3F). These chitinous formations are feebly developed in *L. habei* and *L. mitis*, and their structure differs from those described in species of the Cryptophialidae by Smyth [1986]. In *L. habei* and some specimens of *L. mitis* the lateral bars are chitinous thickenings of triangular form with a curved tip. Externally they are covered by ordinary cuticle and bordered by two clear furrows (Fig. 3F).

The barnacle body

In all acrothoracicans the body consists of an oral cone and a very elongate (in Lithoglyptidae and Cryptophialidae), and S-shaped thorax with cirri grouped at the posterior end (Figs. 1A, 2A, 6A).

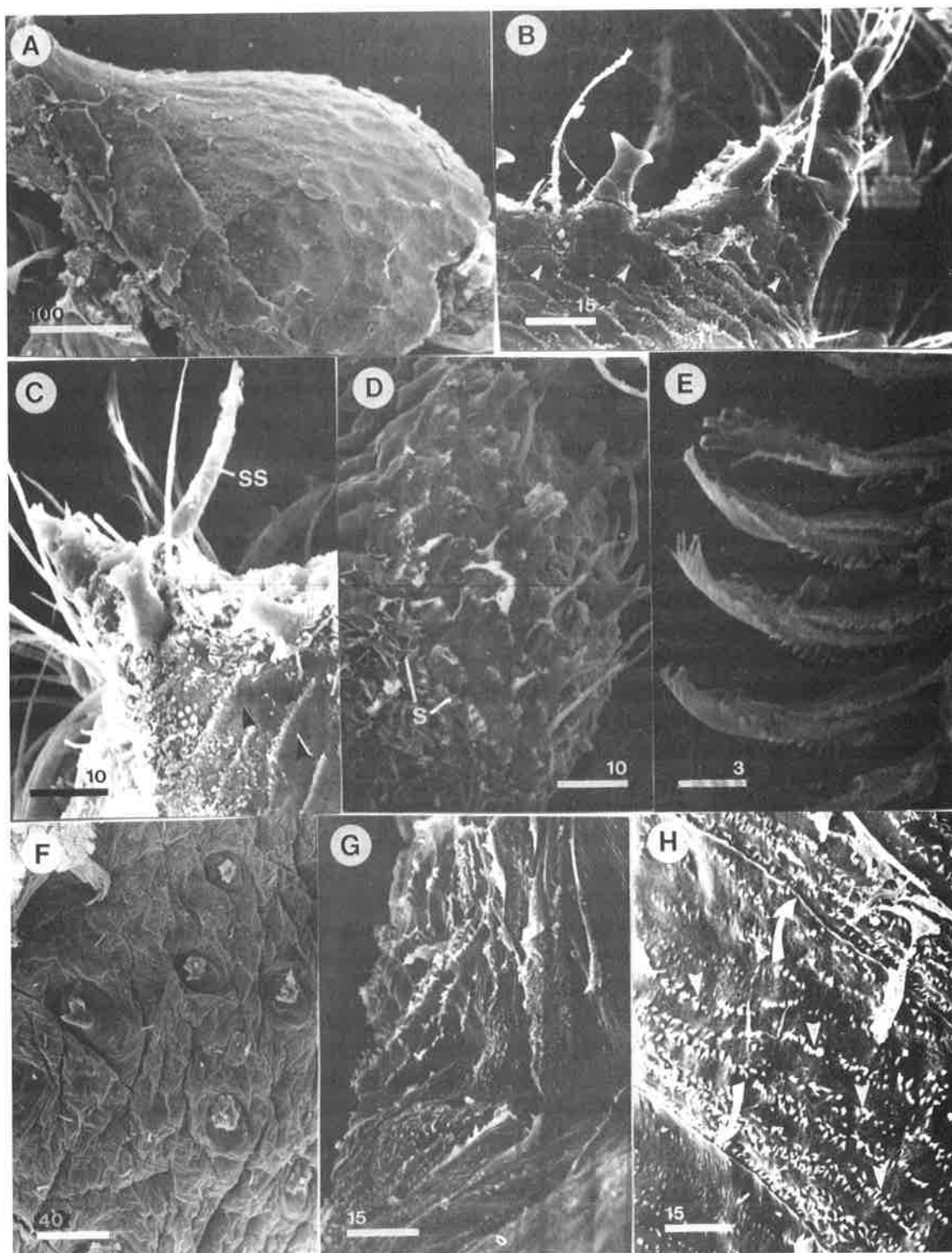


Fig. 4. A — calcareous plate; B,C — opercular conical processes, with rows of massive multifid scales below (arrowheads); D — orificial knob; E — comb collar of juvenile female; F — mantle teeth, near lower part of attachment disk; G,H — surface of attachment disk, H with two putative growth lines (curved arrows) and rows of papillae (arrowheads) (A,B,G,H — *L. mitis*, C,D,E,F — *L. babai*, A,F,H — adults, B–E,G — juveniles). Abbreviations: S — scales of orificial knob; SS — spur-like spine. Scale bars in μm .

Рис. 4. А — известковая табличка; В,С — оперкулярный конический вырост с рядами массивных чешуек (указаны стрелками); D — устьевой бугорок; E — гребневидный воротничок; F — мантийный зуб у нижней части прикрепительного диска; G,H — поверхность прикрепительного диска, H с двумя предполагаемыми линиями роста (загнутые стрелки) и рядами папилл (обычные стрелки) (A,B,G,H — *L. mitis*, C,D,E,F — *L. babai*, A,F,H — взрослые, B–E,G — ювенили). Обозначения: S — чешуйки устьевого бугорка; SS — шпоровидный шип. Масштаб в мкм.

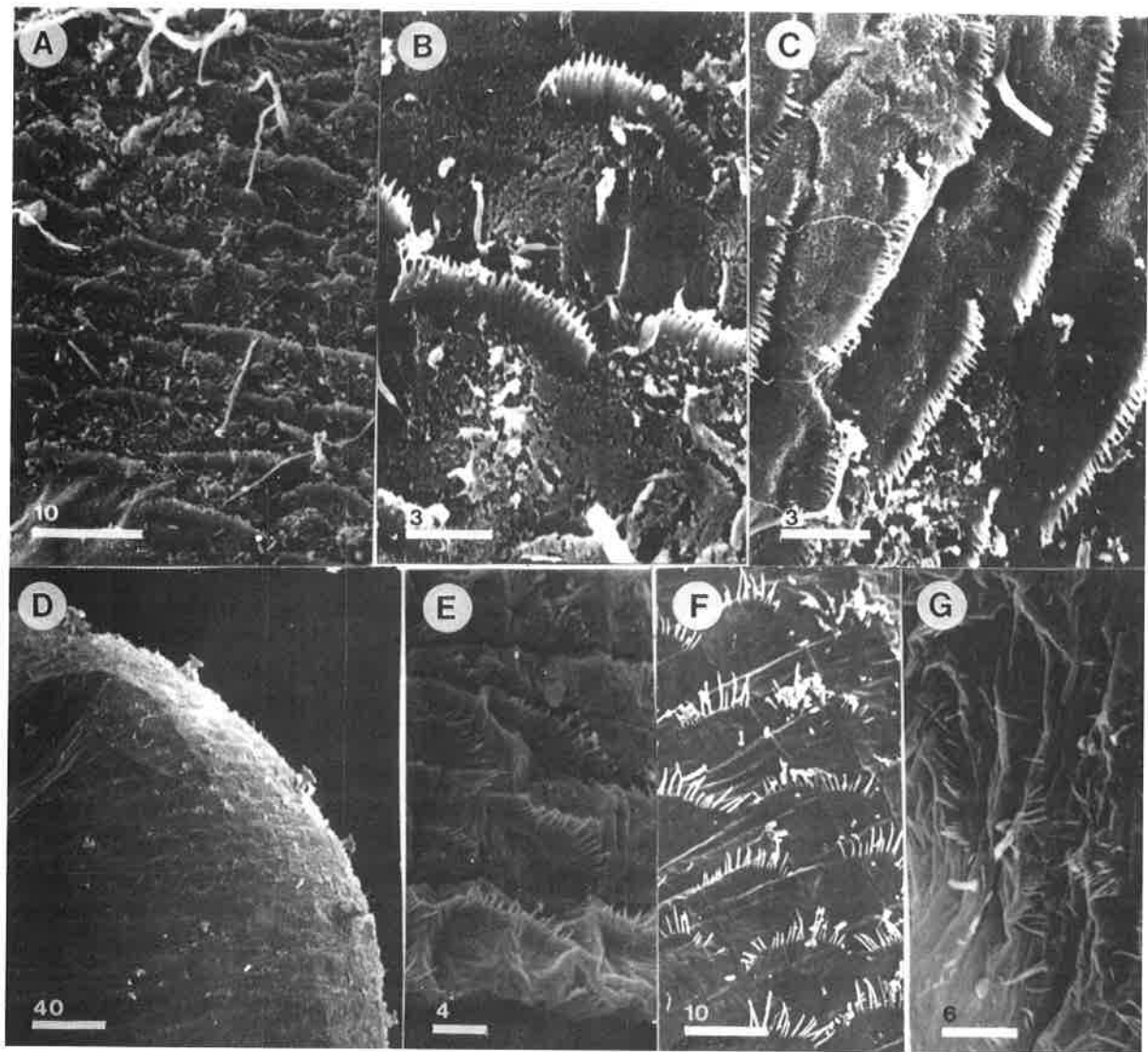
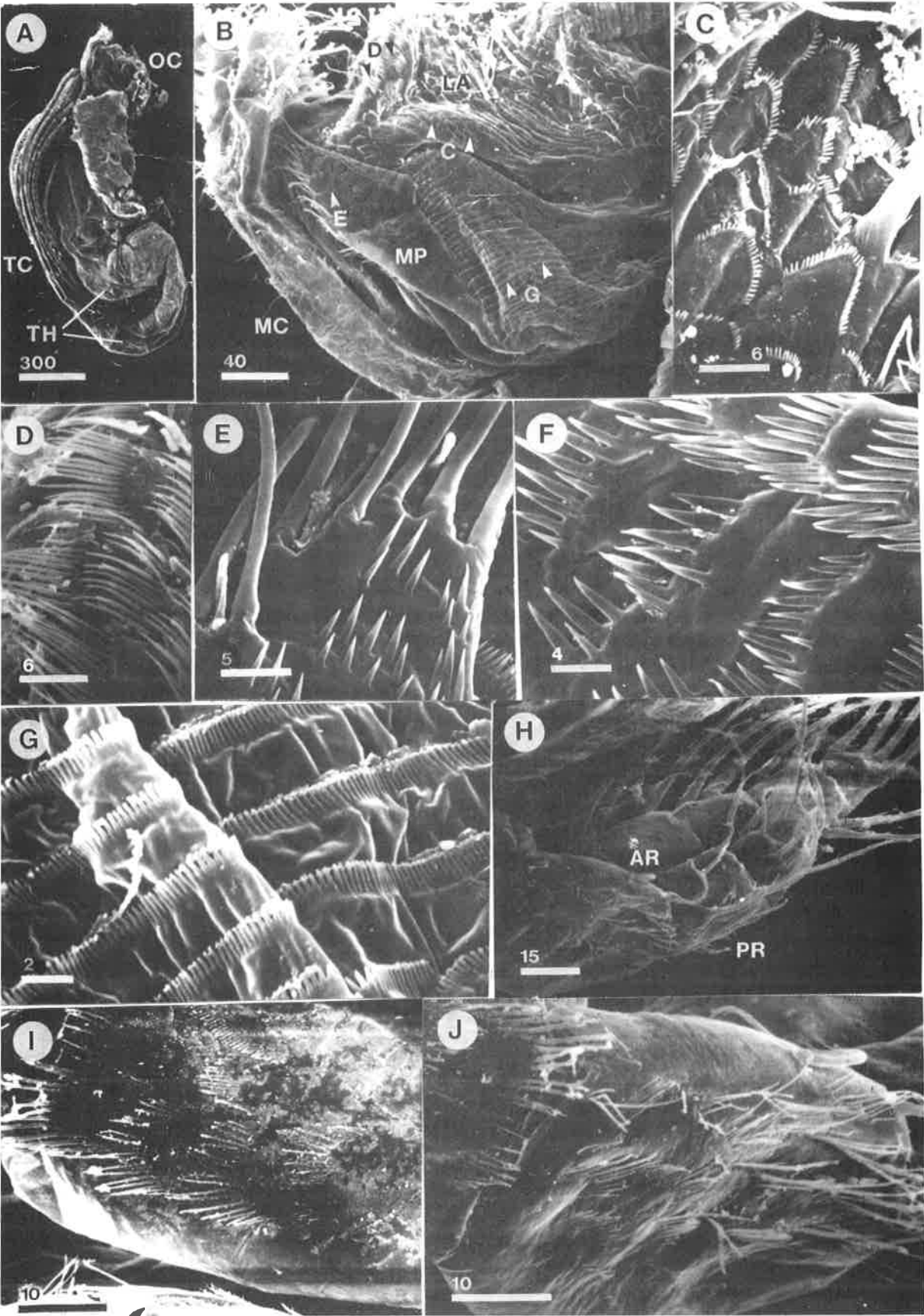


Fig. 5. A — posterior part of opercular area with rows of massive multifid scales; B,C — massive multifid scales under opercular conical process; D — midposterior area with rows of feeble multifid scales; E,F — feeble multifid scales in midposterior area; G — scale-like denticles setae in lower posterior area. A,C,E,G — *L. habei*, B,D,F — *L. mitis*, A,B,E — adults, C,D,F,G — juveniles. Scale bars in μm .

Рис. 5. А — задняя часть оперкулярной области с рядами массивных чешуек; В,С — массивные чешуйки под оперкулярным коническим выростом; D — срединная задняя область с рядами слабых чешуек; E,F — слабые чешуйки середины задней области; G — чешуйковидные шипики нижней части задней области. А,С,Е,Г — *L. habei*, В,Д,Ф — *L. mitis*, А,В,Е — взрослые, С,Д,Ф,Г — juveniles. Масштаб в мкм.

Fig. 6. A — internal body (mantle removed); B — oral cone with labrum (LA) and mandibular palp (MP), (details shown in Figs. C,D,E,G marked with letters and arrowheads); C — arc-shaped scale on lateral surface of labrum; D — bushy scales on distal part of labrum; E — tip of mandibular palp; F — scales on upper (distal) part of mandibular palp; G — rows of lappets on basal part of mandibular palp; H — rami of mouth cirri; I — mouth cirrus, lateral surface of coxa; J — mouth cirrus, lateral surface of basis; (A–G — *L. habei*, H–J — *L. mitis*, all adults. Abbreviations: AR — anterior ramus; LA — labrum; MC — mouth cirri; MP — mandibular palps; OC — oral cone; PR — posterior ramus; TC — terminal cirri; TH — thorax; Scale bars in μm .

Рис. 6. А — внутреннее тело (мантия удалена); В — ротовой конус с лабрумом (LA) и мандибулярным шупиком (MP), (детали показаны на рис. 3 C,D,E,G и отмечены стрелками и буквами); С — арковидные чешуйки боковой поверхности лабрума; D — кустистые чешуйки дистальной части лабрума; E — верхушка мандибулярного шупика; F — чешуйки на верхней (дистальной) части мандибулярного шупика; G — ряды складок на базальной части мандибулярного шупика; H — ветви ротовой усоножки; I — ротовая усоножка, боковая поверхность коксы; J — ротовая усоножка, боковая поверхность базиса. (А–Г — *L. habei*, H–J — *L. mitis*, взрослые). Обозначения: AR — передняя ветвь; LA — лабрум; MC — ротовые усоножки; MP — мандибулярные шупики; OC — ротовой конус; PR — задняя ветвь; TC — терминальные усоножки; TH — торакс. Масштаб в мкм.



Oral cone (Figs. 1 A, 6 A, B). The oral cone has a complicated structure. Surrounding the mouth it carries the labrum, mandibles with mandibular palps, first and second maxillae and cirri I (so-called 'mouth cirri'). We could observe the external structure of the labrum, mandibular palps and mouth cirri. Mandibles, first and second maxillae are situated inside the oral cone and could not be seen from the outside with the SEM.

Labrum (Fig. 6B, C, D). The labrum has a saddle-like form, with a horseshoe-like distal part, and its surface bears different types of setae and scales. Individual setae occur in the middle of the lateral side (Fig. 6B). So-called 'bushy scales' occur in the distalmost part of the labrum (Fig. 6D). They are 6–7 μm wide and 8–9 μm high and consist of a row of 7–15 closely spaced and very slender denticles (setae?). Elsewhere the labrum carries arc-shaped multifid scales (Fig. 6C), which are 4–7 μm high, 4–7 μm wide and have a crenulated edge of denticles. Smyth [1986] found identical arc-shaped multifid scales in the upper part of the mantle sac of *Cryptophialus coronophorus*, but in *L. habei* and *mitis* they occur only on the labrum.

Mandibular palps (Fig. 6B, E, F, G). The palps consist of a basal and a distal part separated by a distinct fold. The lateral sides of the basal part are covered by long, wavy rows of short and very closely spaced denticle-like protrusions, which are directed distally (Fig. 6G). The distal part of the palp carries long, simple setae on the tip and along the upper edge and short setae on the outer (posterior) edge (Figs. 6B, E). The lateral surface of the distal part, especially the inner edge (near labrum), carries spiny scales, loosely organized into rows (Figs. 6E, F). These 7–10 μm wide scales bear strong and sharp spines without any basal articulation. The number and size of these spines differ between individual scales.

Mouth cirri (Figs. 1B, 6B, H–J). Cirri I, or mouth cirri, exist in all members of the Lithoglyptidae and articulate with the body just under the maxillae II. They are part of the oral cone and therefore widely separated from the terminally sited cirri.

A single mouth cirrus (Fig. 1C) consists of a long coxa, a short basis, and two short rami (endopod and exopod). The outer edge of the basis carries a few plumose setae. The edges and surfaces of both rami carry also well-developed plumose setae. The numerous setules on the basal and ramal setae are very delicate and difficult to observe even with SEM (Fig. 6H). The lateral surfaces of the coxa and the basipodite have a dense cover of long and sharp spines, often united into scales (Figs. 6I, J). The lateral surface of the coxa also carries simple multifid scales with short spines, similar to those found by Smyth [1986] in the distal part of *C. coronophorus*. The anterior ramus is 3–4 segmented and longer than the 2–3 segmented posterior one (Fig. 1C).

Thorax (Figs. 1A, 6A, 7A, B). The thorax is the body region (including the mouth cirri) behind the oral cone and consists of a straight anterior part and a strongly S-shaped posterior part carrying the terminal cirri (Figs. 1A, 6A). The cuticle of the posterior part bears closely spaced, transverse rows of "thoracic lappets" [Smyth,

1986] (Figs. 1A, 2A, 7A). The thoracic lappets appear as transverse striations in the light microscope. SEM reveals them as closely spaced denticle-like (combs of fringes) protrusions with a common base, a structure very reminiscent of the multifid scales (Fig. 7B). Each lappet consists of 50–80 protrusions (fringes). These 1.5 μm high lappets point posteriorly and small irregular gaps separate the fringe-like protrusions of a single row.

In *L. mitis* and *L. habei* the rows of thoracic lappets cover the entire surface of the posterior (terminal) part of the thorax, whereas Smyth [1986] showed that they occur in three separate sets in *C. coronophorus*. Tomlinson [1973] first tried to determine the structure of these striations using SEM and mentioned "longitudinal striations" between "transverse striations". Smyth [1986] truly described this thoracic structure and stated 'that only the "longitudinal striations" mentioned by Tomlinson actually exist' formed by fringes, and called them "thoracic lappets".

Terminal cirri (Figs. 1A, 2A, 6A, 7C–F). Four pairs of biramous cirri originate on the terminal part of the thorax. They consist of a two-segmented protopod (coxa, basis) carrying two multisegmented rami (endo- and exopod). The protopod carries two pairs of serrate setae on its posterior distal margin. Both protopod and rami also bears separate rows of lappets on the posterior (outer) margin, resembling multifid scales and similar to the rows of thoracic lappets (Figs. 7C, E). Undulating combs with fringed edges occur in the sutures between the basis and first ramal segments (Figs. 7C, D).

The ramal segments are 2–3 times longer than wide. Each segment carries two pairs of setae on the distal and middle parts of the anterior (inner) margin and a pair of serrate setae on the distal part of the posterior margin of each second segment (Fig. 7F). The first ramal segment carries about 10 rows of lappets on its posterior margin (Figs. 7C, E). The more distal ramal segments carry only two such rows (Fig. 7F).

Caudal appendages (Fig. 1G). The rudimentary abdomen bears two-jointed caudal appendages. The basal segment carries a single seta, whereas the distal segment has a group of plumose setae (normally 4) on its tip.

Discussion

With this paper we follow upon and extend the works of Smyth [1986] and Kolbasov [1999]. We shall first discuss the individual characters in order to set the stage for a discussion of the phylogenetic position of the Acrothoracica.

Opercular bars. The Acrothoracica lack any opercular calcareous plates along the rims of the mantle aperture. The distinctive chitinous opercular bars may therefore serve to reinforce the opercular area during sweeping of the cirri and abrasion movements. The opercular bars also carry numerous setae and projections, which likely serve to detect foreign objects and guard against their ingress into the mantle sac [Kolbasov, 1999]. Nevertheless, we found one *L. mitis* with a harpacticoid copepod inside the mantle sac.

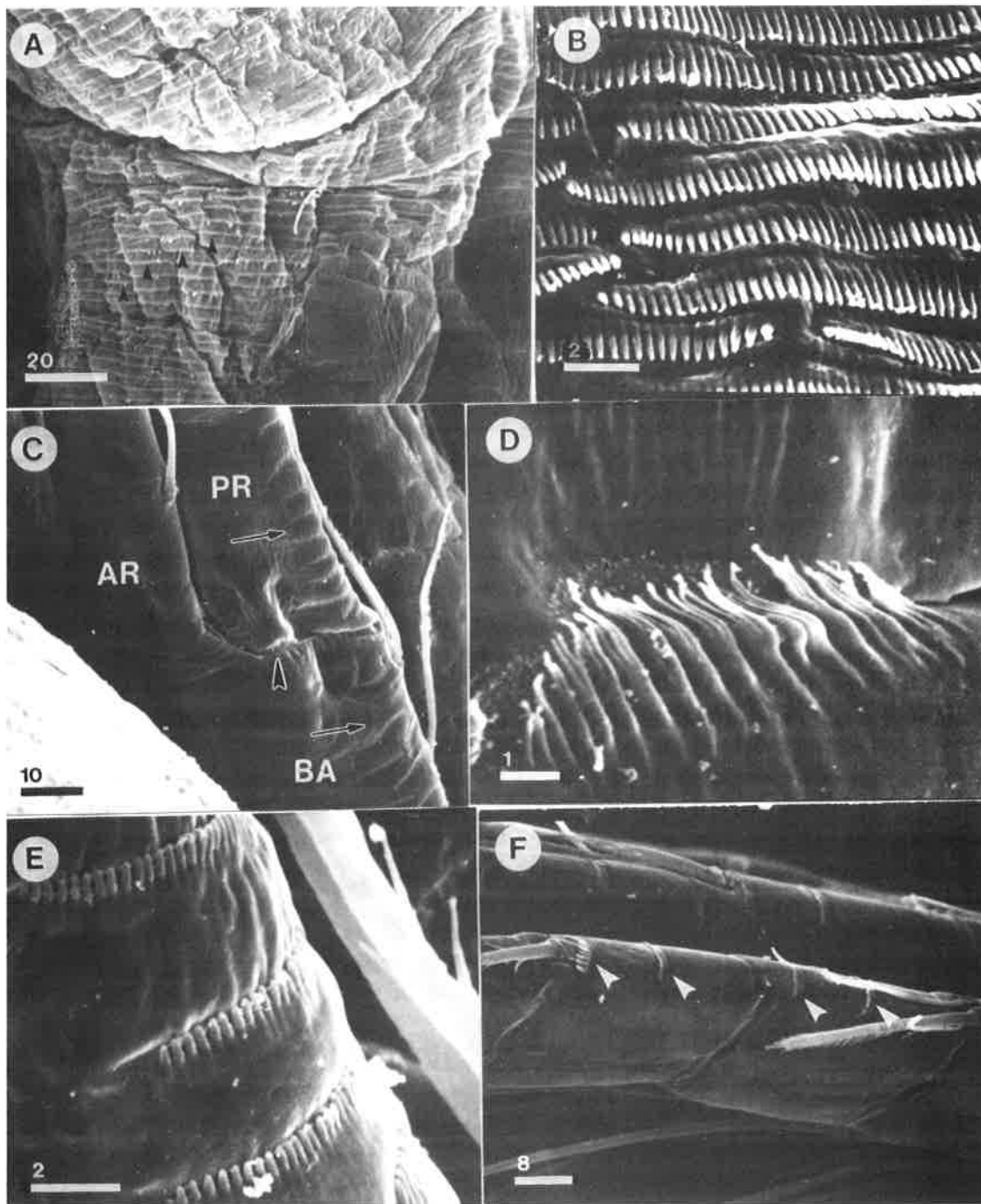


Fig. 7. A — thorax near terminal end, with rows of thoracican lappets (arrowheads); B — transverse rows of thoracican lappets; C — third terminal cirrus, basis (BA) and origin of rami, undulating ridge (arrowhead) in suture between basis (BA) and first ramal segment, lappet-like scales on posterior margin of basis and posterior ramus (arrows); D — undulating ridge in suture between basis and first segment of posterior ramus (at arrowhead in C); E — several lappet-like scales on posterior margin of first ramal segment (arrow in C); F — distal segments of fourth terminal cirrus, only two lappet-like scales per segment (arrowheads). All adults of *L. habei*. Abbreviations: AR — anterior ramus of cirrus; BA — basis; PR — posterior ramus of cirrus. Scale bars in μm .

Рис. 7. А — поверхность торакса у терминального конца с рядами торакальных складок (показаны стрелками); В — поперечные ряды торакальных складок; С — терминальная усоножка (III пара), базис (ВА) и отходящие ветви, волнистый гребень (крупная стрелка) у соединения между базисом (ВА) и первым сегментом ветви, складковидные чешуйки на задних краях базиса и задней ветви (мелкие стрелки); D — волнистый гребень у соединения базиса и первого сегмента задней ветви (указан на рис. 7 С); E — несколько складковидных чешуек на заднем крае первого сегмента задней ветви (указаны на рис. 7 С); F — дистальные сегменты IV пары терминальных усоножек, присутствуют только две складковидных чешуек (указаны стрелками). Все — взрослые особи *L. habei*. Обозначения: AR — передняя ветвь усоножки; BA — базис; PR — задняя ветвь усоножки. Масштаб в мкм.

The comb collar. According to Batham and Tomlinson [1965] the comb collar projects into the mantle aperture and is pressed against the cirri, when they are extended. They therefore suggested that the collar serves to groom the cirri by means of its apical comb and to securely close the mantle aperture during extension of the cirri. Smyth [1986] similarly concluded that the comb collar in *Cryptophialus coronophorus* protrudes into the opercular area and prevents ingress of foreign particles, when the opercular bars are spread apart.

We agree with such a guarding and cleaning function of the comb collar, and it may perhaps also serve to retain captured food particles within the mantle cavity. However, while the comb collar bulges into the mantle aperture in the Cryptophialidae, it protrudes to the outside in the Lithoglyptidae, and we surmise that this must also be the case during cirral beating. The outward bulging comb collar of lithoglyptids therefore provides the necessary room for extension of the cirri, since the oral cone blocks almost the whole space under the opercular bars.

Utinomi [1957] mentioned without giving any reference that *Ibla*, sole among thoracicans, has a comb collar. This interesting statement needs reinvestigation. Glenner et al. [1995] did not include the comb collar character in their matrix, but if a comb collar were coded present for *Ibla* and optimized on their favoured tree the comb collar possibly becomes a ground pattern feature for all Cirripedia.

Lateral bars. The lateral bars serve as reinforcing structures and as attachment for various muscles. The relative size of the bars depends on the form of the opercular area, and they are very large in the Cryptophialidae, which have a long 'opercular neck'. This indicates that the lateral bars assist in supporting this region. Utinomi [1957] observed that the lateral bars follow the line, where the body proper connects with the mantle and that they serve as attachments for short transverse muscles connecting them with the upper part of the attachment disk. The lateral bars probably have other functions, e.g., a fulcrum for the contraction of longitudinal muscles and support of the aperture by their elasticity [Darwin, 1854; Berndt, 1907], a fulcrum pressing the mantle against the side walls of the burrow [Utinomi, 1957; Tomlinson, 1969].

Orificial knob. The orificial knob fills the unprotected gap in the burrow aperture between the attachment area and the flexible operculum. Tomlinson [1969] therefore concluded that the orificial knob guards against ingress of particles between mantle exterior and the burrow wall in the inflexible attachment area. Naturally, densely situated long setae and teeth form an effective mesh guarding the burrow against ingress of particles. Furthermore, the presence of multifid scales around the orificial knob, especially in juveniles, indicates that this structure also functions in the abrading process.

Mantle teeth, multifid scales and burrowing. Many authors have attributed burrowing to the action of the mantle teeth [Batham & Tomlinson, 1965; Grygier &

Newman, 1985; Newman, 1971; Tomlinson, 1955, 1969; Utinomi, 1957, 1961]. Turquier [1968] also described a carbonic anhydrase, which apparently softens the calcareous substrate during burrowing in *Trypetesa nassaroides*. We suggest that the mantle teeth primarily serve to fasten the mantle sac within the burrow during body movement such as abrading and beating of the cirri. The teeth are irregularly arranged on the mantle surface. However, many of them occur in areas where body motility is low and burrowing therefore likely to be minimal or absent such as along the ventral margin and in the lower body part near the attachment disk (Figs. 4F, 5D). The degree of teeth development and their density also vary significantly between various species. This disagrees with a function in burrowing since all Acrothoracica penetrate into solid (calcareous as a rule) substrates.

We see no evidence for a homology between the chitinous mantle teeth in the Acrothoracica and the burrowing spicules of the thoracican genus *Lithotrya*. The latter appear to be calcitic, are densely distributed on the peduncle, and their organic component is penetrated by duct-like structures [Dineen, 1988].

Following to Kolbasov [1999], we suggest that burrowing is primarily facilitated by multifid scales, which occur in all acrothoracican families. Our reasons to say so are: (i) these massive scales have strong and sharp edges of denticles (teeth) and seem well adapted for an abrading process; (ii) rows of multifids would act like an abrasive file and polish the surface of the burrow; (iii) the burrow and its aperture have an allometric form and growth; the location of massive multifids and of multifids on the ventral surface, which may also partake in burrowing, agrees fully with the directions of burrow excavation; (iv) the multifid scales lack in fixed, immotile regions of the mantle sac, whereas the mantle teeth are densely studded there. These facts indicate on different distributional patterns of multifid scales and mantle teeth.

In addition to other functions, all kinds of multifid scales may also assist in removing abraded material from the burrow.

Oral cone and terminal cirri. Høeg et al. [1994] used SEM to study the oral cone in thoracicans. However, no previous data exist for comparison with our SEM observations on the oral cone and the terminal cirri in the Acrothoracica. The distal setae on the mandibular palps, the bushy scales of the labrum, and the setae of the mouth cirri form a mesh for food intake. The bushy scales on the distal part of the labrum and the scales of the mouth cirri probably assist in grasping food objects. The arc-shaped multifid scales on the labrum and the spiny scales and lappets on the mandibular palps probably function as cleaning structures.

Thoracic lappets. Smyth [1986] suggested that the thoracic lappets serve in respiration, since they increase the surface area. We believe that they primarily assist in cleaning the mantle sac from foreign particles and feces for the following reasons: (i) they are situated on the movable region of the body; (ii) the edges of the lappets

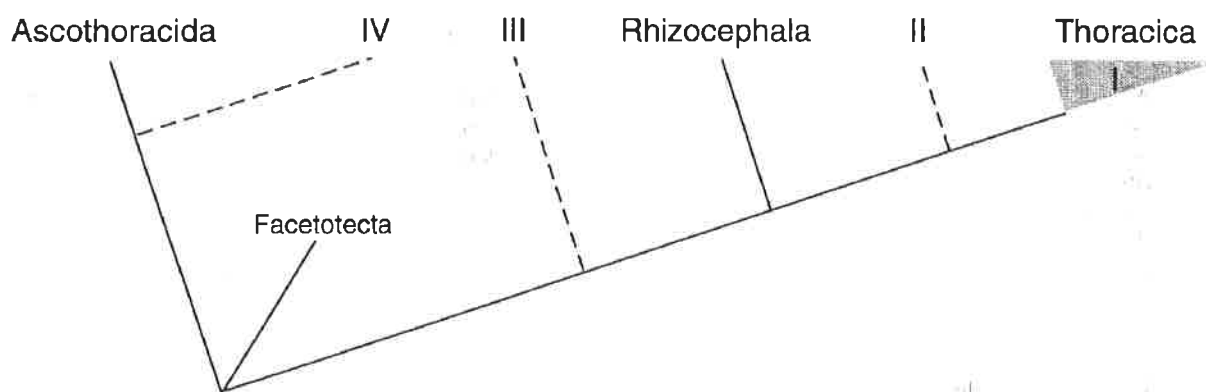


Fig. 8. Putative cladogram of the Crustacea Thecostraca, indicating four possible positions of the Acrothoracica; (I) ingroup in Thoracica, Thoracica paraphyletic; (II) sistergroup to a monophyletic Thoracica; (III) sistergroup to a monophyletic Thoracica + Rhizocephala; (IV) sistergroup to the Ascothoracida, Cirripedia paraphyletic; the exact position of the Facetotecta remains uncertain. Position (III) agrees best with all available data. See text for further discussion.

Рис. 8. Предполагаемая кладограмма родственных связей Crustacea Thecostraca, включающая 4 возможных положения Acrothoracica; (I) внутри Thoracica, Thoracica — парафилетический таксон; (II) сестринская группа монофилетическим Thoracica; (III) сестринская группа монофилетическим Thoracica + Rhizocephala; (IV) сестринская группа Ascothoracida, Cirripedia — парафилетический таксон; точное положение Facetotecta остается неясным. Положение (III) лучше всего согласуется с имеющимися данными. Объяснения в тексте.

always point towards the distal part of the thorax and therefore form an effective mesh for the expulsion of unwanted particles; (iii) the thoracic lappets resemble the lappets of the mandibular palps and the scales on the dorsal surface of the terminal cirri, which probably also serve in a cleaning function; (iv) some acrothoracicans (*Berndtia*, *Cryptophialus*) possess both thoracic lappets and structures similar to the filamentary appendages of the thoracicans, which may serve for respiration.

The calcareous plate. The origin and homology of the calcareous plate and the associated attachment disk were discussed by Kolbasov [1999] as one of unsolved problems in modern systematics and in the evolution of the acrothoracicans. It also relates both to the origin of mantle mineralization in the Cirripedia and to the sister group relationships among the three Cirripede orders [Newman, 1982; Newman, 1987; Glennner et al., 1995].

Within the Acrothoracica several authors have described calcareous formations which appear to be a secretion product of the barnacle [Aurivillius, 1892; Tomlinson, 1955; Utinomi, 1961]. Newman [1971] explicitly claimed that *Weltneria hessleri* Newman possesses a calcareous plate homologous to the rostrum of the Thoracica. This plate was later found in other deep sea lithoglyptids and used to suggest a scalpeloid origin for the Acrothoracica [Grygier & Newman, 1985; Newman, 1974, 1982]. If true, this would make the Thoracica as normally defined paraphyletic. However, as discussed below, the Acrothoracica possess several plesiomorphies incompatible with the hypothesis that they diverge inside the Thoracica or at least after *Ibla*. For these reasons Newman [1987] rejected a "scalpeloid origin" for the Acrothoracica and realized that the acrothoracican calcareous plate may not be homologous with the thoracican rostrum.

Likely functions for the calcareous plate are: fixation of the mantle sac inside the burrow and forming a base for mantle muscle attachment; both necessary for contractions during abrasion process. It also protects the body area that connect directly with the burrow wall [Kolbasov, 1999].

Phylogenetic position of the Acrothoracica

Acrothoracican monophyly. Among the three cirripede orders the Acrothoracica is the most assuredly monophyletic. We suggest that the opercular bars, the orificial knob, the lateral bars, the thoracic lappets and the burrowing apparatus of multifid scales (not multifids themselves, which are, perfectly, homoplasies) represent autapomorphies for the Acrothoracica. This adds to several previously recognized characters such as the burrowing life form, the separation of anterior and terminal cirri, the 180° bending of the body within the burrow, and several peculiarities of metamorphosis [Anderson, 1994]. Monophyly receives support also from 18S rDNA data [Spears et al., 1994; Mizrahi et al., 1998].

Phylogenetic positions. Fig. 8 illustrates four possible phylogenetic positions for the Acrothoracica within the crustacean subclass Thecostraca: (I) ingroup in the Thoracica (=Thoracica paraphyletic); (II) sister group to the Thoracica; (III) sister group to the Thoracica + Rhizocephala, or, (IV) sister group to the Ascothoracida (=Cirripedia paraphyletic).

Relation to the Thoracica (Fig. 8, I, II). Only the putative homology between the acrothoracican calcareous plate and the calcareous rostrum of non-iblid Thoracica speaks for position I. However, as discussed above, we follow Turquier [1978], Newman [1987], Kolbasov [1999] and reject this proposed homology.

The Acrothoracica possess several characters that are with high confidence plesiomorphies when compared with the condition in most or all Thoracica. The thoracican mandibular palp is apomorphically separated from the mandible, but in acrothoracicans the palp retains its plesiomorphic association with the mandible. The Acrothoracica and the thoracican genus *Ibla* both retain the plesiomorphic, postoral position of the adult adductor muscle also seen in the outgroup Ascothoracida and in the cyprid larva [Utinomi, 1960; Turquier, 1970; Batham, 1945; Anderson, 1987]. The remaining Thoracica share the apomorphy of developing a new, preoral adductor muscle during metamorphosis while the postoral, larval adductor degenerates [Glenner & Høeg, 1998]. This is important, because *Ibla* is a strong candidate for being the sister group to all remaining Thoracica [Klepal, 1985; Glenner et al., 1995]. *Ibla* may also possess a structure similar to the acrothoracican comb collar [Utinomi, 1957] and Anderson [1994] enumerated additional similarities between the two taxa in the pattern of cirral beat. These characters associated with feeding cannot be compared to states seen in the outgroup Ascothoracida, but they could well represent general cirripede plesiomorphies. Taken together the morphological evidence from adults comply with phylogenetic positions (II–IV) above, but not with an ingroup position in the Thoracica (I). Most recently, Mizrahi et al. [1998] presented evidence from 18S rDNA sequences indicating that *Ibla* diverged high up on the thoracican tree. This controversial phylogeny would entail that thoracican evolution entailed numerous homoplasies in morphological features such as mandibular palp, adductor muscle, and shell plate number and mineralization.

Relation to the Rhizocephala (Fig. 8, III). Adult Rhizocephala cannot be scored for adductor muscle, mandibular palp or any other appendage character. However, ultrastructural details in cyprid larvae [Jensen et al., 1994] and in rDNA sequences [Spears et al., 1994; Mizrahi et al., 1998] point to a sister group relation between the Rhizocephala and a monophyletic Thoracica and are in agreement with positions (II) and (IV) above.

Relation to the Ascothoracida (Fig. 8, IV). The 18S rDNA sequence data of Spears et al. [1994] suggested for a controversial sister group relationship between the Acrothoracica and the non-cirripede Ascothoracida. This would violate numerous synapomorphies in larval morphology [Moyse et al., 1995; Kolbasov et al., 1999] and the authors also note that rDNA secondary structure supports a monophyletic Cirripedia. Wägele [1996] elegantly showed that the result of Spears et al. [1994] is due to plesiomorphies in the sequence data retained in Ascothoracida and Acrothoracica but not present in their single out-group Branchinecta. Adding the Spears et al. [1994] data to a much more extensive matrix and using chelicerate and polychaete out-groups, Wägele obtained a phylogeny with very high bootstrap values for a monophyletic Thoracica, Thoracica + Rhizocephala, and Cirripedia.

Conclusion

All larval and adult morphological characters, and apparently also the 18S rDNA data set, agree with a monophyletic Cirripedia and within these a sister group relation between the Acrothoracica and a monophylum comprising the Thoracica and the Rhizocephala (Fig. 8, position III). A character optimization on this phylogeny of the Glenner et al. [1995] matrix results in the total absence of capitular plates (valves) as a plesiomorphic condition retained in the Acrothoracica. It is also noteworthy that both the out-group Ascothoracida, the Acrothoracica and the Rhizocephala are symbiotic organisms with separate sexes. This indicates that the both the ur-cirripede and ur-theostracan had a symbiotic mode of life with attached females associated with dwarfish males [Høeg, 1995; Kolbasov, 1996]. Unfortunately, we do not possess the complete information on the character of this coexistence, but we know some facts indicating on symbiotic connections between the acrothoracicans and their hosts. All species of the *Trypetesa* inhabit the columella of gastropod shell occupied by the hermit-crabs and use their excrement for food. Batham and Tomlinson [1965] indicated on the harmful influence of *Cryptophialus melampygos* for its bivalve host. Utinomi [1961] wrote that *Berndtia purpurea* may mask itself as a separate polyp. Cementation to the inanimate substratum and the development of hermaphroditism seems to be apomorphic conditions that evolved within the Thoracica. We end stating that a consistent evaluation of the phylogenies and scenarios discussed above requires an across-the-board analysis of all Thecostraca. This would be based on the Glenner et al. [1995] matrix extended with the morphological information now available from cirripede larvae [Jensen et al., 1994; Moyse et al., 1995; Kolbasov et al., 1999], from adult Acrothoracica [Smyth, 1986; this paper] and from gene sequences [Spears et al., 1994; Mizrahi et al., 1998; Wägele, 1996].

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