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Revision of the Lithoglyptidae sensu Tomlinson, 1969 and *Lithoglyptes* Aurivillius, 1892 (Cirripedia, Acrothoracica,), including a new species from Bermuda

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Abstract

The morphology of the females and males of the ancient acrothoracican burrowing barnacle family, the Lithoglpytidae Aurivillius, 1892, was surveyed. It became evident that by resurrecting a previously described family-group taxon and proposing a new family-group taxon, the Lithoglyptidae could readily be divided into three subfamilies, the Lithoglyptinae s.s. Aurivillius, 1892 stat. nov., the Weltneriinae subfam. nov., and the Kochlorininae Gruvel, 1905 stat. nov. The largest and relatively generalized lithoglyptine genus, *Lithoglyptes* s.l., was investigated utilizing SEM as well as conventional means. From gross morphological characteristics it became evident these species fell into three natural groups for which we propose the genera *Lithoglyptes* s.s., *Auritoglyptes* gen. nov., and *Armatoglyptes* gen. nov. The relationships between the species as well as the genera are explored cladistically, a new species of *Armatoglyptes* is described from Bermuda, the biogeography of the subfamily is discussed, and a key to the genera and species is provided.

Key words: Morphology, SEM, systematics, new subfamilies, new genera, phylogeny

Introduction

The Acrothoracica, one of three superorders of the Cirripedia, is represented by small burrowing barnacles found largely in carbonate sediments and skeletons of marine invertebrates. Representatives were first discovered at relatively high latitudes (Hancock 1849; Darwin 1852) but the greatest diversity is found in the tropical seas of the world. Berndt (1907) divided it into two orders, the relatively generalized Pygophora and the rather specialized Apygophora. The former is presently divided into two families, the

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Lithoglyptidae Aurivillius, 1892 and the Cryptophialidae Gerstaeker, 1866 (Martin & Davis 2001). The Lithoglyptidae includes the most generalized genus, *Weltneria* Berndt, 1907, the species of which have all of their trunk limbs (six pairs of cirri and a pair of caudal appendage). *Lithoglyptes* Aurivillius, 1892, the species-rich genus to be revised in the present paper, differs from *Weltneria* largely in having lost the second pair of cirri. Otherwise, the two are quite similar, as are their burrows, the likes of which are not infrequently encountered in marine carbonate substrates as far back at the Middle Devonian (Baird et al. 1990). Therefore, in contrast to the higher Lithoglyptidae (*Kochlorine* Noll, 1872 and *Kochlorinopsis* Stubbings, 1967), the Cryptophialidae and the apygophoran Trypetesidae, the relatively generalized lithoglyptids represent survivors of conservative clades that have apparently diverged little over the 280 million years of their existence, if not substantilaly longer (Perez-Losada et al. 2004).

Lithoglyptes s.l. Aurivillius, 1892 is second only to *Cryptophialus* Darwin, 1854 in species richness and geographic range. As presently known it includes 14 species from different regions, depths, and carbonate substrates largely from warm and tropical seas of the world, and a new species from Bermuda will be added in the present paper.

The species presently referred to *Lithoglyptes* display a wide range of morphologies involving the form and armament of the opercular bars including the development of posterior opercular processes, and the degree of development of lateral bars and orificial knobs, the presence of a pedestal supporting the two-segmented caudal appendages, and sometimes the details of the mandible. In addition, the dwarf males of the species of the genus differ in the form of the sac-like body and the support of the antennules by which they remain attached for life. Furthermore, a so-called "rostral" calcareous plate has been found in some species of the genera *Weltneria* and *Lithoglyptes* (Newman 1971, 1974; Grygier & Newman 1985; Kolbasov 1999a, 2000a; Kolbasov & Høeg 2000). In addition, several ultrastructural characters having taxonomic value were revealed in the acrothoracicans with SEM (Turquier 1978; Smyth 1986; Kolbasov 1999a, 2000b, 2000c, 2000d, 2000e; Kolbasov & Høeg 2000). Such characters serve to elucidate the differences between the subfamilies of the Lithoglyptidae as well as the relationships between the genera and species of the new subfamily, the Lithoglyptinae.

Grygier and Newman (1985) commented on the plesiomorphic characters defining the Lithoglyptidae, and suggested the non-monotypic genera might be paraphyletic or polyphyletic. That may be, since the number of terminal cirri (4) and the condition of the caudal appendages in females are the sole diagnostic characteristics of *Lithoglyptes* s.l., a genus that includes more than a dozen species having a variety of potentially unrelated morphologies. However, Kolbasov (1998, 2000d) recognized and informally proposed several apparently natural groups within *Lithoglyptes* s.l. In the present paper we extend those studies by determining that the groups within *Lithoglyptes* s.l. are not only likely natural but also are apparently phylogenetically related. Therefore, we will propose they be divided between three distinct genera. Since it is evident these three genera, plus three long established genera, form three natural groups within the Lithoglyptidae, we will propose the family itself be subdivided into three subfamilies of two genera each.

Materials and methods

The species involved in this study are listed below and an asterisk indicates those for which SEM data are available. The last is the new species from Bermuda to be described following the description of the new genus to which it belongs.

For the proposed status of the first four species, see *Lithoglyptes* s.s. herein:

1) *Lithoglyptes indicus* Aurivillius, 1892. We analysed descriptions and drawings of specimens of Aurivillius (1892, 1894) found in corals and mollusc shells from different regions of the Indian Ocean, the Java Sea and the west coast of Sumatra, and of Tomlinson (1969) from the Red Sea.

2) *Lithoglyptes viatrix* Grygier & Newman, 1985*. Approximately 24 females, and two males, in the coral *Enallopsammia ampheloides* from 378–500 m off the Hawaiian Islands (Grygier & Newman 1985) and one female in an unidentified scleractinian coral from 310–350 m, the Coral Sea, 26º46.2'S, 159º30.2'E (investigated with SEM in Kolbasov 2000a).

3) *Lithoglyptes tectoscrobis* Grygier & Newman, 1985. Holotype female in *Enallopsammia ampheloides*, Tonga Offshore Survey Station, 19º25.0'S, 174º13.4'W, 250–290 m (Grygier & Newman 1985).

4) *Lithoglyptes ivanovi* Kolbasov, 1998. One female in the shell of a gastropod, *Thais* sp., occupied by a hermit-crab, Chilachap, Java, approximately 7°45'S, 109°E, subtidal zone (described in Kolbasov 1998).

For the proposed status of the following species see *Auritoglyptes* gen. nov. herein.

5) *Lithoglyptes bicornis* Aurivillius, 1892*. [=*L. ampulla* Aurivillius, 1892 and *L. spinatus* Tomlinson & Newman, 1960 (cf. Newman & Tomlinson 1974)]. Genego I., Maldives, approximately 3°49'N, 73°06'E, coral reef, tidal zone, two females and two males in *Turbo argirostoma*; coral reef, 1.0–1.5 m, three females in *Morula cavernosa*; tidal zone, a female in *Pteria avicula*; Bay Assab, 13°04.8'N, 42°42.7'E, 0.5 m, three females and two males in *Barbatia decussata (=velata)*; Pung I., Vietnam, approximately 12°N, 109°E, 3 m, a female in *Drupa ricinus*; Gulf of Aden, 13°59'5"N, 48°24'7"E, 10 m, one female and one male in *Pinctada margaritifera*; Colombia, 12°26.3'N, 81°43.6'W, 1–2 m, one female in dead madreporarian coral (studied with SEM in Kolbasov 2000e); Bermuda, with the new species described herein.

For the proposed status of the following 10 species see *Armatoglyptes* gen. nov. herein.

6) *Lithoglyptes balanodytes* Kolbasov, 2000*. (? =*Balanodytes taiwanus* of Tomlinson 1969:84, cf. Kolbasov 2000c). Three mature and one young female, and one dwarf male in a hydrocoral colony, 40 m, Fiji Sea, 29°29.5'S, 167°52.0'E (described with SEM in

Kolbasov 2000c).

7) *Lithoglyptes cornutus* Kolbasov, 2000*. Two females with four dwarf males (one and three respectively) in *Turbo argirostoma*, and one dried female in *Conus vexillum*, Silhouette I., Seychelles, approximately 4º36'S, 56º48'E, subtidal zone (described with SEM in Kolbasov 2000d).

8) *Lithoglyptes echinoideus* Kolbasov, 2000. Two dried specimens in hydrocoral *Distichopora* sp., Nauru I., approximately 00°30'S, 166°55'E, 19–20 m (described in Kolbasov 2000f).

9) *Lithoglyptes egorovi* Kolbasov, 1999. One female in *Morula cavernosa*, Genego I., Maldives, 3°48'N, 73°05'E, 1.8 m (described in Kolbasov 1999b).

10) *Lithoglyptes habei* (Tomlinson, 1963)* (= *Kochlorine habei* Tomlinson, 1963:270). Silhouette I., Seychelles, 4°36'S, 56°48'E, subtidal zone, six females in *Mancinella mancinella*; Genego I., Maldives, 3°49'N, 73°06'E, subtidal zone, coral-reef, one female in *Hipponix* sp.; Gulf of Aden, 13°59'5"N, 48°24'7"E, subtidal zone, 10 females in *Turbo* sp.; Maxfield Bay, South-China Sea, 80 m, four females in *Xenophora* sp.; Wizard I., Kosmoledo Atoll, 10°30'S, 47°30'E, subtidal zone, one female in *Latirus polygonus* (studied with SEM in Kolbasov & Høeg 2000).

11) *Lithoglyptes mitis* Tomlinson, 1969*. Shumma I., Dahlak Arch., Red Sea, 15°05.7'N, 41°41'E, 2 m, three females in *Trochus pyramis*; Feartu I., Maldives, 3°48'N, 73°05'E, subtidal zone, seven females in *Trochus virgatus*, 1.5-3 m, three females in *Turbo argirostoma*; Genego I., 3°49'N, 73°06'E, subtidal zone, approximately 20 females in *Mancinella alauina*, *Latirolagena smaragdula*, *Morula cavernosa* and *Hipponix* sp. (studied with SEM in Kolbasov & Høeg 2000).

12) *Lithoglyptes scamborachis* Tomlinson, 1969. We studied Tomlinson’s description and drawings of specimens, in *Tridacna maxima* from Heron Island, Queensland, Australia (Tomlinson 1969).

13) *Lithoglyptes stirni* Turquier, 1987. We studied Turquier’s (1987) descriptions and drawings of specimens from the corals *Caryophyllia cyathus*, *Errina asperta*, *Lophelia pertusa*, *Madrepora occulata*, and *Paracyathus pulchellus* from near Gibraltar.

14) *Lithoglyptes wilsoni* Tomlinson, 1969. We analysed Tomlinson’s description and drawings of specimens which came from the shell of a gastropod, *Turbo lajonkairi*, from Wake I., from unspecified shells from Koror, Palau Is., Western Caroline Is., and from the blue coral, *Heliopora* sp. from Ulul I., Namonuito Atoll in the Central Caroline Is. Tomlinson figures females and males from both Wake and Koror. While the two populations do appear related, differences in the armature of the opercular bars and gross form of the males suggest they may not be the same species.

15) We also describe a new species of *Armatoglyptes* gen. nov. from Bermuda (see below).

All material collected by Kolbasov was preserved and maintained in 70% alcohol. The margins of the burrow containing a barnacle were treated in 2% HCl, or the burrow was excavated mechanically to remove the animal. The latter extraction method preserves the calcareous plates characterising some lithoglyptid species. KOH-treated material was washed in water and transferred to glycerine for light microscopy (Tomlinson 1969). For SEM, from one to five adults and one-five juvenile stages of each species were post-fixed in 2% OsO_4 for 2 hrs., dehydrated in acetone, critical point dried in CO_2, sputter coated with platinum-palladium or gold, and examined in a HITACHI S405A or a JEOL JSM-840 (15 kV) scanning electron microscopes with accelerating voltages of 15 kV.

The dried specimens of *L. viatrix* and *L. tectoscrobis* investigated by Grygier and Newman (1985) "… were reconditioned in a weak trisodium phosphate solution… Animals were extracted from their burrows either by dissolution of the coral in dilute HNO_3 or by mechanically excising the surrounding coral…".

Systematics

Infraclass Cirripedia Burmeister, 1834

Superorder Acrothoracica Gruvel, 1905

Order Pygophora Berndt, 1907

Family Lithoglyptidae Aurivillius, 1892:133

See synonymy of Tomlinson 1969:31, less Kochlorininae Gruvel, 1905, nom. trans. herein.

Early attempts to provide a meaningful classification of the pygophoran acrothoracicans at the familial level appeared largely unnatural and, therefore, while Tomlinson (1969) rightly spared the Cryptophialidae Gerstaecker, 1866, he synonymized five extant and the two fossil families with the Lithoglyptidae. The Cryptophialidae is distinguished from the Lithoglyptidae by numerous characters including having a more or less well-developed neck supporting the opercular bars and internally by vestigial maxillipeds (the first or so-called mouth cirri) and a much elongate rather than a short, bullate or moderately pointed labrum.

The Lithoglyptidae, as envisaged by Tomlinson (1969), included six genera, some of which appear more closely related to each other than to other genera, and to add to the potential confusion we propose splitting the principal genus, *Lithoglyptes* s.l., into three genera. Thus, in order to formally ally the closely related lithoglyptid genera, we propose the resurrection of one of the families synonymized by Tomlinson (1969), but at the subfamilial rather than the familial level, and to erect a new subfamily to accommodate the remainder. These are, in addition to Lithoglyptinae Aurivillius, 1892, Weltneriinae subfam. nov. and Kochlorininae Gruvel, 1905 nom. trans herein. The justification for uniting *Berndtia* Utinomi, 1950a with *Weltneria* under the Weltneriinae is their having five pairs of terminal cirri and relatively similar opercular bars, the lack of caudal appendages in *Berndtia* being an autapomorph separating them. The underlying rational is that loss of a pair of cirri is a much greater change than the loss of caudal appendages and, therefore, *Berndtia* is more closely allied to *Weltneria* than to say *Lithoglyptes*. These same arguments apply to allying *Lithoglyptes* and *Balanodytes* under the Lithoglyptinae (four pairs of terminal cirri, caudal appendages lost in *Balanodytes*). On the other hand, Stubbings (1967) utilized a different criterion in distinguishing his *Kochlorinopsis* from *Kochlorine* since their appendages were the same. These subfamilies, in ascending order of increasing specialization (apomorphies), their distinguishing characteristics, included genera and the numbers of species are as follows:

1) Subfamily Weltneriinae nov., characterized by five pairs of terminal cirri, with or without caudal appendages. *Weltneria* Berndt, 1907:289 with caudal appendages, 12 spp., *W. spinosa* Berndt, 1907:289 the type; *Berndtia* Utinomi, 1950a:7, without caudal appendages, three spp., *B. purpurea* Utinomi, 1950a:7 the type.

2) Subfamily Lithoglyptinae Aurivillius, 1892 (*nom. trans.* Lithoglyptidae Aurivillius, 1892 herein, = Chytraeidae Utinomi, 1950c:457 and Balanodytidae Utinomi, 1950b:99 in part), characterized by four pairs of terminal cirri, with or without caudal appendages. *Lithoglyptes* Aurivillius, 1892 with caudal appendages, 15 spp., *L. indicus* Aurivillius, 1892 the type; *Balanodytes* Utinomi, 1950b:95* without caudal appendages, monotypic, *B. taiwanus* Utinomi, 1950b the type. This subfamily will include the new species and the two new genera to be described below.

*Utinomi (1950b:95) proposed a monotypic genus, *Balanodytes*, for a new species, *B. taiwanus* from Taiwan. Tomlinson (1969) subsequently described what he believed to be *Balanodytes taiwanus* Utinomi from the Marshall Islands. In both cases not only had the material been damaged by fungi and in preparation, it was no longer available. Therefore, when Kolbasov (2000c) discovered several specimens from Fiji similar to the form Tomlinson attributed to *B. taiwanus*, but having caudal appendages, he suggested that not only might Tomlinson's form be a *Lithoglyptes*, it could be a representative of his new species, *L. balanodytes* Kolbasov, 2000c. Furthermore, if *Balanodytes taiwanus* Utinomi, 1950b also proved to a *Lithoglyptes*, *L. habei* Tomlinson, 1963 would be a potential junior synonym. But more importantly, the status of the genus *Balanodytes* as well as forms purportedly representing it would also be open to question. However, it will take material from the original localities to settle this matter.

3) Subfamily Kochlorininae Gruvel, 1905 (*nom. trans.* Kochlorinidae Gruvel, 1905 herein), characterized by three pairs of terminal cirri and caudal appendages, *Kochlorine* Noll, 1872, seven spp., *K. hamata* Noll, 1872 the type; *Kochlorinopsis* Stubbings, 1967, monotypic, *K. discoporellae* Stubbings, 1967 the type.

Subfamily Lithoglyptinae Aurivillius, 1892

Lithoglyptidae Aurivillius, 1892 nom. trans. herein.

The Lithoglyptinae has been proposed to accommodate *Lithoglyptes* s.l. and *Balanodytes*. In the following we will propose that the former be subdivided into *Lithoglyptes* s.s. and two new genera, *Auritoglyptes* gen. nov. and *Armatoglyptes* gen. nov., the diagnostic characteristics of which accompany the discussion of each genus.

(N.B., the opening to the mantle cavity in acrothoracicans is guarded by “apertural lips”, but since they consist of a pair of hard chitinous bars and a comb collar, they are effectively an operculum and will be referred to as such herein).

***Lithoglyptes* s.s. Aurivillius, 1892**

(Figs. 1, 2)

Diagnosis: Lithoglyptinae having two-segmented caudal appendages plus pedestals, an operculum with a pair of posterior lobes (inconspicuous in *L. indicus* and *L. ivanovi*), opercular bars without long posterior projections or auricles, and a mantle without orificial knob or lateral bars.

Four of the 14 species attributed to *Lithoglyptes* s.l. are retained in *Lithoglyptes* s.s. They are the type, *L. indicus* Aurivillius, 1892; *L. viatrix* Grygier & Newman, 1985; *L. tectoscrobis* Grygier & Newman, 1985; and *L. ivanovi* Kolbasov, 1998. They are united by a common morphology such as their opercular bars lacking the long projections (Fig. 1 B, F, H, J). Such anteriorly or posteriorly hooked projections on the opercular bars are seen in species belonging to the new genera proposed herein (Figs. 3 A; 4 A; 5 A-D, E; 6 A, B). The opercular bars of three of the four species are armed with small, simple teeth and denticles (Figs. 1 B, H; 2 A, B), but in the fourth, *L. ivanovi*, they bear some bifid teeth (Fig. 1 J), a feature seen in the two new genera. The presence of short posterior or "carinal" lobes on the opercular bars is characteristic of *L. viatrix* and *L. tectoscrobis* (Fig. 1 B, F), the same area in *L. indicus* and *L. ivanovi* being marked by a patch of spines (Fig. 1 H, J). Lateral bars and/or an orificial knob are completely absent in the armament of the mantle in these four species (Figs. 1 A, F, H; 2 A).

A calcareous, “rostral” plate (Fig. 1 A, C), associated with the attachment disk cementing it to the substratum, was described for *L. viatrix* and *L. tectoscrobis* (Grygier & Newman 1985; Kolbasov 2000a). It is possible the other two species also have such a calcareous plate, but they would have to be removed mechanically from the substratum to find out. The caudal appendages of the species of this genus each consist of two segments supported by a pedestal on either side of the anus. The basal segment supports one or two setae and the terminal segment supports a tuft of four or more long, plumose setae at the distal end (Figs. 1 G, I, K; 2 G).

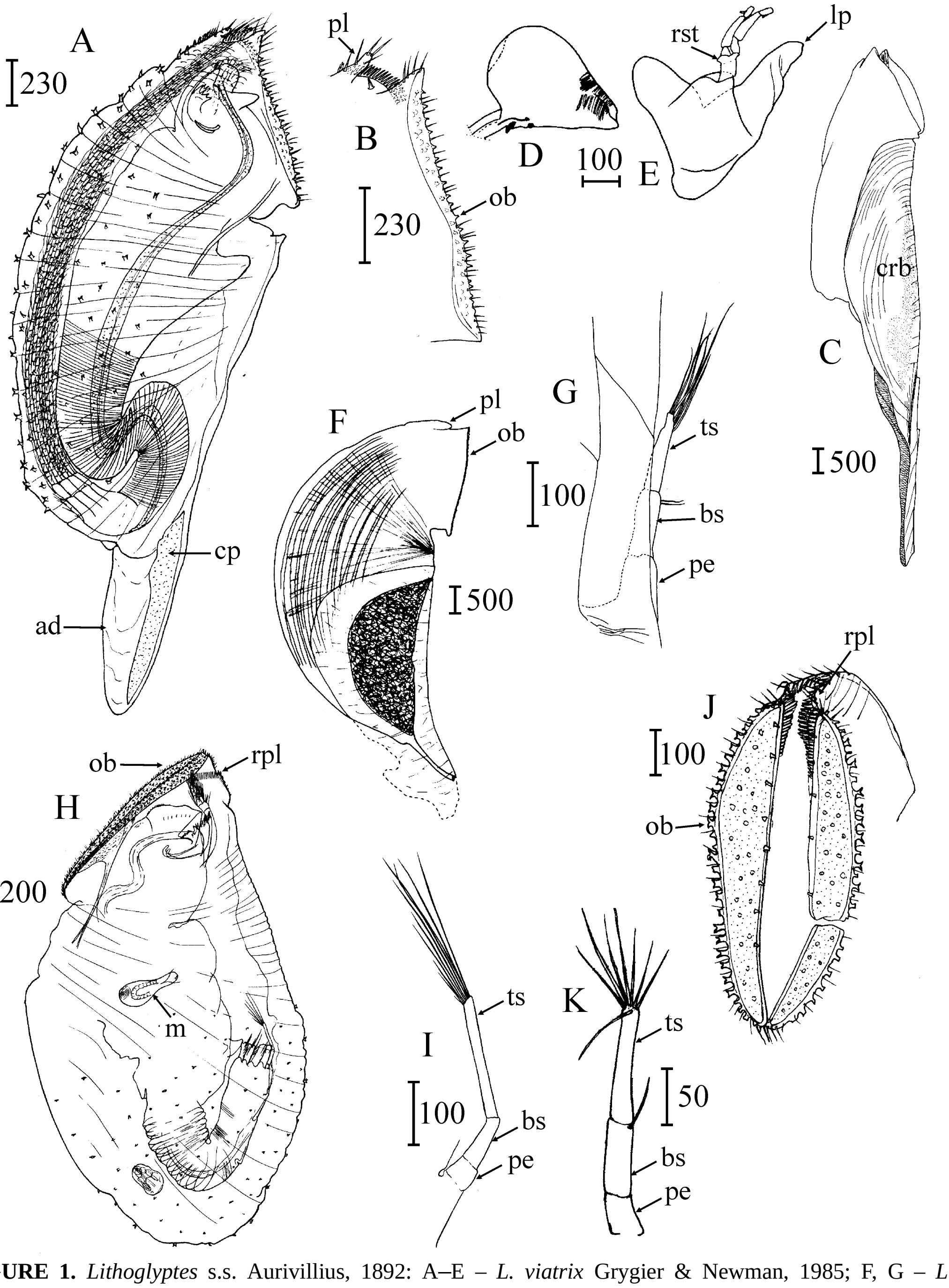

FIGURE 1. *Lithoglyptes* s.s. Aurivillius, 1892: A–E – *L. viatrix* Grygier & Newman, 1985; F, G – *L. tectoscrobis* Grygier & Newman, 1985; H, I – *L. indicus* Aurivillius, 1892; J, K – *L. ivanovi* Kolbasov, 1998. A, C – views of left side; B – left opercular bar of A; D, E – young and mature dwarf males respectively; F – view of left side; G – pedestal of last right cirrus and its caudal appendage; H –view of right side; I – caudal appendage; J – opercular bars viewed from above; K – caudal appendage. (A - from Kolbasov, 2000a; C–G – from Grygier & Newman, 1985; H, I – from Tomlinson, 1969; J, K – from Kolbasov, 1998). Abbreviations: ad – attachment disk; bs – basal segment; cp – calcareous plate “rostrum”; crb – cement roofing burrow; lp – lateral projection (wing); ob – opercular bar; pe – pedestal; pl – posterior lobe; rpl – rudimentary (incipient) posterior lobe; rst – rudimentary (incipient) stalk; ts – terminal segment. Scale bars in µm.

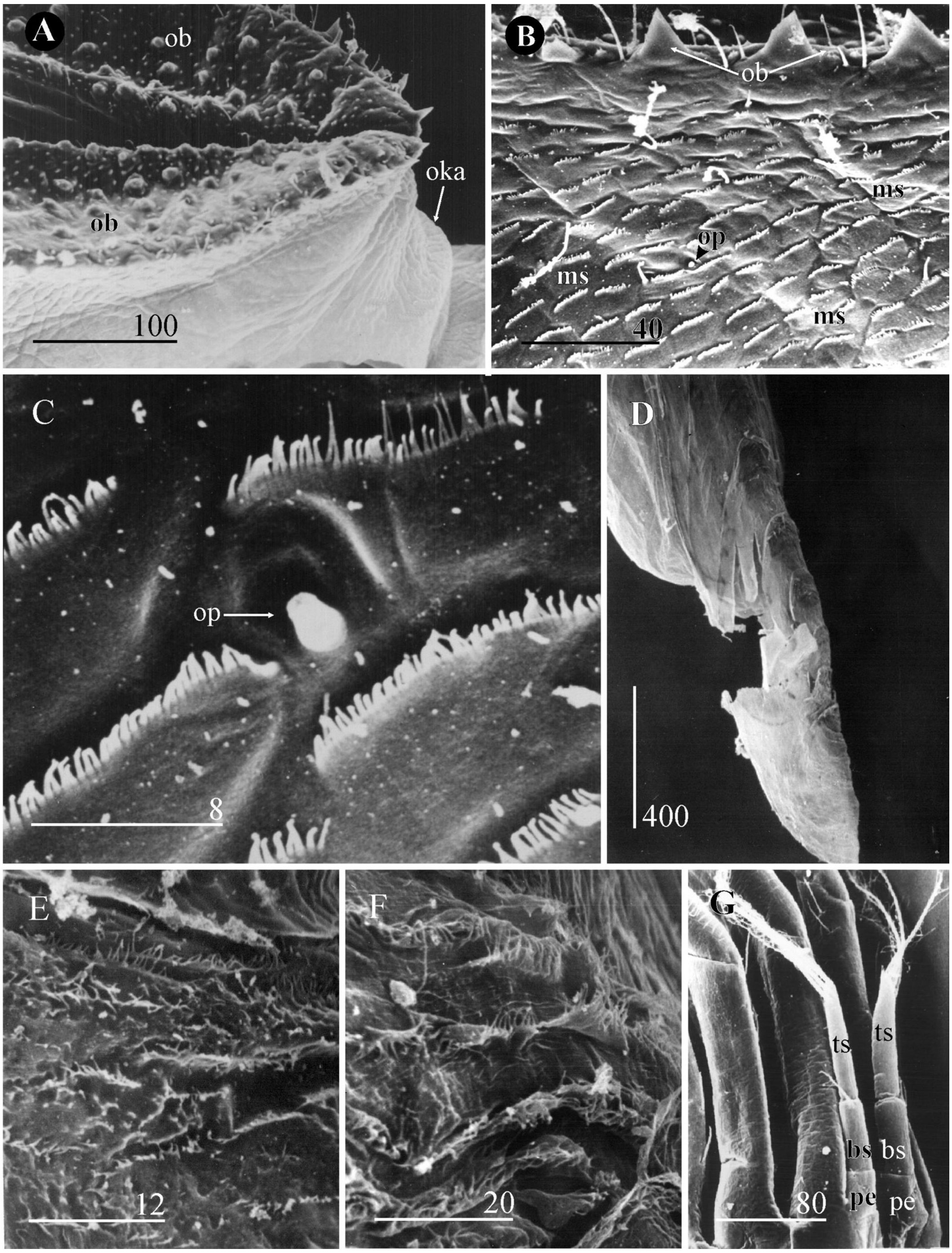

FIGURE 2. *Lithoglyptes* s.s. Aurivillius, 1892: *L. viatrix* Grygier & Newman, 1985. A – anterior portion of operculum, oblique view; B – lateral surface of operculum; C – opercular papilla; D – attachment disk, lower part; E – cuticle of attachment disk, lower part; F – cuticle of attachment disk, upper part; G – caudal appendages. (D, E, F – from Kolbasov, 2000a). Abbreviations: bs – basal segment; ms – massive multifid scales; ob – opercular bar; oka – orificial knob area; op – opercular papillae; pe – pedestal; ts – terminal segment. Scale bars in µm.

The sac of mature dwarf males, known for some species, may possess lateral projections and a short, thick stalk between the body and the antennules (Fig. 1 E).

Surficial ultrastucture of *L. viatrix* was studied in detail utilizing SEM (Fig. 2). Rows of large multifid scales, common to most Acrothoracica (Smyth 1986; Kolbasov 1999a, 2000b, 2000c, 2000d, 2000e; Kolbasov & Høeg 2000), occupy the lateral faces of the opercular area. Occasionally papillae and short setae (Fig. 2 B, C) occur between the large multifid scales. The cuticle of the area occupied by an orificial knob, when present, lacks teeth, setae or multifid scales (Fig. 2 A). Exposed cuticle of the attachment disk has rounded, transverse lines apparently corresponding to the growth lines of the calcareous plate (Fig. 2 D).

In *Lithoglyptes* s.s., as in all lithoglyptid species studied with SEM (Kolbasov 1999a, 2000a, 2000c, 2000d, 2000e; Kolbasov & Høeg 2000; Kolbasov, unpublished data), the surface of the sheets of cuticle forming the attachment disk are covered with dense, filiform structures arranged in irregular, transverse rows (Fig. 2 E, F) and it has been suggested they serve as passages for the secretion of cement (Kolbasov 1999a; Kolbasov & Høeg 2000).

Distribution: Representatives of the genus are found in the Red Sea, Indian Ocean, Sumatra, Java, Java Sea, Coral Sea, and Hawaii. Depth: subtidal zone (*L. indicus* and *L. ivanovi*) or at approximately 500 m (*L. viatrix* and *L. tectoscrobis*).

Hosts: Mainly in scleractinians such as *Enallopsammia ampheloides* and some undetermined corals. Also in *Thais* sp. and some undetermined molluscs.

***Auritoglyptes* gen. n.**

(Figs. 3, 4)

Lithoglyptes Aurivillius, 1892:133, in part.

Chytraea Utinomi, 1950c:458, *nom. nud.* (does not satisfy the requirements of ICZN Articles 13.1.1 and 13.3, and hence Chytraeidae Utinomi, 1950c:457 also *nom. nud.*).

Diagnosis: Lithoglyptinae having two-segmented caudal appendages plus pedestals, an operculum with a pair of long, articulated, posterior, setose, ear-like processes, or “auricles” (Fig. 3A), opercular bars with well developed, anteriorly hooked (decurved) opercular projections, and a mantle without an orificial knob or lateral bars.

Etymology: from the Latin *auritus* – eared, in reference to the pair of posterior processes (“auricles”) of the operculum, and the Greek *glyptes* – carver, in reference to its affinities with the rock carver, *Lithoglyptes*.

A monotypic genus represented by *Auritoglyptes bicornis* (Aurivillius, 1892) the type, morphologically although not necessarily genetically a senior synonym of *L. spinatus* Tomlinson & Newman, 1960 (cf. Newman & Tomlinson 1974).

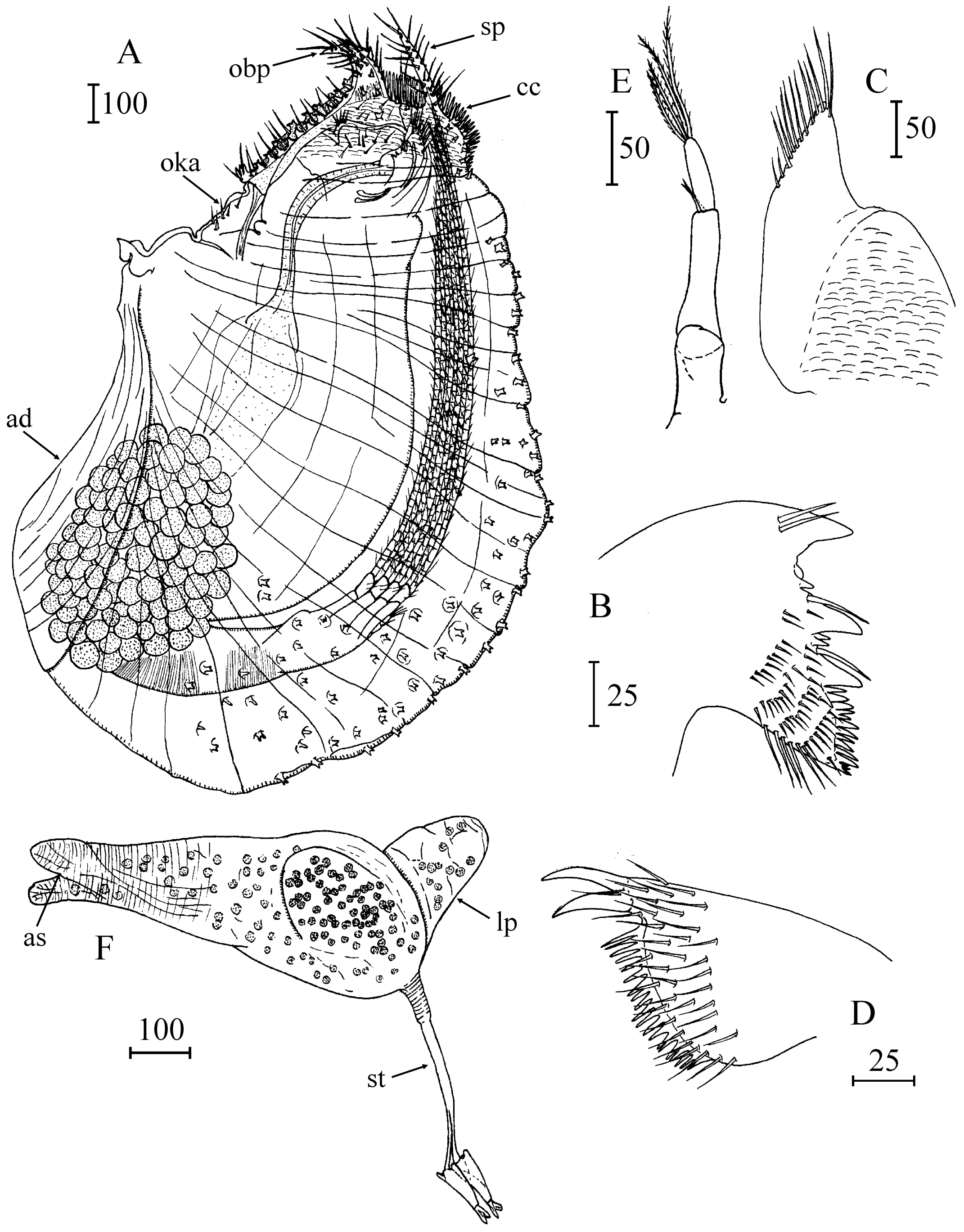

FIGURE 3. *Auritoglyptes* gen. nov.: *A. bicornis* (Aurivillius, 1892). A – viewed from right side; B – mandible; C – mandibular palp; D – maxillule; E – caudal appendage; F – dwarf male. (A, E, F – from Kolbasov, 2000e). Abbreviations: ad – attachment disk; as – apertural slit; cc – comb collar; lp – lateral projection (wing); obp – opercular bar, posterior projection; oka – orificial knob area; sp – long, articulated posterior setose process (“auricle”) ; st – stalk. Scale bars in µm.

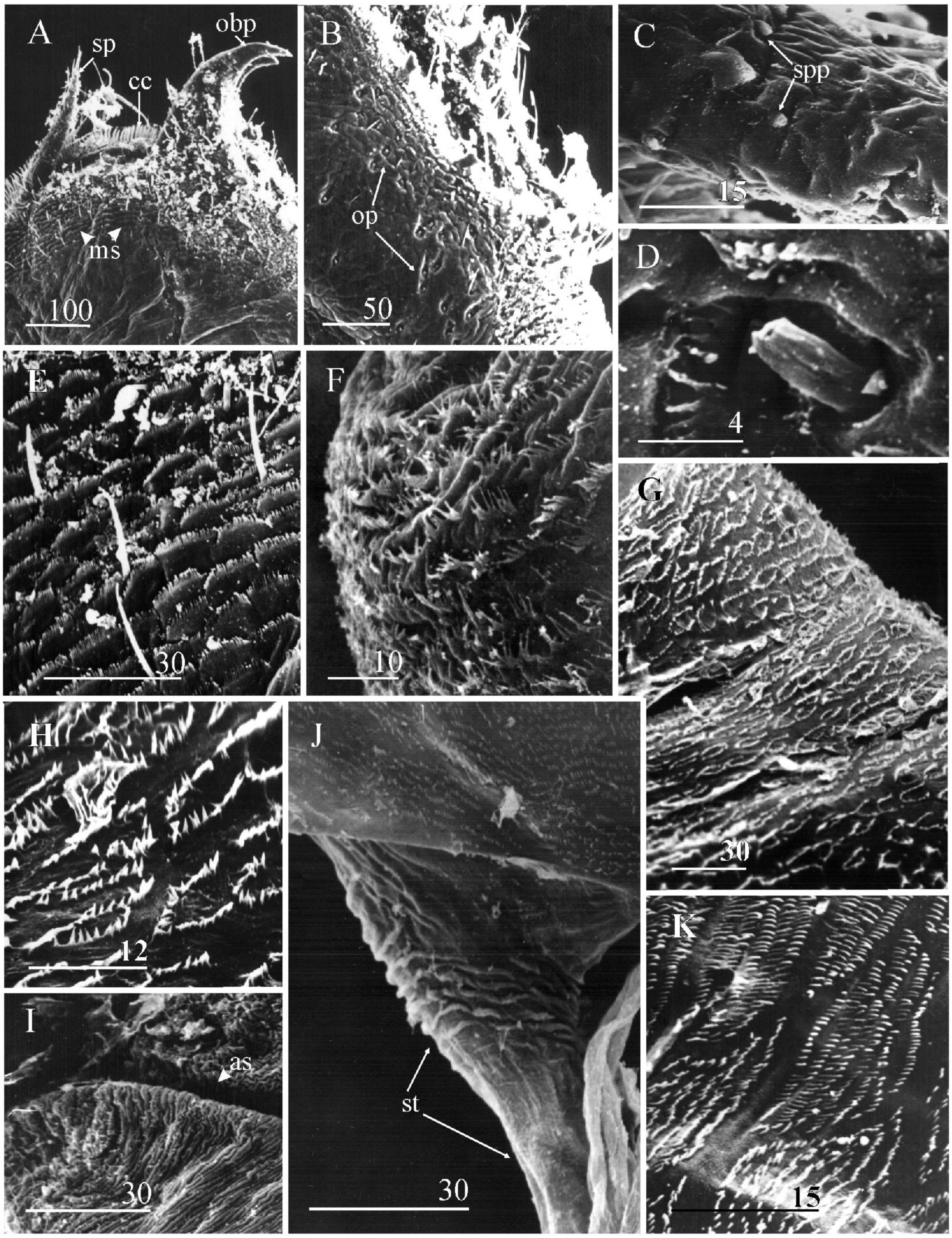

FIGURE 4. *Auritoglyptes* gen. nov.: *A. bicornis* (Aurivillius, 1892). A, B – posterior and anterior portions of operculum respectively; C – surface of an auricle; D – opercular papilla; E – massive multifid scales; F – surface of orificial knob area; G – cuticle of attachment disk; H – flexible cuticular extensions of attachment disk (G) enlarged; I – dwarf male, apertural slit; J – dwarf male, base of stalk; K – dwarf male, rows of fringes or denticles on the middle part of body (all photos from Kolbasov, 2000e). Abbreviations: as – apertural slit; cc – comb collar; ms – massive multifid scales; obp – opercular bar, posterior projection; op – opercular papillae; sp – auricle; spp –papillae of an auricle; st – stalk. Scale bars in µm.

Description: The opercular bars are armed with long setae and bifid and simple teeth, and a pair of strong, anteriorly hooked, posterior projections (Figs. 3 A; 4 A). A pair of long, articulated, setose processes ("auricles") inserted posterior to the opercular bars are diagnostic for the genus. Well-developed apertural (opercular) papillae are located beneath the opercular bars in conspicuous pits, between the rows of prominent multifid scales, (Fig. 4 B, D), and on the surface of the auricles (Fig. 4 C). Typical prominent multifid scales, with scattered small setae coming up between them, cover the lateral faces of the operculum (Fig. 4 E). Lateral bars are absent. The orificial knob area lacks teeth but bears setae and dense multifid scales (Figs. 3 A; 4 F).

The oval or teardrop shaped attachment disk has indistinct growth lines and its cuticle is covered with dense, flexible extensions united into groups with oval outlines (Fig. 4 G, H).

The caudal appendages consist, as in *Lithoglyptes* s.s., of two segments supported by a pedestal, although the distal segment, with four plumose setae, is shorter than the proximal one (Fig. 3 E).

The mantle of the dwarf males (Fig. 3 F) has well-developed, wing-like lateral body projections. The apertural slit, situated on the elongated end of mantle, is without teeth, setae or denticles (Fig. 4 I). There is a long, thin stalk between the mantle and antennules (Figs. 3 F; 4 J). The cuticle of the body is covered by small, sharp and dense extensions characteristic for all lithoglyptids (Fig. 4 K).

Distribution: Almost all tropical and subtropical waters: Red Sea, Aden, Maldives, Thailand, Java, Vietnam, New Guinea, Japan, Great Barrier Reef (Heron Island) Australia, Marshall Islands, Line Islands, Caribbean and Bermuda (re habitat and associates, cf. *A. thomasi* sp. nov. herein). Depth: from subtidal zone to 10 m.

Hosts. On *Acropora palmata*, *Acropora studeri*, *Dendrophylla axifuga* and some undetermined corals. Bivalve molluscs - *Barbatia decussata*, *Pinctada margaritifera*, *Pteria avicula*, *Tridacna maxima*; and gastropods - *Drupa ricinus*, *Morula cavernosa*, *Turbo argirostoma*. Also in skeletons of dead invertebrates and limestone.

***Armatoglyptes* gen. nov.**

(Figs. 5–8)

Lithoglyptes Aurivillius, 1892:133, in part.

Diagnosis: Lithoglyptinae having two-segmented caudal appendages without pedestals, an operculum without posterior processes ("auricles"), opercular bars with posterior projections, mantle with or without an orificial knob as well as lateral bars.

Etymology: from the Latin *armatus* – armed, in reference to the well-developed posterior projections of the opercular bars, and the Greek *glyptes* - carver, in reference to affinities with the rock carver, *Lithoglyptes*.

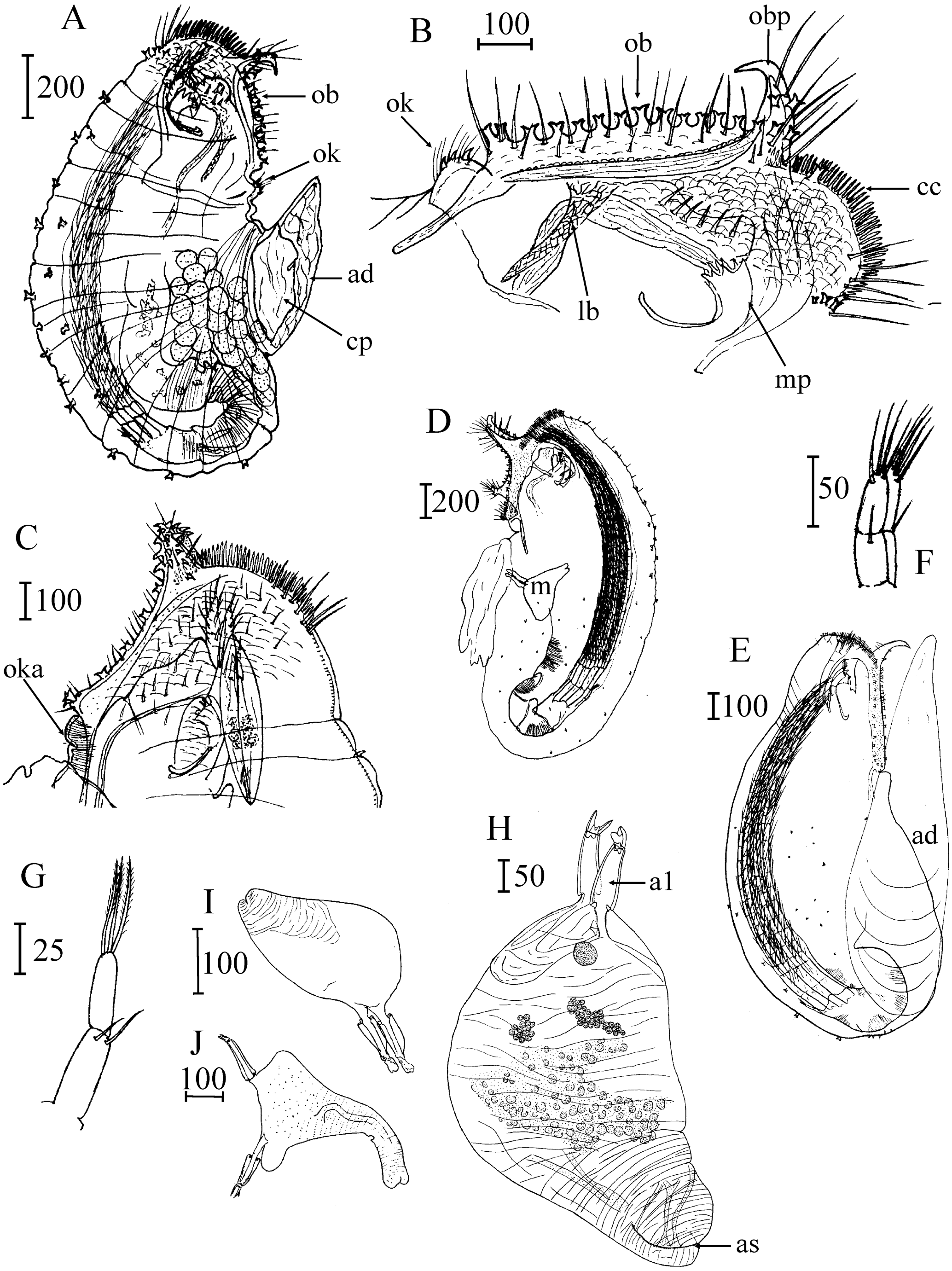

FIGURE 5. *Armatoglyptes* gen. nov.: A, B, F – *A. habei* (Tomlinson, 1963); C, G – *A. echinoideus* (Kolbasov, 2000); D – *A. scamborachis* (Tomlinson, 1969); E, I, J – *A. wilsoni* (Tomlinson, 1969); H – *A. mitis* (Tomlinson, 1969). A – view of left side; B – detail of right opercular area; C – right opercular area; D – view of right side; E –view of left side; F, G – caudal appendages; H – dwarf male; I, J – dwarf males (Wake & Koror, respectively). (A – from Kolbasov, 2000a; C, G – from Kolbasov, 2000f; D, E, I, J – from Tomlinson, 1969; H – from Kolbasov, 2002). Abbreviations: a1 – antennules; ad – attachment disk; as – apertural slit; cc – comb collar; cp – calcareous plate; lb – lateral bar; m – dwarf male; mp – mouth parts; ob – opercular bars; obp – opercular bar, posterior projection; ok – orificial knob; oka – orificial knob area. Scale bars in µm.

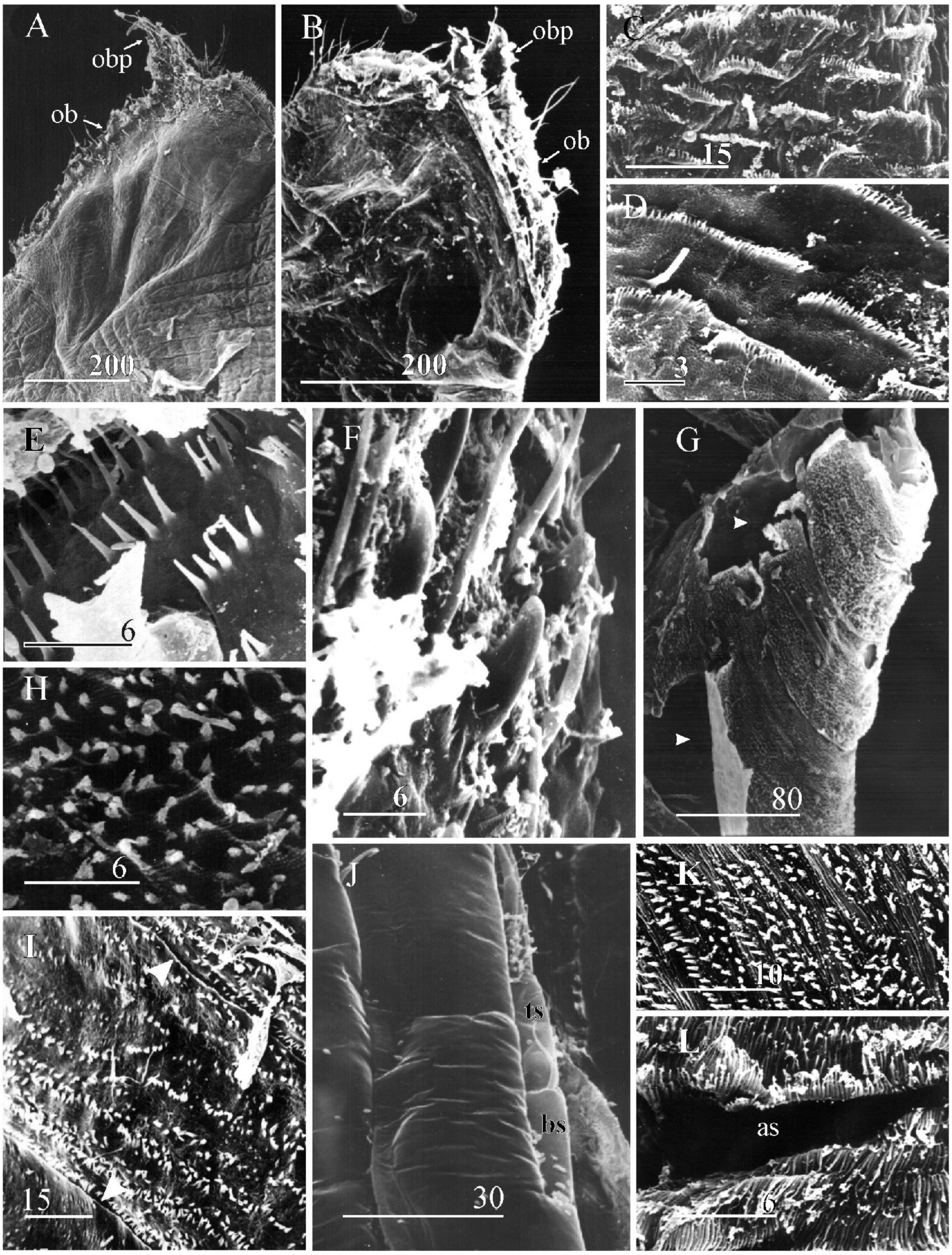

FIGURE 6. *Armatoglyptes* gen. nov.: A, D – *A. habei* (Tomlinson, 1963); B, E, G, H, J – *A. cornutus* (Kolbasov, 2000); C – *A. balanodytes* (Kolbasov, 2000); F, I, K, L – *A. mitis* (Tomlinson, 1963). A, B – opercular area, right and left views respectively; C, D – massive multifid scales; E – multifid scales in posterior part of operculum; F – surface of orificial knob; G – cuticle of attachment disk, cavity between exterior and interior cuticular layers arrowed; H – cuticular flexible extensions of attachment disk; I – cuticle of attachment disk, two growth lines arrowed; J – left caudal appendage and pedestal of last cirrus; K – dwarf male, cuticle of middle of body; L – apertural slit. (A, D, F, I – from Kolbasov & Høeg, 2000; E, G, H – from Kolbasov, 2000d; C – from Kolbasov, 2000c; L – from Kolbasov, 2000e). Abbreviations: as – apertural slit; bs – basal segment; ob – opercular bar; obp – opercular bar, posterior projection; ts – terminal segment. Scale bars in µm.

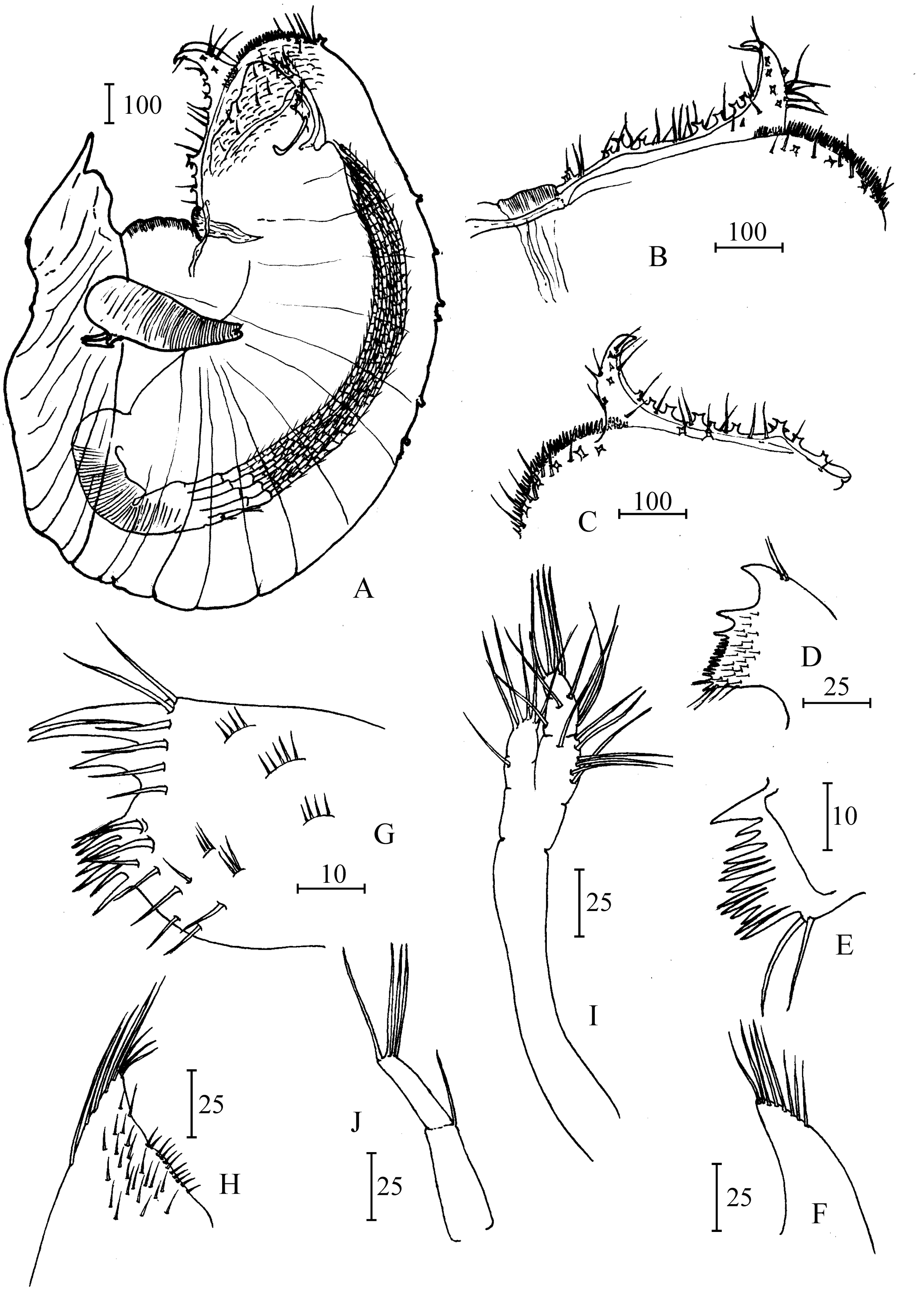

FIGURE 7. *Armatoglyptes thomasi* gen. et sp. nov. (holotype): A - female with attached dwarf male, viewed from right side; B, C, right and left opercular bars respectively; D - mandible; E - inferior angle of mandible; F - mandibular palp; G - maxillule; H - maxilla; I - mouth cirrus; J - caudal appendage. Scale bars in µm.

The genus consists of nine species formerly included in *Lithoglyptes* s.l. and the new species from Bermuda described herein. They are *A. balanodytes* (Kolbasov, 2000c), *A. cornutus* (Kolbasov, 2000d), *A. echinoideus* (Kolbasov, 2000f), *A. egorovi* (Kolbasov, 1999), *A. habei* (Tomlinson, 1963), *A. mitis* (Tomlinson, 1969), *A. scamborachis* (Tomlinson, 1969), *A. stirni* (Turquier, 1987), *A. wilsoni* (Tomlinson, 1969), and *A. thomasi* sp. nov.

Description: These species exhibit much morphological diversity, but share several unifying characters; 1) opercular bars of adult females that always have a pair of well-developed posterior projections, often covered by setae and teeth [the projections maybe straight in *A. echinoideus*, *A. egorovi*, and *A. mitis* (Fig. 5 C), recurved (hooked posteriorly) in *A. balanodytes*, *A. cornutus*, and *A. scamborachis* (Figs. 5 D; 6 B), or decurved (hooked anteriorly) in *A. habei*, *A. stirni*, *A. wilsoni*, and *A. thomasi* (Figs. 5 A, B, E; 6 A, 7 A–C)], 2) an operculum (apertural lips) lacking posterior lobes or processes (“auricles”), and 3) the sides of operculum typical bearing prominent multifid scales without papillae scattered between them (Fig. 6 C, D, E). The lateral bars may be feebly developed (Figs. 5 A, B, D; 6 A) in *A. egorovi*, *A. habei*, *A. mitis*, and *A. scamborachis*, or absent (Fig. 5 C, E; 7 A) in *A. balanodytes*, *A. cornutus*, *A. echinoideus*, *A. stirni*, *A. wilsoni*, and *A. thomasi* and a distinct orificial knob, armed with setae and teeth (Figs. 5 A, B; 6 F) is present in *A. mitis*, and *A. habei*, but absent in *A. balanodytes*, *A. cornutus*, *A. echinoideus*, *A. egorovi*, *A. scamborachis*, *A. stirni*, *A. wilsoni*, and *A. thomasi* (Figs. 5 C, D, E; 6 B; 7 B).

A teardrop-shaped attachment disk (Figs. 5 A, E; 6 G) is present in all species. It bears transverse, curved growth-lines, and is covered by dense cuticular extensions grouped into transverse rows in *A. balanodytes*, *A. habei*, *A. mitis* (Fig. 6 I), but irregularly distributed in *A. cornutus* (Fig. 6 G, H). A ”rostral” calcareous plate (Fig. 5 A), covered by the cuticle of the attachment disk, has been described in *A. habei* and *A. mitis* (Kolbasov, 1999a; Kolbasov & Høeg, 2000). It is quite possible that other species of the *Armatoglyptes* have a calcareous plate that was dissolved during extraction with acid from the substratum (Fig. 6 G).

Caudal appendages (Figs. 5 F, G; 6 J; 7 J) two-segmented but without pedestals. The basal segment bears one-two simple setae, whereas the distal one bears a tuft of four plumose setae.

The dwarf males of *Armatoglyptes*, as well as those of *Lithoglyptes* s.s., lack a slender stalk between the mantle and the antennules seen in the males of *Auritoglyptes*. On the other hand, their form differs between species groups within the genus (Fig. 5 D, I–H), and it may change during the maturation within a species (Fig. 5 I, J). Generally the males are pear-shaped (*A. balanodytes*, *A. habei*, *A. mitis*, *A. stirni*, and *A. wilsoni*) and the posterior end may be considerably elongated (Fig. 5 J). Heart-shaped dwarf males were described for *A. cornutus*, and *A. scamborachis* (Fig. 5 D). The distinct apertural slit situated at the posterior end may be equipped with long and dense setiform denticles (Fig. 6 L). The cuticle of the body is covered by characteristic small, sharp and densely arranged cuticular extensions (Fig. 6 K).

Distribution: Mediterranean, Red Sea, Seychelles, Gulf of Aden, Persian Gulf, Maldives, Indonesia, Vietnam, Taiwan, Japan, North-Eastern Australia, Southern Australia, Melanesia, Micronesia, Polynesia, Bermuda. Depth: from subtidal zone to 390 m.

Hosts: Corals – *Caryophyllia cyathus*, *Distichopora nitida*, *Distichopora* sp., *Errina aspera*, *Heliopora* sp., *Lophelia pertusa*, *Madrepora occulata*, *Paracyathus pulchellus*. Molluscs – bivalves *Ostrea angasi*, *Pecten liridus*, *Spondylus* sp., *Tridacna maxima*, *Tridacna* sp.; gastropods – *Berylsma waitei*, *Bursa bubo*, *Bursa bufo*, *Bursa rubeta*, *Charonia sauliae*, *Conus vexillum*, *Cronia pseudamygdala*, *Dinassovica jourdani*, *Fasciolaria filamentosa*, *Fulgetrum* sp., *Hipponix* sp., *Kelletia lischkei*, *Latirolagena smaragdula*, *Latirus polygonus*, *Mancinella alauina*, *Mancinella mancinella*, *Morula cavernosa*, *Plecuna lobata*, *Ricinula rubicunda*, *Siphonalia tasmaniensis*, *Tectus ochrolencus*, *Thais aperta*, *Thais tuberosa*, *Throchus incrassatus*, *Throchus obeliscus*, *Throchus pyramis*, *Throchus virgatus*, *Turbo argyrostoma*, *Turbo lajonkairi*, *Turbo marmorostoma crassus*, *Turbo petholatus*, *Turbo* sp., *Xenogalea stadialus*, *Xenophora* sp.; Cirripedia – *Megabalanus tintinnabulum* s.l..

***Armatoglyptes thomasi* sp. n.**

Figs. 7, 8

Diagnosis. An *Armatoglyptes* having an indistinct orificial knob lacking armament but without lateral bars, opercular bars supporting a pair of well-developed recurved posterior projections and a pair of small armed elevations at approximately 1/3 back along the length of the aperture, and a mandible with a comb of sharp spines along the lower half of the cutting edge.

Material: Three females with three dwarf males (one on holotype and two on one of the paratypes). The holotype and a paratype were boiled in KOH for light microscopy investigations. The dissected holotype (Fig. 7) and the paratype (Fig. 8 A, B), together with dwarf males, are deposited in the Zoological Museum of Moscow State University (no. Mg 1213). From the undersides of limestone slabs from seaward lips and cup reef rims, up to 3 m depth, 2.4 km north of East Blue Cut, Bermuda, July 1988, Dr. M.L.H. Thomas (University of New Brunswick) collector. Accompanied on slabs by an occasional specimen of the largely insular species *Catophragmus imbricatus* and *Tesseropora atlantica*, and other attached organisms (Thomas & Stevens 1991), and by *Auritoglyptes bicornis* (Aurivillius, 1892) (herein).

Etymology. Named in the honor of Dr. M.L.H. Thomas who discovered the new species and, upon the advice of Dr. Wolfgang Sterrer, provided us with material from Bermuda.

Description: Female. Holotype (Fig. 7 A): 1.5×1.0 mm, aperture 0.5 mm long from anterior end of opercular bars to posterior end of comb collar, colour off-white in alcohol. Opercular bars (Fig. 7 B, C) approximately 0.38 mm long, 1) equipped with several bifid teeth and simple setae, 2) a pair of small elevations (hillocks), about 1/3 the length from the anterior end, bearing one or two bifid teeth at their tops which are slightly larger than the surrounding bifid teeth, 3) a pair of well-developed, recurved (anteriorly bent) posterior processes having small bifid teeth and simple setae long their lengths but only simple teeth at their tips, 4) followed by a long, typical comb collar and 5) scattered setae and bifid teeth at the posterior end of the aperture.

Lateral surfaces of opercular area sparsely covered with short setae among a dense covering of prominent multifid scales, discernible as fine striations and sparse short setae under light microscopy. Lateral bars absent but a feeble apertural reinforcing bar arises from the anterior end of the opercular bars. The orificial knob lacks setae, teeth and denticles, but has a strongly wrinkled cuticle that appears as a densely striated area (Fig. 7 A, B). The region between the knob and the attachment disk is approximately three times its length and also appears densely striated (Fig. 7 A). The remainder of the mantle, except for a few scattered teeth along the “carinal” margin, lacks armament. The attachment disk is composed of successive layers of striated cuticle, but whether or not it was calcified is unknown.

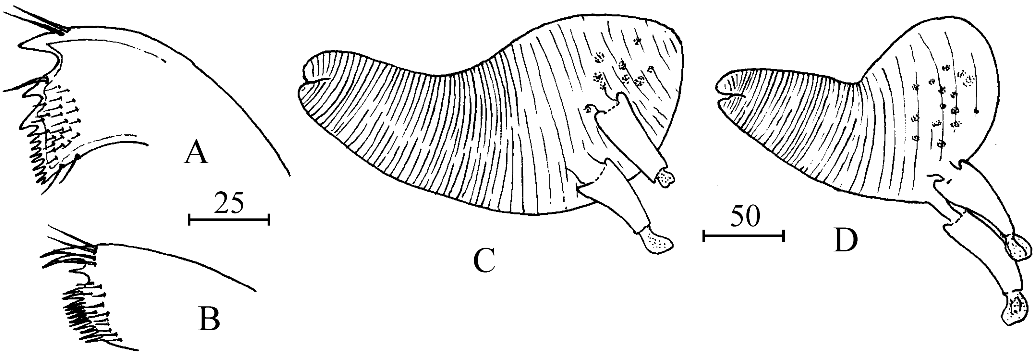

FIGURE 8. *Armatoglyptes thomasi* gen. et sp. nov., A, B (paratype): C, D - dwarf males. A - mandible; B - maxillule; C, D - dwarf males, general view. Scale bars in µm.

The mouthparts are surrounded by a typical saddle-shaped labrum. The mandibles (Fig. 7 D, E; 8 A) support three teeth along the upper half and a comb of 9–12 sharp spines along the lower half of the cutting edge, several long setae at upper and lower margins, and numerous small setae on the surface of the blade. Mandibular palps characteristic of lithoglyptids, with trapezoid distal parts bearing long, smooth setae (Fig. 7 F). Superior angle of maxillules (Fig. 7 G; 8 B) with three curved spine-like setae, the upper two longer than the lower one, followed by a notch without spines and an inferior angle supporting a row of small spines; surfaces of blade distally setose, upper setae are longest, with several small setae united into ctenoid scales. Maxillae (Fig. 7 H) are typical of lithoglyptids, triangular, with long setae at the tip and smaller setae scattered on the anterior side and along inner margin.

Mouth or first cirri (maxillipeds) (Fig. 7 I) consist of a long, curved coxa and a quadrangular basis supporting two rami with indistinct segmentation; the anterior ramus perhaps originally three-segmented and almost twice as long as the apparently two - segmented posterior ramus, rami bearing numerous long setae. The four pairs of terminal cirri, and the caudal appendages with the proximal and distal segments bearing one-two setae and four setae respectively (Fig. 7 J), are typical for the genus.

The simple dwarf males (Fig. 7 A; 8 C, D) were attached to the side of the female near or on the side of the attachment disk. Their pear or gourd-shaped mantle measures 200–400 µm long, with an elongated, bent, distal end covered by dense annular striations and bearing a distinct apertural slit.

Affinities. The new species, *Armatoglyptes thomasi* from Bermuda, is similar to *A. habei* (Tomlinson, 1963) from Japan, *A. wilsoni* (Tomlinson, 1969) from Koror and Wake I., and *A. stirni* (Turquier, 1987) from the E. Atlantic in having opercular bars with a pair of large, recurved (anteriorly hooked) posterior projections. The new species is also similar to *A. echinoideus* (Kolbasov, 2000f) from Nauru I. in having a strongly wrinkled cuticle of the orificial knob area, but the latter can be easily be distinguished by the heavy hooked spines found on the posterior projections of its opercular bars. The new species also differs from *A. habei* in having an unarmed orificial knob and in lacking lateral bars. *Armatoglyptes wilsoni* and *A. stirni* also lack these features, but the Koror population of the former has a small elevation supporting a strong bifid tooth about 1/3 the length of each opercular bar from the attachment area, and similar elevations are seen in *A. thomasi*. The mandible in *A. wilsoni* is described as having the upper half of the cutting edge supporting three blunt cusps rather than sharp teeth, and the lower half bearing many tubercles rather that a comb of sharp spines, and the maxillules have two rather than three curved spines at the superior angle (Tomlinson 1969), features that clearly separate it from *A. thomasi*. The two also have markedly different distributions, *A. wilsoni* being known from the Indo-West Pacific whereas *A. thomasi* is known only from Bermuda.

This leaves *A. stirni* on the eastern side of the Atlantic (near Gibraltar) and, therefore, evidently geographically the closest relative of *A. thomasi*. However, it generally has the hooked tips of the posterior opercular bar projections bifid rather than simple, and there is no elevation between them and the anterior ends of the opercular bars as there is in *A. wilsoni* and *A. thomasi*. In addition, the mandible of *A. stirni* has denticles between the second and third teeth and a thick and short rather than a long comb of relatively long, thin spines between the third tooth and the inferior angle, which further distinguish it from *A. thomasi*. Furthermore, *A. stirni* differs from both *A. wilsoni* and *A. thomasi* in having the basis of the first or mouth cirrus longer than wide and the anterior and posterior rami perhaps three and clearly four segmented respectively. Thus, while all these species are more or less closely related, *A. thomasi* is apparently closer to the Indo-W. Pacific forms, particularly *A. wilsoni* form Koror, than it is to *A. stirni* from the E. Atlantic.

Phylogeny

What are the phylogenetic relations between the genera *Lithoglyptes* s.s., *Auritoglyptes* and *Armatoglyptes;* e.g., how do the species of *Lithoglyptes* s.l. align with these genera cladistically? We are limited to characters of the adult stages (females and dwarf males) for the phylogenetic reconstruction, since only the cyprid larvae of *Armatoglyptes* have been investigated (Kolbasov et al. 1999).

We developed a matrix of 13 characters for Nexus Data Editor 5.0 (Table 1). Data were scored "0" or"1", or "0,1" when both conditions were present (with or without lateral bars for *Weltneria,* for example), and "0", "1" and "2" for multistate characters. We tried to avoid multistates in our analysis (only character 10). Uninformative characters, such as 1, 3 and 6 (number of terminal cirri, strong posterior processes and unpaired projection), do not contribute to this parsimony analysis. But at least 1 and 3 may represent synapomorphies or symplesiomorphies and, therefore, we consider these features as very important in the lithoglyptine evolution.

TABLE. Character matrix. Unknown states marked by (?).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13
Weltneria	0	0	0	0,1	0,1	0	0,1	0	1	0	0	0,1	0,1
L. indicus	1	1	0	0	0	0	0	1	?	0	1	0	?
L. viatrix	1	1	0	0	0	0	0	1	1	0	0	1	1
L. tectoscrobis	1	1	0	0	0	0	0	1	?	0	?	?	?
L. ivanovi	1	1	0	0	0	0	1	1	?	0	1	?	?
Au. bicornis	1	0	1	0	1	0	1	1	1	1	1	1	1
Ar. balanodites	1	0	0	0	1	0	1	0	0	0	1	0	0
Ar. cornutus	1	0	0	0	1	0	1	0	0	0	1	0	0
Ar. echinoideus	1	0	0	0	1	0	1	0	?	1	1	?	?
Ar. egorovi	1	0	0	1	1	0	1	0	?	0	1	?	?
Ar. habei	1	0	0	1	1	0	1	0	0	2	1	0	0
Ar. mitis	1	0	0	1	1	0	1	0	0	2	1	0	0
Ar. scamborachis	1	0	0	1	1	1	1	0	?	0	1	0	0
Ar. stirni	1	0	0	0	1	0	1	0	?	0	1	0	0
Ar. wilsoni	1	0	0	0	1	0	1	0	?	0	1	0	0
Ar. thomasi	1	0	0	0	1	0	1	0	?	1	1	0	0

List of characters

1. Number of cirri (including mouth cirri or maxillipeds): 0 = six pairs (one pair of mouth cirri plus five pairs of terminal cirri), 1 = five pairs (one pair of mouth cirri plus four pairs of terminal cirri). The number of cirri has been considered of importance in the systematics of the Lithoglyptidae as well as the Acrothoracica in general. The reduction of terminal cirri from five pairs in Weltneriinae to 4 in Lithoglyptinae, and to 3 in Kochlorininae, is the trend. We consider the presence of all six pairs (plus caudal appendages) in *Weltneria* (out-group) plesiomorphic compared to five pairs because six

represents the ground pattern for all thecostracans. Thus, the presence of five pairs of cirri (one pair of mouth cirri and four pairs of terminal ones plus caudal appendages) represents a synapomorphy uniting the genera *Lithoglyptes, Auritoglyptes* and *Armatoglyptes* under the Lithoglyptinae.

2. Small posterior lobes of operculum: 0 = absent, 1 = present. These structures are characteristic of species of *Lithoglyptes* s.s. (weakly developed in *L. indicus* and *L. ivanovi*). Similar structures are seen elsewhere only in *Berndtia fossata* Tomlinson, 1969 and *B. purpurea* Utinomi, 1950a. We consider the small posterior lobes an apomorphy because they are unique structures not found in *Weltneria* (out-group). On the other hand, the pair of auricles on the operculum of *Auritoglyptes bicornis* could have evolved from these lobes.

3. Auricles: 0 = absent, 1 = present. This pair of long, posterior, articulated, setose processes represents an autapomorphy of *Auritoglyptes*. As noted above under character 2, they could have evolved from the posterior lobes.

4. Lateral bars: 0 = absent, 1 = present. Development of a pair of elongate, chitinous thickenings representing extensions of the operculum and serving to support it is a common trend within the Acrothoracica. Weakly developed lateral bars found in some species of *Weltneria* and Lithoglyptinae become conspicuous in apomorphic *Kochlorine*, species of which develop the most ornate operculum in the Lithoglyptidae, and they apparently develop independently in the family Cryptophialidae, along with a pronounced elongation of the included mantle into a “neck”. We consider the presence of lateral bars the apomorphic condition.

The majority of the species of *Weltneria* lack lateral bars, but a few species have short, weak, granulated extensions of the operculum that Tomlinson (1969) considered the “evolutionary beginning of the lateral bars”. Therefore we scored this state as “0,1” for *Weltneria*. While all species of *Lithoglyptes*, the six species of *Armatoglyptes* and the sole species of *Auritoglyptes* lack lateral bars, four species of *Armatoglyptes* have developed reticulated ones.

5. Posterior projections of opercular bars: 0 = absent, 1 = present. Such projections represent armament that likely serves to deter other organisms from attempting to enter the mantle cavity and parasitizing and/or eating them (Kolbasov 1999a; Kolbasov & Høeg 2000). Their presence is apparently an apomorphy for the Lithoglyptidae. While several species of *Weltneria* lack such projections, others like *W. aapta*, *W. spinosa*, *W. zibrowii* have short, posterior projections of the opercular bars. Therefore, we mark this character as “0,1” for *Weltneria*. Species of the genus *Lithoglyptes* lack these projections. *Auritoglyptes* has developed, anteriorly hooked posterior projections of the opercular bars. All species of *Armatoglyptes* have developed straight, decurved or recurved posterior projections.

6. An unpaired, toothed median projection occurring on one of the opercular bars: 0 = absent, 1 = present. Such an unpaired, toothed median projection is conspicuous and

armed with several teeth. It is an autapomorphy for only a single species of the Lithoglyptinae, *Armatoglyptes scamborachis*, but a similar structure has been described for several species of the genus *Kochlorine*. While its function is unclear, one or the other of the small elevations of the operculum bars found in *A. thomasi* and *A. wilsoni* may have given rise to this structure in *A. scamborachis*.

7. Minor armament of the opercular bars: 0 = with small denticles, 1 = with big teeth (simple, bifid, complex). We assume complex armament, including that of the opercular bars, increased during acrothoracican evolution. Therefore, big teeth, apparently serving for the defence of the entrance to the mantle cavity, should be considered as an apomorphic condition in comparison with small denticles. In general, opercular bar armament in the out-group *Weltneria* is made up of small denticles, as in most species of *Lithoglyptes* s.s. (except *L. ivanovi*). Species of *Armatoglyptes* and *Auritoglyptes* have the opercular bars armed with relatively large teeth.

8. Caudal appendages*: 0 = two-segmented, without basal pedestal 1 = two-segmented plus basal pedestal. The first type is more common among the acrothoracicans, including *Weltneria* (out-group) than the second type. Kolbasov et al. (1999) showed that the furcal rami of the acrothoracican cyprid larva, the homolog of caudal appendages in the adult, each consists of a single segment. Therefore, the additional segment in the adult must either bud off from the cleaved telson or be acquired by subdivision of the primary segment seen in the cyprid. Aurivillius (1892) and Tomlinson (1969) illustrate an “incipient” or “vestigial “ division of the proximal of the two segments in *Lithoglyptes indicus* and *Auritoglyptes bicornis* respectively, but there is presently no way of telling whether each now has the potential of becoming three-segmented or that it had been three-segmented. The origin of the pedestals of the caudal appendages in *Lithoglyptes* and *Auritoglyptes* is likewise unclear. It may be nothing more than an extension of the telson of the adult female. The out-group, *Weltneria*, has all six pairs of cirri plus two-segmented caudal appendages without pedestals. Caudal appendages consisting of two segments plus pedestals are characteristic of *Lithoglyptes* and *Auritoglyptes*. Therefore, it appears these pedestals are apomorphic.

*Newman and Tomlinson (1974:205) discuss the number of segments of the caudal appendages described for *L. indicus* Aurivillius, 1892 (cf. Tomlinson 1969:47, fig. 5d) and *L. spinatus* Tomlinson & Newman, 1960 [cf. Tomlinson 1969:51, fig. 7b {= *Auritoglyptes bicornis* (Aurivillius, 1892)} herein]. At the time not only was the pedestal counted as a segment but an incomplete “articulation” increased the count by one. However, since the incomplete “articulation” appeared late if at all in the ontogeny of *A. bicornis* (cf. Newman & Tomlinson 1974), and it does not appear to function as an articulation in this species, or in *L. indicus* in which it involves the basal rather than terminal segment, we conclude it is not a vestigial segment.

9. Opercular or apertural pores/papillae: 0 = absent, 1 = present. Opercular or apertural pores and papillae have not been found in other cirriped taxa (Thoracica and

Rhizocephala) and, therefore, apparently represent a synapomorphy for the Acrothoracica (Kolbasov 1999a). They have been observed in most species of *Weltneria*, *Lithoglyptes*, *Auritoglyptes* and *Kochlorine*, but not in *Armatoglyptes,* or in species of the families Trypetesidae and Cryptophialidae (Kolbasov 1999a; Kolbasov 2001; Kolbasov & Høeg 2000, 2001). Thus, we interpreted the opercular pores/papillae as part of the ground pattern of the acrothoracicans; e.g., their absence in such advanced families as Trypetesidae and Cryptophialidae being interpreted as a loss rather than descent from ancestors lacking opertural papillae with pores. By the same token, their absence in the species of *Armatoglyptes* investigated with SEM is considered an apomorphy.

10. Orificial knob: 0 = absent, 1 = present but not armed with conspicuous teeth, 2 = present and armed with conspicuous teeth. An orificial knob protects the "rostral" region of the burrow against ingress of foreign particles and organisms. We consider its development and armament with conspicuous teeth as an apomorphic condition for the Lithoglyptidae. In addition, an orificial knob is present in a number of species of the Trypetesidae and may represent a synapomorphy with the Lithoglyptidae.

11. Labrum: 0 = with anterior portion pointed, 1 = with anterior portion rounded, presumably reduced. Species of *Weltneria* and *Lithoglyptes*, representing the generalised acrothoracicans, have a labrum with a noticeable projection at the anterior end rather than broadly rounded (bullate) as in higher, more apomorphic lithoglyptid genera, the Trypetesidae, and the most lower thoracicans. However, while we conclude that the development of a pointed labrum is a plesiomorphic character that was lost in the higher lithoglyptids, it needs to be mentioned that it likely led to the much elongated labrum of the cryptophialids.

12. Body of mature dwarf male: 0 = without lateral lobes/wings, 1 = with lateral lobes/ wings. Kolbasov (2002) wrote, "Following Klepal (1987), the pear-shaped males (*Weltneria* and some species of *Lithoglyptes* s.l.) may be viewed as the most generalized ones". Their form differs only slightly from that of the cyprid body, and there are no wings/lobes. These males have no long attachment stalk, thus the distance between the male and the aperture of the female remains relatively large. Therefore, Kolbasov (2002) wrote "…the males with lateral lobes/wings and thus a larger mantle cavity to serve as an internal sheath for the penis, and a long attachment stalk, 'peduncle', or 'orchid/testicular lobe', represent the more apomorphic evolutionary forms." Such an evolutionary advanced morphology is characteristic for the males of *Lithoglyptes viatrix* (Fig. 1E), *Auritoglyptes bicornis* (Fig. 3F), *Kochlorine* spp., and *Trypetesa* spp.. While in general this is true, Klepal (1987) had neither described nor illustrated the markedly advanced male of *Weltneria exargilla* Newman, 1974 nor did she note its similarities to the male of *Lithoglyptes spinatus* Tomlinson & Newman, 1960, (= *Auritoglyptes bicornis* (Aurivillius, 1892), which, as she notes, may lack a penis. The males of *W. exargilla* and *A. bicornis* have the antennules extended on a stalk (character 13), but those of the former are stockier and the T-shaped flange between the pair of antennules is less well developed (much as in

L. viatrix, Fig. 1E), whereby the polarity would be from the former to the latter. The same can be said for the “wings”, and the loss of the penis, which again suggests the polarity is towards *Auritoglyptes*. In any event, this is why *Weltneria* is scored 1 as well as 0.

13. Antennules of mature dwarf males: 0 = without stalk between body and antennules, 1 = with stalk. As noted above under character 12 above, we consider the absence of an antennular stalk the plesiomorphic state and its presence an apomorphy.

These data were subjected to parsimony analysis and search of the shortest trees (PAUP 4.0, Swofford, 1998). All characters were entered unordered and of equal weight, and all trees were unrooted. We reconstructed bootstrap 50% majority-rule consensus, quartet puzzling and neighbor-joining trees (Fig. 9). We used two kinds of matrices – with data on *Weltneria* as an out-group (trees on Fig. 9 A, C, E) and without data on *Weltneria* (trees on Fig. 9 B, D, F). Removal of *Weltneria* from analysis emphasizes those synapomorphies (posterior projections of opercular bars and lateral bars in some species) or symplesiomorphies (two-segmented caudal appendages and pear-shaped males without antennular stalk) found in this genus and *Armatoglyptes*, but absent in *Lithoglyptes* and/or *Auritoglyptes*. Thus, we may more precisely estimate the position of those species related to *Armatoglyptes* within the Lithoglyptinae. All trees, especially the puzzle and neighbor-joining trees (Fig. 9 C & D and E & F respectfully), show that *Lithoglyptes*, *Auritoglyptes* and *Armatoglyptes* form a monophylum on the basis of a synapomorphy – the four pairs of terminal cirri. *Lithoglyptes* and *Auritoglyptes* are closer to each other than to *Armatoglyptes*, in spite of the fact both *Auritoglyptes* and *Armatoglyptes* have developed posterior projections of opercular bars, in having such synapomorphies as two-joined caudal appendages plus pedestals and dwarf males with an antennular stalk and lateral wings. Autapomorphies for *Lithoglyptes* include the small posterior lobes of the operculum (shared only with two species of *Berndtia*), and for *Auritoglyptes,* the auricles of the operculum. Their relationship would be closer if these structures were homologous: (both short and long posterior lobes occupy a similar region of the operculum, and there is the possibility the latter evolved from the former).

We could not find common autapomorphies for all species of *Armatoglyptes*. The genus shares synapomorphies with other genera, such as four pairs of terminal cirri with *Auritoglyptes* and *Lithoglyptes*, posterior projections (hooks, spines) of the opercular bars with *Auritoglyptes* and some species of *Weltneria*, armament of the opercular bars with bifid or complex teeth as in some species of *Weltneria* and one species each of *Lithoglyptes* and *Auritoglyptes*, and a labrum with a rounded rather than pointed anterior margin in two species of *Lithoglyptes* and *Auritoglyptes*. Several species of *Armatoglyptes* have additional apomorphies such as a conspicuous and armed orificial knob and the advent of lateral bars (shared with some species of *Weltneria*), but other species lack them. We tentatively assume the absence of the opercular papillae/pores is a synapomorphy for *Armatoglyptes* but not all species have been investigated.

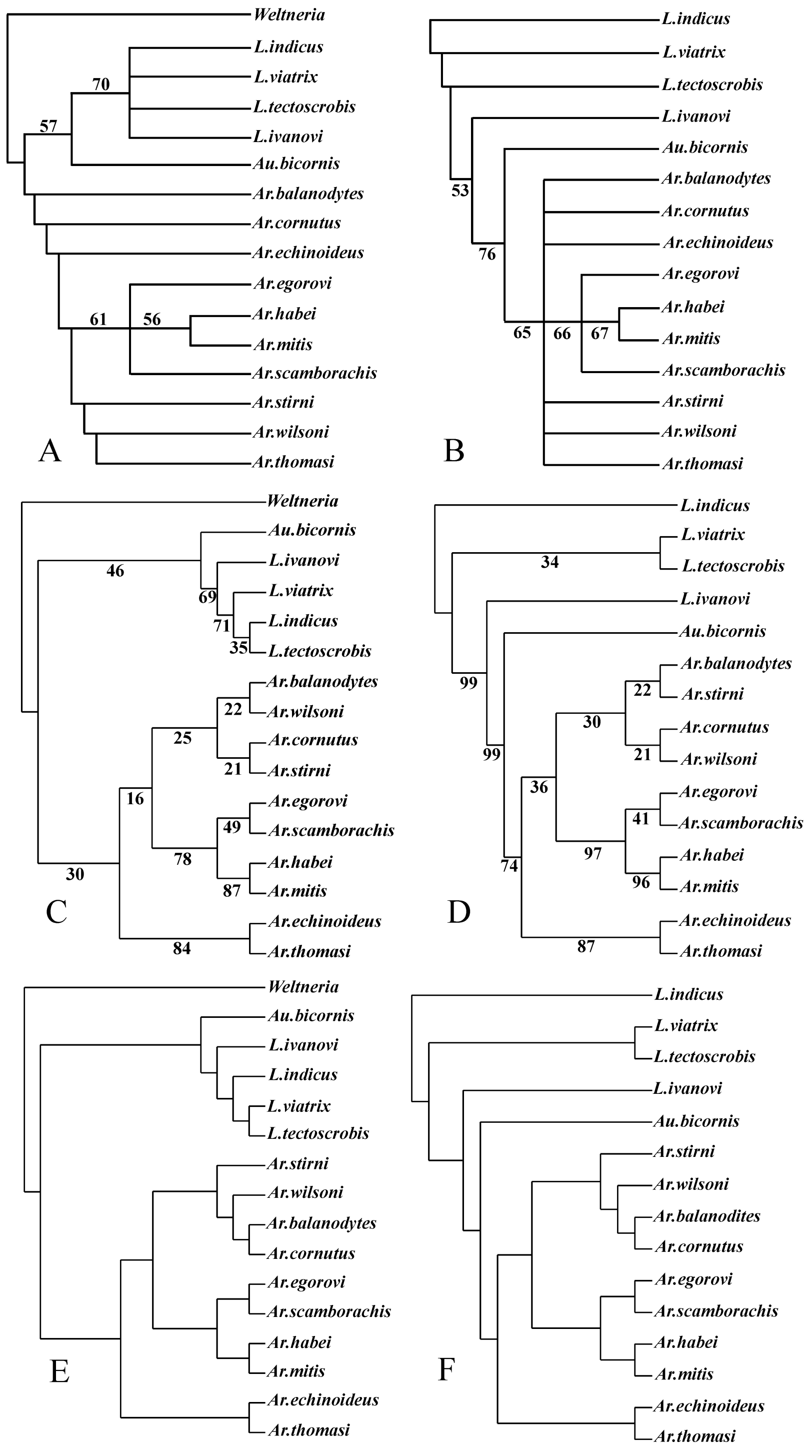

FIGURE 9. Phylogenetic reconstruction cladograms of *Lithoglyptes* s.l. and the species of the resulting genera, *Lithoglyptes* s.s., *Auritoglyptes* and *Armatoglyptes* (all characters unordered and of equal weight; PAUP, Swofford 1998): A, C, E - with *Weltneria* as out-group; B, D, F – without out-group). A & B – Bootstrap 50% majority-rule consensus trees. Percentages at nodes denote frequency of occurrence among 251 trees; C & D – Quartet puzzling trees, number of puzzling steps = 1000. Percentages at nodes denote frequency of occurrence of bipartitions found in one or more trees; E & F – Neighbor-joining trees.

From the foregoing, *Lithoglyptes* and *Auritoglyptes* can be interpreted as monophyletic taxa on the base of autapomorphies. On the other hand, while *Armatoglyptes* can be distinguished from other lithoglyptines on the basis of symplesiomorphies such as the two-segmented caudal appendages and the pear-shaped dwarf males without antennular stalks, its monophyly can be questioned. The genus could evolve directly from a *Weltneria*-like ancestor, by the reduction and loss of a pair of terminal cirri and the development of an armed orificial knob, lateral bars and posterior projections of the opercular bars, but not all of its species necessarily share a common ancestor.

The origin of *Lithoglyptes* and *Auritoglyptes* is also obscure. *Auritoglyptes* could have evolved from a *Lithoglyptes*-like ancestor by elongation of the small posterior lobes into long posterior processes ("auricles") and the development of opercular bar armament, or these genera could originate independently. *Armatoglyptes*, on the one hand, and *Lithoglyptes* and *Auritoglyptes*, on the other, could have evolved from different ancestors. While we do not exclude the possibility that *Lithoglyptes* and *Armatoglyptes* evolved from a common ancestor having unarmed opercular bars and dwarf males without a stalk between the antennules and the body, this route seems dubious. It is highly unlikely that *Armatoglyptes* evolved from *Auritoglyptes* since the latter has the apomorphic "auricles" and the long stalk between the antennules and the body of its male.

All known species of the *Weltneria* lack posterior opercular processes and lobes, have two-segmented caudal rami without pedestals, and all except one have dwarf males with simple attachment antennules. On the other hand, species of *Berndtia*, like *Lithoglyptes*, have feebly armed opercular bars without posterior projections, and they too lack lateral bars and an orificial knob. Furthermore, two species of *Berndtia* have conspicuous posterior opercular lobes perhaps reminiscent of those in *Lithoglyptes*. *Berndtia* has a suite of characters suggestive of *Lithoglyptes* and, therefore, these two genera likely share a common ancestor having caudal appendages.

Key to the genera and species of Lithoglyptinae

(four pairs of terminal cirri plus caudal appendages).

1 Caudal appendages each of two segments plus a pedestal.. 2
- Caudal appendages each of two segments but without a pedestal ..... 6 (*Armatoglyptes*)
2 Opercular bars without well-developed posterior projections, operculum with short posterior lobes or rudiments thereof..3 (*Lithoglyptes*)
- Opercular bars with hooked posterior projections, operculum with long, articulated posterior setose lobes (auricles) .... *Auritoglyptes bicornis*
3 Opercular bars armed with bifid teeth.. *L. ivanovi*
- Opercular bars lacking bifid teeth, with simple teeth and/or small denticles 4
4 Posterior lobes of operculum well developed 5
- Posterior lobes of operculum rudimentary... *L. indicus*

5 Proximal end of mantle attenuated, extending to point of initial attachment .... *L. tectoscrobis*
- Proximal end of mantle not extending to initial point of attachment............... *L. viatrix*
6 Opercular bars asymmetrical, one with a medial projection................ *A. scamborachis*
- Opercular bars symmetrical 7
7 Orificial knob with conspicuous teeth... 8
- Orificial knob without teeth, or absent.. 9
8 Posterior projections of opercular bars straight, without long recurved hooks or spines .... *A. mitis*
- Posterior projections recurved or straight, but when straight with long anterior, recurved spines .... *A. habei*
9 Posterior projections of opercular bars decurved in adults 10
- Posterior projections of opercular bars recurved anteriorly or straight in adults 11
10 Posterior projections equal to or greater than the length of opercular bars .... *A. balanodytes*
- Posterior projections less than the length of opercular bars ....*A. cornutus*
11 Opercular bars with upturned anterior ends............................. *A. wilsoni* (Koror form)
- Opercular bars without upturned anterior ends 12
12 Opercular bars each with a small elevation at 1/3 of length from anterior end .... *A. thomasi*
- Opercular bars straight, without such an elevation 13
13 Posterior projections of opercular bars straight, without curved spines near tip 14
- Posterior projections of opercular bars decurved, usually with 1–2 curved spines near tip (often broken off in adults) .... *A. stirni*
14 Posterior projections of opercular bars with several longitudinal rows of curved teeth. .... *A. echinoideus*
- Posterior projections of opercular bars without longitudinal rows of curved teeth .... *A. egorovi*

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Literature cited

Aurivillius, C.W.S. (1892) Neue Cirripeden aus dem Atlantishchen, Indischen und Stillen Ocean. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm*, 3, 123–134.

Aurivillius, C.W.S. (1894) Studien über Cirripeden. *Kongliga Svenska Vetenskaps- Akademiens Handlingar, Uppsaala,* 26, 7, 5–107 + 9 pls. 1–9.

Baird, G.C., Brett, C.E. & Tomlinson, J.T. (1990) Host specific acrothoracid barnacles on Middle Devonian platyceratid gastropods. *Historical Biology,* 4, 221–244.

Berndt, W. (1907) Über das System der Acrothoracica. *Archiv für Naturgeschichte, Berlin*, 73, 1, 287–289.

Burmeister, H. (1834) *Beiträge zur Naturgeschichte der Rankenfüsser (Cirripedia)*. G. Reimer, Berlin, pp. i–viii, 1–60 + pls. 1–2.

Darwin, C.R. (1852) *A monograph on the sub-class Cirripedia, with figures of all the species. The Lepadidae; or, pedunculated cirripedes*, Ray Society, London (1851), 400 pp + pls. 1–10.

Darwin, C.R. (1854) *A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile cirripedes); the Verrucidae, etc., etc., etc.*, Ray Society, London, 684 pp + pls. 1–30.

Gerstaecker, A. (1866–1879) Arthropoda. *H.G. Bronn. Die Klassen und Ordungen*. C.F. Winter , Leipzig und Heidelberg, 5, 1, 406–589.

Gruvel, A. (1905) *Monographie des Cirrhipèdes ou Thécostracés*. Masson et C^{ie}, éditeurs, Paris (reprinted 1965, A. Asher & Co., Amsterdam), 472 pp.

Grygier, M.J. & Newman, W.A. (1985) Motility and calcareous parts in extant and fossil Acrothoracica (Crustacea: Cirripedia), based primarily upon new species burrowing in the deep-sea coral *Enallopsammia. Transactions of the San Diego Society of Natural History,* 21, 1, 1–22.

Hancock, A. (1849) Notice of the occurrence on the British coast of a burrowing barnacle belonging to a new order of the class Cirripedia. *Annals and Magazine of Natural History,* 4, 2, 305–314 + pls. 8–9.

Klepal, W. (1987) A review of the comparative anatomy of the males in cirripedes. *Oceanography and Marine Biology Annual Reviews*, 25, 285–351.

Kolbasov, G.A. (1998) A new species of the genus *Lithoglyptes* (Cirripedia: Acrothoracica) from the Indian Ocean (Isl. Java). *Arthropoda Selecta*, 7, 3, 175–178.

Kolbasov, G.A. (1999a) The external mantle morphology of burrowing barnacles of the families Lithoglyptidae and Cryptophialidae (Cirripedia, Acrothoracica). *Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, 1998*, 1, 139–149.

Kolbasov, G.A. (1999b) A new species of the burrowing barnacles of the genus *Lithoglyptes* (Cirripedia: Acrothoracica: Lithoglyptidae) from the Maldives. *Zoologicheskiy Zhurnal,* 78, 9, 1125–1128 (in Russian).

Kolbasov, G.A. (2000a) Calcareous plates of the barnacles of the superorder Acrothoracica, morphology and functions, homology with calcareous plates of the barnacles of the superorder Thoracica (Thecostraca, Cirripedia). *Zoologicheskiy Zhurnal*, 79, 11, 1284–1289 (in Russian).

Kolbasov, G.A. (2000b) New species of a boring barnacle *Cryptophialus hoegi* (Cirripedia: Acrothoracica: Cryptophialidae) from the Aden Gulf. Description of the female and dwarf male ultrastructure. *Zoologicheskiy Zhurnal*, 79, 9, 1027–1035 (in Russian).

Kolbasov, G.A. (2000c) A new species of the genus *Lithoglyptes* (Crustacea: Cirripedia: Acrothoracica) from the Fiji Sea, with some data on its ultrastructure. *Arthropoda Selecta,* 9, 2, 85–89.

Kolbasov, G.A. (2000d) *Lithoglyptes cornutus,* new species (Cirripedia: Acrothoracica), a boring barnacle from the Seychelles, with some data on the ultrastructure. *Hydrobiologia*, 438, 1–3, 185–191.

Kolbasov, G.A. (2000e) External morphology of the burrowing barnacle *Lithoglyptes bicornis* (Crustacea: Cirripedia: Acrothoracica: Lithoglyptidae). *Hydrobiologia*, 438, 1–3, 193–204.

Kolbasov, G.A. (2000f) A new species of the burrowing barnacles of the genus *Lithoglyptes* (Cirripedia: Acrothoracica: Lithoglyptidae) off Island Nauru (Micronesia). *Zoologicheskiy Zhurnal*, 79, 3, 372–376 (in Russian).

Kolbasov, G.A. (2001) A new species of burrowing barnacle, *Weltneria bekae* (Cirripedia, Acrothoracica) from Papua (New Guinea): Description of external morphology. *Zoologicheskiy Zhurnal,* 80, 10, 1–10 (in Russian).

Kolbasov, G.A. (2002) Cuticular structures of some acrothoracican dwarf males (Crustacea: Thecostraca: Cirripedia: Acrothoracica). *Zoologischer Anzeiger,* 241, 85–94.

Kolbasov, G.A. & Høeg, J.T. (2000) External morphology of females in the burrowing barnacles *Lithoglyptes mitis* and *L. habei* (Lithoglyptidae) and the phylogenetic position of the Cirripedia Acrothoracica (Crustacea: Thecostraca). *Arthropoda Selecta,* 9, 1, 13–27.

Kolbasov, G.A. & Høeg, J.T. (2001) External morphology of cypris larvae of two species of *Trypetesa* Norman, 1903 (Crustacea, Thecostraca, Cirripedia, Acrothoracica, Trypetesidae). *Arthropoda Selecta*, 10, 2, 87–92.

Kolbasov, G.A., Høeg J.T. & Elfimov, A.S. (1999) Cypris morphology in two species of *Lithoglyptes* using scanning electron microscopy (Crustacea, Thecostraca, Cirripedia, Acrothoracica, Lithoglyptidae). *Contribution to Zoology,* 63, 3, 143–160.

Martin, J.W. & Davis, G.E. (2001) *An updated classification of the Recent Crustacea*. Natural History Museum of Los Angeles County, Science Series 39, 123 pp.

Newman, W.A. (1971) A deep-sea burrowing barnacle (Cirripedia: Acrothoracica) from Bermuda. *Journal of Zoology, London*, 165, 423–429.

Newman, W.A. (1974) Two new deep-sea Cirripedia (Ascothoracica and Acrothoracica) from the Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 54, 2, 437-456.

Newman, W.A. & Tomlinson, J.T. (1974) Ontogenetic dimorphism in *Lithoglyptes* (Cirripedia, Acrothoracica). *Crustaceana*, 27, 2, 204–208.

Noll, F.C. (1872) *Kochlorine hamata* N., ein bohrender Cirripede. *Bericht über die Senckenbergische naturforschende Gesellschaft,* 4, 50–58.

Perez-Losada, M.J., Høeg, J.T. & Crandall, K.A. (2004) Unraveling the evolutionary radiation of the thoracican barnacles using molecular and morphological evidence: A comparison of several divergence time estimation approaches. *Systematic Biology,* 53, 2, 244–264.

Smyth, M. (1986) *Cryptophialus coronophorus*, new species (Cirripedia, Acrothoracica), a boring barnacle from Guam, Mariana Islands, with new insights into cryptophialid ultrastructure. *Journal of Crustacean Biology,* 6, 1, 143–157.

Stubbings, H.G. (1967) The cirriped fauna of tropical West Africa. *Bulletin of the British Museum (Natural History), Zoology,* 15, 6, 229–319 + pl. 1.

Swofford, D.L. (1998) PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. *Sinauer Associates, Sunderland, Massachusetts*.

Thomas, M.L.H. & Stevens, J.A. (1991) Communities of constructional lips and cup reef rims in Bermuda. *Coral Reefs,* 9, 225–230.

Tomlinson, J.T. (1963) Two new acrothoracican cirripeds from Japan. *Publications of the Seto Marine Biological Laboratory,* 11, 2, 263–280.

Tomlinson, J.T. (1969) *The burrowing barnacles (Cirripedia: order Acrothoracica)*. Bulletin of the United States National Museum, 296, 1–162.

Tomlinson, J.T. & Newman, W.A. (1960) *Lithoglyptes spinatus*, a new burrowing barnacle from Jamaica. *Proceedings of the Unites States National Museum,* 113, 3445, 517–526.

Turquier, Y. (1978) Le tégument des cirripèdes acrothoraciques. *Archives de Zoologie Experimentale et Générale,* 119, 107–125.

Turquier, Y. (1987) Cirripèdes acrothoraciques des côtes occidentales de la Mediterranée et de l'Afrique du Nord III. Lithoglyptidae et Trypetesidae. *Bulletin du Museum national d'Histoire naturelle,* Paris, 4, 9 A, 2, 391–408.

Utinomi, H. (1950a) A new remarkable coral-boring acrothoracican cirriped. *Memoirs of the College of Science, University of Koyoto,* Series B, 19, 3, 87–94, including Pl. 1.

Utinomi, H. (1950b) On another form of Acrothoracica, newly found from Formosa. *Memoirs of the College of Science, University of Koyoto,* Series B, 19, 3, 95–100.

Utinomi, H. (1950c) General account of Acrothoracica. *In*: Nakamura, K. (Ed.), *Some Problems in Modern Biology,* Osaka, Japan, pp. 428–461 (in Japanense).