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# Revision of the coral-inhabiting genus *Conopea* (Cirripedia: Archaeobalanidae) with description of two new species of the genera *Conopea* and *Acasta*

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## Abstract

The morphology of archaeobalanid barnacles of the genera *Conopea* and *Acasta* inhabiting cnidarians of the orders Alcyonacea and Antipatharia was surveyed. Based on morphological characteristics, it became evident that the species of the nominal genus *Conopea* fell into three natural groups affiliated to three archaeobalanid genera, *Conopea* s.s., *Acasta* and *Solidobalanus*. The relationships between the species of *Conopea* s.l. and those of *Acasta* inhabiting alcyanaceans are analyzed using a cladistic approach. The barnacles of the genus *Conopea* s.s. are characterized by a strong, firm shell; the orifice is not dentate; rostral and sometimes carinal plates are often elongated in their basal parts; the rostro-carinal axis of the basis is often elongated and clasps the axis of the host coral; the radii have summits parallel to the basal margin of the parietes, and denticulated sutural margins; the scutum has simple growth ridges without longitudinal striation or ribs; the basitergal angle is truncated (sinusoid); and the basidorsal point of the penis is developed. The genus *Conopea* s.s. encompasses 20 epizoic species from tropical and temperate seas, inhabiting alcyonaceans (sea fans or gorgonians) and antipatharians. A new species of *Conopea* and a new species of *Acasta* are described, and a key to the species of *Conopea* s.s. is provided.

**Key words:** morphology, systematics, phylogeny, *Conopea*, *Acasta*, new species

## Introduction

The archaeobalanid genus *Conopea* Say, 1822, and some species of the mostly sponge-inhabiting genus *Acasta* Leach, 1817, are symbiotic barnacles associated with cnidarians of the orders Alcyonacea and Antipatharia (Hiro 1937). *Conopea* s.l. encompasses 28 described species and all, except *C. merrilli* Zullo, 1966, live in 'galls' and are almost completely covered by host tissue, with only the opercular opening exposed. Often the basis of the shell clasps the axis of the host coral. *Conopea* species are found in tropical and temperate seas around the world from shallow subtidal to deep water.

Although the genus *Conopea* was erected by Say in 1822 to accommodate the species *C. elongata*, which is currently known as *C. galeata* (Say 1822), the barnacles of this group as well as species of the genus *Acasta* were affiliated for more than 150 years as subgenera of the genus *Balanus* Da Costa, 1778. Say (1822) defined *Conopea* as "Shell sessile, fixed, composed of two cones joined by their bases, the lines of junction carinate each side: inferior cone entire, attached by its anterior side and tip to marine bodies; with an aperture at the summit, closed by a quadrivalved operculum." Darwin (1854, p. 216) characterized these barnacles by "Parietes and basis sometimes permeated by pores, sometimes not; radii not permeated by pores, shell elongated in its rostrocarinal axis, basis boat-shaped, attached to Gorgoniae and Milleporae." He considered *Conopea* as closely related to the genera *Megabalanus* Hoek, 1913 and *Acasta,* whereas Hoek, (1913) thought *Conopea* to be closely related to *Balanus*. Pilsbry (1916, p. 235) discussed the possible diphyletic nature of *Conopea*: "I have been unable to decide whether

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the species of *Conopea* with poreless compartments are secondarily so by reason of the filling up of pores solidly or whether, like *Acasta*, parietal pores have never been evolved. It is possible, though it does not appear probable, that the group is diphyletic, composed of one series of species related to the poreless Balani and *Acasta*, and another related to the porous Balani." Recently Van Syoc *et al.* (2014) described several species of *Conopea* with secondarily filled longitudinal tubes of the parietes and the basis. Broch (1922, 1931) and Hiro (1937) indicated the close relationship between some *Conopea* and *Acasta* species inhabiting octocorals and antipatharians. This taxonomic uncertainty is the reason why certain octocoral-inhabiting barnacles were described as *Conopea*, whereas others were described as *Acasta*.

In a recent paper on the genus *Conopea* Carrison-Stone *et al.* (2013) noted that "*Conopea* is not a well documented group. There is very little data on host associations, species ranges are not well defined, published descriptions are often incomplete and occasionally contain questionable information." Van Syoc *et al.* (2014) indicated that "The acastine species living in gorgonians differ from *Conopea* species in several ways, the most obvious is the form of their attachment to the host. *Conopea* species are cemented directly, and firmly, to the surface of the gorgonian axis. The coenenchyme of the gorgonian overgrows the shell of *Conopea* species, but the proteinaceous axis generally does not. On the other hand, individuals of Acastinae become completely embedded in the proteinaceous axis rather than living attached to the surface of the gorgonian axis. The wall plates of most *Conopea* are heavily cemented to each other at the contact sutures, whereas those of acastines are loosely attached to each other and disarticulate very easily with handling or treatment in dilute sodium hypochlorite."

In the course of the present survey different barnacle species were detached from octocorals and antipatharians hosts in museum collections (National Museum of Natural History, Leiden The Netherlands, Muséum national d'histoire naturelle, Paris, and Western Australian Museum, Western Australia). Based on examination of the original material and of literature data, we have concluded that barnacles of the genus *Conopea* form two distinct morphological clades. The first is characterized by a strong, firm shell with thick compartments, an elongated basis that clasps the axis of the host coral, an orifice that is not dentate but smooth or even, radii with summits parallel to the basal margin of the parietes and denticulated sutural margins, a scutum with simple growth ridges and a truncated (sinusoid) basitergal angle, and a penis with a developed basidorsal point. The second clade possesses morphological characters of acastine barnacles, such as a shell with thin, feebly connected compartments with spines or bumps externally, a basis that does not firmly clasp the axis of the host coral, a dentate orifice, radii with oblique summits, a scutum with a rounded basitergal angle and often with longitudinal ribs or striations, and a penis without a basidorsal point. In our material these barnacles were covered by coral coenenchyme only and were not overgrown by the proteinaceous material of the axis as occurs in *Acasta vipensis* (Van Syoc *et al.* 2014).

In the present study we split the genus *Conopea* s.l. and propose that the first clade represents the genus *Conopea* s.s., while the second belongs to the genus *Acasta*. We also describe two new species of the genera *Conopea* and *Acasta*.

## Material and methods

Barnacles belonging to the genera *Acasta* and *Conopea* from alcyonacean and antipatharian hosts fixed in 70% or absolute alcohol were selected from various natural history museum collections. For the phylogenetic analysis, a specimen of the acorn barnacle *Pachylasma* sp., found on an alcyonacean, was used as an out-group. The phylogenetic analysis of the Balanomorpha (Pérez-Losada *et al.*, 2014) indicates that the Pachylasmatidae are a basal clade. The species examined in this study were:

1) *Acasta alcyonica* Rosell, 1991: National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Indonesia, Sulawesi, Spermonde Archipelago, 4º40'S, 118º57'E, 1 specimen covered by a white-rose alcyonacean *Astrogorgia* sp. (Plexauridae).

2) *Acasta antipathidis* Broch, 1916: Swedish Museum of Natural History, syntypes SMNH-Type-4249. Locality: Indian Ocean, Western Australia, 72 km WSW Sta Cape Jaubert, 01.07.1911, photographs only, on denuded dead axis of alcyonacean coral.

3) *Acasta echinata* Hiro, 1937: National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Seychelles, 5º23'S, 53º19'E, 2 specimens (Fig. 13H–K) covered by a red alcyonacean of family Plexauridae.

4) *Acasta* (*Conopea*) *navicula* (Darwin, 1854) = *Archiacasta spinitergum* (Broch, 1931): National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Indonesia, Sulawesi, 5º05'S, 119º19'E, 3 specimens (Fig. 13A–G) covered by a brownish alcyonacean *Trimuricea* sp. (Plexauridae).

5) *Acasta* (*Conopea*) *pygmaea* (Broch, 1931): Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4628. Locality: 23°22'S, 168°05'E, 260 m, 2 dead specimens covered by a white alcyonacean *Parisis* sp. (Parisididae).

6) *Acasta vivicava* **sp. nov.**: National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Seychelles, 6º12'S, 53º02'E, one specimen (Figs 6–8) covered by a white alcyonacean *Briareum* sp. (Briareidae).

7) *Conopea calceola* (Ellis, 1758): Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4706. Locality: MUSORSTOM 3, stn. CP134, Philippines, 12°01.1'N;121°57.3'E, 92–95 m, 2 specimens (Figs 9A, E–G, 10A, B, 11A, B, 12A, D, G) covered by a white alcyonacean *Eunicella* sp. (Gorgoniidae).

8) *Conopea cymbiformis* (Darwin, 1854): Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4672. Locality: NORFOLK 1, stn. DW1724, 23°17'S, 168°14'E, 291 m, 27.06.2001, Lozouet P., Boisselier & Richer de Forges coll., 2 specimens (Fig. 12H) covered by a white alcyonacean of family Isididae. Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4704. Locality: TERRASSES, stn. DW3090, 22°16'S, 167°08'E, 260 m, 25.10.2008, Samadi S, Lozouet P. & Castelin M. coll., 2 specimens (Fig. 12B, E). Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4780. Locality: TERRASSES, stn. DW3072, 23°19'S, 168°16'E, 220m, 23.10.2008, Samadi S, Lozouet P. & Castelin M. coll., 2 specimens (Figs 9C, I, 10C, D, 11C, D) on an antipatharian *Myriopathes* sp. (Myriopathidae). Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4753. Locality: SALOMONS 1, stn. DW1756, 8°52'S, 159°50'E, 511 m, 10.03.2001, Bouchet, Dayart, Warén & Richer de Forges coll., 1 specimen (Fig. 9 H) covered by a reddish alcyonacean of family Ellisellidae. National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Indonesia, Sulawesi, 5º06'S, 119º17'E, 1 specimen covered by a white yellowish alcyonacean *Menella* sp. (Plexauridae).

9) *Conopea scandens* (Pilsbry, 1916): Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4632. Locality: TERRASSES, 23°42'S, 168°01'E, 260 m, 20.10.2008, Samadi S., Lozouet P. & Castelin M. coll., 1 dried specimen. National Museum of Natural History (Naturalis), Leiden, The Netherlands. Locality: Indonesia, Sulawesi, Spermonde Archipelago, 4º40'S, 118º57'E, 2 live (Figs 9D; 10E, F; 11E, F; 12C, F, I) and 2 dead specimens covered by a brownish alcyonacean of family Plexauridae.

10) *Conopea titani* sp. nov.: Holotype: Western Australian Museum (WAM), Western Australia, Ningaloo Marine Park, 24°00.8'S, 113°24.5'E, st. RVS 4545/2008/D104, epibenthic sledge, coll. Drs. Salotti M.P., Slack-Smith S.M., 06.02.2008, 57 m, one specimen (Figs 1-5) covered by a reddish alcyonacean of family Ellisellidae. Two paratypes: Western Australian Museum (WAM), Western Australia, Rowley Shoals, Imperieuse REEF , L23, 18 27'37"-18 27'43"S, 120°08'41"-120°08'41"E, st. SS0507/082, coll. Drs. Gomez O.A., Whisson C.S., 19.06.2007, 80-81 m. Nine paratypes: Western Australian Museum (WAM), Western Australia, Adele Island Kimberley, 15 30'00"S, 123°05'00"E, st. 09/K09-T72, coll. Drs. Gomez O.A., Hossie A., 16.10.2009, 14 m.

11) *Pachylasma* sp.: Muséum national d'histoire naturelle (MNHN), Paris, IU-2011-4705. Locality: 22°16'S, 167°08'E, 260m, 1 specimen (Fig. 14) on alcyonacean of family Plexauridae

Following soft parts dissection, host coral tissues from the surface of the barnacle shells, scutum, and tergum were removed by forceps and immersed in bleach (2% sodium hypochlorite) for ~two hours, to completely digest the organic tissue, and rinsed five times with distilled water, then adhering chitin and organic debris were removed using entomological pins and ultrasonic cleaner (1–3 seconds). The six pairs of cirri, the penis and the oral cone were dissected from the somatic bodies, and the trophi, cirri and penis mounted in glycerol on glass slides. Photographs of the morphological characteristics of the shell parts (basis, plates, scutum and tergum) and somatic bodies (six pairs of cirri, the penis and the oral cone) were made using a stereomicroscope Leica MZ 6 and an Olympus BX 51 microscope with Nomarski differential interference contrast microscopy. The resulting photographs were touched up using a CorelDRAW X3 Graphics Suite.

## Taxonomy

**Subclass Cirripedia Burmeister, 1834**

**Superorder Thoracica Darwin, 1854**

**Order Sessilia Lamarck, 1818**

**Suborder Balanomorpha Pilsbry, 1916**

**Superfamily Balanoidea Leach, 1817**

**Family Archaeobalanidae Newman & Ross, 1976**

**Genus *Conopea* Say, 1822**

**Diagnosis** (modified, see section 'Phylogeny'): Archaeobalanids with strong, firm shells that cannot be easily disarticulated into separate compartments after separation from host; shell orifice with even summits; rostral plate often elongated in basal part along host axis; basis firmly clasping axis of host coral; outer surface of parietes smooth, lacking spines; inner surface with longitudinal ribs prominent along basal margin; radii solid, with summits parallel to basal margin of parietes and denticulated sutural margins; margin of basis with deep, rounded pits to interlock with corresponding inner ribs of parietes; scutum with simple growth ridges and truncated (sinusoid) basitergal angle; penis with developed basidorsal point. The genus *Conopea* includes of 20 epizoic species from tropical and temperate seas, inhabiting alcyonacean and antipatharian corals. Type species *Conopea calceola* (Ellis, 1758).

***Conopea titani*** **sp. nov.**
Figures 1–5.

**Type material.** Western Australia, Ningaloo Marine Park, 24°00.8'S, 113°24.5'E, st. RVS 4545/2008/D104, epibenthic sledge, coll. Drs. Salotti M.P., Slack-Smith S.M., 06.02.2008, 57 m, one specimen covered by a reddish calcaxonian alcyonacean of family Ellisellidae in pure ethanol. Holotype WAM C50309 (shell compartments in ethanol, mouth parts and cirri mounted in glycerol on microscope slides) is deposited in Western Australian Museum, Perth. Two paratypes WAM C49287 are deposited in Western Australian Museum, Perth: Western Australia, Rowley Shoals, Imperieuse REEF , L23, 18 27'37"-18 27'43"S, 120°08'41"-120°08'41"E, st. SS0507/082, coll. Drs. Gomez O.A., Whisson C.S., 19.06.2007, 80-81 m. Nine paratypes WAM C43609 are deposited in Western Australian Museum, Perth: Western Australia, Adele Island Kimberley, 15 30'00"S, 123°05'00"E, st. 09/K09-T72, coll. Dr. Gomez O.A., Mr. Hossie A., 16.10.2009, 14 m.

**Diagnosis**. Shell very large, strong, elongated in both basal areas of carina and rostrum, parietes and basis solid, parietes with prominent basal ribs, margin of basis with rows of deep pits. Opercular plates thick, scutum with simple growth ridges, tergum with blunt apex and short, broad spur. Crests of labrum without teeth. Anterior rami of cirri III and IV with sharp denticles. Penis with large basidorsal point.

**Description**. Shell very large, strong, cannot be disarticulated into separate compartments. External surface of shell smooth, covered by firmly attached, horny, brownish coenosarc of gorgonian (Fig. 1A). Color ivory, carina and carinolaterals 2 slightly tinted with rose, radii white, paler than parietes (Fig. 1B). Maximum axis length 62.7 mm, height 13.6 mm, width 16.4 mm, orifice maximal diameter 6.8 mm. Basal parts (basis, carina and rostrum) elongated in both carinal and rostral portions. Parietes with radii and alae solid (Figs 1C, D; 2B). Radii with rectangular summits parallel to basal margin of parietes and extending from apex to apex of adjoining plates, orifice of shell not dentate (Fig. 1A–C). Sutural margins of radii denticulated, striated with transverse ridges (septa) (Fig. 1D). Alae narrow, summits oblique. Parietes with basal ribs forming several rows of prominent outgrowths at basal margin; sheath with transverse ridges, slightly less than half total length of parietes (Figs 1C; 2B).

Carinolatus 2 narrow, basal width 1/9 to 1/10 basal width of carinolatus 1. Basis elongated in rostro-carinal axis, boat-shaped, completely clasping thick, horny axis of gorgonian (Fig. 1B), solid, with numerous deep and rounded pits organized in irregular rows along margin, pits articulated with basal ribs of parietes (Fig. 2A, B).

Scutum (Fig. 2C–F) triangular, width less than height, thick, color ivory, distinct growth ridges, without longitudinal striation, apex acute, occludent margin dentate, tergal margin straight, basal margin curved, basitergal corner slightly truncated. Articular ridge distinct, not prominent, ~2/3 length of tergal margin, truncated, oblique ridges in upper part, articular furrow present. Adductor ridge absent, pit of adductor muscle indistinct and shallow, pit of lateral depressor muscle shallow but distinct.

Tergum (Fig. 3) broad, thick, color ivory, scutal margin straight, longer than convex carinal margin, apex blunt, almost rounded, exterior with conspicuous growth ridges, spur furrow absent. Spur broad, short, corners rounded, not separated from basiscutal corner, ~2/3 width of tergum. Articular ridge low, removed from scutal margin, ~1/3 length of scutal margin, 5 faint depressor muscle crests.

Labrum (Fig. 4A) with deep medial notch, teeth absent on crests. Mandibular palps (Fig. 4A) club like, long, dense setae distally, short setae along outer edge. Mandibles (Fig. 4B–D) with 4 teeth on cutting edge, decreasing in size from upper to lower, first, second and third teeth well separated from each other, third and fourth teeth close, tooth 3 bifid, tooth 4 with 3–4 small denticles on tip, inferior angle with 1–3 denticles, inferior margin setose. Maxillules (Fig. 4E, F) with 12–15 cuspidate setae of different lengths and widths along straight cutting edge, notch absent, fine setae along outer and inner edges and lateral surfaces of blade. Maxillae (Fig. 4G), small, bilobed, long setae on distal ovate lobes.

Cirri I with unequal rami, anterior rami (10, 11 segments) considerably longer than posterior rami (9 segments), both rami covered with moderately dense setae. Cirri II with unequal rami, posterior rami (8 segments) shorter than anterior (10, 11 segments), with dense setae. Cirri III (Fig. 5A) with thick, unequal rami, anterior rami (11, 12 segments) longer than posterior (10 segments), several pairs of setae of different sizes along anterior edges of segments, tuft of stout setae at posterio-distal angle, segments of anterior ramus with 5–8 sharp denticles on anterior edges. Cirri IV (Fig. 5B) with long, subequal rami, anterior rami (18 segments), posterior (17, 21) segments, anterior edges of segments with several pairs of setae of different sizes, few setae at posterio-distal angle, several sharp denticles along anterior edges of basis and basal (1–7) segments of anterior ramus. Cirri V and VI with long, subequal rami, anterior rami (20–21 segments) and posterior (20 segments) bearing several pairs of short, long setae on anterior edges, and tuft of posterio-distal setae.

Penis (Fig. 5C, D) long, annulated, without conspicuous setae, basidorsal point prominent.

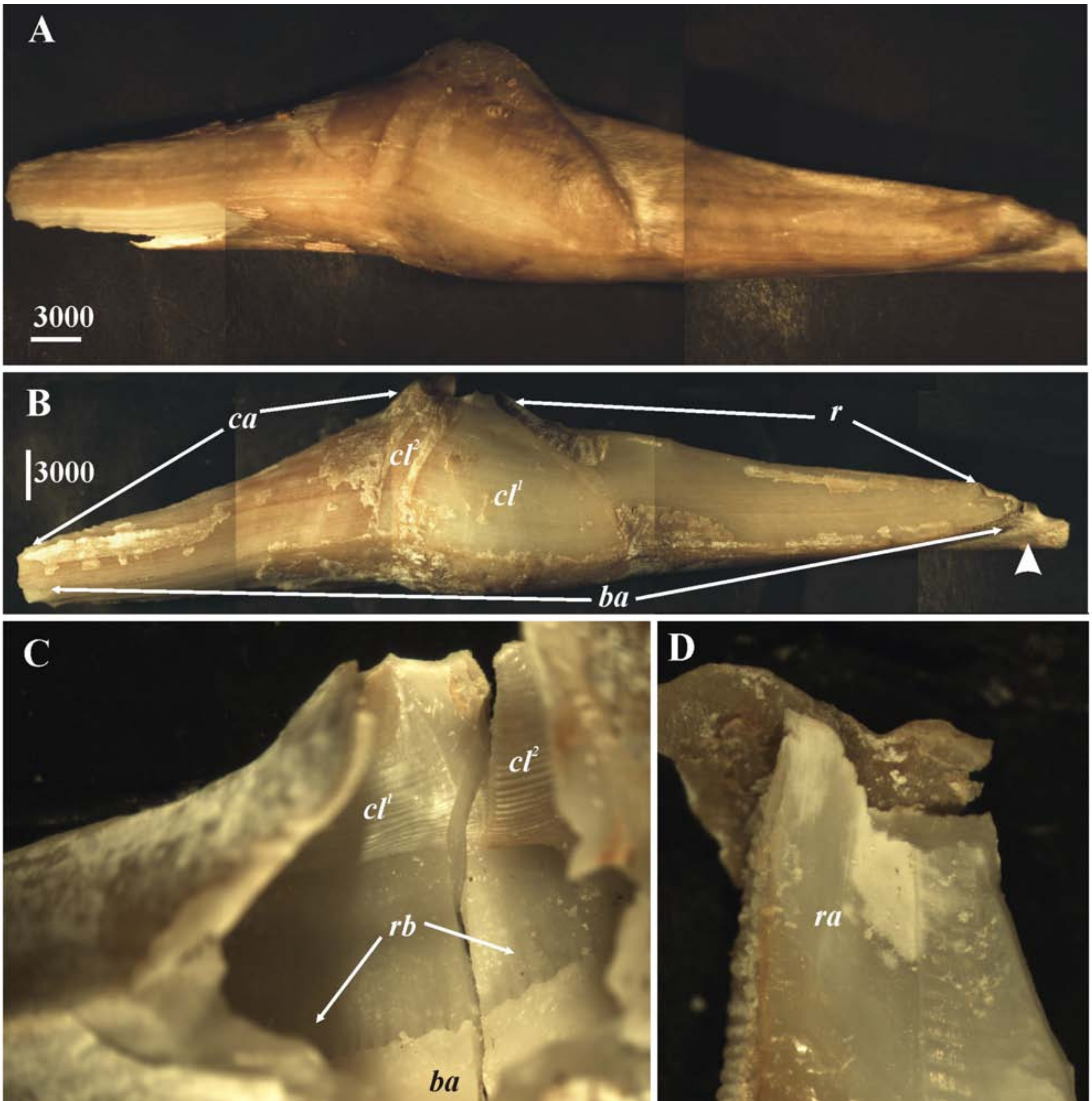


**FIGURE 1.** *Conopea titani* **sp. nov.**, general appearance of shell. (A) Shell covered by underlaying chitinous membrane of gorgonian coenosarc, lateral view. (B) Shell with removed underlaying chitinous membrane of gorgonian coenosarc, lateral view, axis of gorgonian indicated by arrowhead. (C) Inner surface of carinolaterals 1 and 2 showing inner basal ribs of parietes and strong articulation with basis. (D) Part of carinolatus 1 showing deticulated sutural margin of radius. Abbreviations: *ba*—basis, *ca*—carina, $cl^1$—carinolatus 1, $cl^2$—carinolatus 2, *r*—rostrum, *ra*—radius, *rb*—inner ribs of parietes. Scale bars in µm.

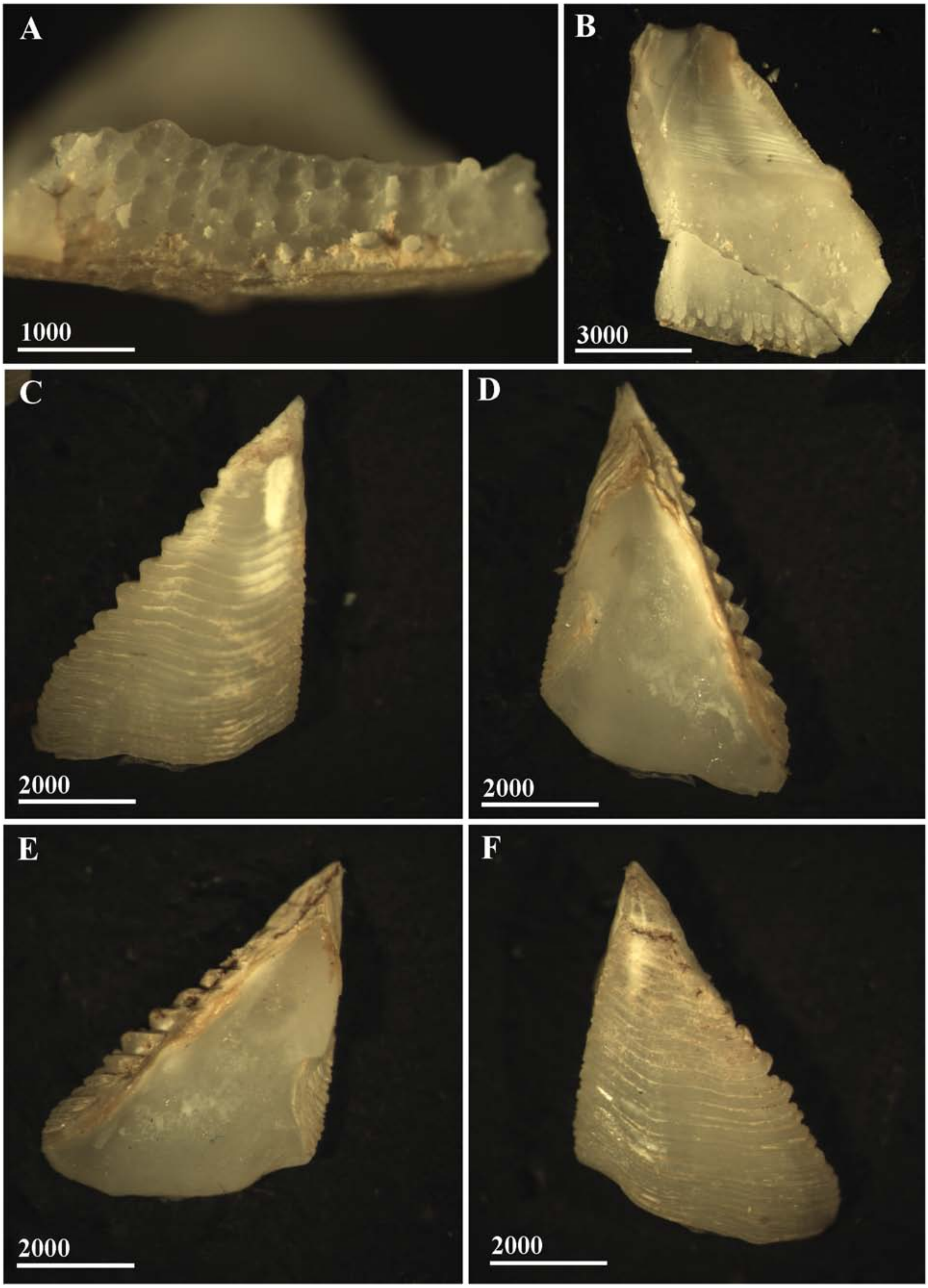


**FIGURE 2.** *Conopea titani* **sp. nov.**, shell compartments and scuta. (A) Margin of basis showing irregular rows of deep pits for articulation with basal ribs of parietes. (B) Inner surface of carinolatus 2 showing sheath and prominent basal ribs. (C), (D) Right scutum, outer and inner view. (E), (F) Left scutum, inner and outer view. Scale bars in µm.

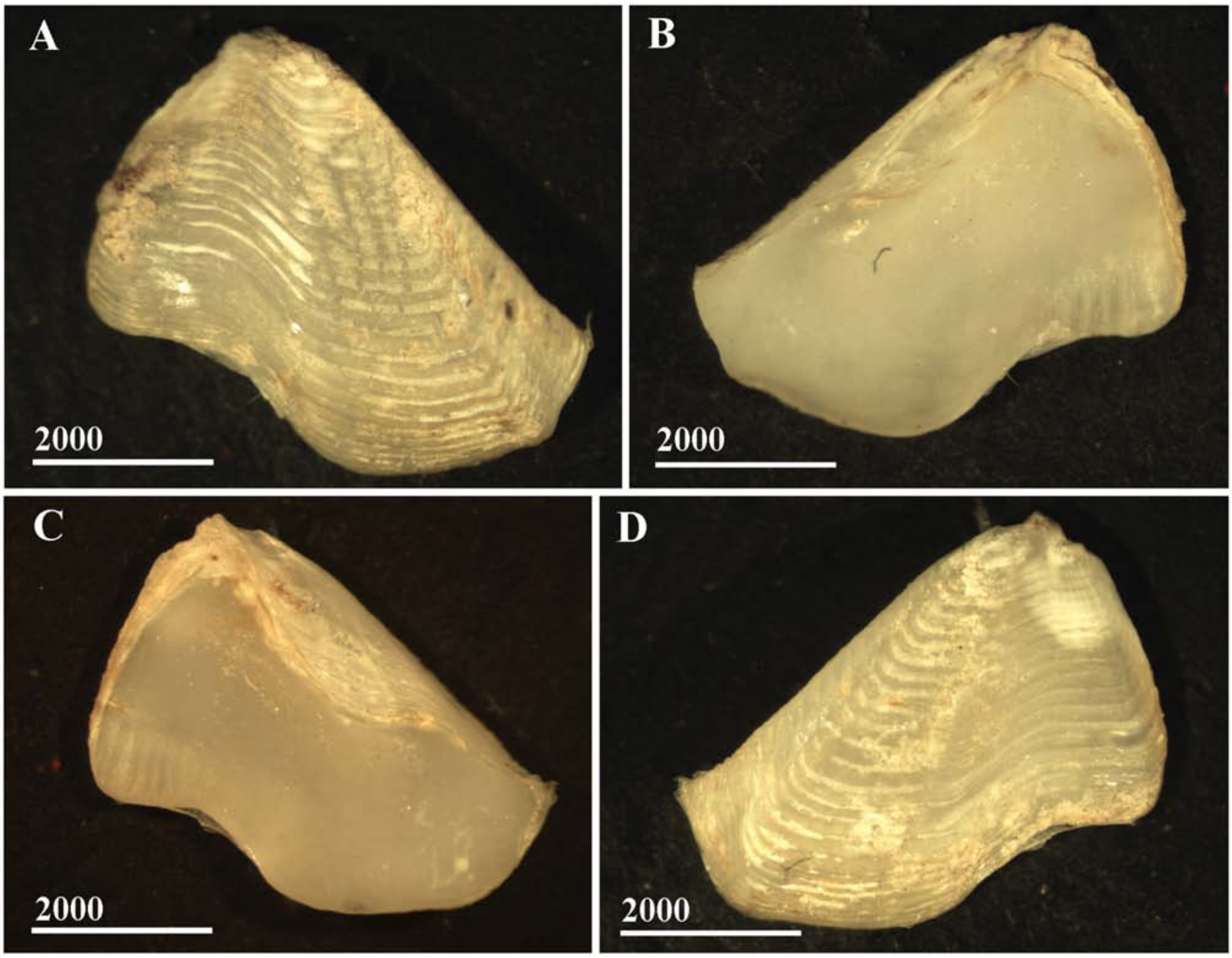


**FIGURE 3.** *Conopea titani* **sp. nov.**, terga. (A), (B) Left tergum, outer and inner view. (C), (D) Right tergum, inner and outer view. Scale bars in µm.

**Remarks**. The new species, *Conopea titani*, is related to species of the genus *Conopea* that have a strong, rigid shell with thick compartments and an elongated basis, an even orifice (not dentate), the basitergal margin of the scutum truncated and with simple growth ridges, and the penis with a developed basidorsal point. These species include *C. acuta* (Nilsson-Cantell, 1921); *C. basicuneata* Van Syoc, Carrison-Stone, Madrona & Williams, 2014; *C. calceola* (Ellis, 1758); *C. cornuta* (Hoek, 1913); *C. cymbiformis* (Darwin, 1854); *Conopea exothobasis* Van Syoc, Carrison-Stone, Madrona & Williams, 2014; *C. fidelis* Carrison-Stone, Van Syoc, Williams & Simison, 2013; *C. galeata* (Linnaeus, 1771); *C. granulata* (Hiro, 1937); *C. investita* (Hoek, 1913); *C. minyrostrum* Van Syoc, Carrison-Stone, Madrona & Williams, 2014; *C. mjobergi* (Broch, 1916); *C. propriens* (Hoek, 1913); *C. sabangensis* Van Syoc, Carrison-Stone, Madrona & Williams, 2014; *C. saotomensis* Carrison-Stone, Van Syoc, Williams & Simison, 2013; *C. scandens* (Pilsbry, 1916); *C. sinensis* (Ren et Liu, 1978); and *C. willhearsti* Van Syoc, Carrison-Stone, Madrona & Williams, 2014. *Conopea titani* is most similar to *C. margaretae*. These two species share very large shells that are conspicuously elongated in both basal carinal and rostral portions, and are similar in the form of the opercular valves, the armament of sharp denticles on the anterior rami of cirri III and IV,

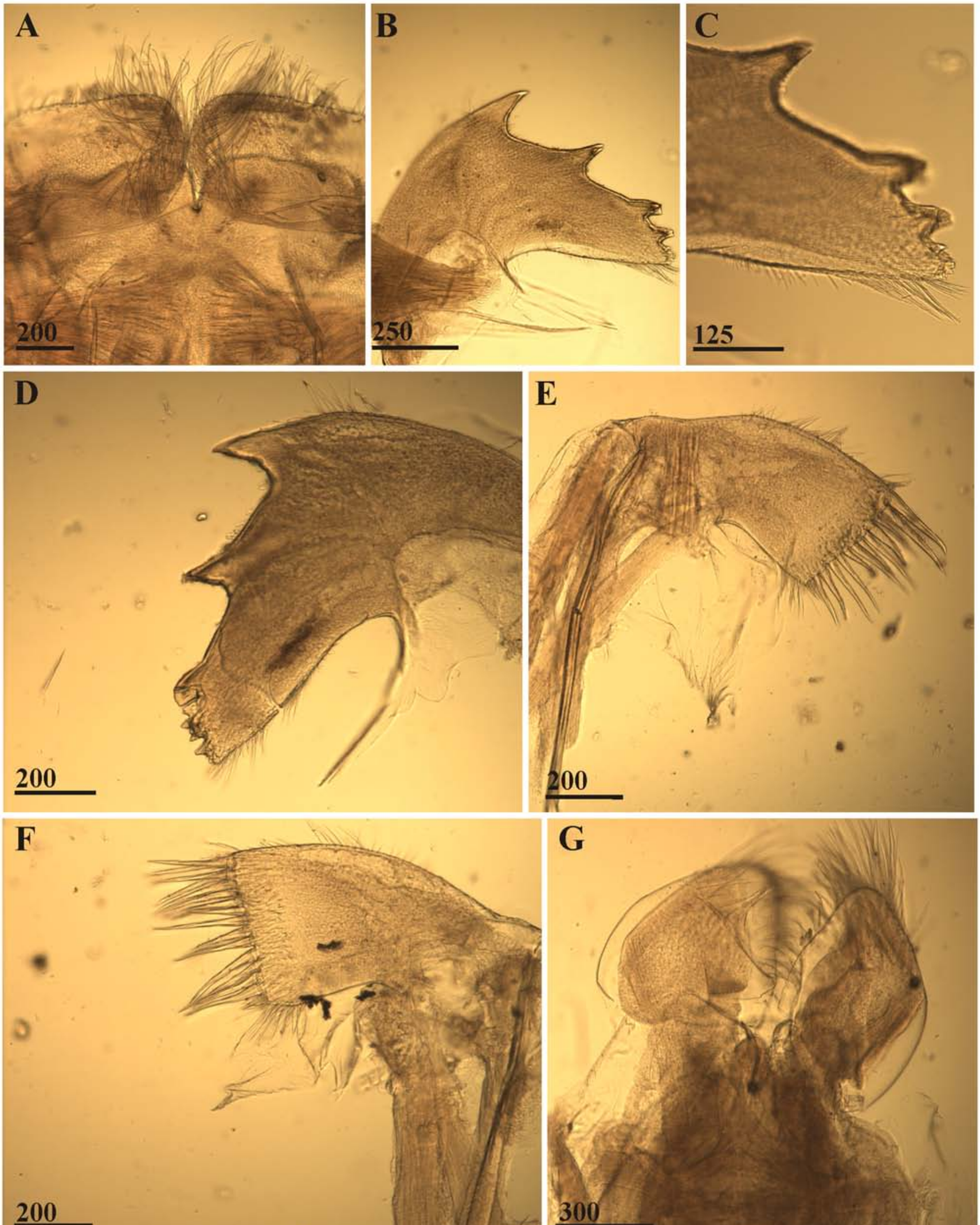


**FIGURE 4.** *Conopea titani* **sp. nov.**, mouth parts. (A) Labrum with palps. (B), (D) Mandibles. (C) Lower part of mandible (inferior angle). (E), (F) Maxillules. (G) Maxillae. Scale bars in µm.

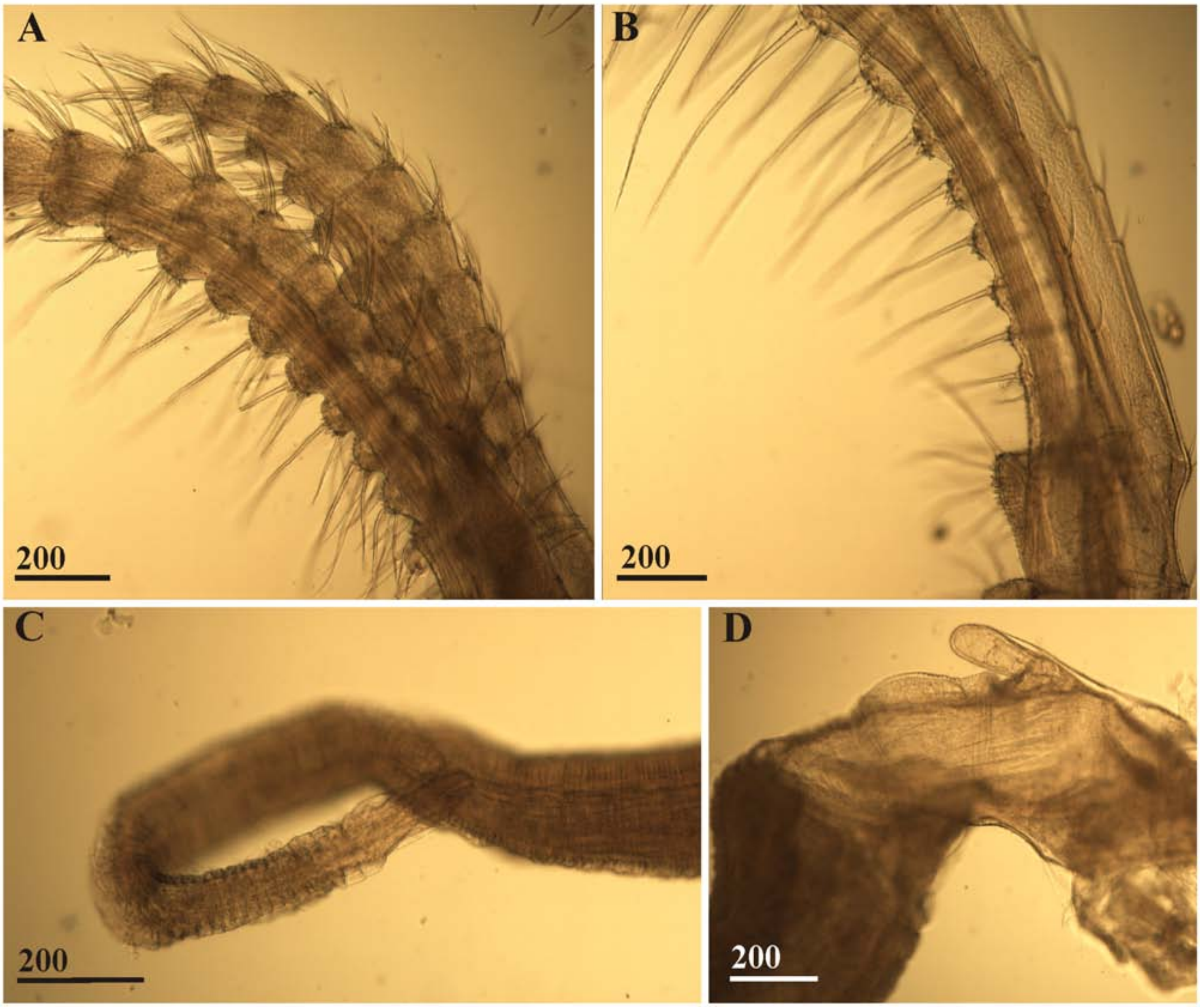


**FIGURE 5.** *Conopea titani* **sp. nov.**, cirri and penis. (A) Cirrus IV. (B) Cirrus IV, basis and basal segments. (C) Tip of penis. (D) Base of penis with basidorsal point. Scale bars in µm.

and the rounded tip of the basidorsal point of the penis. However, *C. titani* has a solid basis and parietes, rather than secondarily filled longitudinal tubes as in *C. margaretae*. The articular ridge of the scutum is not prominent in *C. titani* but is prominent in *C. margaretae*. The spur of the tergum is wider in *C. titani*, being 2/3 the width of the basal margin and ½ width in *C. margaretae*; the end is truncated in *C. titani* and rounded in *C. margaretae*, and without a furrow in *C. titani* but with a shallow, distinct furrow in *C. margaretae*. The shell of *C. titani* is twice the length of *C. margaretae*. *Conopea titani* was found in Western Australia, whereas *C. margaretae* is from the Philippines. *Conopea titani* also resembles *C. proripiens* in shell shape and the structure of the opercular valves, but the carina of *C. titani* is much more elongated than that of *C. proripiens*, and the crest of the labrum of *C. titani* lacks teeth. *Conopea titani* differs from *C. minyrostrum* by the more elongated basal parts of the rostrum and the carina, by the presence of a solid basis rather than one with secondarily filled longitudinal tubes, by the paler rose coloration of the shell, and by the absence of teeth on the crest of the labrum. *Conopea titani* differs from *C. calceola*, *C. fidelis* and *C. saotomensis*, which represent a complex of cryptic species (Carrison-Stone *et al.* 2013), by the absence of a beak-shaped apex to the tergum, and denticles on the terminal end of the tergal spur. The new species can be easily distinguished from *C. galeata* by the absence of the unique broad, square summit of the tergum. *Conopea titani* differs from *C. cornuta*, *C. cymbiformis*, *C. granulata*, *C. investita*, *C. mjobergi*, *C scandens* and *C. siniensis* in having an extremely elongated basal part of the carina, a blunt and rounded tip to the tergum, and the absence of teeth on the crests of labrum.

*Conopea titani* represents the largest species known for the genus *Conopea*. The rostro-carinal basal length does not usually exceed 10 mm for most species of *Conopea*. The basal length of *C. basicuneata* is ~51 mm, in *C. exothobasis* and *C. margaretae* it is~33 mm, and in some specimens of *C. cymbiformis* and *C. galeata* it may reach ~20–25 mm (Darwin 1854; Broch 1931; Rosell 1991), but it never reaches the extreme size of 63–83 mm of the basal length that is characteristic of *C. titani*.

**Etymology**. The specific name *titani*, from the Greek *titan* (*Τιτάν*) meaning giant, represents the size of this species, it being the largest known species of this genus.

## Subfamily Acastinae Kolbasov, 1993

### Genus *Acasta* Leach, 1817

**Diagnosis.** Archaeobalanids with shell with thin, feebly connected compartments, basal parts of rostrum and carina not elongated, radii with oblique summits, parietes solid, usually with internal longitudinal ribs, wall plates often separated by splits or windows covered by delicate membrane; basis not elongated, deeply cup-shaped, rarely flat, margin often serrated; scutum with or without external radial striation; segments of anterior ramus of cirrus IV either bearing hooks or thorns or lacking them. The genus *Acasta* includes of 38 epizoic species from tropical and temperate seas, inhabiting sponges, alcyonaceans and antipatharians. Type species *Acasta spongites* (Poli, 1791).

#### ***Acasta vivicava*** **sp.nov.**

Figures 6–8.

**Type material.** National Museum of Natural History (Naturalis), Leiden, Holland. Locality: 'Oceanic Reef's Expedition' 1992–93, Seychelles, Amirante Islands, 6º12'S, 53º02'E, SCUBA diving, 02.01.1993, one specimen covered by a white scleraxonian alcyonacean *Briareum* sp. (Briareidae). Holotype RMNH.CRUS.C.10234 (shell compartments in ethanol, mouth parts and cirri mounted in glycerol on glass slide) is deposited in National Museum of Natural History (Naturalis), Leiden, The Netherlands.

**Diagnosis**. Shell white, with thin, feebly connected compartments, parietes with small dense external projections and developed basal longitudinal ribs on internal surface, carinolatus 2 narrow, basis saucer-shaped, with crenated margin, width of scutum equal to height, articular ridge prominent, tergum with long, sharp, beak-shaped apex, basidorsal point of penis absent. Embedded in alcyonacean coenenchyme.

**Description**. Shell covered with host tissue forming gall ~8.8 mm long with small orifice ~0.9 mm long (Fig. 6A, B). Shell white, slightly elongated in rostro-carinal axis, rostro-carinal basal length 4.5 mm, basal width 3 mm, height 4.0 mm, opercular orifice dentate, ~1.5 mm maximum length, compartments and basis feebly connected (Fig. 6 C, D). Basis saucer-shaped, with concentric growth lines, crenated margin, irregular depression in centre marking connection to axis of gorgonian, junction between basis and axis of host weak. Parietes (Fig. 6F–H) with small, dense, external projections and fine growth lines, sheath ~1/2 total length, with horizontal striations, internal basal longitudinal ribs distinct. Radii and alae with oblique summits, radii reaching bases of parities and with fine oblique external striations, alae with horizontal striations. Carinolatus 2 narrow (Fig. 6H), with parie only about 1/19 width of carinolatus 1.

Scutum (Fig. 7A–C) thin, semitransparent, broad, width and height equal, external growth ridges crossed with few short, feeble longitudinal ridges, occludent margin dentate. Articular ridge ~1/2 length of tergal margin, prominent, with smooth, not truncated lower end, articular furrow developed, adductor ridge feeble, pits for adductor and depressor muscles not developed.

Tergum (Fig. 7D–G) thin, semitransparent, with growth lines, apex long, sharp, beak-shaped, scutal margin concave, spur truncated, ~1/2 width of basal margin, distinctly separated from basiscutal angle, spur furrow shallow, wide. Articular ridge developed, ~1/2 total height, crests of depressor muscles absent.

Labrum (Fig. 8A) with deep medial notch, 2 small teeth on each crest. Mandibular palps (Fig. 8A) club-shaped, with long, dense setae distally. Mandible (Fig. 8B–E) cutting edge with 5 teeth decreasing in size from upper to lower, teeth 1–3 well separated from each other, teeth 2–5 with bifid, inferior angle serrated, with 2 sharp denticles, inner margin with long, dense setae, outer margin with rare long, paired setae, lateral surface of blade

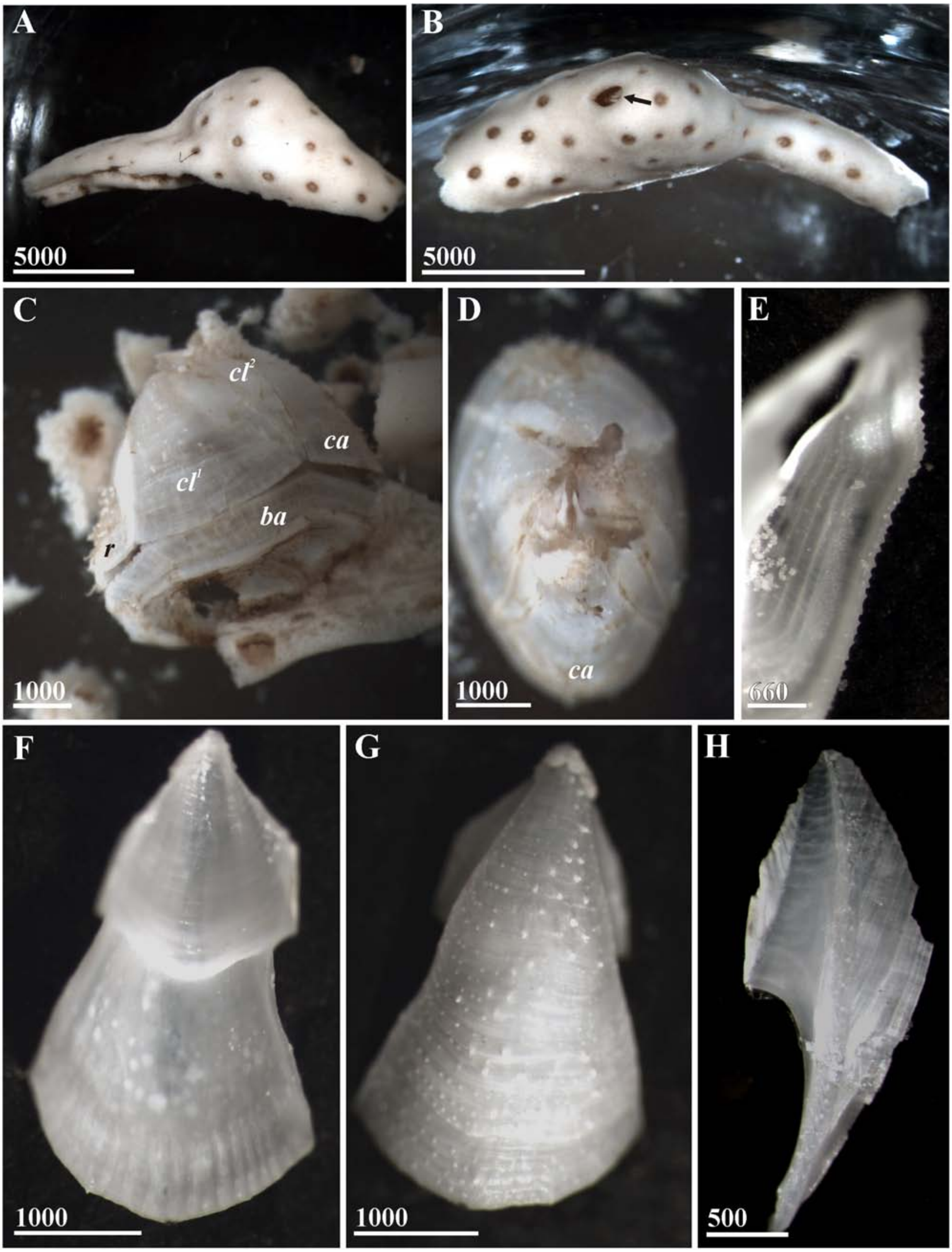


**FIGURE 6.** *Acasta vivicava* **sp. nov.**, general appearance, shell compartments. (A), (B) Gall on gorgonian host, lateral and top view, orifice indicated by arrow. (C), (D) Shell, lateral and top view. (E) Margin of basis. (F), (G) Carina, inner and outer view. (H) Carinolatus 2, outer view. Abbreviations: *ba*—basis, *ca*—carina, *cl*$^1$—carinolatus 1, *cl*$^2$—carinolatus 2, *r*—rostrum. Abbreviations: bp—basidorsal point of penis. Scale bars in µm.

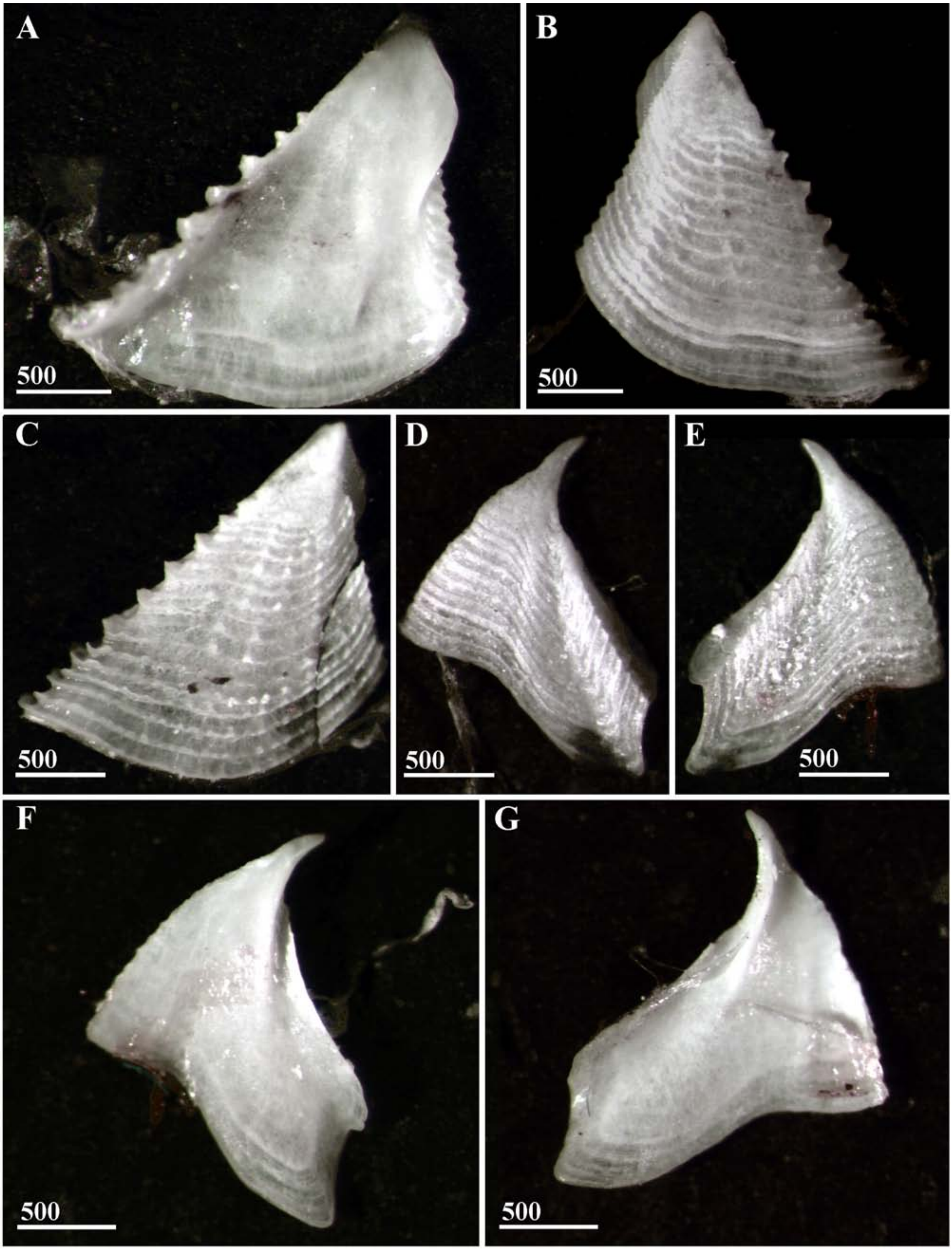


**FIGURE 7.** *Acasta vivicava* **sp. nov.**, opercular plates. (A), (B) Left scutum, inner and outer view. (C) Right scutum, outer view. (D), (E) Left and right terga, outer view. (F), (G) Right and left terga, inner view. Scale bars in µm.

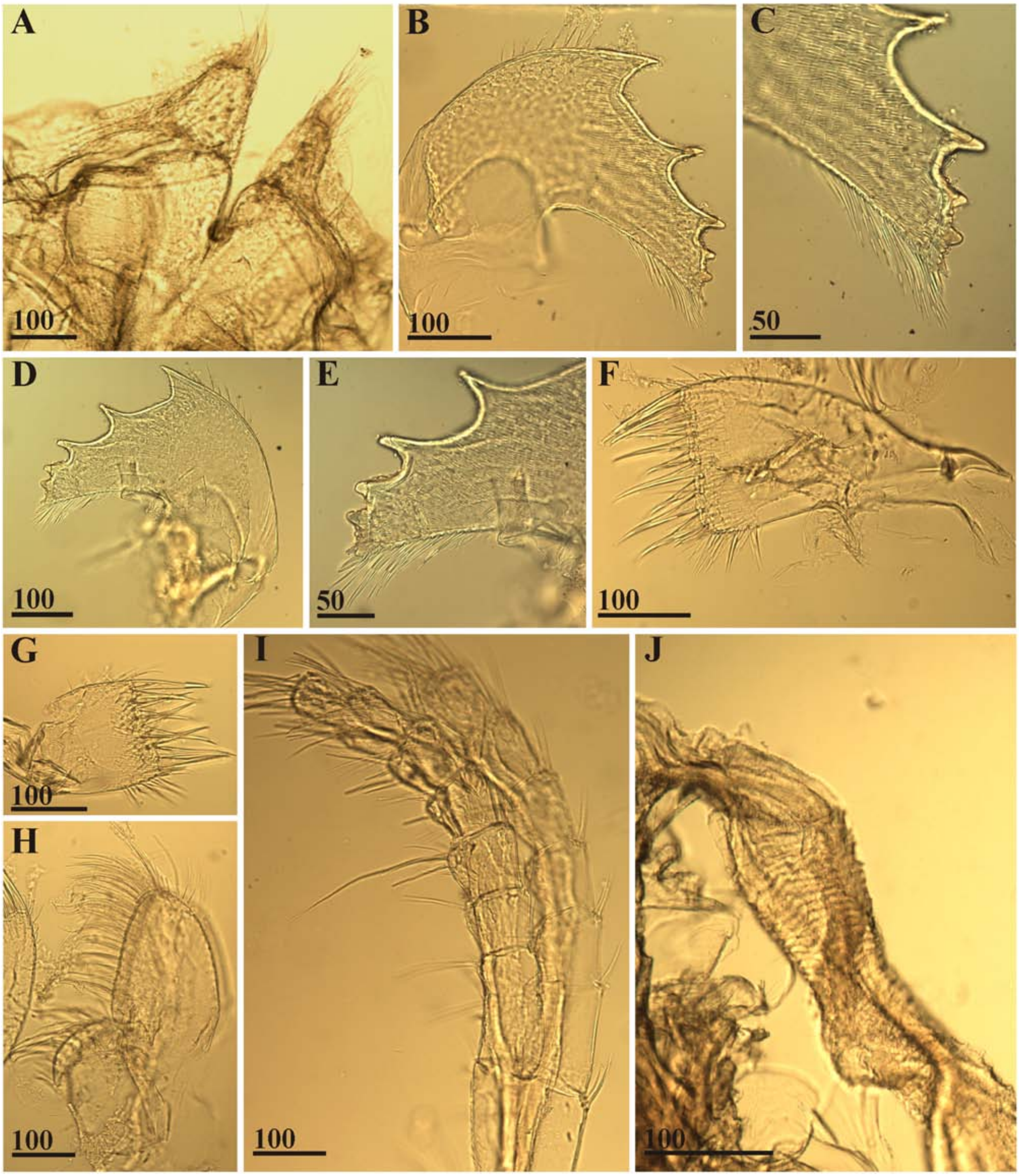


**FIGURE 8.** *Acasta vivicava* **sp. nov.**, mouth parts, cirri and penis. (A) Labrum with palps. (B), (D) Mandibles. (C), (E) Lower parts of mandibles (inferior angles). (F), (G) Maxillules. (H) Maxilla. (I) Cirrus III. (J) Base of penis. Scale bars in µm.

with dense, small setae. Maxillules (Fig. 8F, G) with 9–10 cuspidate setae of different lengths along straight cutting edge, notch absent, upper and lower pairs of cuspidate setae largest, long fine setae along outer and inner margins and on lateral surfaces of blade. Maxillae (Fig. 8H) bilobed, with long setae along inner margins of lobes and on tip.

Most of the cirri of the specimen studied were dried and rami broken. Cirrus I with rami unequal, anterior ramus (12 segments) twice as long as posterior ramus (6 segments), both rami covered with moderately dense setae. Cirrus II with rami unequal, anterior ramus (7 segments) longer than posterior (5 segments), segments with dense setae. Cirri III (Fig. 8I) with anterior ramus (8 segments) slightly longer than posterior (6 segments), several pairs of setae of different sizes along anterior edges of ramal segments, pair of stout setae at posterio-distal angle, segments of both rami without denticles or teeth. Cirri IV–VI with broken rami. Basal segments of cirrus IV without teeth and denticles. Penis (Fig. 8J) long, annulated, basidorsal point absent.

**Remarks**. Nine species of the genus *Acasta* were found in alcyonaceans—*A. alcyonica* Rosell, 1991; *A. alcyonicola* Utinomi, 1953; *A. echinata* Hiro, 1937 (Fig. 13H–K); and *A. umitosaka* Utinomi, 1962 from alcyoniinan alcyonaceans; *A. antipathidis* Broch, 1916 (this species was previously reported to have an antipatharian host; however, study of photographs of the syntypes revealed that the colony reported as a black coral in fact represents a denuded dead axis of an alcyonacean); *A. gregaria* Utinomi, 1959; *A. hirsuta* Broch, 1916; *A. purpurata* Darwin, 1854; and *A. vipensis* Van Syoc, Carrison-Stone, Madrona & Williams, 2014 from alcyonaceans (gorgonians). The new species, *A. vivicava*, differs from these species in having a narrower CL2, a scutum with a prominent articular ridge and a tergum with an elongated sharp apex. The new species can also be distinguished from *A. alcyonica*, *A. purpurata* and *A. umitosaka* by the absence of large slits or windows between the shell plates, and from *A. alcionica*, *A. gregaria* and *A. hirsuta* and *A. vipensis* by the absence of the longitudinal striation of scutum.

It should be noted that several archaeobalanid species that are epibionts of alcyonaceans and antipatharians also representing acastines were erroneously assigned to the genus *Conopea*, as demonstrated by the phylogenetic analyses (see below). These include *C. canaliculata* (Ren et Liu, 1978); *C. dentifer* (Broch, 1922); *C. folliculus* (Hiro, 1937); *C. fragilis* (Broch, 1931); *C. longibasis* (Hiro, 1937); *C. navicula* (Darwin, 1854) (Fig. 13A–G); *C. pygmaea* (Broch, 1931); and *C. squamosa* (Rosell, 1991). *Acasta vivicava* also differs from *C. canaliculata, C. dentifer, C. fragilis, C. longibasis, C. navicula* and *C. pygmaea* in having the scutum with equal basal and tergal margins and with a prominent articular ridge, the tergum with an elongated sharp apex and a narrower carinolatus 2. The new species has opercular valves slightly similar to *C. follisculus*, but differs by the scutum having a more prominent articular ridge and by the absence of a depressor muscle pit. *Acasta vivicava* differs from *C. squamosa* by possessing a narrower carinolatus 2 and by the elongated, sharp apex of the tergum. *Acasta vivicava* also can be distinguished from *C. canaliculata*, *C. dentifer*, *C. longibasis*, *C. fragilis* and *C. navicula* by the absence of developed longitudinal striation of the scutum.

**Etymology**. The specific name represents the similarity to a bird living in the tree hollow, from the Latin '*vivet*' meaning live and '*cavae*' hollow.

## Phylogeny

We used a cladistic approach for the study of the phylogenetic relationship between species of the genus *Conopea* s.l. and species of the genus *Acasta* inhabiting alcyonaceans, using morphological characters. The characters comprise the morphology of the shell, the shell compartments, the opercular plates, the armament of cirri III and IV and the penis, and the mode of the attachment to the host substrate.

We composed the list of 28 characters for our analysis, where only two are multistates, character 19: structure of basitergal margin of scutum, and character 26: armament of anterior ramus of cirrus. Six characters are uninformative, 1–5, and 28, structure of rostral plate, radii, labrum, mandible, presence/absence of caudal appendages and character of attachment to the host substratum. These do not contribute to the parsimony analysis. However, they represent synapomorphic or symplesiomorphic characters, 1–5 between the out-group and *Conopea-Acasta* clade and, therefore, these features were included in our analysis. We developed a matrix of 28 characters for Nexus Data Editor 5.0 (Table 1). Data were scored "0" or"1", and "0", "1" and "2" for multistate characters. Generally in the matrix the plesiomorphic character was scored "0".

**List of characters.**

1. Structure of rostral plate: 0 = tripartite rostral plate formed by incomplete fusion of rostrum and rostrolaterals, 1 = a single rostral plate made of completely fused rostrum and both rostrolaterals. A concrescent compound rostral plate consisting of partially fused rostrum with rostrolaterals (RL-R-RL) with traces of fusion sutures (Fig. 14A, B) as found in *Pachylasma* is regarded as plesiomorphic character, the (RL-R-RL) state is found also in Catophragmidae (Chthamaloidea) and only in a few coronulids. A single rostral plate without fusion sutures such as found in *Conopea* and *Acasta* (Fig. 9G) is the derived state.

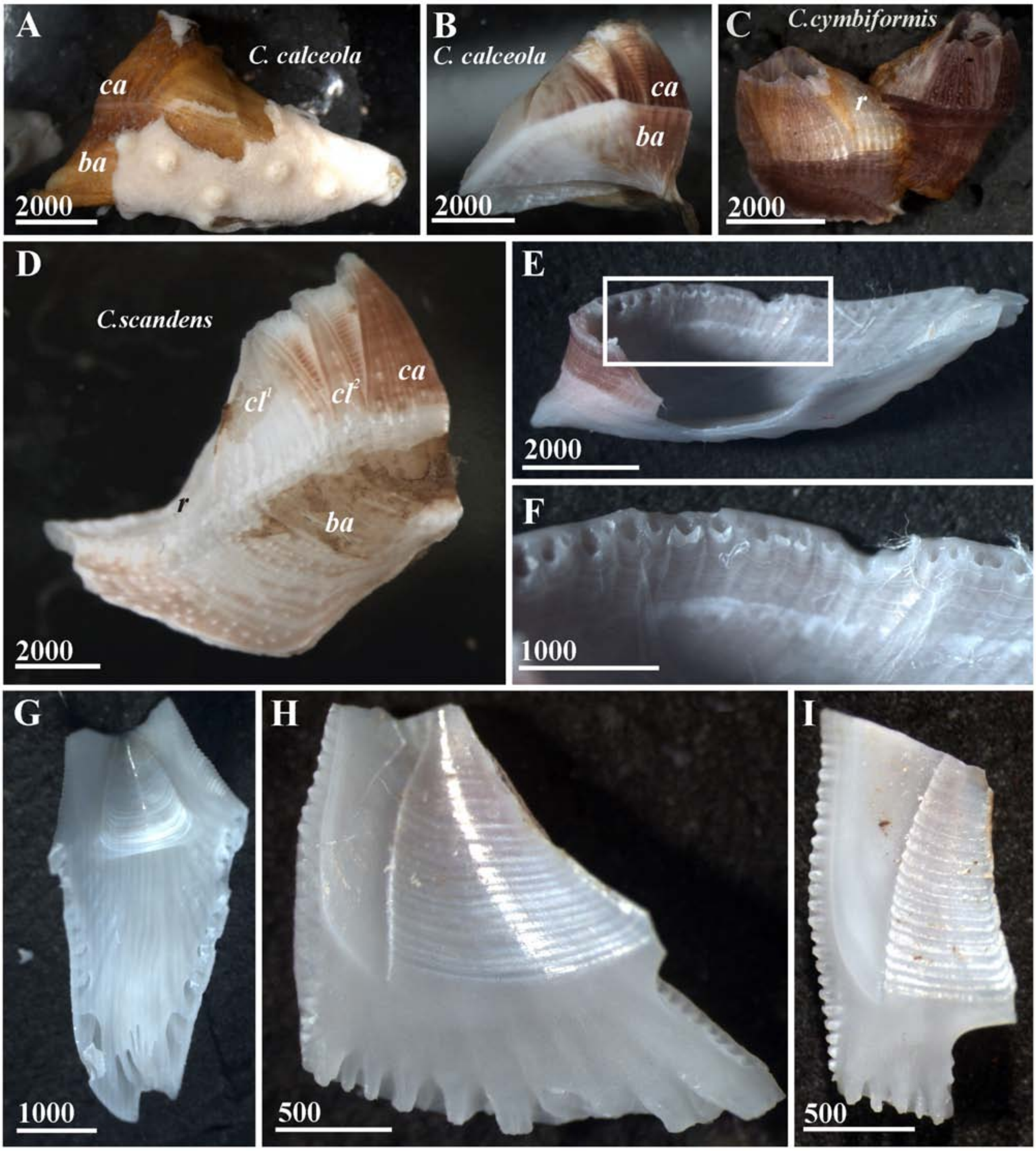


**FIGURE 9.** Shell morphology of 3 species of genus *Conopea* (*C. calceola*—A, B, E–G; *C. cymbiformis*—C, H, I; and *C. scandens*—D). (A) Shell covered by host tissues, lateral view. (B–D) Shells with host tissues removed, lateral view. (E) Basis. (F) Margin of basis from rectangle area in 'E' showing longitudinal inner tubes/canals with openings/pits for articulation with basal ribs of parietes. (G) Rostrum with longitudinal ribs and internal longitudinal tubes/canals, inner view. (H) Carinolatus 1 with protruding inner ribs and denticulated sutural margin of radius. (I) Carinolatus 2 with protruding inner ribs and denticulated sutural margin of radius. Abbreviations: *ba*—basis, *ca*—carina, *$cl^1$*—carinolatus 1, *$cl^2$*—carinolatus 2, *r*—rostrum. Scale bars in µm.

2. Radii of shell plates: 0 = absent,1 = present. The absence of radii is a plesiomorphic character found in Pachylasminae (Fig. 14A), whereas the development of radii from the margins of parietes to overlap alae of the adjacent parietes is characteristic for advanced forms such as *Conopea* and *Acasta* (Figs 9H, I, 13A, B).
3. Crest of labrum: 0 = without median incision, 1—with deep median incision. Labrum without a median

incision presents in pedunculate barnacles, and lower acorn barnacles such as Chthamaloidea and Pachylasmatoidea (*Pachylasma*) (Fig. 14C), median incision is an apomorphic feature found in Balanoidea including *Conopea* and *Acasta* (Figs 4A, 8A).

4. Structure of mandible: 0 = generalized blade of incisiform teeth, 1 = molariform blade. Mandible of generalized form with incisiform teeth is a plesiomorphic character found in *Pachylasma*, (Fig. 14D), the derived character is molariform blade of mandible (Figs 4B, D, 8B, D).

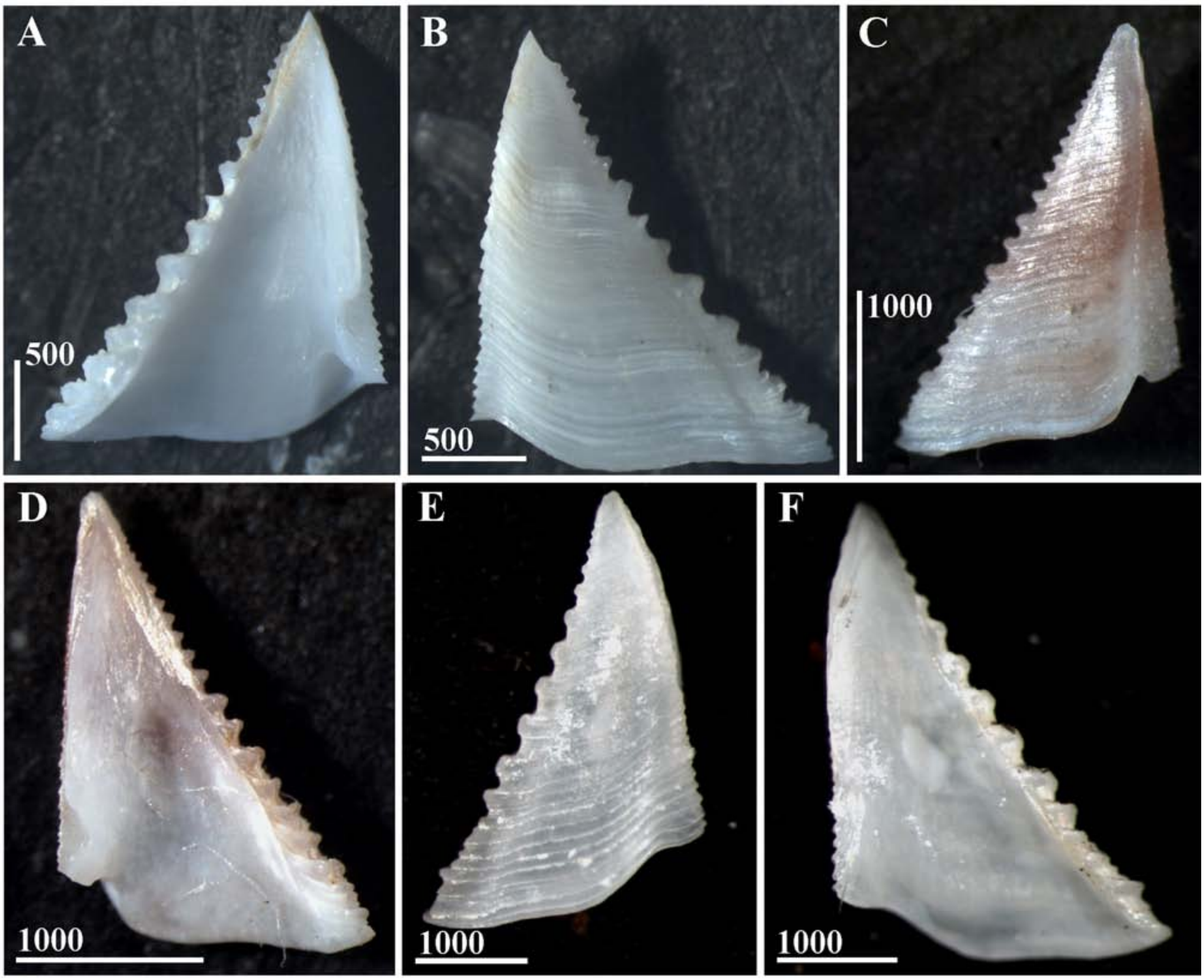


**FIGURE 10.** Scuta of 3 species of genus *Conopea* (*C. calceola*—A, B; *C. cymbiformis*—C, D; and *C. scandens*—E, F). (A), (D), (F) Inner surface. (B), (C), (E) Outer surface. Scale bars in µm.

5. Caudal appendages: 0 = present,1 = absent. Caudal appendages are found in pedunculate barnacles and lower balanomorphans such as *Pachylasma* (Fig. 14E) but absent in advanced Balanomorpha.
6. Shell solidity: 0 = shell strong and cannot be disarticulated , 1 = shell with thin, often semitransparent and feebly connected compartments, which often are disarticulated after removal of host tissue. Some species of the genus *Conopea* have a shell with strong articulated compartments that cannot be easily disarticulated after separation from the host, whereas other species of *Conopea*, as well as species of the genus *Acasta*, have a shell with thin and feebly connected compartments that maybe considered as an adaptive pattern of epibiotic life.
7. Basis attachment to host: 0 = basis does not clasp host (axis of coral), 1 = basis clasps firmly to host (axis of coral). Basis clasping the horny axis of the alcyonacean is a derived character found in some species of the genus *Conopea,* leading to the rostrocarinal elongation of the basis due to the growth of the coral and forming an axial groove (Figs 1B, 9A, D). Other species of the genera *Conopea* and *Acasta* have a basis that does not clasp the axis of host and can be easily separated from the host (Figs 6C, 13A, H).

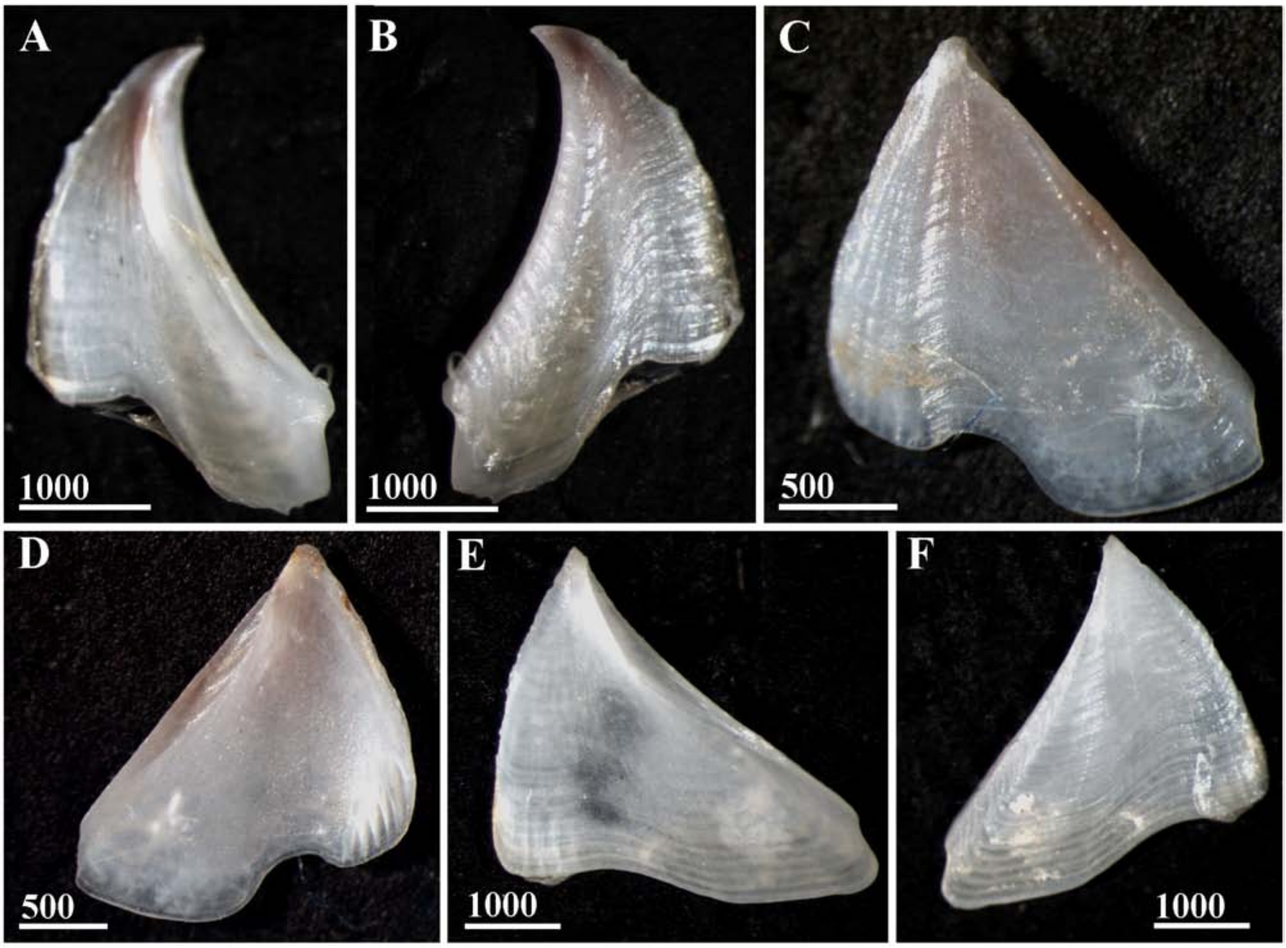


**FIGURE 11.** Terga of 3 species of genus *Conopea* (*C. calceola*—A, B; *C. cymbiformis*—C, D; *C. scandens*—E, F). (A), (D), (E) Inner surface. (B), (C), (F) Outer surface. Scale bars in µm.

8. Margin of basis: 0 = margin serrate, with small teeth, 1 = margin not serrate. The basis of several species of *Conopea*, as well as a majority of *Acasta*, has a serrated margin (Figs 6E, 13G, K), whereas other species of *Conopea* have the margin of the basis without small teeth (Fig. 9F).
9. Deep pits on margin of basis. 0 = deep pits absent , 1 = margin of basis with deep and rounded pits. A series of species of *Conopea* have deep rounded pits along the margin of the basis (Figs 2A, 9E, F); these pits may or may not correspond to the inner longitudinal tubes of the basis; these pits interlock with the inner longitudinal ribs of the parietes (Figs 2B, 9G–I).
10. Structure of basis: 0 = basis solid, 1 = basis tubiferous. The majority of species of *Conopea* and all species of *Acasta* have a solid basis (Figs 2A, 13G, K), but a few species of *Conopea* have a tubiferous basis made of inner radiating canals (Fig. 9E, F). The tubiferous basis is regarded as an apomorphic trait and the solid basis as a plesiomorphic trait, but in some species the radiating canals are filled by calcareous deposition that can be traced by the peripheral deep pits.
11. Structure of parietes: 0 = solid, non tubiferous, 1 = tubiferous. Solid parietes are the rule in pedunculate barnacles, verrucomorphans, chthamaloids and certain balanomorphans; tubiferous parietes with inner canals are considered as an apomorphic condition. All species of *Acasta* have solid parietes (Figs 6F, 13B); only a few species of *Conopea* have tubiferous parietes (Fig. 9G). However, solid parietes of some *Conopea* are regarded as a derived characteristic, where the inner tubes are secondarily filled by calcareous deposition. Pilsbry (1916) indicated that "I have been unable to decide whether the species of *Conopea* with poreless compartments are secondarily so by reason of the filling up of pores solidly, or whether, like *Acasta*, parietal pores have never been evolved" which may be evidence in favor of a dyphyletic nature of *Conopea*.

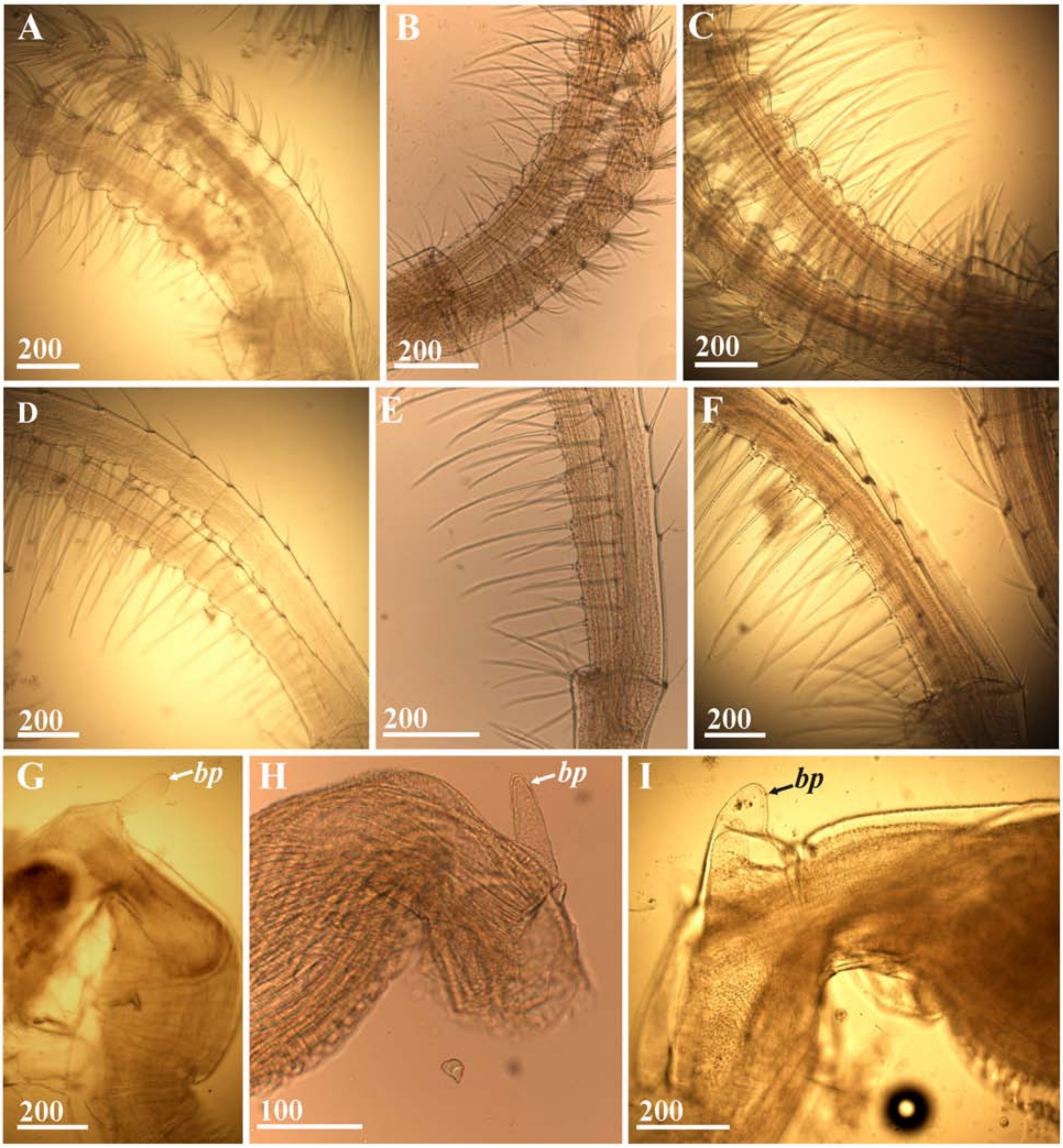


**FIGURE 12.** Cirri and penes of 3 species of genus *Conopea* (*C. calceola*—A, D, G; *C. cymbiformis*—B, E, H; *C. scandens*—C, F, I). (A), (B), (C) Cirri III. (D), (E), (F) Cirri IV, basal segments. (G), (H), (I) Basal parts of penes with basidorsal point. Scale bars in µm.

12. External surface of parietes: 0 = smooth or with minute granules, 1 = with conspicuous projections. Parietes with smooth external surfaces are found in several species of *Conopea* and in some cases they are ornamented with minute granules (Figs 1B, 9A–D), but other species of *Conopea* and the majority of *Acasta* species have conspicuous projections/spines on the external surface of the parietes (Figs 6C, G, 13A, H) serving for better fixation in the friable host tissues (Kolbasov 1993).
13. Inner surface of parietes beneath sheath: 0 = smooth, without longitudinal ribs, 1 = with longitudinal ribs. Longitudinal ribs on the inner surface, beneath the sheath of the parietes, are present in the majority of species of *Conopea* and *Acasta* (Table 1) (Figs 1C, 2B, 6F, 9G–I, 13B).
14. Structure of inner longitudinal ribs of parietes: 0 = longitudinal ribs do not project beyond basal margin of parietes, 1 = longitudinal ribs project beyond basal margin of parietes to interlock with corresponding tubes or

the pits of the basis. Parietes of all investigated species of *Acasta* and some species of *Conopea* have inner longitudinal ribs that do not project beyond the basal margin (Figs 6F, 13B), whereas several species of *Conopea* possess longitudinal ribs projecting beyond the basal margin (Figs 2B, 9H, I). These projecting ribs interlock with corresponding deep pits on the margin of the basis.

15. Structure of rostrum: 0 = not elongated in basal portion, 1 = conspicuously elongated of basal portion. Some species of *Conopea* have basis that clasps the axis of coral firmly characterized by conspicuously elongated basal portion of rostrum (Figs 1B, 9A, B, D). In these cases the carino-rostral growth of the barnacle correspond to the elongation of the host that leads to the elongation of basal parts of rostrum and carina.

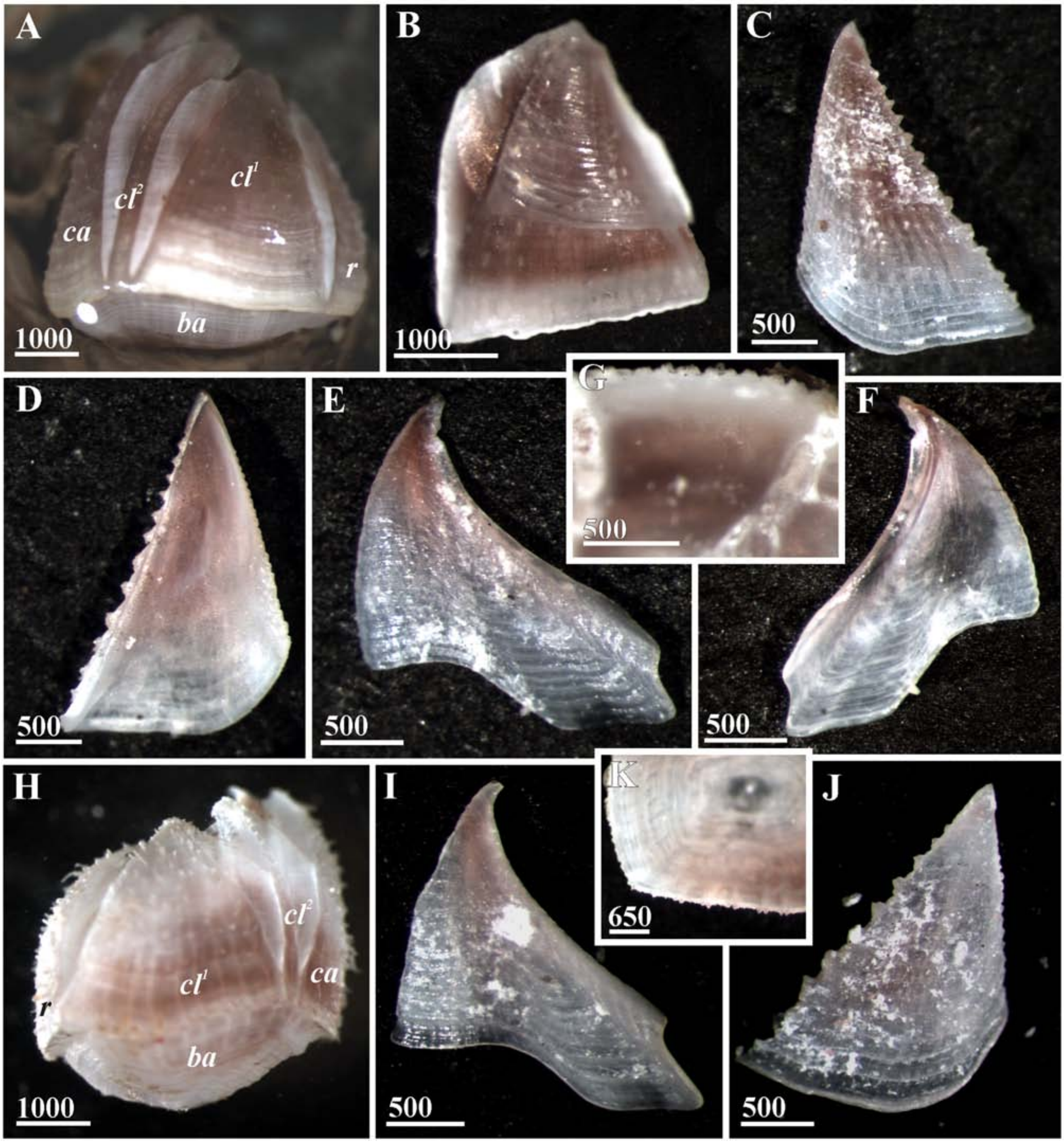


**FIGURE 13.** Shell morphology of 2 species of genus *Acasta* from octocorals (*Acasta (Conopea) navicula*—A–G; *A. echinata*—H–K). (A), (H) Sell, general appearance, lateral view, host tissue removed. (B) Carinolatus 1, inner view. (C), (D) Left scutum, outer and inner surface. (E), (F) Left tergum, outer and inner surface. (G) Serrated margin of basis. (I) Tergum, outer surface. (J) Scutum, outer surface. (K) Serrated margin of basis. Abbreviations: *ba*—basis, *ca*—carina, $cl^1$—carinolatus 1, $cl^2$—carinolatus 2, *r*—rostrum. Scale bars in µm.

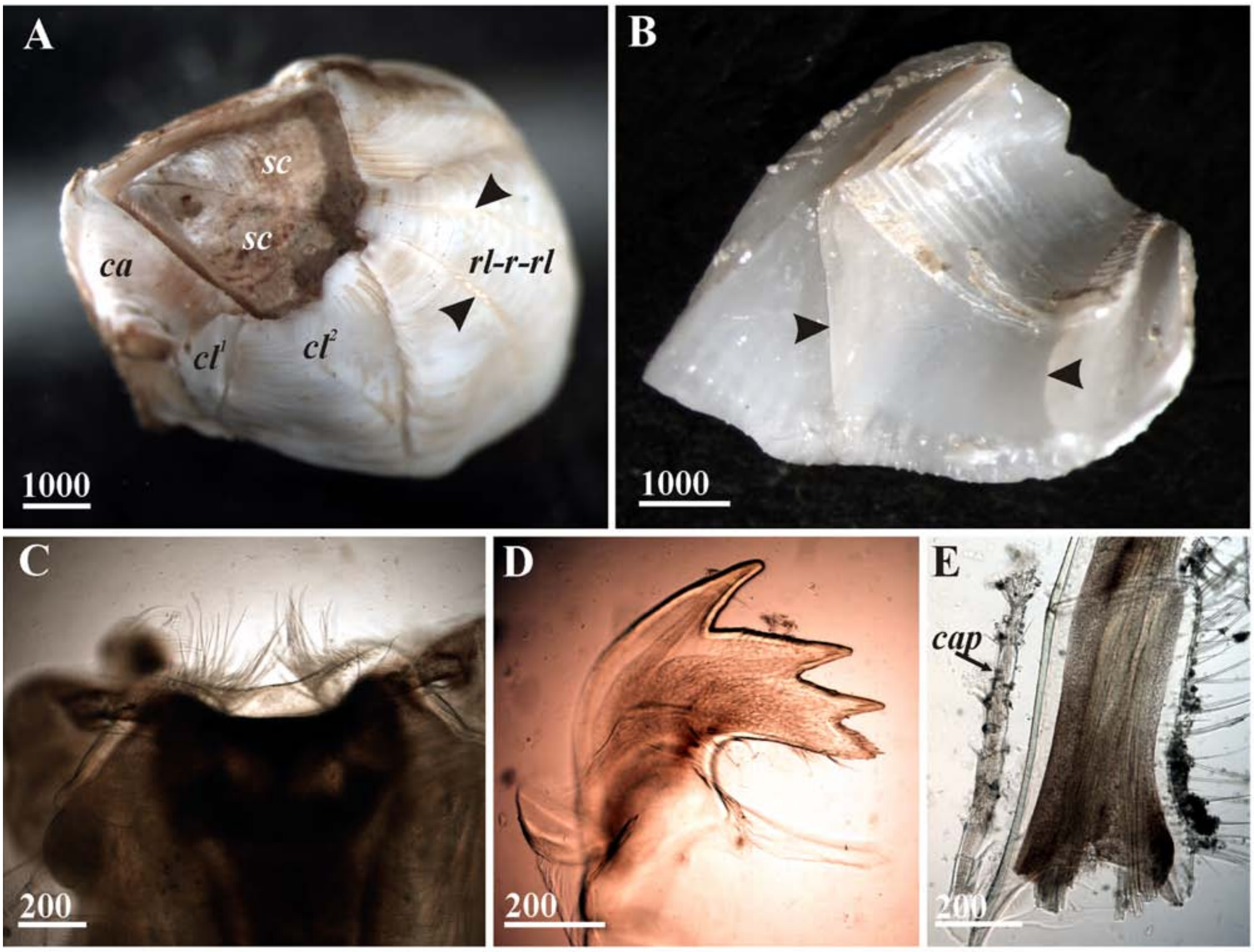


**FIGURE 14.** *Pachylasma* sp., general morphology. (A), Shell, top view, fusion sutures between rostrum and two rostrolaterals indicated by arrowheads. (B), Tripartite rostral plate, inner surface, sutures between fused rostrum and two rostrolaterals indicated by arrowheads. (C), Labrum without deep median incision. (D), Mandible of generalized form with incisiform teeth. (E), Protopod of cirrus 6 and caudal appendage. Abbreviations: *ca*—carina, *cap*—caudal appendage, $cl^1$—carinolatus 1, $cl^2$—carinolatus 2, *rl-r-rl*—tripartite rostral plate, *sc*—scuta. Scale bars in µm.

16. Summits of radii: 0 = radii with oblique summits, orifice of shell dentate, 1 = radii with summits parallel to basal margins of parietes, orifice of shell even. Radii with summits parallel to the basal margins of the parietes are found in species of *Conopea* with strong robust shells (Fig. 9B–D); radii with oblique summits are found in *Acasta* and in species of *Conopea* with thin weak shells (Figs 6C, D, H, 13A, B, H).
17. Structure of sutural margins of radii: 0 = not dentate, 1 = strongly dentate. Radii with strongly dentate sutural margins are characteristic for species of *Conopea* having strong robust shells (Figs 1D, 9G–I), providing a firm connection between the adjoining plates. A few species of *Conopea*, as well as the species of *Acasta* studied, possess radii but lack dentate sutural margins.
18. External surface of scutum: 0 = with radial (longitudinal) striae or ribs, 1 = without radial (longitudinal) striae or ribs. The external surface of the scutum with longitudinal striae or ribs of different degrees of development (Figs 7B, C, 13C, J) are characteristic for several species of *Conopea* and the majority of studied *Acasta*, and their scuta often appear latticed. In species of *Conopea* with strong robust shells, the scuta are without radial striae or ribs (Figs 2C, F, 10B, C, E).
19. Structure of basitergal margin of scutum: 0 = rounded, not truncated, 1 = truncated (sinusoid), 2—straight. A rounded basitergal margin of the scutum is found in all species of *Acasta* and some species of *Conopea* (Table 1) (Figs 7A–C, 13C, D, J). Species of *Conopea* with strong shells have a scutum with a truncated (sinusoid) basitergal margin (Figs 2E, F, 10) and a straight basitergal margin only occurs in *Conopea merrilli* (Zullo 1966).

20. Pit of depressor muscle of scutum: 0 = not distinct, 1 = distinct, directly at basitergal margin. Species of *Conopea* with strong shells possess scuta with a distinct depressor muscle pit at different degrees of development (depth) situated directly at the basitergal margin (Figs 2D, E, 10A, D, F).
21. Apex of tergum: 0 = strongly curved, produced, beak-shaped, 1 = blunt, square or sharp but not produced. The apex of the tergum may be strongly curved, produced and beak-shaped in some species of *Conopea* and *Acasta* (Figs 7D–J, 11A, B, 13E, F, I) or blunt, square or sharp but not produced in other species (Figs 3, 11C–F). There is no correlation with the morphology of the shell, shell compartments or the soft body.
22. Crests of depressor muscles of tergum: 0 = present, 1 = reduced. The inner surface of the tergum of some species of both genera is equipped with distinct depressor muscle crests (Figs 3B, C, 11D). There is no correlation with other morphological characters.
23. Width of spur of tergum: 0 = about 2/3 of basal margin, 1 = ½ of basal margin or less. The species of *Acasta* and *Conopea* may possess different widths of the tergal spur without correlation with other morphological characters.
24. Tergal spur structure: 0 = does not separate from basiscutal margin distinctly, 1 = separated from basiscutal margin distinctly. In different species of *Conopea* and *Acasta* the tergal spur may be distinctly separated (Figs 7D–J, 11A, B, 13E, F, I) or not (Figs 3, 11C–F) from the basiscutal margin of the tergum. We did not trace a correlation of this character with other morphology.
25. Armament of anterior ramus of cirrus III: 0 = segments without denticles, 1 = segments with denticles. The segments of the anterior ramus of cirrus III in several species of both *Acasta* and *Conopea* may be armed with noticeable sharp denticles along the anterior margin (Fig. 5A), while other species lack these denticles (Figs 8I, 12A–C). There is no strong correlation with other morphology (Table 1).
26. Armament of anterior ramus of cirrus IV: 0 = segments without denticles, 1 = segments with denticles, 2 = segments with curved teeth. The segments of the anterior ramus of cirrus IV in several species of *Acasta* and *Conopea* may be armed with noticeable sharp denticles along the anterior margin (Fig. 5B) or lack these denticles (Fig. 12D–F), and a few species of these genera possess conspicuous curved teeth on the basal segments (Table 1). These curved teeth, serving for grooming of the host tissues in sponge-inhabiting species of *Acasta* (Kolbasov 1993), are also characteristic for some *Acasta* species found on octocorals (Table 1). In *Conopea navicula* the presence of such teeth may indicate its relationship to *Acasta*.
27. Basidorsal point of penis: 0 = present, 1 = absent. A developed basidorsal point of the penis is characteristic of species of *Conopea* with strong robust shells (Table 1) (Figs 5D, 12G–I). The penis without a basidorsal point is found in species of *Conopea* with feeble, thin shells and in species of *Acasta* (Fig. 8J).
28. Substrate character: 0 = barnacles attach to both coral and to each other, 1 = attach only to coral. Generally specimens of *Conopea* and *Acasta* attach solely to, or are embedded in the host coral. Specimens of *C. merrilli* were found attached to the host coral and to each other, and were not covered by host tissue (Zullo 1966). This fact evidences that *C. merrilli* cannot be considered as truly symbiotic and does not belong to *Conopea*. We suspect that specimens of *Pachylasma* sp. from our material also attach to each other, but since we found only a single specimen we scored this character as "?".

These characters were subjected to parsimony analysis using PAUP 4.0, software (Swofford 1998). All characters were entered unordered and of equal weight. We reconstructed bootstrap 50% majority-rule consensus and neighbor-joining trees (Fig. 15). We used two kinds of matrices—with data on *Pachylasma* sp. as an out-group (trees on Fig. 15A, B) and without the data of *Pachylasma* sp. (trees on Fig. 15C, D). Removal of *Pachylasma* sp. from analysis emphasizes the possible synapomorphies (thin shell with feebly connected plates and absence of basidorsal point of penis) or symplesiomorphies (serrated margin of basis without deep rounded pits for interlocking with the parietes) found in some species of *Conopea* s.l. and all species of the genus *Acasta* inhabiting octocorals (Table 1). Thus, we may more precisely estimate the position of those species forming a distinct clade in the bootstrap 50% majority-rule consensus tree (Fig. 15C). Reconstructed trees show that species of the genus *Conopea* s.l. form two distinct clades corresponding to two morphological groups. The first clade includes only species of the genus *Conopea* (Fig. 15A, B), whereas the second clade unites species from both genera, *Conopea* and *Acasta*, from corals (Fig. 15B, C, D). Thus, the genus *Conopea* s.l. presently represents a non-monophyletic taxon. The clade, including the type species *Conopea calceola* (Ellis, 1758), should be considered as the genus *Conopea* s.s. with 20 species. These are *C. acuta*, *C. basicuneata*, *C. calceola*, *C. cornuta*, *C. cymbiformis*, *C.*

*exothobasis*, *C. fidelis*, *C. galeata*, *C. granulata*, *C. investita*, *C. margaretae*, *C. minyrostrum*, *C. mjobergi*, *C. proripiens*, *C. sabangensis*, *C. saotomensis*, *C. scandens*, *C. sinensis*, *C. titani* and *C. willhearsti*. The other species—*C. canaliculata*, *C. dentifer*, *C. folliculus*, *C. fragilis*, *C. longibasis*, *C. navicula*, *C. pygmaea* and *C. squamosa*—should be allocated to the genus *Acasta*. These species, as other representatives of *Acasta*, are characterized by a shell with thin and feebly connected compartments, the basal parts of the rostrum and carina are not elongated, the basis is not elongated significantly in the rostro-carinal axis and does not firmly clasp the axis of the host coral, the orifice is dentate, the radii have oblique summits, the scutum has a rounded basitergal angle and often has longitudinal ribs or striations, and the penis is without a basidorsal point.

**TABLE 1.** Character matrix. Unknown states marked by (?), inapplicable by (-).

| Characters<br>Species | 1 2 3 4 5 6 7 8 9 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2<br>0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 |
|---|---|
| *Pachylasma* sp. | 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 - - - 0 0 1 0 1 0 0 0 1 ? |
| *Conopea acuta* | 1 1 1 1 1 0 1 1 1 0 0 0 1 1 1 1 1 1 1 0 0 1 1 0 0 0 ? 1 |
| *Conopea basicuneata* | 1 1 1 1 1 0 1 1 ? 0 0 0 ? ? 1 1 ? 1 1 1 1 0 1 0 1 1 0 1 |
| *Conopea calceola* | 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 0 0 0 1 |
| *Conopea canaliculata* | 1 1 1 1 1 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 1 ? ? ? 1 |
| *Conopea cornuta* | 1 1 1 1 1 0 1 1 ? ? ? 0 ? ? 1 1 ? 1 1 1 1 0 1 0 1 0 ? 1 |
| *Conopea cymbiformis* | 1 1 1 1 1 0 1 1 1 0 0 0 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 |
| *Conopea dentifer* | 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 1 ? 1 |
| *Conopea exothobasis* | 1 1 1 1 1 0 1 1 ? 1 0 0 ? ? 1 1 ? 1 0 0 1 0 1 1 1 1 0 1 |
| *Conopea fidelis* | 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 0 0 0 1 |
| *Conopea follisculus* | 1 1 1 1 1 1 0 0 0 0 0 1 0 - 0 0 0 1 0 1 0 1 1 1 ? ? ? 1 |
| *Conopea fragilis* | 1 1 1 1 1 1 1 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 |
| *Conopea galeata* | 1 1 1 1 1 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 0 1 0 0 0 0 1 |
| *Conopea granulata* | 1 1 1 1 1 0 1 1 ? 0 0 0 1 ? 0 1 1 1 1 1 1 0 0 0 1 1 0 1 |
| *Conopea investita* | 1 1 1 1 1 1 1 1 1 1 1 0 ? ? 1 1 ? 1 1 ? 0 0 1 0 0 0 ? 1 |
| *Conopea longibasis* | 1 1 1 1 1 1 0 ? 0 0 0 0 1 0 0 0 ? 0 0 0 0 1 1 0 ? ? ? 1 |
| *Conopea margaretae* | 1 1 1 1 1 0 1 1 ? 1 1 0 ? ? 1 1 ? 1 1 1 1 0 1 0 1 1 0 1 |
| *Conopea merrilli* | 1 1 1 1 1 0 0 ? 1 1 0 0 1 0 0 1 1 1 2 1 1 1 1 1 1 1 0 0 |
| *Conopea minyrostrum* | 1 1 1 1 1 0 1 1 ? 1 0 0 ? ? 1 1 ? 1 1 1 1 0 1 1 1 1 0 1 |
| *Conopea mjobergi* | 1 1 1 1 1 0 1 0 ? 0 0 0 1 ? 1 1 1 1 1 1 0 0 1 0 ? ? ? 1 |
| *Conopea navicula* | 1 1 1 1 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 2 0 1 |
| *Conopea proripiens* | 1 1 1 1 1 0 1 1 ? 0 0 0 1 ? 1 1 1 1 1 1 1 0 0 0 1 1 ? 1 |
| *Conopea pygmaea* | 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 |
| *Conopea sabangensis* | 1 1 1 1 1 0 1 1 ? 0 0 0 ? ? 1 1 ? 1 1 1 1 0 1 1 1 0 0 1 |
| *Conopea saotomensis* | 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 1 1 1 0 0 0 1 |
| *Conopea scandens* | 1 1 1 1 1 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 |
| *Conopea sinensis* | 1 1 1 1 1 0 1 1 ? 0 0 0 1 ? 0 1 ? 1 1 1 1 0 0 0 1 0 0 1 |
| *Conopea squamosa* | 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 |
| *Conopea titani* | 1 1 1 1 1 0 1 1 1 0 0 0 1 1 1 1 1 1 1 1 1 0 0 0 1 1 0 1 |
| *Conopea willhearsti* | 1 1 1 1 1 0 1 1 1 1 1 0 ? ? 1 1 0 1 1 1 1 0 1 1 1 1 0 1 |
| *Acasta alcyonica* | 1 1 1 1 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 ? 2 1 1 |
| *Acasta alcyonicola* | 1 1 1 1 1 1 0 ? 0 0 0 ? 1 0 0 0 0 0 0 0 0 1 1 1 0 2 1 1 |
| *Acasta antipathidis* | 1 1 1 1 1 ? 0 ? 0 0 0 0 1 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 1 |
| *Acasta echinata* | 1 1 1 1 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 1 1 1 |
| *Acasta gregaria* | 1 1 1 1 1 1 0 1 0 0 0 1 1 0 0 0 0 0 0 1 1 0 1 0 ? ? ? 1 |
| *Acasta hirsuta* | 1 1 1 1 1 1 0 ? 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 1 1 1 |
| *Acasta purpurata* | 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 1 0 ? 0 1 0 0 ? 2 ? 1 |
| *Acasta umitosaka* | 1 1 1 1 1 1 0 1 0 0 0 1 0 - 0 0 0 0 0 0 0 1 1 0 ? ? ? 1 |
| *Acasra vipensis* | 1 1 1 1 1 1 0 ? 0 0 0 1 ? ? 0 0 0 0 0 0 0 1 1 1 1 1 1 1 |
| *Acasta vivicava* | 1 1 1 1 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 |

In our analysis, *C. exothobasis* and *C. merrilli* form a sister clade to the other species of *Conopea* s.s. (Fig. 15D). Although *C. exothobasis* possesses a scutum with a rounded basitergal margin, differing from the sinusoid basitergal margin found in other species of *Conopea* s.s., it shares other common characters of *Conopea*, including an elongated boat-shaped basis, a rostrum with an elongated basal part, and a smooth/even margin of a small

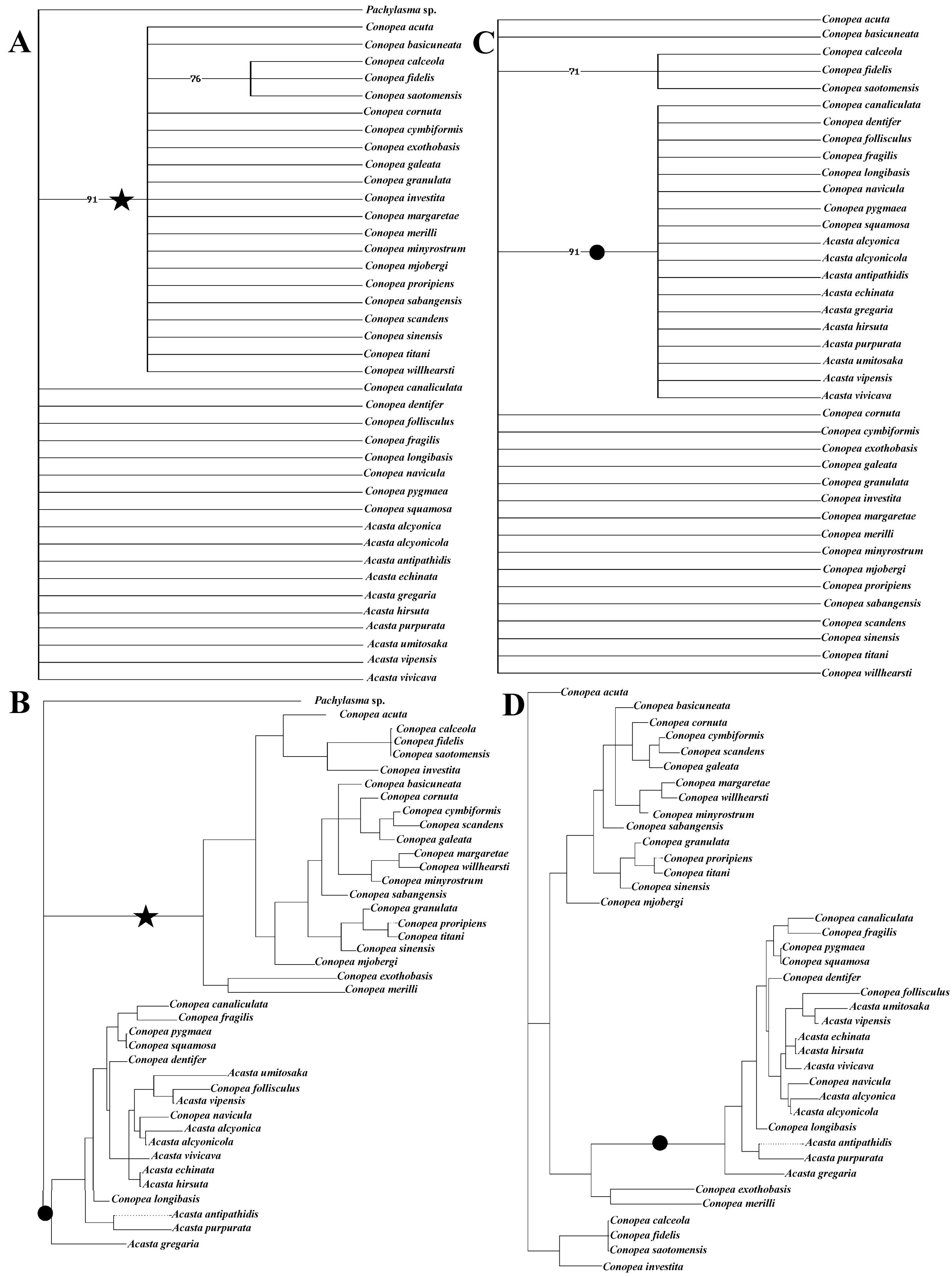


**FIGURE 15.** Phylogenetic reconstruction cladograms of the genus *Conopea* s.l. and coral inhabiting species of the genus *Acasta* and the species of the resulting genera, *Conopea* s.s. (node is indicated by star) and *Acasta* (node is indicated by circle), (all characters unordered and of equal weight; PAUP, Swofford 1998): (A), (B), with *Pachylasma* sp. as out-group; (C), (D), without out-group. (A), (C) Bootstrap 50% majority-rule consensus trees. Percentages at nodes denote frequency of occurrence among 100 trees. (B), (D) Neighbor-joining trees.

orifice. The morphology of *C. merrilli* does not fit either *Conopea* s.s. or *Acasta*. Although it posses quite a strong shell and a penis with a basidorsal point like *Conopea*, its shell is not elongated and it posses a wide orifice, a basis that is absolutely flat and tubiferous, a scutal basitergal margin that is straight, and inner sculpture of the opercular valves that differs from that found in *Acasta* and *Conopea*. Additionally, specimens of this species can attach not only to the alcyonacean but also to each other (Zullo 1966). Zullo (1966) supposed that this species may belong to the genus *Solidobalanus* and we also consider it as a representative of this genus.

Thus, the nominal genus *Conopea* s.l. includes species belong to three genera: *Conopea* s.s. (*C. acuta*, *C. basicuneata*, *C. calceola*, *C. cornuta*, *C. cymbiformis*, *C. exothobasis*, *C. fidelis*, *C. galeata*, *C. granulata*, *C. investita*, *C. margaretae*, *C. minyrostrum*, *C. mjobergi*, *C. proripiens*, *C. sabangensis*, *C. saotomensis*, *C. scandens*, *C. sinensis*, *C. titani* and *C. willhearsti*.), *Acasta* (*A. canaliculata*, *A. dentifer*, *A. folliculus*, *A. fragilis*, *A. longibasis*, *A. navicula*, *A. pygmaea* and *A. squamosa*) and *Solidobalanus* (*S. merrilli*).

Based on these data we have modified a diagnosis for the genus *Conopea* as follows: Archaeobalanids with strong, firm shells that cannot be disarticulated to separate compartments; shell plates and opercular valves often thickened; shell orifice not dentate, with even margin; rostral and sometimes carinal plates often elongated in basal part; basis often elongated and clasping axis of the host coral; outer surface of parietes smooth, without conspicuous projections, inner surface with longitudinal ribs prominent over basal margin; several species having tubiferous parietes; radii solid, with summits parallel to basal margin of parietes and sutural margins denticulated; margin of basis with deep, rounded pits interlocking with corresponding inner ribs of parietes, pits may correspond to inner longitudinal tubes in several species (tubiferous basis); scutum with simple growth ridges without longitudinal striation or ribs, with sinusoid basitergal angle, distinct pit of depressor muscle often situated directly on basitergal margin; annuli of anterior rami of cirri III and IV often armed with sharp denticles; penis with developed basidorsal point. The genus *Conopea* includes 20 epizoic species from tropical and temperate seas, inhabiting alcyonacean and antipatharian corals. Type species *Conopea calceola* (Ellis, 1758).

The suggested phylogeny presented in this study is based on morphological data, and in some respects it does not agree with traditional systematics. The results should be supported by molecular analyses. Regrettably not all taxa used in the analyses are suitable for molecular study. A collective effort is needed to enable molecular analyses that can confirm the present analyses.

## Key to species of the genus *Conopea*

| | | |
|---|---|---|
| 1 | Tergum with broad and square apex | *C. galeata* |
| - | Tergum with sharp or blunt but not square apex | 2 |
| 2 | Tergum with curved beak-shaped apex | 3 |
| - | Tergum without curved beak-shaped apex | 7 |
| 3 | Plates and basis solid | 4 |
| - | Plates and basis tubiferous | 5 |
| 4 | Spur long, about 1/3 width of tergum | *C. mjobergi* |
| - | Spur short, about ½ width of tergum | *C. acuta* |
| 5 | Tergum with developed crests of depressor muscle | *C. investita* |
| - | Tergum with reduced crests of depressor muscle | 6 |
| 6 | Spur of tergum smooth, without denticles on distal end | *C. fidelis* |
| - | Spur of tergum with denticles on distal end | *C. calceola, C. saotomensis** |
| 7 | Shell with two lateral horns at basal parts of carinolaterals 1 | *C. cornuta* |
| - | Shell without lateral horns | 8 |
| 8 | Radii narrow, not exposed | *C. sinensis* |
| - | Radii broad, exposed | 9 |
| 9 | External surface of parietes with dense small granules | *C. granulata* |
| - | External surface of parietes without granules | 10 |
| 10 | Both rostral and carinal parts of basis significantly elongated | 11 |
| - | Basis not significantly elongated in carinal part | 15 |
| 11 | Basal part of carina not elongated, scutum with rounded, not sinusoidal basitergal margin | *C. exothobasis* |
| - | Basal parts of both rostrum and carina conspicuously elongated, scutum with sinusoidal basitergal margin | 12 |
| 12 | Shell with extremely elongated carinal and rostral basal parts conspicuously longer than central part | 13 |
| - | Elongated basal rostral and carinal parts of shell comparable in length with central part | 14 |
| 13 | Spur of tergum about 2/3 of width of basal margin, with truncated end | *C. titani* |
| - | Spur of tergum about ½ of width of basal margin, with rounded end | *C. margaretae* |

| | | |
|---|---|---|
| 14 | Rostrum shorter than carina | *C. minyrostrum* |
| - | Rosrum significantly longer than carina | *C. proripiens* |
| 15 | Basis solid | 16 |
| - | Basis tubiferous | 18 |
| 16 | Rostrum greatly elongated, about ½ or more of total shell length | *C. basicuneata* |
| - | Length of rortrum less than ½ of total length of shell | 17 |
| 17 | Segments of anterior ramus of cirrus III armed with sharp denticles | *C. sabangensis* |
| - | Segments of anterior ramus of cirrus III lack armament of sharp denticles | *C. cymbiformis* |
| 18 | Spur of tergum not separated from basiscutal margin distinctly, cirri III, IV lack armament of sharp denticles | *C. scandens* |
| - | Spur of tergum separated from basiscutal margin, cirri III, IV with armament of sharp denticles | *C. willhearsti* |

* *C. calceola* and *C. saotomensis* represent a complex of cryptic species and cannot be distinguished morphologically (Carrison-Stone *et al.*, 2013)

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