



## Oxynaspididae (Crustacea, Cirripedia): phylogenetics and evolutionary ecology, with descriptions of three new genera and six new species

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### Abstract

A phylogenetic analysis of the Cirripedia family Oxynaspididae yields four monophyletic clades. These are designated as four genera, *Oxynaspis* Darwin, 1852, *Archoxynaspis* gen. nov., *Pycnaspis* gen. nov. and *Minyaspis* gen. nov. Five new species from Astrolabe Reef in Fiji (*Oxynaspis perekrestenkoi* sp. nov., *O. joankovanae* sp. nov., *Minyaspis amylanae* sp. nov., *M. opreskoi* sp. nov. and *M. welchi* sp. nov.) and one from Palau (*Oxynaspis joandianae* sp. nov.) are described. A morphological character dataset and resulting phylogeny supporting the new generic divisions is presented. All but two of the 24 species previously known and all six of the newly described species are intimately associated with antipatharians. *Pycnaspis connectens* was described by Broch (1931) as “fixed to a silicious sponge.” A list of species’ ranges and their known hosts is presented. The earliest known possible antipatharian in the fossil record is Miocene, much later than the Eocene appearance of *Archoxynaspis eocenica* (Withers, 1935). Therefore, the symbiosis of oxynaspidids with antipatharians may have evolved only since the Miocene. However, given the dubious fossil record of antipatharians (known only from a single specimen of uncertain affinity from Miocene Italy) the time of the first antipatharian/oxynaspidid symbiosis is uncertain.

**Key words:** *Archoxynaspis* gen. nov., *Pycnaspis* gen. nov., *Minyaspis* gen. nov., symbiosis, barnacle, black coral, Antipatharia, Cirripedia

## Introduction

Darwin (1852) proposed the genus *Oxynaspis*, placing it within the family Lepadidae. The name is derived from the Greek *oxyno*, to sharpen, and *aspis*, shield, after the pointed scutum of *Oxynaspis celata*, the type species of the genus. Darwin based the genus on the presence of five capitular plates and the medial position of the scutal umbo, derived from growth proceeding from the upper and lower edges of the primordial plate. Darwin (1852) observed that this pattern of scutal growth was closer to that in *Scalpellum* (umbo located medially on occludent margin) than that in *Lepas* (umbo basal). However, *Oxynaspis* is similar to *Lepas* in having only five capitular plates, lacking the lateral plates, rostrum, and sub-carina of *Scalpellum* and the whorl(s) of other small plates around the lower part of the capitulum that occur in various other scalpellomorphs. Darwin (1852: 134) concluded his description of the genus *Oxynaspis*, “In natural position, it appears to lead from *Scalpellum* through *Poecilasma* to *Lepas*.” In other words, Darwin placed *Oxynaspis* as an evolutionary intermediate between the multi-plated *Scalpellum* and the more evolved five-plated lepadomorphs, *Poecilasma* and *Lepas*.

This evolutionary polarity has not been generally accepted. Several authors, beginning with Broch (1922), considered the five-plated thoracicans to be more basal than those possessing additional plates (Newman *et al.* 1969; Newman 1987; Anderson 1994; Glenner *et al.* 1995; Buckeridge and Newman 2006). There is molecular-level data to support this hypothesis (Perez-Losada *et al.* 2004). However, more recent phylogenetic studies combining molecular and morphological data have suggested that at least some of the multi-plated stalked barnacles may be basal to the five-plated forms (Perez-Losada *et al.* 2008). The trees resulting from data used in these recent studies all place oxynaspidids well within the branches containing the other five-plated lepadomorphs.

Gruvel (1905) erected the subfamily Oxynaspinæ for five plated pedunculates with a medial scutal umbo. He placed Oxynaspinæ and Lepadinae within the family Pentaspidæ. Pilsbry (1907b) recognized Gruvel’s subfamily designation, transforming the spelling of Oxynaspinæ into Oxynaspidinae by correctly using the “-d” ending for “aspi”, and placed it within the family Lepadidae. Annandale (1909) followed Pilsbry (1907b), spelling the subfamily Oxynaspidinae. Nilsson-Cantell (1921) raised the sub-family to family level. However, Nilsson-Cantell (1921) and some authors of other subsequent papers mistakenly attributed the family name to Pilsbry (1907b) rather than Gruvel (1905), perhaps because of the difference in spelling. The most recent systematic arrangements unite the three families with five-plated capitula, Oxynaspididae, Lepadidae and Poecilasmatidae, within the Lepadiformes (Buckeridge and Newman 2006).

Given the cryptic nature of these barnacles, it is not surprising that several species were described not by a barnacle taxonomist, but by a coelenterate taxonomist studying the antipatharian collection of the British Museum. A. Knyvett Totton described one new species of *Oxynaspis* in his 1923 monograph on the antipatharians collected by the British Antarctic Expedition of 1910. He added six more in a later publication devoted entirely to oxynaspidids (Totton 1940).

## Material and methods

Specimens used in this study are archived in the research collections at the California Academy of Sciences, Invertebrate Zoology, San Francisco, California (CASIZ) and the Benthic Invertebrate Collections at Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California (SIO-BIC). The Fiji specimens were discovered and collected by hand using SCUBA during a visit to the Dravuni Field Station of the University of the South Pacific. The Palau barnacles were in the CASIZ collection of *Antipatharia*, attached to a coral specimen.

Dissections were performed under a Nikon SMZ-U microscope. SEM photos were taken with the LEO 1450VP SEM at the California Academy of Sciences (CAS). Light microscope photographs of preserved whole holotype specimens attached to their hosts were taken with the Leitz microscope photo-montage equipment at CAS. Photographs of representative examples of the mandible, maxilla I and cirrus I from paratypes of each newly described species were taken using a Spot Flex imaging system mounted on a Leica DMRB compound microscope. The underwater photo of living *Minyaspis amylaneae* on their host *Cirrihipathes anguina* was taken *in situ* in Fiji by RVS with Fujichrome film using a Canon EOS camera with 100 mm macro lens in an Ikelite camera housing and twin Ikelite 50 strobes. The 35 mm slide image of the living *Minyaspis amylaneae* was scanned using a Canon Canoscan 9950 flatbed scanner to create a digital file. Digital image files were adjusted using Adobe Photoshop.

No morphological elements of specimens (other than from color to grayscale for some) were changed by the Photoshop adjustments.

## Systematics

### Subclass Cirripedia Burmeister, 1834

### Order Thoracica Darwin, 1854

### Suborder Lepadiformes Buckeridge & Newman, 2006

### Family Oxynaspididae Gruvel, 1905

#### Genus *Archoxynaspis* gen. nov.

Figure 1

**Type species.** This mono-typic genus contains only the extinct species, *Archoxynaspis eocenica* (Withers, 1935).

**Type locality.** Middle Eocene of England.

**Diagnosis.** All 5 plates completely and thickly calcified; plates closely approximate, not separated by uncalcified areas. Scutum with distinct ridge running from umbo to apex. Tergum with distinct ridge running from umbo (apex) to basal tip. Scutal adductor muscle pit lacking. Carina with basal end recurved; basal margin rounded, not forked.

**Etymology.** From the Greek *arch-*, beginning, *oxyno-*, to sharpen, and *aspi-*, shield (scutum).

**Remarks.** The lack of an adductor muscle pit on the scutum of *Archoxynaspis* gen. nov. distinguishes it from *Minyaspidis* gen. nov., *Pycnaspis* gen. nov. and *Oxynaspis*. The lack of a scutal adductor muscle pit in *Archoxynaspis eocenica* and the two species used as outgroups in our phylogenetic analysis, *Dosima fascicularis* Ellis & Solander, 1786 and *Lepas anatifera* Linnaeus, 1758, indicate that it is a plesiomorphic character state. In addition, this earliest known representative of the Oxynaspididae exhibits other plesiomorphic capitular plate morphology such as complete shell coverage of the capitulum, with no gaps between calcified plates and the basal end of the carina rounded, not forked as it is in *Minyaspidis*.

#### Genus *Pycnaspis* gen. nov.

Figure 2

**Type species.** *Pycnaspis connectens* (Broch, 1931: 34–38).

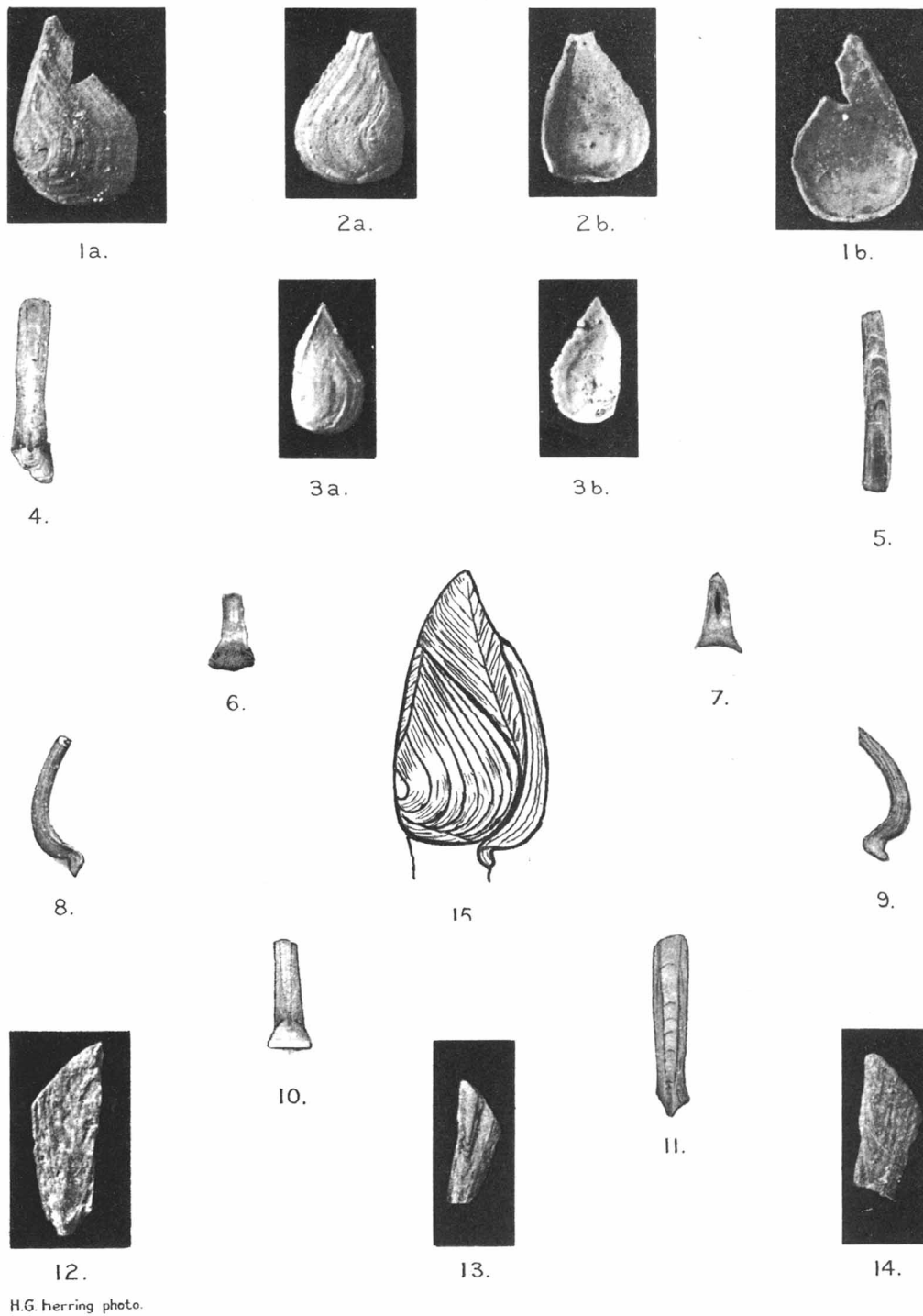
**Type locality.** “Kei-Islands: [Malaysia] St. 49. 5° 37’ S., 132°23’ E., 245 m., sand. May 3<sup>rd</sup>, 1922. One specimen fixed to a silicious sponge”.

**Material examined.** Holotype of *Oxynaspis connectens* Broch, 1931; ZMUC 6068, borrowed from the Zoological Museum of the University of Copenhagen, Denmark.

**Diagnosis.** All 5 plates completely calcified, approximate. Plates more heavily calcified and thicker than those in *Oxynaspis* and *Minyaspidis*. Scutum with shallow adductor muscle pit; lacking distinct ridge running from umbo to apex. Tergum proximal to scutum and carina, without prominent projections on margins or raised bumps on surface. Carinal surface smooth, basal end rounded, not forked. Attached to silicious sponge, not known to be a symbiont of Antipatharia.

**Etymology.** From the Greek, *pycn-*, solid, thick, strong, and *aspi-*, shield (scutum).

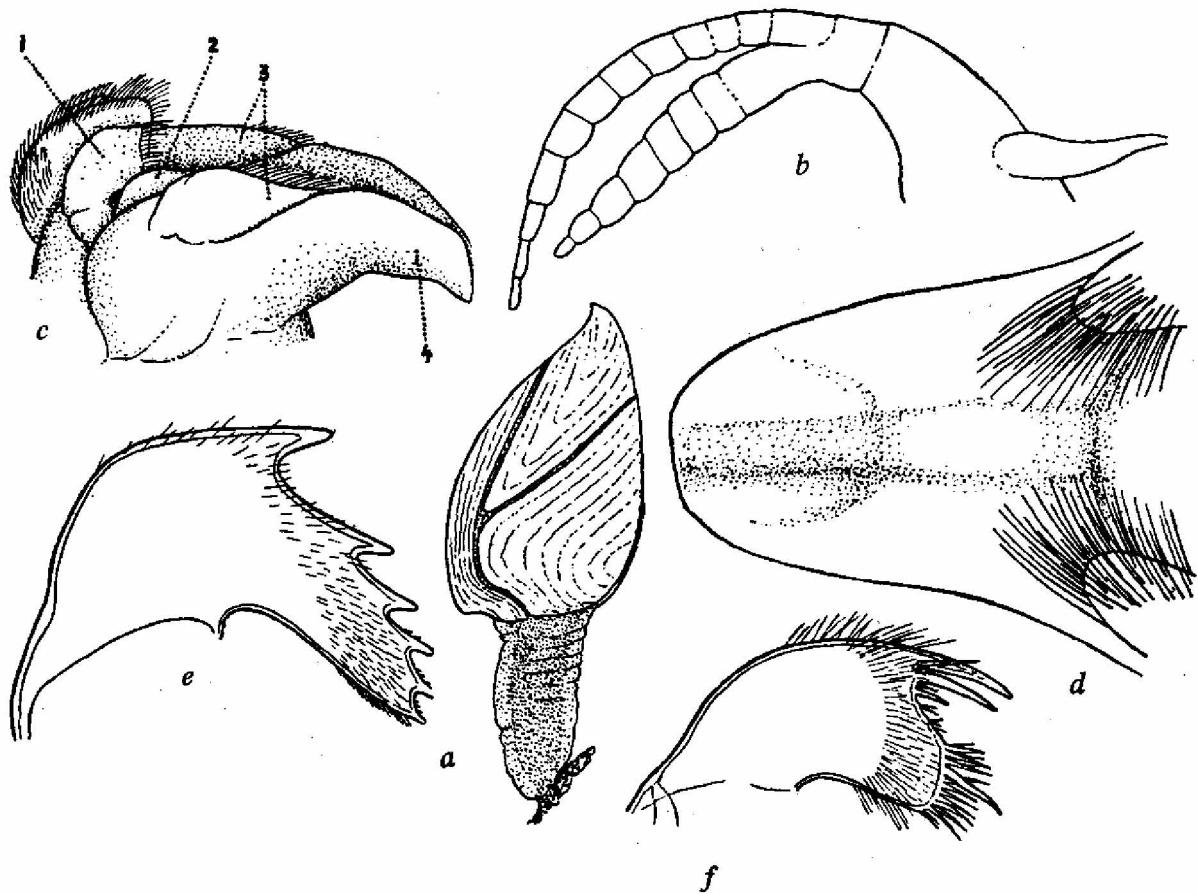
**Remarks.** As with *Archoxynaspis* gen. nov., there are no uncalcified areas between the capitular plates. The plates are not thin and fragile, as they are in *Oxynaspis* and *Minyaspidis* gen. nov., but thick and sturdy; Broch (1931: 34–35) states “On the whole the plates must be characterized as remarkably strong and thick; they are far stronger than in *Oxynaspis celata*.” *Pycnaspis* gen. nov. is similar to *Archoxynaspis* in retaining most of the plesiomorphic features of capitular plates, similar to those exhibited in *Lepas*, with the exception of the shallow adductor muscle pit on the scutum of *Pycnaspis connectens*. It is also noteworthy that Broch (1931) found his specimen on a sponge,



H.G. herring photo.

**LEPAS EOCENICA**, n. sp.

**FIGURE 1.** *Archoxynaspis eocenica* (Withers, 1935), copy of Plate XVI from Withers, 1935. Withers's original caption follows: EXPLANATION OF PLATE XVI. *Lepas eocenica*, sp. n. Middle Eocene, Ledian, Upper Bracklesham Beds: Selsey Bill, Sussex. Figs. 1-3. Scuta. Holotype (fig.1), a, outer view; b, inner view. Figs. 4-11. Carina (incomplete). Figs. 4, 10, outer view of two plates showing basal plate; fig. 5, outer view of apical part; figs. 6,7, inner view of two basal parts, showing variation in outward curvature of basal plate; figs. 8,9, side view of two plates, fig. 8 showing cross-section; fig. 11, plate with basal plate broken away. Figs. 12-14. Terga, outer views. Fig. 15. Reconstruction. (Figs. 1-15, x 6 diam.)



**FIGURE 2.** *Pycnaspis connectens* (Broch, 1931), copy of Figure 13 from Broch, 1931. Specimen in side view (a), first cirrus with basal filamentary appendage (b), mouthparts in side view (c), labrum seen from the ventral side (d), mandible (e), maxilla 1 (f).

not an antipatharian. Our examination of the type specimen did reveal a golden-brown chitin sheath covering the entire animal. We take this as further evidence that the chitin coverings commonly seen on all oxynaspidids are at least in part generated by the barnacle and not exclusively by the host antipatharian.

### Genus *Oxynaspis* Darwin, 1852 (emended)

**Type species.** *Oxynaspis celata* Darwin, 1852: 134–136.

**Type locality.** Madeira, Portugal, attached to an *Antipathes* sp.

**Diagnosis.** All 5 plates completely, or nearly completely, lightly calcified, approximate or nearly so, sometimes with small un-calcified chitinous areas between scuta and carina. Scutum with shallow adductor muscle pit. Tergum with umbo apical. Carina extending up between terga, basal end rounded or truncate, not forked. Obligate symbionts of antipatharians.

**Remarks.** The plates are more fragile than *Archoxynaspis* **gen. nov.** or *Pycnaspis* **gen. nov.** and are easily broken or chipped. They are completely calcified, as in *Archoxynaspis* and *Pycnaspis*, and are not reduced as in *Minyaspis* **gen. nov.** The basal end of the carina is not forked, as it is in *Minyaspis*. Previously described species referable to *Oxynaspis* s.s., ordered alphabetically by species, type localities and their known hosts are listed below:

*Oxynaspis alatae* Totton, 1940: 470–472; Mauritius; *Aphanipathes alata*

*Oxynaspis cancellatae* Totton, 1940: 468–470; Kei Islands [Malaysia]; *Aphanipathes cancellata*

*Oxynaspis celata* Darwin, 1852: 134; Madeira, Portugal; *Antipathes* sp.

*Oxynaspis celata hirtae* Totton, 1940: 474; West Indies; *Parantipathes hirta*  
*Oxynaspis celata indica* Annandale, 1909: 69–71; off Akyab, Northern Burma, 17 fathoms [31 m] and off Orissa, Bengal, India, 20 fathoms [37 m]; antipatharians  
*Oxynaspis celata japonica* Broch, 1922: 275–279; 33°41' N, 128°50' E [between South Korea and Kyushu, Japan]; 75 fathoms [137 m]; *Antipathes* sp.  
*Oxynaspis celata nova-zelandica* Broch, 1922: 275–279; 38°12' S, 149°40' E [east of Paradise Beach, Victoria, Australia]; 100–160 fathoms [183–293 m]; antipatharian  
*Oxynaspis gracilis* Totton, 1940: 472–473; West Indies; *Antipathella gracilis*  
*Oxynaspis pacifica* Hiro, 1931: 143–144; Seto, Prov. Kii; Toba, Prov. Shima; Misaki, Prov. Sagami, Japan; 70–200 fathoms [128–366 m]; *Antipathes* sp.  
*Oxynaspis rossi* Newman, 1972: 203–206; Cabo San Lucas, Baja California, Mexico and Santa Catalina Island, California, U.S.A.; *Antipathes* sp.

***Oxynaspis perekrestenkoi* sp. nov.**

Figures 3, 4

**Material examined.** Holotype: CASIZ 110166, 1 complete intact specimen attached to *Antipathes* cf. *A. pennacea* (CASIZ 113583); Fiji Is, Great Astrolabe Reef, S of Herald Passage, outside of reef, under ledge; 18° 46.26' S, 178° 27.79' E; depth: 24 m; coll. Robert Van Syoc, 4 June 1998 (RVS-405). Paratypes (all from holotype locality). CASIZ 113628, 1 specimen, shell on SEM stub, mouthparts and cirri on glass microscope slide. CASIZ 110123, 1 specimen. CASIZ 110124, 1 specimen. CASIZ 110140, 1 specimen. CASIZ 110143, 1 specimen. CASIZ 110144, 1 specimen. CASIZ 110152, 1 specimen. CASIZ 110153, 1 specimen. CASIZ 110155, 1 specimen. CASIZ 110156, 1 specimen. CASIZ 110165, 1 specimen. CASIZ 110184, 1 specimen. CASIZ 110185, 1 specimen. CASIZ 110187, 1 specimen. CASIZ 110188, 1 specimen. CASIZ 110190, 1 specimen. CASIZ 110191, 1 specimen. CASIZ 110193, 1 specimen. CASIZ 110194, 1 specimen. CASIZ 110125, 2 specimens. CASIZ 110134, 8 specimens. CASIZ 110141, 6 specimens. CASIZ 110175, 48 specimens. CASIZ 110189, 5 specimens. CASIZ 113622, 50 specimens. SIO-BIC C11214, 2 specimens from CASIZ 110175.

**Diagnosis.** Small bumps or protuberances on exterior of all plates (Fig. 3A–G); carina bent at about 90° angle at umbo (Fig. 3C), basal end broadly truncate, not forked or rounded (Fig. 3B,C); tergal scutal margin pectinate with small teeth, occludent margin with broad teeth with flattened ends, many of ends touching and fusing with neighboring teeth (Fig. 3D,E); scutal tergal margin toothed, basal margin nearly flat to slightly rounded and convex, occludent margin above umbo concave (Fig. 3F,G).

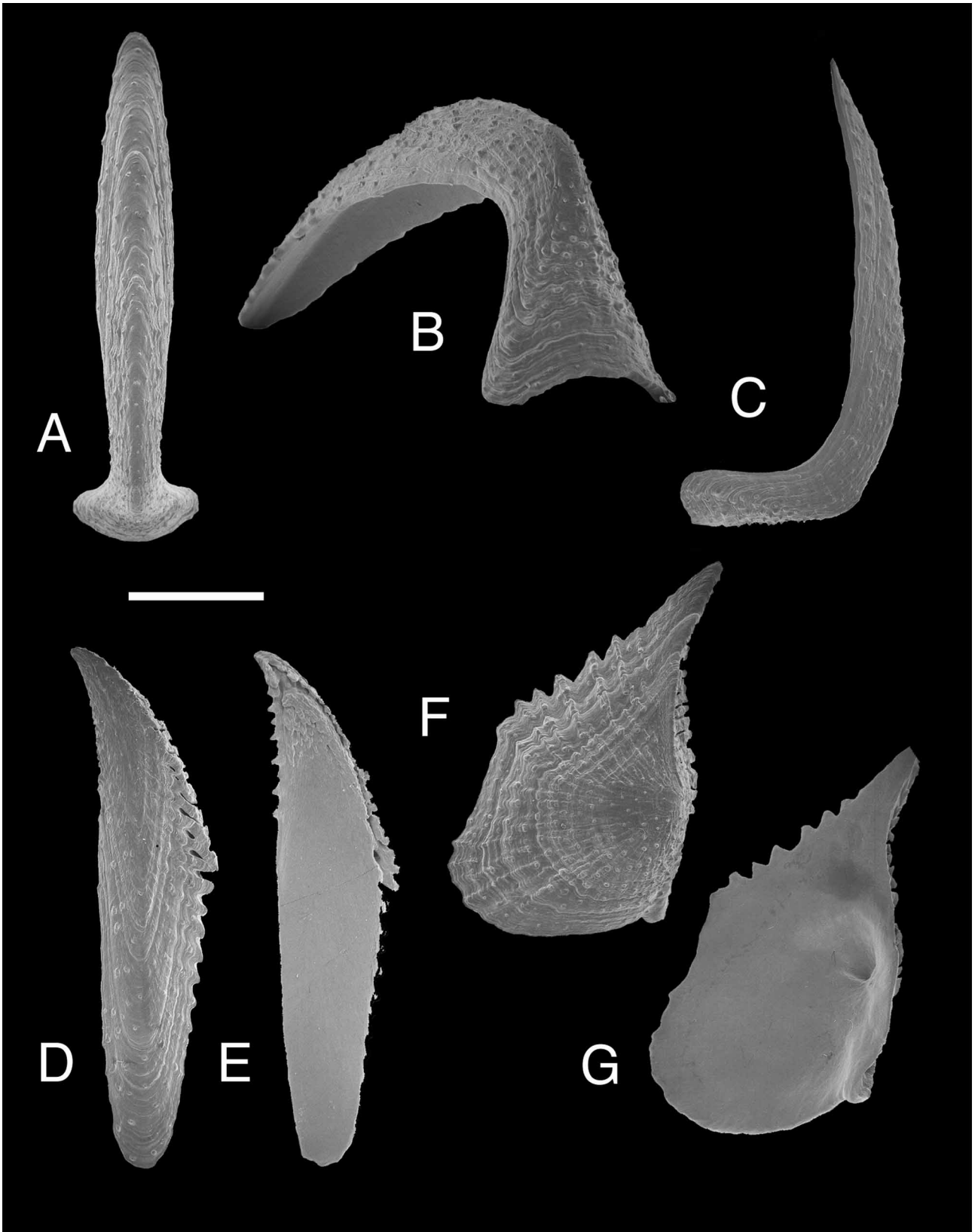
**Description.** Capitulum (Fig. 4A,E) with plates approximate except for space between scutum and carina; capitular height greater than twice its width; low growth ridges and small protuberances on all plates, protuberances extending into low radial ridges on scuta (Fig. 3A–G); covered with tissue, polyps and spines of host antipatharian and chitinous, golden-brown epicuticle (Fig. 4E).

Scutum (Fig. 3F,G) somewhat irregularly quadrangular; umbo subcentral, on occludent margin; basi-carinal angle nearly touching carina at basal end; tergal margin toothed and confluent along entire margin; occludent and basal margins forming angle about or greater than 90°; basal margin nearly flat to broadly convex with small notch or indentation close to occludent margin; entire occludent margin coincident with mantle margin; occludent edge with small tooth-like projections; carinal margin nearly straight; adductor muscle pit well-formed, distinct.

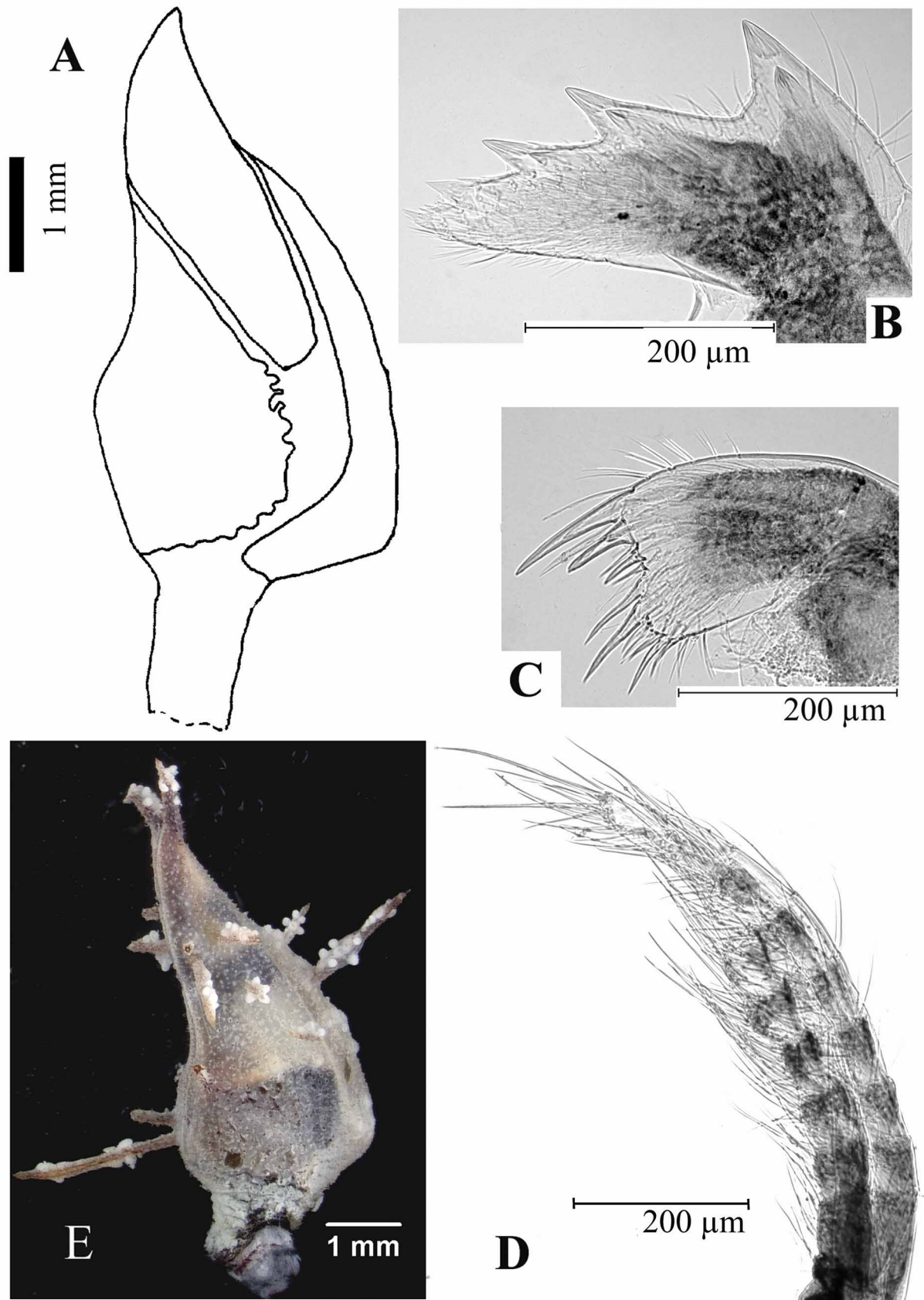
Tergum (Fig. 3D,E) somewhat triangular with rounded carinoscutal angle and shallowly curved carinal margin leading to apex; margins nearly touching carina and scutum; umbo at apex; scutal margin with tooth-like projections on half closest to occludent edge; occludent edge slightly convex, slightly curving away from occludent margin; occludent margin with small tooth-like projections producing pectinate edge (Fig. 3E).

Carina (Fig. 3A,B,C) slightly bent in upper portion, line from apex to umbo passing through part of tergam, similarly line from apex to basal/peduncular margin passing through scutum; umbo between lower one-fifth and lower one-third of total height; basal margin broadly truncate, not forked, not extending across peduncle; longer than scutum; extending up about 1/2 length of tergam; width narrowest at umbo and apex; not inflected between basal margin and umbo.

Labrum bullate.



**FIGURE 3.** *Oxynaspis perekrestenkoi* sp. nov. Paratype, CASIZ 113628. Carina, dorsal view (A), oblique view (B), side view (C). Tergum exterior (D), interior (E). Scutum exterior (F), interior (G). Scale bar equals 1 mm.



**FIGURE 4.** *Oxyaspis perekrestenkoi* sp. nov. Paratype CASIZ 110191; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 3 for plate details. Paratype CASIZ 113628; Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 110166; whole specimen, with host tissue and spines covering capitulum (E).



Mandible (Fig. 4B) with 5 teeth, first largest, second about one half length of first, third and fourth slightly shorter than second, fifth slightly shorter than fourth; face, superior and inferior margins of mandible setose.

First maxilla (Fig. 4C) lacking notch; superior part of cutting edge with slight bulge with 1 large and 1 medium spine protruding; cutting edge flat below bulge with many smaller and 2 longer spines; face, superior and inferior margins setose.

Cirrus I (Fig. 4D) with anterior ramus shorter than posterior; other cirri with equal, or nearly equal, rami. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	8	15	15	16	15	15
Post.	10	15	14	14	15	15
Ant.	7	13	16	16	15	15
Post.	10	13	15	16	16	16

Caudal appendages absent. Filamentary appendages absent at base of cirrus I. Dorsal filamentary appendages lacking.

**Etymology.** Named in honor of Michel Perekrestenko, friend and colleague at the California Academy of Sciences, in appreciation for his translations of Russian scientific literature for researchers at our institution, including the works of Memmi and Zevina cited herein.

**Remarks.** *Oxynaspis perekrestenkoi* **sp. nov.** is most similar morphologically to *O. joankovenae* **sp. nov.**, described below. It differs from *O. joankovenae* in possessing a tergum with a rounded, rather than flat, basal margin and in having the umbo of the scutum on the occludent margin in *O. perekrestenkoi*, which is not the case in *O. joankovenae*. Additionally, the scutum in *O. perekrestenkoi* has a carinal margin that extends out more toward the carina, such that a line from the carina apex to the carinal basal end passes through the scutum, which is not the case in *O. joankovenae*.

### *Oxynaspis joankovenae* **sp. nov.**

Figures 5, 6

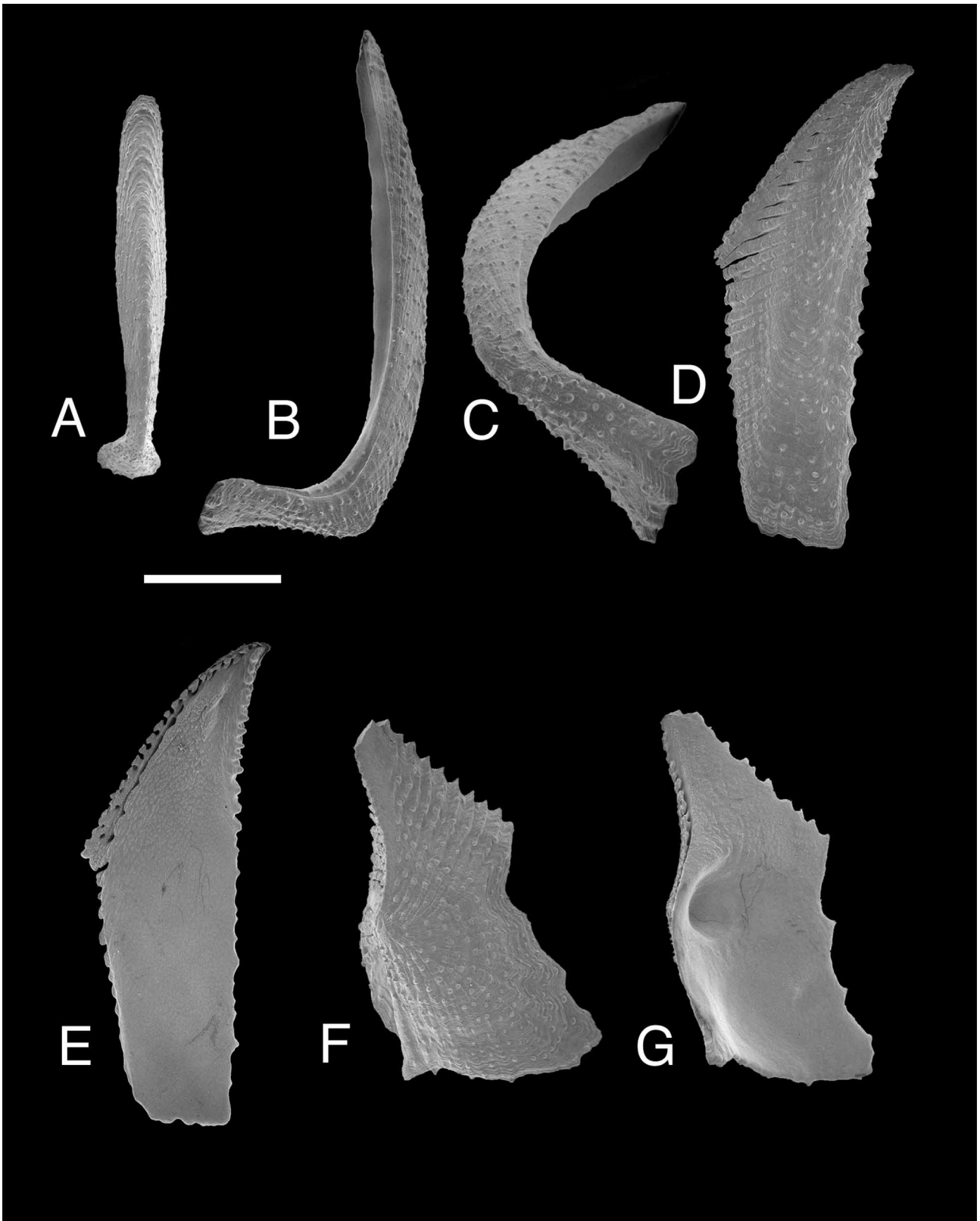
**Material examined.** Holotype: CASIZ 110147, 1 complete intact specimen, attached to *Antipathes myriophylla* Pallas (CASIZ 113586); Fiji Is, N Astrolabe Reef, SE side, wall and steep valley channels; 18° 40.54' S, 178° 31.34' E; depth: 24 m; coll. Robert Van Syoc, 19 June 1998 (RVS-440). Paratypes (all from holotype locality with exception of CASIZ 110174, as noted below): CASIZ 110128, 1 specimen, shell on SEM stub, mouthparts and cirri on glass microscope slide. CASIZ 110127, 1 specimen. CASIZ 110135, 1 specimen. CASIZ 110146, 1 specimen. CASIZ 110158, 1 specimen. CASIZ 110159, 1 specimen. CASIZ 110126, 5 specimens. CASIZ 110171, 3 specimens. SIO-BIC C11213, 2 specimens from CASIZ 110171. CASIZ 110174, 1 specimen; Fiji Is., Great Astrolabe Reef, N of Herald Passage, coral pinnacles outside of reef; 18° 45.06' S, 178° 27.99' E.; depth: 24–27 m.; 6 June 1998; coll. Robert Van Syoc (RVS-410); host specimen CASIZ 110173.

**Diagnosis.** Small bumps or protuberances on exterior of all plates; carina bent at about 90° angle at umbo, basal end truncate, not forked or rounded; tergum with teeth on all margins, teeth on occludent margin with flattened ends, some meeting and fusing along distal half, tergal spur flattened/truncated; scutum angular with teeth on tergal margin, carinal margin slightly concave and broadly scalloped, basal margin nearly straight with small shallow concavity near occludent margin (Fig. 5).

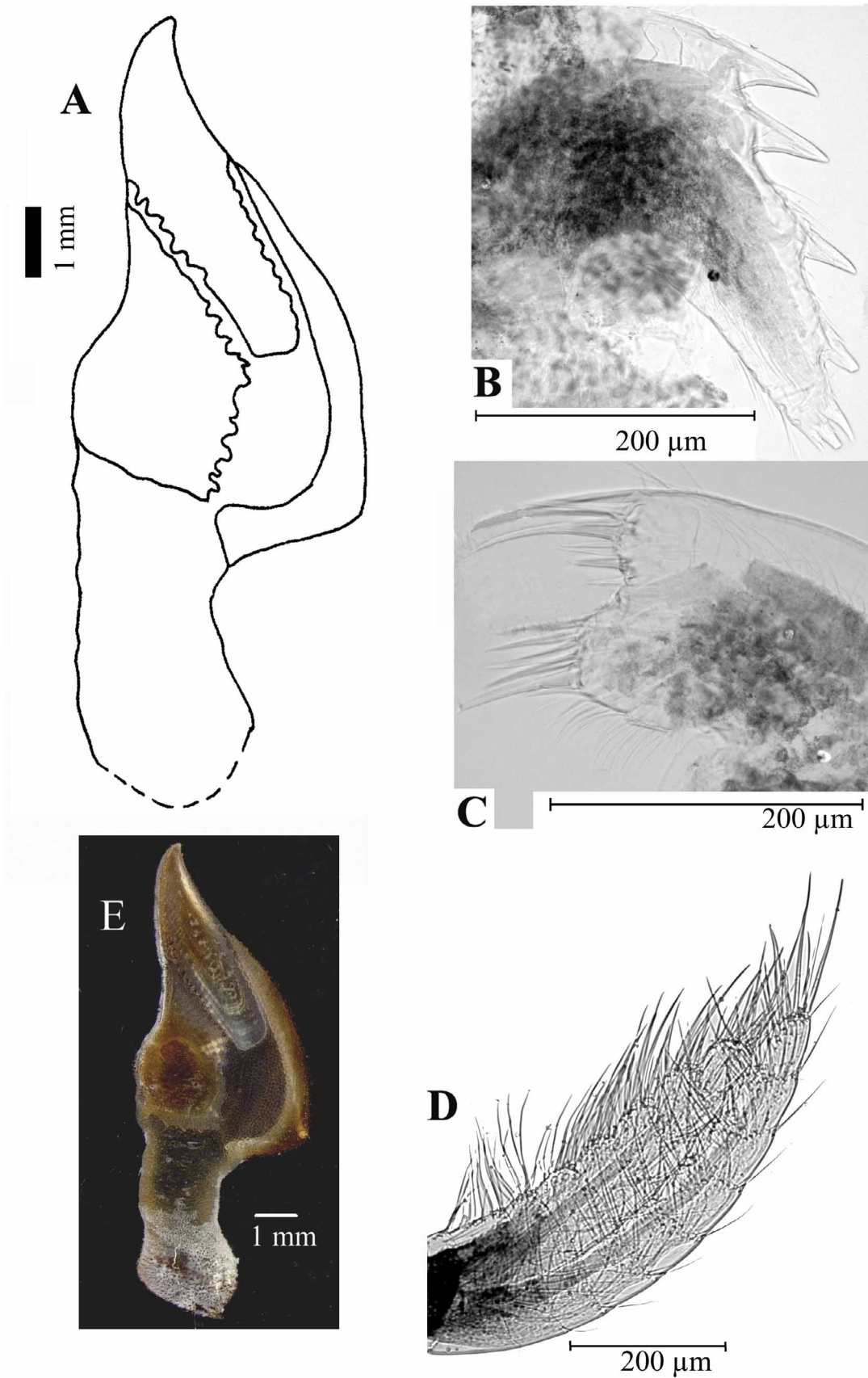
**Description.** Capitulum with plates approximate except for large uncalcified space between scutum and carina (Fig. 6A); capitular height less than twice its width; low growth ridges and small protuberances on all plates, protuberances extending into pronounced radial ridges and grooves on scuta and terga; covered with chitinous, golden-brown epicuticle.

Scutum (Fig. 5F,G; Fig. 6A) somewhat quadrangular with various irregularities along margins; umbo subcentral, inset slightly from occludent margin; basi-carinal angle of scutum proximal to and nearly touching basal end of carina; tergal margin toothed and confluent along entire tergum; occludent and basal margins forming an angle

about or greater than 90°; basal margin broadly convex with shallow notch or concavity near occludent edge; entire occludent margin coincident with mantle margin; occludent edge with small protuberances, concave above umbo, convex or irregular below umbo; carinal margin broadly concave with two broad projections; adductor muscle pit shallow.



**FIGURE 5.** *Oxyaspis joankovenae* sp. nov. Paratype, CASIZ 110128. Carina, dorsal view (A), side view (B), oblique view (C). Tergum exterior (D), interior (E). Scutum exterior (F), interior (G). Scale bar equals 1.5 mm for A; 1 mm for B, D, E, F, G; 750  $\mu$ m for C.



**FIGURE 6.** *Oxyaspididae joankovenae* sp. nov. Holotype CASIZ 110147; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 5 for plate details. Paratype CASIZ 110128: Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 110147; whole specimen, with host tissues removed from capitulum, golden-brown chitinous layer visible (E).

Tergum (Fig. 5D,E; Fig. 6A) broadly triangular; margins nearly touching carina and scutum; umbo at apex; scutal margin with rib-like projections, shallow notch close to occludent edge above scutal apex; occludent edge broadly convex, slightly curving away from occludent margin; occludent margin with small protuberances.

Carina (Fig. 5A,B,C; Fig. 6A) slightly curved in upper portion, line from apex to umbo passing outside carina, similarly line from apex to basal/peduncular margin passing through carinal margin of scutum; umbo between lower one-fifth and lower one-third; basal margin truncate, not forked, not extending across peduncle; longer than scutum; width narrowest at umbo and apex; extending up over one-half length of tergum; slightly inflected between basal margin and umbo.

Labrum bullate.

Mandible with 5 or 6 teeth (Fig. 6B); if 5-toothed, first largest, second about half length of first, third and fourth slightly shorter than second, fifth half length of fourth; if 6-toothed, first 2 teeth about same size, third slightly shorter, fourth and fifth slightly shorter than third, sixth about half length of fifth; face, superior and inferior margins of mandible setose.

First maxilla (Fig. 6C) with notch in superior half of cutting edge, notch about one third length of cutting edge, depth of notch about one seventh length of cutting edge; 2 large spines and 3–5 small spines above notch, many small to medium length spines and 1 large spine below notch; face, superior and inferior margins of maxilla setose.

Cirri I and II (Fig. 6D) with anterior ramus shorter than posterior ramus. Remaining cirri with near equal number of segments per ramus. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	9	11	13	15	13	14
Post.	10	13	12	13	15	14
Ant.	7	12	15	15	15	14
Post.	7	12	14	15	15	14

Caudal appendages uniarticulate. Filamentary appendages absent at base of Cirrus I. Dorsal filamentary appendages lacking.

**Etymology.** In honor of Joan Koven for her vital contributions to the establishment of the field station on Drauni for the study of Astrolabe Reef and for her assistance during the CAS Astrolabe Reef Expedition of 1998.

**Remarks.** Morphologically, the most similar species to *O. joankovenae* **sp. nov.** is *O. perekrestenkoi* **sp. nov.** The differences between the two species are explained in the Remarks section of *O. perekrestenkoi*.

### *Oxynaspis joandianeae* **sp. nov.**

Figures 7, 8

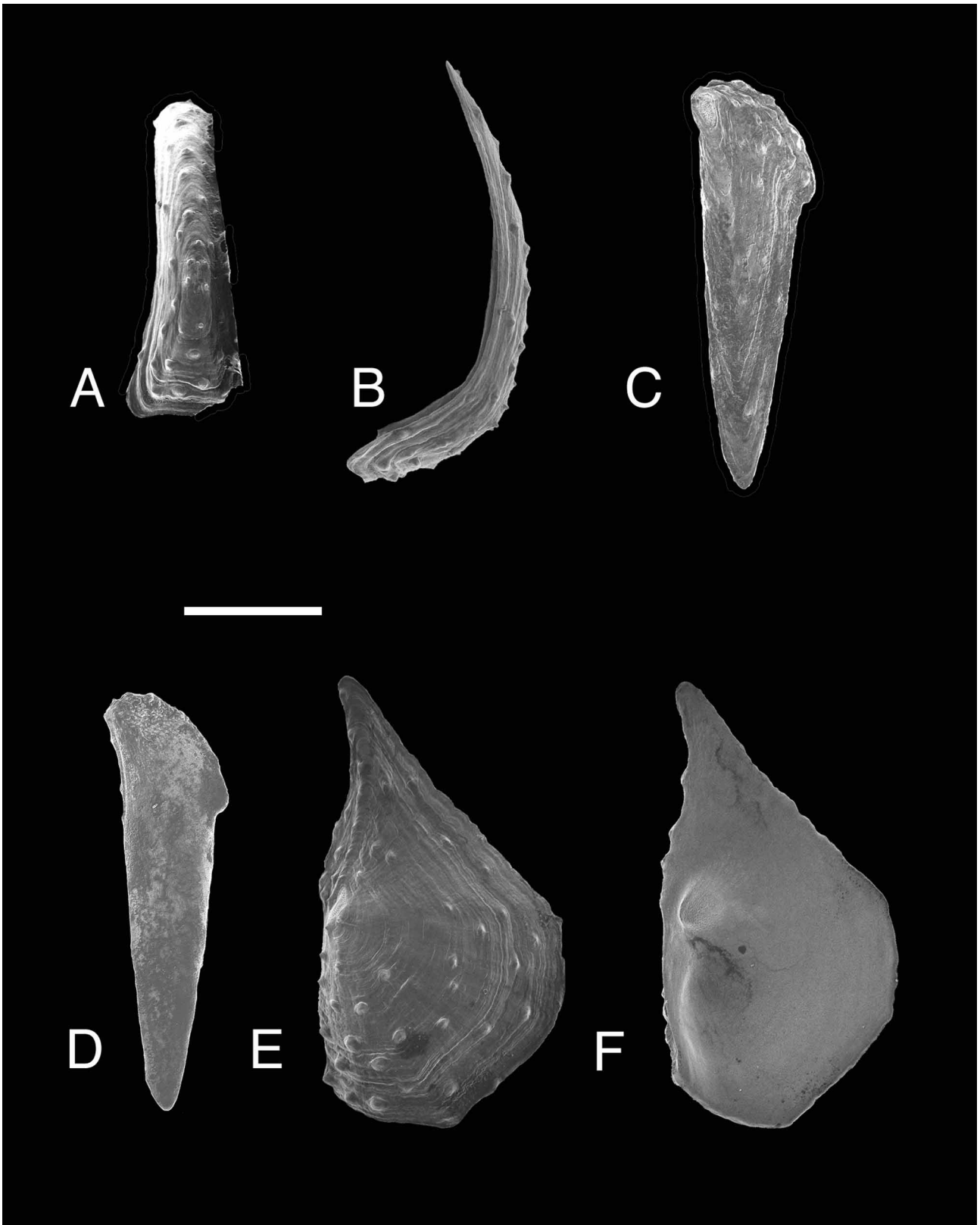
**Material examined.** Holotype: CASIZ 104150, 1 complete intact specimen, attached to *Antipathes* sp. (CASIZ 97824); Pacific Ocean, Caroline Is, Republic of Belau, Ngemelis, steep drop off, Rock Is, 18 m offshore; depth: 15–30 m [Sta. # 22]; 7 August 1974; coll. C. Himmelwright. Paratypes: CASIZ 104151, 5 specimens, attached to *Antipathes* sp. (CASIZ 97805); Pacific Ocean, Caroline Is, Republic of Belau, Ngemelis, Rock Is, steep drop off, 91 m offshore; depth: 41 m; 23 July 1974; coll. C. Himmelwright. CASIZ 172661, 1 whole specimen, same locality as CASIZ 104151. SIO-BIC C11212, 2 specimens from CASIZ 104151. CASIZ 104147, 1 specimen, mouthparts and cirri on glass microscope slide, plates on SEM stub, same locality as holotype.

**Diagnosis.** Bumps or protuberances scattered over exterior of all plates (Fig. 7); carina bent at slightly more than 90° angle at umbo, extending up about one-half length of scutum, basal end flat, not rounded or forked; tergum with occludent margin broadly rounded and slightly inflated at scutal and upper margins to form small protuberances extending slightly beyond margins, spur not truncate; scutum with occludent margin slightly concave above umbo; dorsal filamentary appendage present.

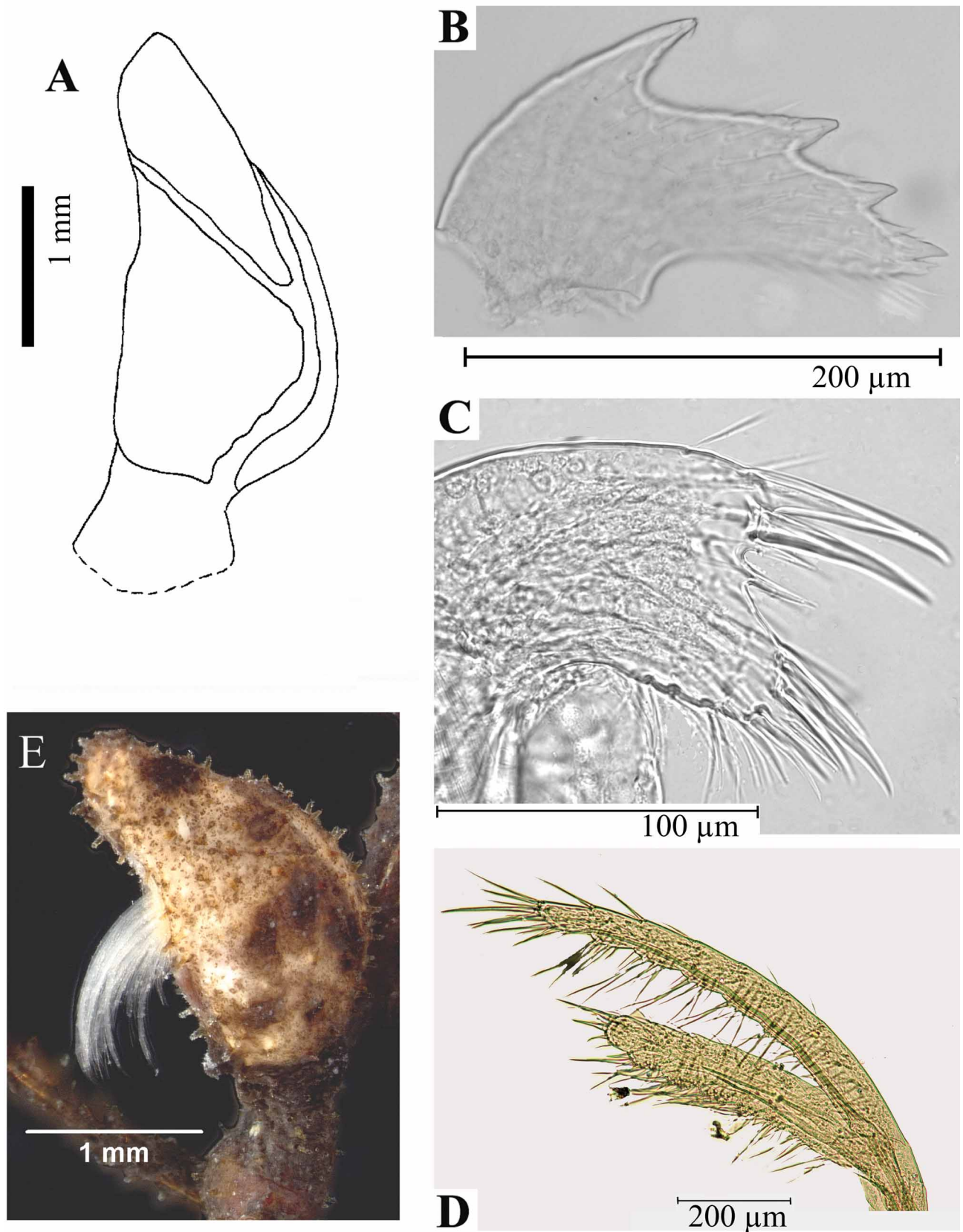
**Description.** Capitulum with all plates approximate (Fig. 8A); capitulum height about twice its width; low growth ridges and small protuberances on all plates; covered with chitinous, golden-brown epicuticle.

Scutum (Fig. 7E,F; Fig. 8A) carinal margin broadly convex, angled, sometimes giving appearance of 2 sides,

producing a 5-sided plate; umbo subcentral, near occludent margin; nearly touching carina along entire margin; tergal margin confluent along entire length; occludent and basal margins forming angle of about 90°; basal margin straight or slightly convex; entire occludent margin coincident with mantle margin; occludent margin with small protuberances; adductor muscle pit shallow.



**FIGURE 7.** *Oxynaspis joandiana* sp. nov. Paratype CASIZ 104147. Carina, dorsal view (A), side view (B). Tergum exterior (C), interior (D). Scutum exterior (E), interior (F). Scale bar equals 600  $\mu$ m.



**FIGURE 8.** *Oxynaspis joandiana* sp. nov. Paratype CASIZ 172661; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 7 for plate details. Paratype CASIZ 104147; Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 104150; whole specimen, attached to branch of host, with host tissue covering capitulum (E).

Tergum (Fig. 7C,D; Fig. 8A) broadly triangular; margins nearly touching carina and scutum; umbo at apex; scutal margin smooth, shallow concavity on scutal margin (at apex of scutum) near occludent margin; occludent edge slightly convex, slightly curving away from occludent margin; occludent margin with small protuberances.

Carina (Fig. 7A,B; Fig. 8A) curved in upper portion, line from apex to umbo passing outside of carina, similarly line from apex to basal/peduncular margin passing through scutum; umbo in lower one-fifth to one-third; basal margin truncate, not forked, not extending across peduncle; about same length as scutum; width narrowing from basal margin to apex; extending up along about one-half length of tergum; not inflected between basal margin and umbo.

Labrum bullate.

Mandible (Fig. 8B) with 3 major teeth along cutting edge, 3 minor teeth at inferior margin of cutting edge, first major tooth longest, second about half length of first, third slightly shorter than second; face of mandible and superior and inferior margins setose.

First maxilla (Fig. 8C) with broad, shallow notch on superior half of cutting edge; 2 large spines above notch, several spines along inferior half of notch, many shorter spines below notch; face of maxilla and superior and inferior margins setose.

Cirri I and II (Fig. 8D) with anterior ramus shorter than posterior ramus; other cirri with nearly equal or equal number of segments per ramus. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	9	13	13	15	17	15
Post.	11	13	13	15	16	15
Ant.	7	13	14	13	15	16
Post.	10	14	15	16	15	17

Caudal appendages absent. Filamentary appendages absent at base of Cirrus I.

One dorsal filamentary appendage present.

**Etymology.** Named in honor of Joan Diane Mitchell Dekelboun.

**Remarks.** *Oxynaspis cancellatae* Totton, 1940 and *O. gracilis* Totton, 1940 are the species most similar to *O. joandianae* **sp. nov.**, which differs from these two species in the presence of a shallow notch just proximal to the scutal/occludent margin (Fig. 7C,D). In addition, the carinal umbo position is between the basal one-fifth and basal one-third of the carina in *O. joandianae*, whereas it is in the basal one-fifth of the carina in *O. gracilis* and above the basal one-third in the carina of *O. cancellatae*.

### *Minyaspis* gen. nov.

**Type species.** *Minyaspis amylanae* **sp. nov.**

**Type locality.** Fiji Is, Great Astrolabe Reef, NE of Dravuni I., 18° 44.08' S, 178° 32.63' E, depth: 14 m.

**Diagnosis.** Scutum thin, fragile, not calcified along carinal and tergal margins, resulting in incomplete coverage of capitulum. Tergum sometimes incompletely calcified. Scutum with pronounced adductor muscle pit. Basal end of carina commonly forked, not rounded or truncate.

**Etymology.** *Miny-* from the Greek, *minys*, small, and *-aspis*, a shield.

**Remarks.** The species placed within this genus are generally defined by partially calcified capitular plates. Although one might consider this reduction in calcification to be a trait commonly found in cirripeds in obligate commensal relationships in which they are closely associated with host taxa tissues (e.g. sponge-inhabiting barnacles, see Kolbasov 1993; Van Syoc and Newman 2010), we contend that in the case of oxynaspidids the reduction of calcification is a synapomorphy of the genus *Minyaspis* **sp. nov.** Independent data sets, such as those derived from DNA sequences, could test this hypothesis. To date, however, we have not been able to obtain suitable tissues for DNA extraction from the great bulk of oxynaspidid species. Previously described species of *Oxynaspis*, newly referred to the genus *Minyaspis*, ordered alphabetically by species, with the known hosts of type specimens and type localities, are listed below.

*Minyaspid acapitula* (Foster and Buckeridge, 1995: 351–353); Réunion; 120 m; host not mentioned  
*Minyaspid aurivillii* (Stebbing, 1900: 675, pl. 74c); New Britain, Papua New Guinea; 40 fathoms [73 m.]; antipatharian  
*Minyaspid bocki* (Nilsson-Cantell, 1921: 228–230); Goto Islands, Kyushu, Japan; 230 m; “Hornkorallen”  
*Minyaspid faroni* (Totton, 1940: 483–486); Red Sea; *Antipathes lentispina*  
*Minyaspid floridana* (Pilsbry, 1953: 15–16); off Palm Beach, Florida; 50–60 fathoms [91–110 m.]; antipatharian  
*Minyaspid granti* (Totton, 1940: 480–482); 80 miles [133 km] south of Penang, Malaysia; antipatharian  
*Minyaspid michi* (Zevina, 1983: 1636–1637); Nazca Ridge; 25°45' S, 85°22' W; 240–210 m; host not mentioned  
*Minyaspid patens* (Aurivillius, 1892: 38, pl. III, Figs 1, 2); West Indies, Anguilla; *Antipathes*  
*Minyaspid pulchra* (Nilsson-Cantell, 1934: 46–54); 10°27'46" S, 126°4'30" E [south of Timor Island, Indonesia];  
“from telegraph cable”, no host mentioned in text, however the holotype is illustrated (Nilsson-Cantell, 1934: 48, Fig. 1a) attached to what appears to be an antipatharian axis  
*Minyaspid reducens* (Foster, 1982: 221–223); Fung Head, Sai Kung Peninsula, Hong Kong; 12 m; *Antipathella japonica* and *Cirripathes anguina*  
*Minyaspid sinensis* (Ren, 1983: 85–86, Fig. 2); East China Sea; 29°30' N, 126°00' E; 96 m; antipatharian  
*Minyaspid terranova* (Totton, 1923: 116–118); New Zealand; 189 m; *Antipathes lilliei*

### ***Minyaspid amylanae* sp. nov.**

Figures 9, 10

**Material examined.** Holotype: CASIZ 110160, 1 complete, intact specimen, attached to *Cirripathes anguina* Dana (CASIZ 113593); Fiji Is, Great Astrolabe Reef, NE of Dravuni I., 18° 44.08' S, 178° 32.63' E; depth: 14 m; 18 June 1998; coll. Robert Van Syoc (RVS-439). Paratypes: CASIZ 110132, 1 specimen, mouthparts and cirri on microslide; same locality as holotype. CASIZ 113621, 1 specimen, plates on SEM stub, no body; Fiji Is., N Astrolabe Reef, S end; 18° 40.54' S, 178° 31.34' E; depth: 14 m; 20 June 1998; coll. Robert Van Syoc (RVS-444). CASIZ 110132, 1 specimen, mouthparts and cirri on glass microscope slide; same locality as holotype. CASIZ 110133, 1 specimen; same locality as holotype. CASIZ 110167, 1 specimen; same locality as holotype. CASIZ 110136, 1 specimen; Fiji Is, N Astrolabe Reef, SW side, outer reef, sheer wall with shallow caves; 18° 40.17' S, 178° 31.04' E; 24–27 m; 13 June 1998; coll. Robert Van Syoc (RVS-426). CASIZ 113617, 1 specimen; Fiji Is, N Astrolabe Reef, SW side, outer reef, sheer wall with shallow caves; 18° 40.17' S, 178° 31.04' E; 24–27 m; 13 June 1998; coll. Robert Van Syoc (RVS-426). CASIZ 113618, 1 specimen; Fiji Is, N Astrolabe Reef, SW side, outer reef, sheer wall with shallow caves; 18° 40.17' S, 178° 31.04' E; 24–27 m; 13 June 1998; coll. Robert Van Syoc (RVS-426). CASIZ 113615, 3 specimens; Fiji Is, N Astrolabe Reef, SW side, outer reef, sheer wall with shallow caves; 18° 40.17' S, 178° 31.04' E; 24–27 m; 13 June 1998; coll. Robert Van Syoc (RVS-426); CASIZ 113616, 2 specimen; Fiji Is, N Astrolabe Reef, SW side, outer reef, sheer wall with shallow caves; 18° 40.17' S, 178° 31.04' E; 24–27 m; 13 June 1998; coll. Robert Van Syoc (RVS-426). CASIZ 113619, 2 specimens; Fiji Is, Great Astrolabe Reef, SE corner of outer reef; 18° 41.47' S, 178° 31.24' E; depth: 21 m; 22 June 1998; coll. Robert Van Syoc (RVS-448). CASIZ 113620, 21 specimens, Fiji Is, N Astrolabe Reef, S end; 18° 40.54' S, 178° 31.34' E; depth: 14 m; 20 June 1998; coll. Robert Van Syoc (RVS-444); SIO-BIC C11215, from CASIZ 113620.

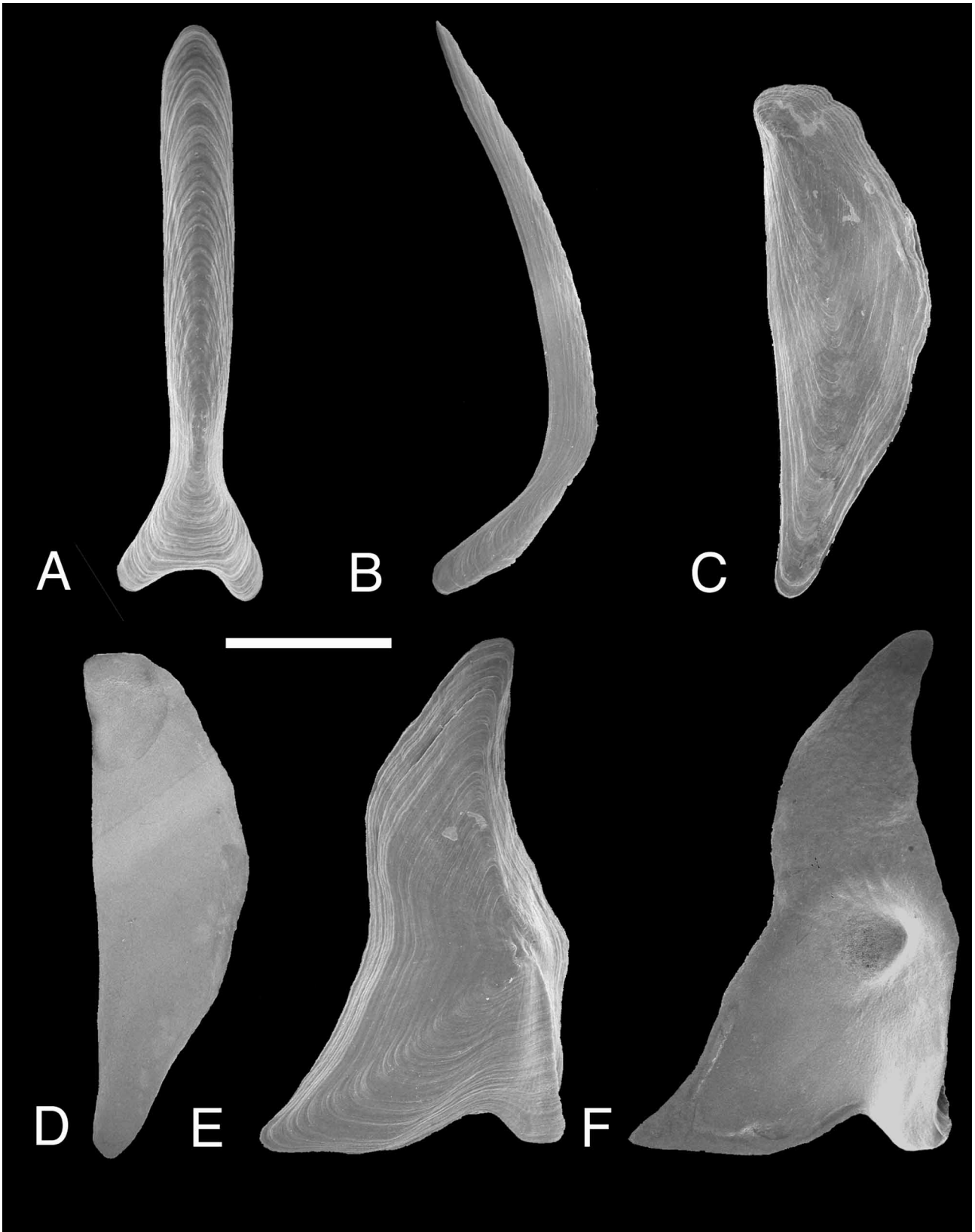
**Diagnosis.** Single filamentary appendages on either side at base of cirrus I; caudal appendages absent; tergum and scutum without toothed or jagged margins; carina forming angle greater than 90° at umbo, basal end with shallow fork (Fig. 9).

**Description.** Capitulum with large non-calcified area between scutum and carina (Fig. 10A); capitular height less than twice its width; low growth ridges on all plates; scuta and terga with opaque white markings approximate to adductor muscle attachment sites; covered with chitinous, golden-brown epicuticle.

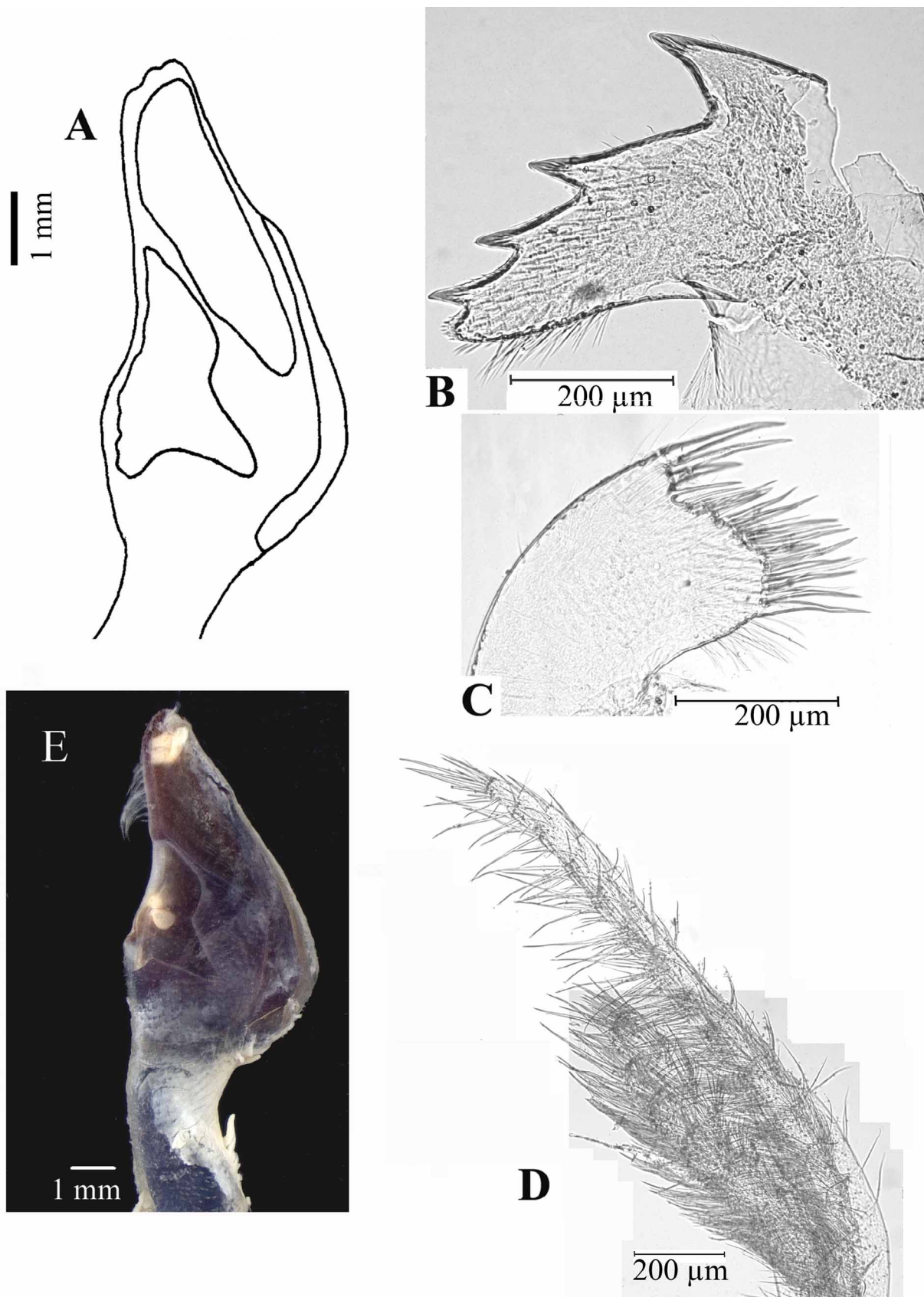
Scutum (Fig. 9E,F; Fig. 10A) irregularly shaped, not quadrangular; umbo subcentral, not on occludent margin; separated from carina by wide non-calcified area except near basal margin of carina; near tergum at slightly less than one-half length of tergum; occludent and basal margins forming an angle less than 90°; basal margin with well-defined concavity; occludent margin coincident with mantle margin; occludent edge smooth, broadly concave in upper half; carinal margin shallowly concave; adductor muscle pit shallow.

Tergum (Fig. 9C,D; Fig. 10A) broadly triangular; margins nearly touching carina and scutum; umbo below apex; scutal margin smooth; occludent edge broadly convex.





**FIGURE 9.** *Minyaspis amylanae* **sp. nov.** Paratype, CASIZ 113621. Carina, dorsal view (A), side view (B). Tergum exterior (C), interior (D). Scutum exterior (E), interior (F). Scale bar equals 1.5 mm for A, B, C, D; 1 mm for E and F.



**FIGURE 10.** *Minyaspis amylianae* sp. nov. Paratype CASIZ 110136; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 9 for plate details. Paratype CASIZ 110132; Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 110160; whole specimen, with host tissues covering capitulum except where abraded away from handling (E).

Carina (Fig. 9A,B; Fig. 10A) straight in upper portion, line from apex to umbo passing only through carina, similarly line from apex to basal/peduncular margin passing through scutum; umbo between basal one-fifth and one-third; basal margin deeply forked, extending less than halfway across peduncle; longer than scutum; width narrowest at umbo; extending up about one-half length of tergum; lacking shallow inflection between basal margin and umbo.

Labrum bullate.

Mandible (Fig. 10B) with 4 teeth and rounded fifth subtooth at cutting edge inferior margin, first tooth largest, second about half length of first, third and fourth slightly shorter; face of mandible and superior and inferior margins setose.

First maxilla (Fig. 10C) with deep notch in superior half of cutting edge; 2 large, long spines above notch, many slightly shorter spines below notch; setae in notch, on face of maxilla and along superior and inferior margins.

Cirrus I (Fig. 10D) with anterior ramus shorter than posterior; other cirri with rami about equal. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	6	12	16	14	16	17
Post.	10	12	16	14	15	17
Ant.	7	16	17	17	17	15
Post.	14	17	17	15	16	16

Caudal appendages absent. Single filamentary appendages absent at base of Cirrus I. Dorsal filamentary appendages lacking.

**Etymology.** Named in honor of Amy Lane Palenscar Van Syoc, who assisted in collecting specimens on the CAS Dravuni Astrolabe Reef Expedition of June 1998.

**Remarks.** Although they are somewhat similar in outward appearance, the terga of *M. reducens* (Foster, 1982) have prominently toothed edges while those of *M. amylandae* **sp. nov.** have smooth edges. *Minyaspis amylandae* falls between the *M. granti* (Totton, 1940/*M. bocki* (Nilsson-Cantell, 1921) and the *M. michi* (Zevina, 1983/*M. sinensis* (Ren, 1983) branches in the phylogenetic tree herein based on morphological characters (Fig. 15). It can be distinguished from these closest species by the proximity of the basal margins of the scutum and carina in *M. amylandae*. These two plates are not close to each other in any of the other four species. *Minyaspis amylandae* also has the carinal umbo above the basal one-fifth and below the basal one-third of the carina, whereas in *M. granti* and *M. bocki* the umbo is located in the basal one-fifth of the carina and in *M. michi* and *M. sinensis* it is located above the basal one-third of the plate.

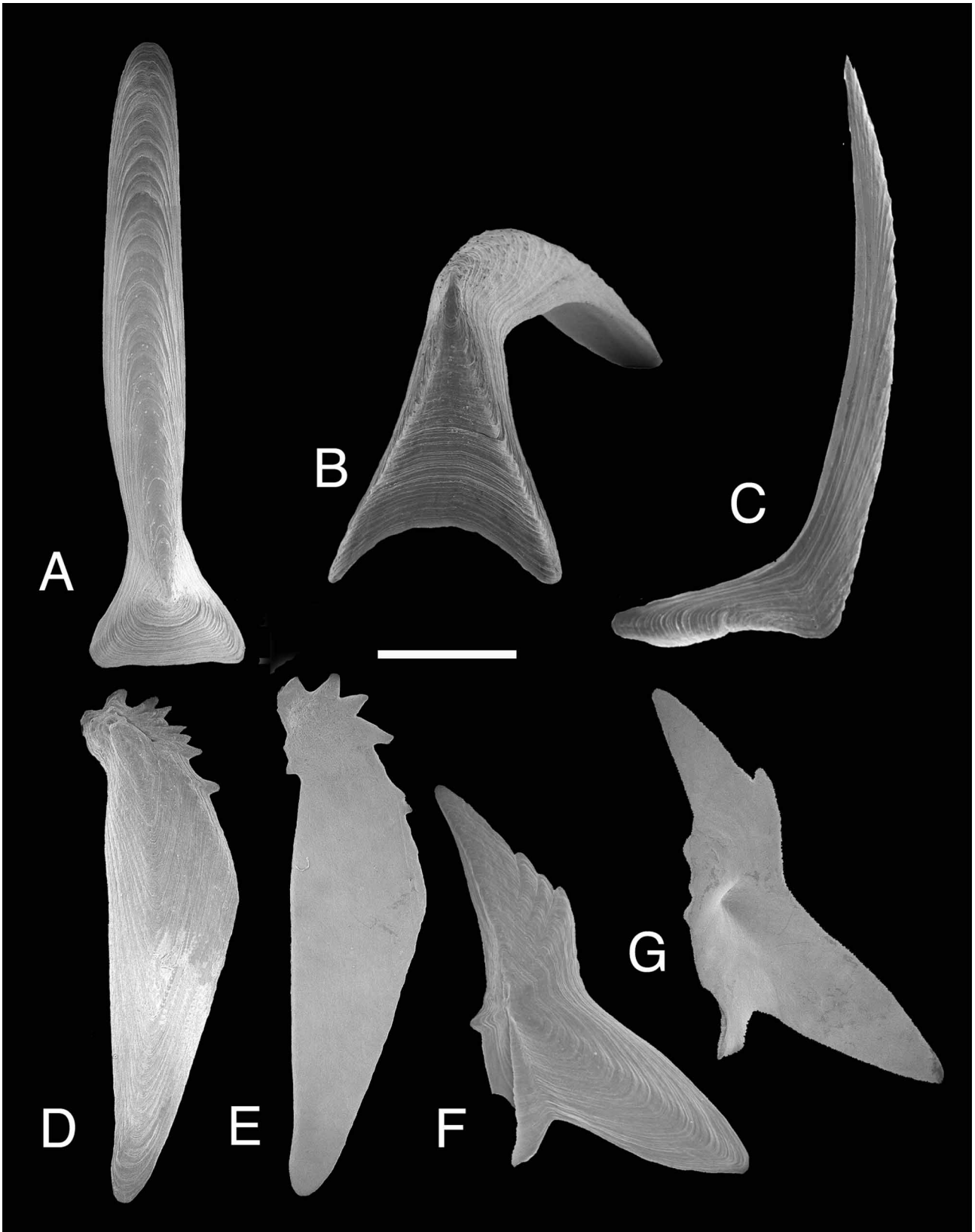
### *Minyaspis opreskoi* **sp. nov.**

Figures 11, 12

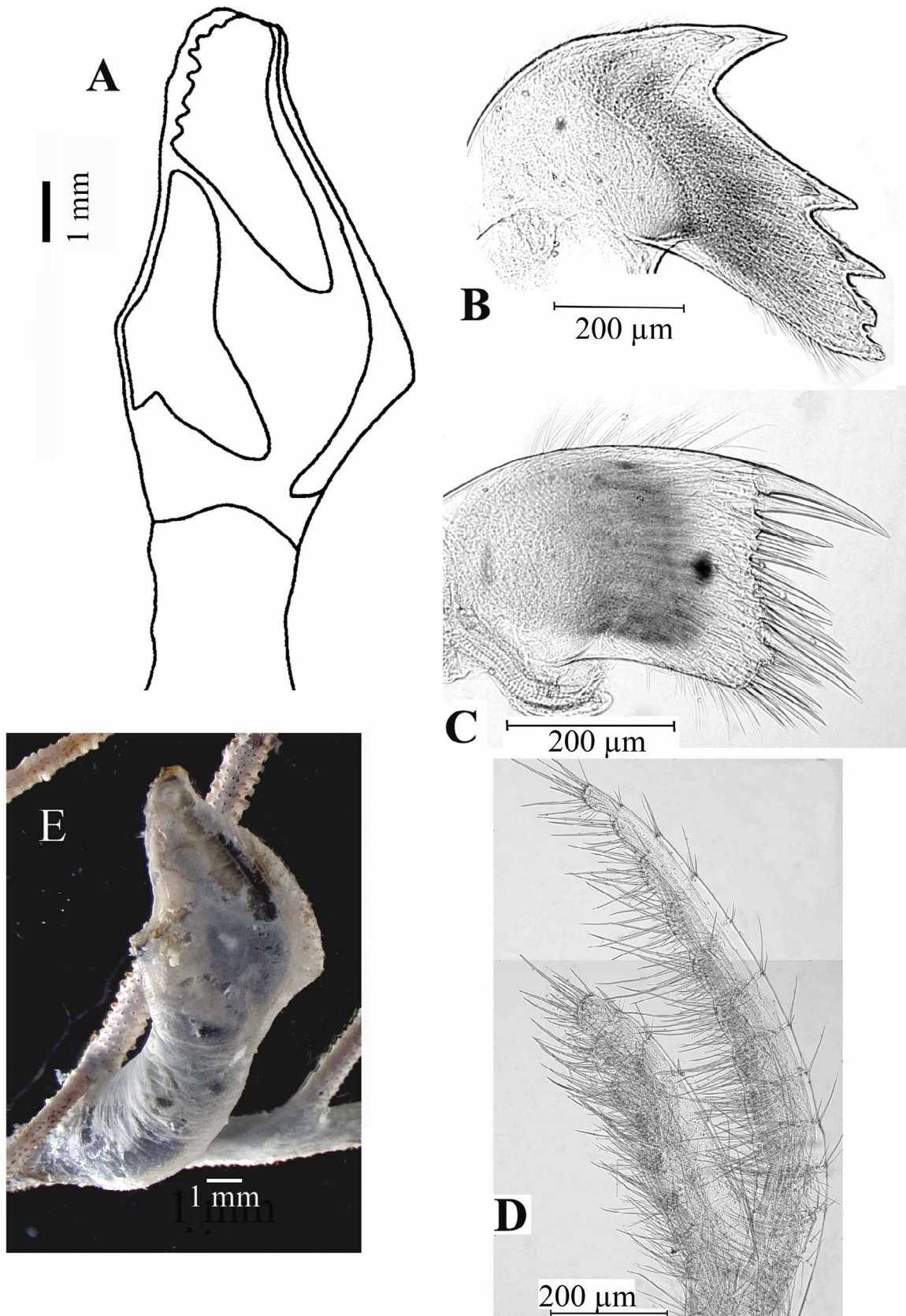
**Material examined.** Holotype: CASIZ 110163, 1 complete intact specimen, attached to *Antipathes* cf. *A. spinulosa* (Schultze) (CASIZ 113587); Fiji Is, N Astrolabe Reef, outer SW corner; 18° 40.54' S, 178° 31.34' E; depth: 17 m; 20 June 1998; coll. Robert Van Syoc (RVS-443). Paratypes (all from same locality as holotype): CASIZ 172660, 1 specimen. CASIZ 110162, 1 specimen, shell plates mounted on SEM stub, mouthparts and cirri on glass microscope slide, peduncle preserved in 75% EtOH. CASIZ 110161, 9 specimens. SIO-BIC C11216, from CASIZ 110161.

**Diagnosis.** Carina forming nearly 90° angle at umbo, basal end with broad, shallow fork (Fig. 11A,B); tergum with large tooth-like projections on occludent margin (Fig. 11D,E); scutum possessing sharply produced corners, basal margin deeply incised (Fig. 11F,G); filamentary appendages lacking on dorsum and at base of Cirrus 1.

**Description.** Capitulum with large non-calcified areas between plates; capitular height less than twice its width; low growth ridges on all plates; covered with chitinous, golden-brown epicuticle.



**FIGURE 11.** *Minyaspis opreskoi* sp. nov. Paratype CASIZ 110162. Carina, dorsal view (A), oblique view (B), side view (C). Tergum exterior (D), interior (E). Scutum exterior (F), interior (G). Scale bar equals 1.5 mm for A, C, D, E, F and G; 1 mm for B.



**FIGURE 12.** *Minyaspis opreskoi* sp. nov. Paratype CASIZ 172660; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 11 for plate details. Paratype CASIZ 110162, Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 110163; whole specimen, attached to branch of host, with host tissue covering capitulum (E).

Scutum (Fig. 11F,G; Fig. 12A) irregularly shaped, not quadrangular; umbo subcentral, not on occludent margin; separated from carina by wide non-calcified area except near basal margin of carina; near tergum at single point at apex; occludent and basal margins forming angle about or slightly greater than 90°; basal margin with deep concavity on half closest to occludent edge; entire occludent margin coincident with mantle margin; occludent edge with 1–3 large protuberances; carinal margin broadly concave in upper half; adductor muscle pit shallow; exterior lacking small protuberances.

Tergum (Fig. 11D,E; Fig. 12A) broadly triangular; margins nearly touching carina and scutum only near their respective apices; umbo not apical; scutal margin smooth; occludent edge irregular, with large tooth-like projections producing pectinate edge; exterior lacking protuberances.

Carina (Fig. 11A,B,C; Fig. 12A) curved in upper portion, line from apex to umbo passing outside of carina, similar line from apex to basal/peduncular margin not passing through scutum; umbo between lower one-fifth and lower one-third; basal margin truncate, not deeply forked, not extending across peduncle; longer than scutum; width narrowest at umbo; extending up more than one-half length of tergum; with shallow inflection between basal margin and umbo; exterior with small protuberances.

Labrum bullate.

Mandible (Fig. 12B) with 5 teeth, first largest, second and third about half length of first, fourth and fifth smaller; face of mandible, superior and inferior margins setose.

First maxilla (Fig. 12C) lacking notch, cutting edge very slightly depressed from superior margin until about midpoint of cutting edge where it bulges out, rounding broadly into inferior margin; face of maxilla, superior and inferior margins setose.

Cirrus I (Fig. 12D) with anterior ramus shorter than posterior; other cirri with rami of about equal length. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	10	13	19	19	18	20
Post.	13	14	19	19	18	20
Ant.	10	14	18	21	19	18
Post.	13	15	19	19	19	19

Caudal appendages uniarticulate with several spines on dorsal surface close to tips. Filamentary appendages lacking at base of cirrus I. Dorsal filamentary appendages lacking.

**Etymology.** Named for Dennis Opresko for his work on antipatharian taxonomy and his identifications of the host taxa of the cirriped species described herein.

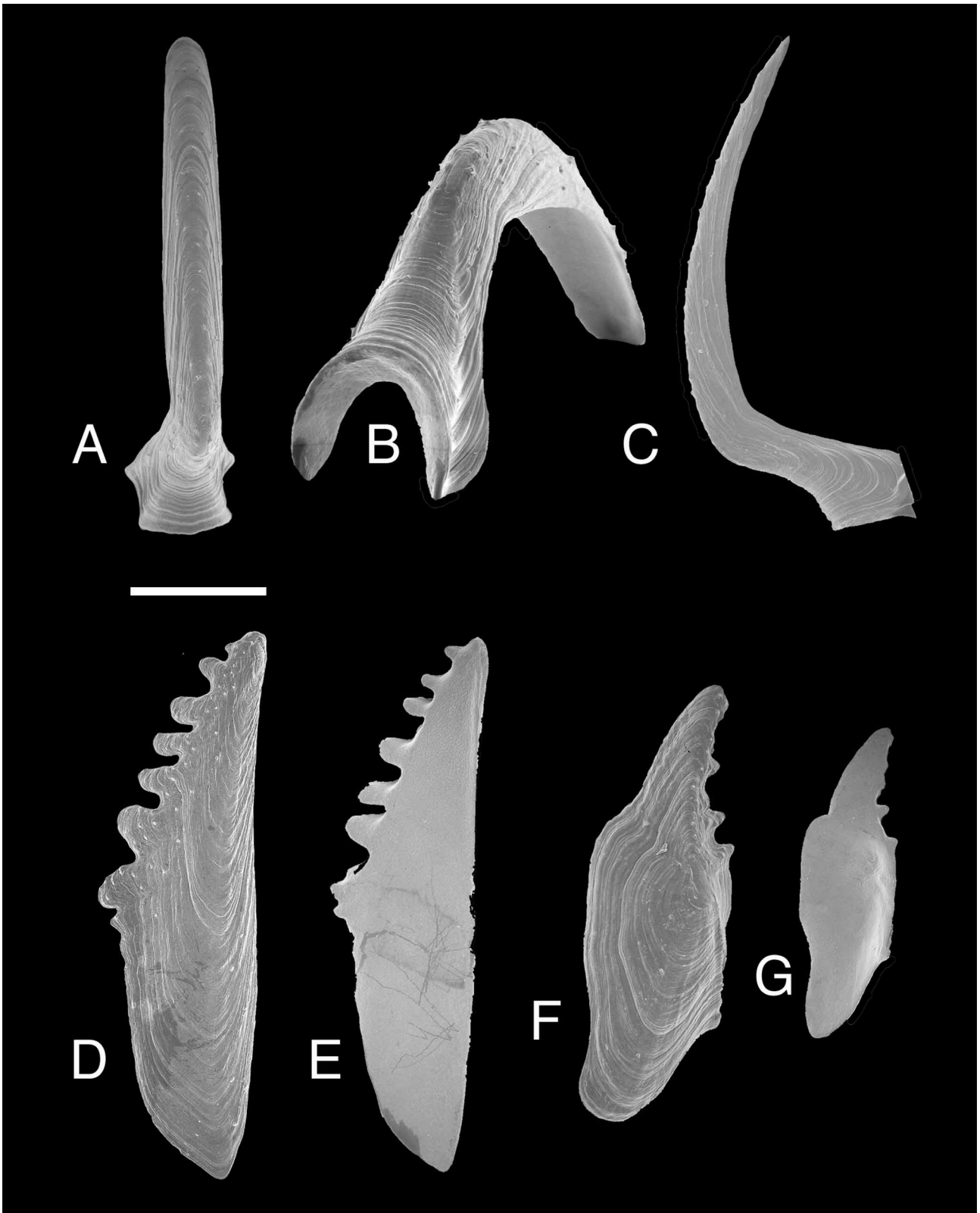
**Remarks.** *Minyaspis opreskoi* **sp. nov.** lies closest to the branch of *M. aurivilli* (Stebbing, 1900) and *M. welchi* **sp. nov.** in our phylogenetic tree (Fig. 15). It differs from these two taxa by having the scutum with a smooth occludent margin and external surface, without teeth or protuberances (Fig. 11E). The tergum of *M. opreskoi* is also smooth on the external surface and along the scutal margin (Fig. 11C). The tergal umbo on *M. opreskoi* is not apical (Fig. 11C); however, it is apical in *M. aurivilli* and *M. welchi*. Similarly, the carinal base of *M. opreskoi* is not inflected (Fig. 11B), whereas it is inflected in *M. aurivilli* and *M. welchi* (Fig. 13A–C).

### *Minyaspis welchi* **sp. nov.**

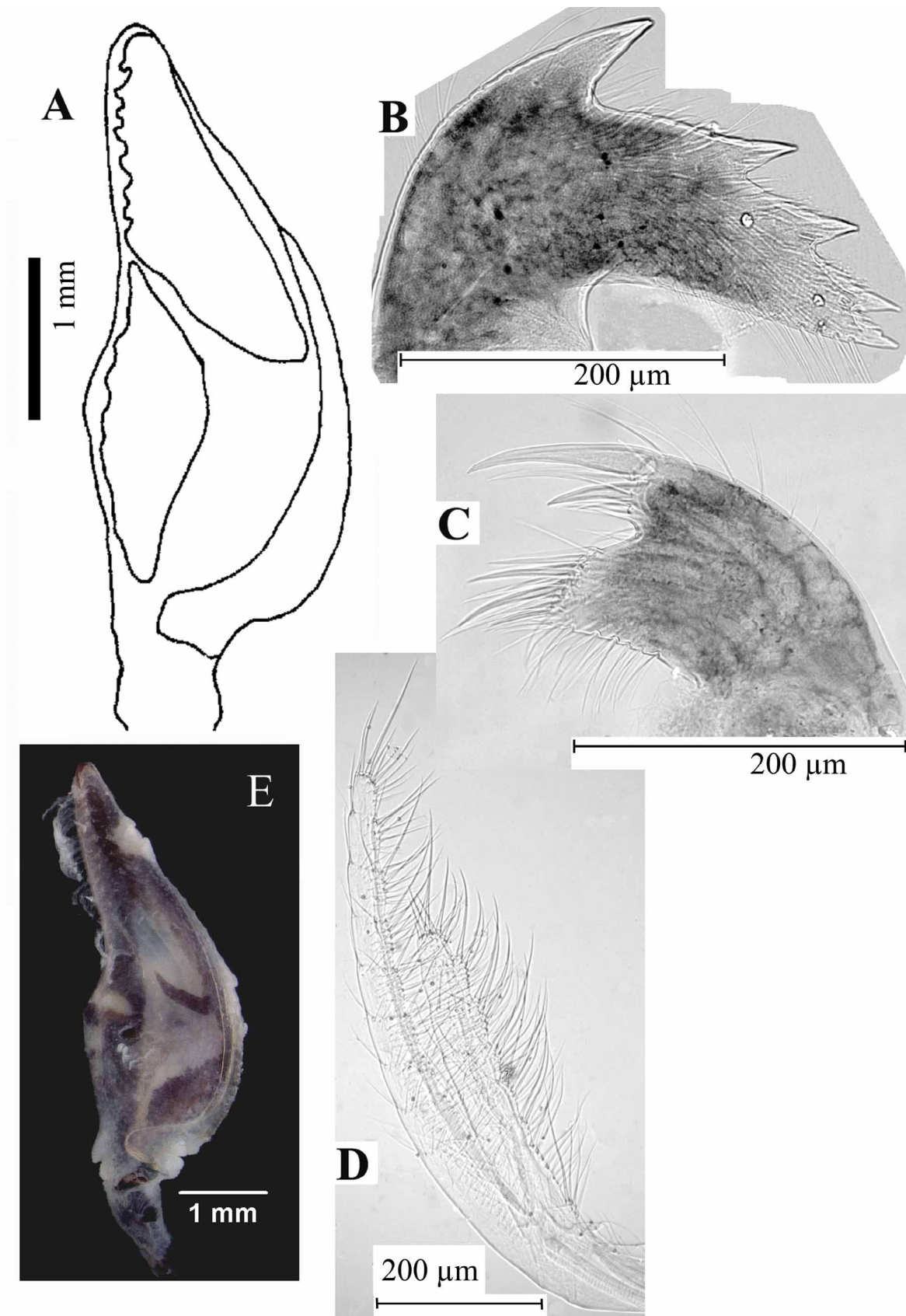
Figures 13, 14

**Material examined.** Holotype: CASIZ 110150, 1 complete intact specimen, attached to *Antipathes* sp. (CASIZ 113590); Fiji Is, Great Astrolabe Reef, W of Vanuakula I., small pass through reef; 15–18 m; 5 June 1998; coll. Robert Van Syoc (RVS-409). Paratypes: CASIZ 110149, 1 specimen, plates on SEM stub; same locality as holotype. CASIZ 110129, 1 specimen; same locality as holotype. CASIZ 110131, 1 specimen; same locality as holotype. CASIZ 110169, 1 specimen, mouthparts and cirri on glass microscope slide; Fiji Is, Great Astrolabe Reef, S of Herald Passage, outside of reef, under ledge; 18° 46.26' S, 178° 27.79' E; depth: 24 m; 4 June 1998; coll. Robert Van Syoc (RVS-405). CASIZ 110170, 1 specimen; same locality as CASIZ 110169. CASIZ 113623, 1 specimen;

same locality as CASIZ 110169. CASIZ 113626, 1 specimen; Fiji Is, Great Astrolabe Reef, NE corner, under overhang; 18° 42.41' E' 178° 32.32 S; depth: 18 m; 23 June 1998; coll. Robert Van Syoc (RVS-452). CASIZ 113627, 1 specimen; same locality as CASIZ 113626. CASIZ 110148, 8 specimens; same locality as holotype. SIO-BIC C11217, from CASIZ 110148.



**FIGURE 13.** *Minyaspis welchi* sp. nov. Paratype CASIZ 110149. Carina, dorsal view (A), oblique view (B), side view (C). Tergum exterior (D), interior (E). Scutum exterior (F), interior (G). Scale bar equals 750  $\mu$ m for A, B, C; 600  $\mu$ m for D, E, and F; 850  $\mu$ m for and G.



**FIGURE 14.** *Minyaspis welchi* sp. nov. Paratype CASIZ 110170; outline of whole specimen showing general arrangement of plates in relation to each other (A), plate details are not shown in this simple outline drawing, see SEMs in Fig. 13 for plate details. Paratype CASIZ 110169; Mandible (B), Maxilla 1 (C), Cirrus I (D). Holotype CASIZ 110150; whole specimen, with host tissue covering capitulum (E).



**Diagnosis.** Small bumps or protuberances on exterior of all plates (Fig. 13); carina forming about 90° angle at umbo, basal end broadly, roundly forked, ends truncated; tergal occludent margin with large, broad, round teeth along entire margin; scutal occludent margin with a few rounded teeth above umbo, basal margin rising steeply to occludent margin.

**Description.** Capitulum (Fig. 14A) with large non-calcified area between scutum and carina; capitular height greater than twice its width; low growth ridges and small protuberances on all plates; covered with chitinous, golden-brown epicuticle.

Scutum (Fig. 13F,G; Fig. 14A) irregularly shaped, not quadrangular; umbo subcentral, not on occludent margin; separated from carina by wide non-calcified area; near tergum at slightly more than one-half length of tergum; occludent and basal margins forming angle greater than 90°; basal margin broadly convex with very shallow concavity near occludent margin; occludent margin coincident with mantle margin; occludent edge irregular in upper half, with large tooth-like protuberances; carinal margin shallowly concave; adductor muscle pit shallow.

Tergum (Fig. 13D,E; Fig. 14A) broadly triangular; margins nearly touching carina and scutum; umbo at apex; scutal margin smooth with shallow notch above scutal apex; occludent edge irregular with large, tooth-like protuberances.

Carina (Fig. 13A,B,C; Fig. 14A) bent in upper portion, line from apex to umbo passing outside of carina, similarly line from apex to basal/peduncular margin not passing through scutum; umbo between basal one-fifth and one-third; basal margin deeply forked, extending more than halfway across peduncle; longer than scutum; width narrowest at umbo; extending up less than one-half length of tergum; with shallow inflection between basal margin and umbo.

Labrum bullate.

Mandible (Fig. 14B) with 5 teeth, first largest, second about half length of first, third and fourth slightly shorter than second, fifth about half length of third and fourth; face of mandible, superior and inferior margins setose.

First maxilla (Fig. 14C) with deep notch in superior half of cutting edge; 2 large, long spines and few shorter spines above notch, many shorter spines below notch, some approaching size of large spines above notch; face of maxilla, superior and inferior margins setose.

Cirrus I (Fig. 14D) with anterior ramus shorter than posterior, remaining cirri with rami about equal. Setae simple. Cirral counts are as follows:

	CI	CII	CIII	CIV	CV	CIV
Ant.	9	16	-	21	21	20
Post.	10	16	16	18	20	20
Ant.	8	13	17	16	19	20
Post.	9	14	16	18	-	20

Caudal appendages lacking. Filamentary appendages lacking on either side at base of cirrus I. Dorsal filamentary appendages lacking.

**Etymology.** Named in honor of Captain Dennis Welch, a friend and supporter of research at the California Academy of Sciences.

**Remarks.** *Minyaspis welchi* **sp. nov.** is most similar morphologically to *M. aurivilli* (Stebbing, 1900) and *M. opreskoi* **sp. nov.** It differs from *M. aurivilli* in states for 8 characters and from *M. opreskoi* in states for 12 characters in our data matrix. The three most obvious differences are that *M. welchi* has 1) a basally forked carina, 2) with the basal forked ends extending more than halfway across the peduncle, and 3) the carina extends along less than one-half the length of the tergum.

## Phylogenetic analysis of the Oxynaspididae

For our phylogenetic analysis of the relationships within the Oxynaspididae, we used two out-group species, *Lepas anatifera* and *Dosima fascicularis*. These 5-plated Lepadomorph species are “free-living” pelagic species. *Lepas*

*anatifera* attaches to flotsam or other drifting or slow moving objects, including other organisms (Darwin 1852, Van Syoc and Roletto 1986), while *Dosima fascicularis* can form its own gas-filled float as well as attach to flotsam and drifting organisms (Darwin 1852).

Memmi erected the family Dosimidae for *Dosima* as he considered it distinct from and intermediate to the remaining Lepadidae and the Oxynaspididae (Memmi 1983). There are a number of characters in *Dosima* that Memmi noted as being more similar to *Oxynaspis* than to *Lepas*, including the non-basal umbo of the scuta and carina (Memmi 1983). He also noted a similarity of the chitinous covering with minute spines on *Dosima* with the chitinous covering possessed by species in the Oxynaspididae (Memmi 1983). Although we have not found such a “chitinous covering” on any of the *Dosima fascicularis* specimens in the CASIZ collection, Darwin observed *Dosima fascicularis* with “plates generally covered throughout by thin chitine membrane, which is thickly clothed, especially in the interspaces between the plates, with minute spines, barely visible to the naked eye” (Darwin 1852). Therefore, *Dosima* seems the most closely allied outgroup taxon to compare phylogenetically with the Oxynaspididae.

#### Character list

- 1: Scutum, umbo on occludent margin, basal = 0; on occludent margin, not basal = 1; not on occludent margin, not basal = 2
- 2: Scutum nearly touching carina along entire margin = 0; at base only = 1; margins not proximal = 2
- 3: Scutum/tergal margins confluent along entire margin = 0, margins not entirely confluent, but confluent for more than ½ of margin = 1, confluent for less than ½, but more than a single pt = 2, margins proximal at a single point, or less = 3
- 4: Scutum, occludent and basal margins about right angle or greater = 0, less than 90 degree angle = 1
- 5: Scutum, basal margin straight = 0, not straight = 1
- 6: Scutum, entire occludent margin coincident with mantle margin = 0, recessed from mantle margin = 1
- 7: Scutum, shape quadrangular (or nearly so) = 0, triangular = 1, other = 2
- 8: Scutum, carinal margin convex or straight = 0, concave = 1, irregular = 2
- 9: Scutum, multiple radial grooves: none, smooth (except for a few folds) = 0; yes, radial grooves/ridges present = 1
- 10: Scutum, occludent margin with protuberances: none, smooth = 0; yes, small protuberances present = 1; large teeth present on occludent margin = 2
- 11: Scutum, protuberances on external surface: none, smooth = 0; protuberances present on external surface = 1
- 12: Scutum, adductor muscle pit: absent = 0; present = 1
- 13: Tergum, margin nearly touching scutum = 0, not proximal to scutum = 1
- 14: Tergum, scutal margin smooth = 0; tooth-like protuberances present = 1; margin pectinate = 2
- 15: Tergum, umbo at apex = 0; umbo not apical = 1
- 16: Tergum, notch under scutal/occludent margin = 0; notch not present = 1
- 17: Tergum, occludent margin straight = 0; convex, curving away from occludent margin = 1; irregular = 2
- 18: Tergum, occludent margin smooth = 0; with tooth-like protuberances = 1; margin pectinate = 2
- 19: Tergum, external margin smooth = 0; with protuberances = 1
- 20: Carina, line from apex to umbo passes through scutum: no = 0; yes = 1
- 21: Carina, line from apex to basal end passes through scutum: yes = 0; no = 1
- 22: Carina, umbo position: basal one-fifth = 0; basal one-fifth to one-third = 1; umbo positioned above lower one-third = 2
- 23: Carina, basal end spoon-shaped = 0; blunt, not forked = 1; forked = 2
- 24: Carina, basal end without fork tips extended across peduncle = 0; fork tips extended up to 1/2 width of peduncle = 1; extending more than ½ width of peduncle = 2
- 25: Carina longer than scutum: no = 0; yes = 1
- 26: Carina narrower above and below umbo = 0; not narrower = 1
- 27: Carina, external surface smooth = 0; protuberances present on external surface = 1
- 28: Carina extends up tergum more than 1/2 length of tergum = 0; about 1/2 length of tergum = 1; obviously less than 1/2 length of tergum = 2

29: Carina base, inflected: yes = 0; no = 1

30: Space between scutum and carina: less than 1/3 of scutum width = 0, greater than 1/3 of scutum width = 1

#### Data Matrix

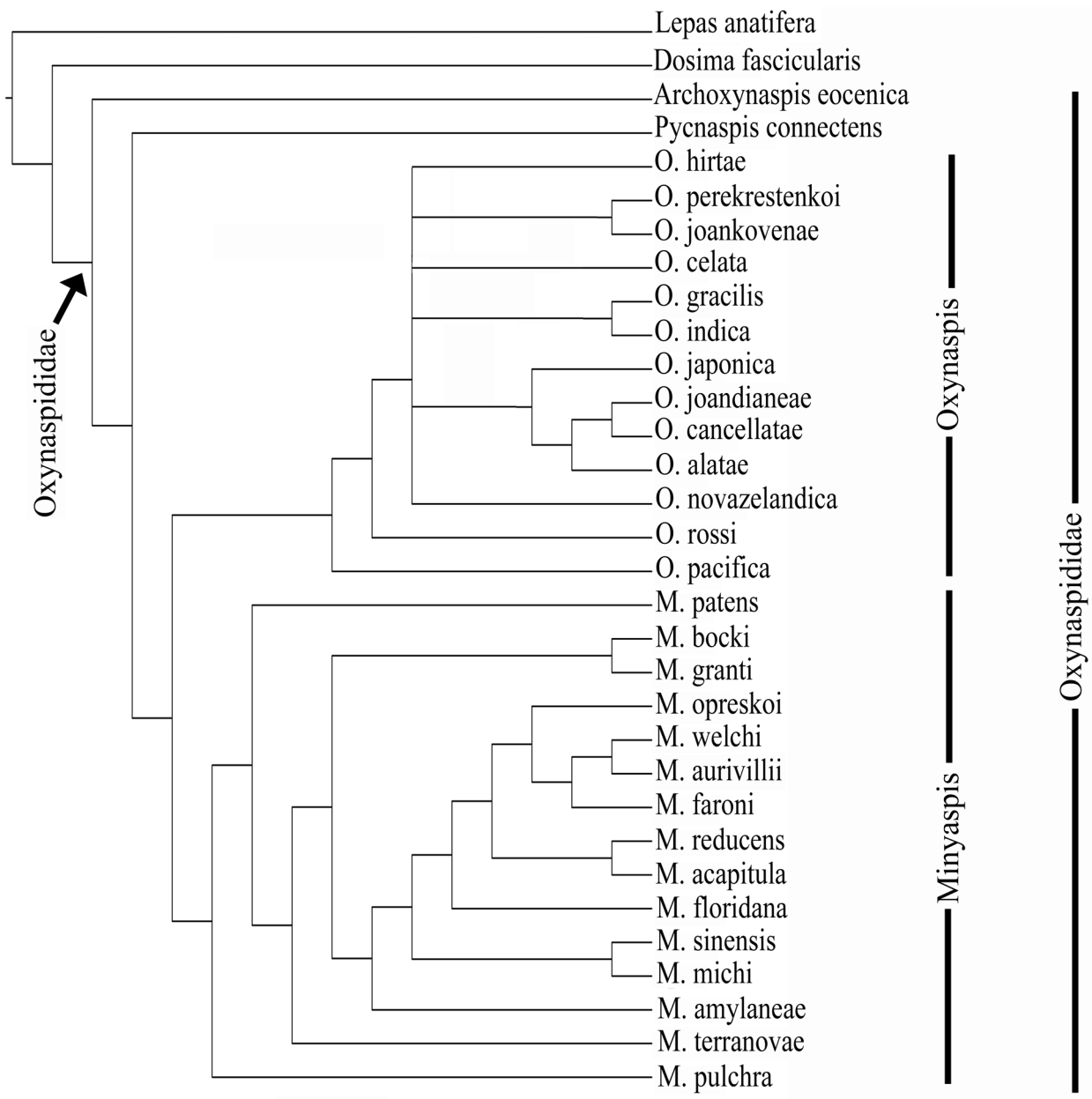
<i>Lepas anatifera</i>	000000000000000110000020000010
<i>Dosima fascicularis</i>	000000000000000110000100010000
<i>Archoxynaspis eocenica</i>	100000000000000110000000100000
<i>Pycnaspis connectens</i>	1000000000010001100000001x0000
<i>O. hirtae</i>	100000001111010011110110111100
<i>O. novazelandica</i>	110010001111010001110010111100
<i>O. perekrestenki</i>	110000001111010112100110111110
<i>O. japonica</i>	1000000010110x00100101101xx110
<i>O. joankovenae</i>	210000001111020112100110111111
<i>O. joandianae</i>	100000000111000110100110011110
<i>O. celata</i>	1000000012110100121101101x1110
<i>O. gracilis</i>	110000000111000011110200101110
<i>O. cancellatae</i>	100000000111000110110010011100
<i>O. alatae</i>	100010100111000100010112111110
<i>O. rossi</i>	110000001011110011110010100100
<i>O. indica</i>	110000001111020011110210001110
<i>O. pacifica</i>	110000001101010101000110100100
<i>M. patens</i>	121000010001000010011210111211
<i>M. bocki</i>	1221102200011000100010211x0111
<i>M. pulchra</i>	121010010001000110001020110101
<i>M. opreskoi</i>	212110210101001022001120110101
<i>M. amylineae</i>	222110210001001110001121110111
<i>M. welchi</i>	213111220211000021101122111201
<i>M. reducens</i>	223111210001121122011200100111
<i>M. floridana</i>	223111210001101110011110100111
<i>M. aurivillii</i>	213111220011020022111022101101
<i>M. sinensis</i>	22211121000100101001120010x111
<i>M. terranova</i>	112010200001000010000110110211
<i>M. granti</i>	123111220001100011001012110101
<i>M. michi</i>	22211121000x000010x112001xx111
<i>M. acapitula</i>	22311122000x021022x1110010x111
<i>M. faroni</i>	213111210001101122001122100111

The 32 taxa with 30 ordered characters were subjected to a parsimony analysis in PAUP\* 4.0b10 using ordered character states for a heuristic search. There were 18 shortest trees of 147 steps each. A consensus tree consists of 2 major oxynaspidid clades representing the species in the genera *Minyaspis* and *Oxynaspis*, and two single taxon branches representing *Archoxynaspis eocenica* and *Pycnaspis connectens* between the two major clades and the two basal branches of the outgroup taxa, *Lepas anatifera* and *Dosima fascicularis* (Fig. 15).

#### Natural key to genera of the family Oxynaspididae

- 1 Scutum with adductor muscle pit ..... 2
- Scutum without adductor muscle pi . . . . . *Archoxynaspis* **gen. nov.**; *A. eocenica* (Withers, 1935) Eocene of England, extinct.
- 2 Plates completely or nearly completely calcified; no spaces (or only a little space) between plates ..... 3
- Plates not completely calcified; large uncalcified spaces between scuta, terga and carina; carina commonly forked at basal end. .... *Minyaspis* **gen. nov.**
- 3 Plates not fragile, sturdy, as thick as *Lepas* plates; no uncalcified areas between plates .....

..... *Pyncaspis* **gen. nov.**; *Pyncaspis connectens* (Broch, 1931) from “siliceous sponge”.  
 - Plates fragile, easily broken; sometimes small uncalcified area between scuta and carina ..... *Oxynaspis* Darwin, 1852



**FIGURE 15.** Phylogenetic consensus of 18 shortest trees (147 steps each) using morphological characters for known taxa of Oxynaspididae and two outgroup species, *Lepas anatifera* and *Dosima fascicularis*.

**Evolutionary ecology and biogeography of the Oxynaspididae**

The evolutionary sequence proposed by Darwin (1852) and echoed by Withers (1953) for the stalked thoracicans placed the heavily armored Scalpellomorphs, with their “armored” peduncles covered with small calcareous plates and many small plates on the basal portion of the capitulum beneath the scuta and terga, in the earliest position. Darwin and Withers claimed that the five plated thoracicans derived from a Scalpellomorph ancestor, with *Oxynaspis* the intermediate form leading to the more recently evolved lepadids.

There is evidence from fossils (*Cyprilepas holmi* Wills, 1962, Wills 1963; *Priscansermarinus barnetti* Collins and Rudkin, 1981) and molecular phylogenetics (Perez-Losada *et al.* 2004) that the earliest thoracicans were likely

unarmored with chitinous plates and that those forms with five plated capitula are basal to the remaining, more heavily armored, groups (Briggs *et al.* 2005). If this is the case, the five plated Oxynaspididae would then be basal to the multi-plated Scalpellidae. However, as noted in the introduction in the present paper, molecular and morphological data analyzed by Perez-Losada *et al.* (2008) place the oxynaspidids squarely within the five-plated lepadomorph clade with a high degree of support, while the scalpellomorphs are not a monophyletic group in that analysis.

Unarmored thoracicans and those with only five relatively lightly calcified plates are subject to predation by jawed fish and predatory arthropods. The fossil record indicates that at least some early unarmored forms found refuge as symbionts of other organisms (e.g. *Cyprilepas holmi* Wills, 1962; on a Silurian eurypterid). Lepadomorphs currently find refuge from predation by living in the open sea far from coastal predators (e.g. *Lepas* spp on flotsam) or as symbionts of other organisms (e.g. *Octolasmis* spp on decapod crustaceans).

Those lepadomorph species escaping from predation pressure by finding refuge in either distance from high densities of predators (*Lepas* spp and *Dosima fascicularis*) or symbiosis with other organisms (oxynaspidids and poecilasmatids) have evolved less heavily calcified and smaller calcified areas on their capitular plates. Similarly, *Heteralepas* spp have no calcified regions on their capitulum and now live only as symbionts of other organisms.

Another evolutionary consequence of symbiosis is a small body size. The free-living lepadids are nearly all larger than any oxynaspidids. The poecilasmatids have evolved a body size of only a few millimeters in most cases, especially those living beneath the carapace of decapod crustacea. There is considerable variation in size among living species of Oxynaspididae, from capitula a few millimeters to around a centimeter in length. It is worth noting here that the earliest known fossil oxynaspidid, *Archoxynaspis eocenica* (Withers, 1935), is similar in capitular length to the medium-sized extant species (about 8 mm).

Other than four species where a host organism was not recorded, all but one of the described species of Recent oxynaspidids, including those described herein, were described as symbionts of antipatharians. *Pycnaspis connectens* (Broch, 1931) is the only non-fossil member of the family that was described from a non-antipatharian host. Broch (1931) found this species attached to a “silicious” sponge.

Careful examination of the holotype of *Pycnaspis connectens* revealed it to be covered with chitinous cuticle. The source of similar cuticle coverings of antipatharian symbiont oxynaspidids has been discussed in previous studies. Aurivillius (1894), Darwin (1852) and Nilsson-Cantell (1921) considered that the cuticle and spines covering the capitulum and peduncle of oxynaspidids are formed by the antipatharian host. However, Annandale (1909) considered the chitinous layer covering his specimens of *Oxynaspis celata* to be solely the product of the cirriped. Broch (1931) in his description of the species, and Totton, in his 1940 review of the genus, noted (and we have confirmed) that although the holotype of *Pycnaspis connectens* was not found in association with an antipatharian, it has a well-developed spiny chitinous cuticle. Broch (1931), Totton (1940), and Newman (1972) took this as evidence that oxynaspidids were fully capable of producing the chitinous cuticle on their own. It now seems clear that, as Broch (1931: 37) suggested, both the barnacle and the coral produce exterior chitin layers that, being similar in nature, are difficult to distinguish from each other. This may be an important factor in the successful colonization and survival of oxynaspidids on antipatharian colonies. In life, the tissue of antipatharian hosts completely envelops the barnacles, leaving only the orifice of the barnacle’s capitulum uncovered by tissue and polyps (Fig. 16, photograph of living *M. amylianeae* with coral tissues).

Very few other groups of Cirripedia associate with antipatharians. Some species of the archaeobalanid barnacle subfamily Acastinae are known from antipatharian hosts. However, the Acastinae are most commonly associated with Porifera (Kolbasov 1993; Van Syoc and Winther 1999). Additionally, a few species of *Octolasmis* (*Dichelaspis*) associate with either antipatharians or hydroids (Hoek 1907: *Dichelaspis tydemani* on “spines”, now known to be antipatharian; Pilsbry 1907a: *Dichelaspis hawaiiensis* on “slender gorgonian”, now known to be an antipatharian; Pilsbry 1907b: *Octolasmis* (*Dichelaspis*) *americanum* on a hydroid stalk).

Most oxynaspidid species are known only from a few specimens from a few localities. Therefore, our data set regarding geographic ranges is quite limited. However, several species are now known from isolated oceanic islands (e.g. Hawaii and Fiji). This fact leads us to conclude that not all speciation events within the family have been due to vicariance. Some agent of dispersal must be involved. Furthermore, oxynaspidid larvae are not known to attach to drifting flotsam or moving organisms that might transport juveniles and adults great distances. In fact, they have been found attached only to fixed benthic organisms; antipatharians and a siliceous sponge. Therefore, planktonic larvae must be an important agent in dispersal to oceanic island habitats. Furthermore, the larvae must

be relatively long lived to survive and successfully colonize island habitat (antipatharian colonies) after such long distance dispersal. Withers (1953: 25), however, notes that “several specimens in the *Cypris*-stage were found in an individual of *O. cancellatae*, showing that the development took place within the mantle cavity of the female. This would at any rate considerably limit the extent to which the animal could travel and they would already be in their required habitat.” Certainly, direct development to the cyprid stage prior to larval release from the parent would hinder long-range larval dispersal.



**FIGURE 16.** Living specimens of *Minyaspis amylanae* **sp. nov.**, CASIZ 113620, *in situ* prior to collection. Photograph by Robert Van Syoc, underwater at depth of 14.7 meters at collection site on North Astrolabe Reef, Fiji. Polyps of *Antipathes* cf. *A. spinulosa* symbiont visible on the capitula and peduncles of the barnacles.

Little is known regarding host species specificity. However, if a high degree of host species specificity is eventually found, we expect that the barnacle species range will largely overlay that of their antipatharian host species.

The only reported fossil record of an antipatharian is from the Miocene of Italy, whereas the earliest known oxynaspidid, *Archoxynaspis eocenica* (Withers, 1935), is from mid-Eocene of England. However, the antipatharian record (originally described as *Antipathes vetusta* by Michelotti in 1839) is suspect. Even though Wells and Hill (1956: F166) associate this record with the antipatharian genus *Leiopathes*, many earlier workers were of the opinion that it might be a gorgonian. Examination of a specimen upon which this record is based indicated that it has "no distinguishable features (i.e., spines or a central axial canal) that really prove that it is an antipatharian" (Opresko pers. comm.). Therefore, in the absence of a well-supported fossil record, it would be rash to assume that earliest oxynaspidids either were or were not associated with antipatharians.

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