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Diversity and systematics of Haminoeidae gastropods (Heterobranchia: Cephalaspidea) in the tropical West Pacific Ocean: new data on the genera *Aliculastrum, Atys*, *Diniatys* and *Liloa*

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Abstract

Four genera of Haminoeidae gastropods inhabiting the tropical West Pacific (*Aliculastrum*, *Atys*, *Diniatys*, and *Liloa*) were studied based on the combined analyses of live animals, external morphology, anatomy and shells aided by scanning electron microscopy and molecular sequencing. Eleven species are described including two new to Science, namely ***Atys pittmani*** **sp. nov.** and ***Atys ukulele*** **sp. nov.**. The putative synapomorphies of the genera *Aliculastrum*, *Diniatys*, and *Liloa* are discussed. High levels of morpho-anatomical variability were found among representatives of the genus *Atys*, which hampered the recognition of synapomorphies.

Key words: Mollusca, cephalaspids, bubble-shells, diversity, taxonomy

Introduction

Haminoeidae is the most genera-rich family of Cephalaspidea gastropods (Burn & Thompson 1998). It was first proposed by Pilsbry (1895) with the name Hamineinae as a subfamily of Akeridae with the single genus *Haminea* (=*Haminoea*). Species in this family are found worldwide in both tropical and temperate waters. Their shells show great variability ranging from typical bulloid to cylindrical-elongate. Spiral grooves can be present either at the ends or covering the entire shell. Shells are usually thin, translucent, and fragile but some species in the genera *Atys* and *Aliculastrum* possess solid thick shells. The mantle and other body parts are usually dull and cryptically coloured, although some species can be colourful and be even capable of changing colour to suit the environment (Edlinger 1982; Gosliner *et al.* 2008). They have a muscular buccal bulb containing chitinous jaws and a radula formed by a central tooth that varies in shape between genera plus hook-shaped lateral teeth in variable numbers. A gizzard is present with three plates containing pointed rods for shredding algal tissue and diatoms, the main diet of haminoeids (Gosliner 1991; Mikkelsen 1996; Malaquias *et al.* 2009a; Malaquias 2010).

Thirteen to 17 genera are often recognized as valid in recent literature, namely *Aliculastrum* Pilsbry, 1896, *Atys* Montfort, 1810, *Austrocylichna* Burn, 1974, *Bullacta* Bergh, 1901, *Cylichnatys* Kuroda & Habe, 1952, *Cylichnium* Dall, 1908, *Diniatys* Iredale, 1936, *Haloa* Pilsbry, 1921, *Hamineobulla* Habe, 1950, *Haminoea* Turton & Kingston, 1930, *Liloa* Pilsbry, 1921, *Limulatys* Iredale, 1936, *Mnestia* H. Adams & A. Adams, 1854, *Nipponatys* Habe, 1952, *Phanerophthalmus* Adams, 1850, *Smaragdinella* Adams & Reeve, 1848, and *Weinkauffia*, Monterosato, 1884 (Habe 1952; Burn & Thompson 1998; Carlson & Hoff 2003; Qi 2004; Gosliner *et al*. 2008; Bouchet 2014). Malaquias *et al*. (2009b) showed by molecular phylogenetic analysis that contrary to the traditional view, *Ventomnestia* is not part of Haminoeidae and later (Malaquias, 2010) confirmed the inclusion of the genera *Atys*, *Bullacta*, *Haminoea*, *Phanerophthalmus*, and *Smaragdinella* in the family using multi-locus Bayesian molecular phylogenetics.

Several studies have been conducted in the West Pacific since the 19th century and major expeditions yielded significant contributions to the knowledge of cephalaspids in the region. The Astrolabe Expedition produced some

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of the first insights into the diversity of cephalaspids from the Australasian region (Quoy & Gaimard 1833). The Challenger Expedition led to a detailed catalogue of cephalaspidean species (Watson 1886). Bergh (1901) produced a major contribution to the knowledge of West Pacific cephalaspids with focus on the Philippines. Schepman (1913) published an extensive account on the molluscs, including the cephalaspids collected during the Dutch Siboga Expedition. Major monographs with a global focus such as Adams (1850), Sowerby (1868; 1870; 1873), and Pilsbry (1895; 1896), also included significant accounts of cephalaspids from the Indo-West Pacific. In addition, the works of Pease (1860), Pilsbry (1917, 1921), and Kay (1979) described a high number of species from the Hawaiian archipelago. A common point shared by all these publications is that the taxonomic work is mostly based upon the shells alone and very limited anatomical data was included.

Numerous regional checklists, short anatomical accounts and books with chapters devoted to the Haminoeidae have been published. Examples are Pease (1860), Pilsbry (1917, 1921), Kay (1979) and Malaquias (2011) (for the Hawaiian islands), Habe (1952, 1970) (Japan and western Pacific in general), Lin (1990, 1997) (China), Preece (1995) (Pitcairn Islands), Carlson & Hoff (2000, 2003) (Mariana Islands), Qi (2004) (China), Burn (2006) (SE Australia), Noseworthy *et al*. (2007) (Jeju Island, South Korea), Gosliner *et al*. (2008) (Indo-West Pacific), Tan & Woo (2010) (Singapore), and Willan & Tagaro (2010) (Philippines).

As with other cephalaspidean gastropods, haminoeids have experienced extensive taxonomic confusion due to intraspecific variation and interspecific similarity of shells, until now the chief character used for species description and diagnoses. In the present account the diversity of four genera of Haminoeidae (*Aliculastrum*, *Atys*, *Diniatys*, and *Liloa*) inhabiting shallow waters of the tropical West Pacific Ocean is studied. New morpho-anatomical and shell characters are given to understand the extent of intraspecific variability and help in species delimitation.

Materials and methods

Taxa sampling. Specimens were obtained from museum collections (University Museum of Bergen [ZMBN], Museum national d'Histoire Naturelle, Paris [MNHN], Museum für Naturkunde, Berlin (ZMB) and Florida Museum of Natural History [UF]) and fieldwork carried out in Guam, Hawaii and the Philippines. Collection of specimens was conducted on the intertidal and subtidal down to 30 m deep. Sand, seagrass and algae substrates were examined. Whenever possible live animals were photographed, relaxed, and preserved in 10% formalin and absolute ethanol (> 96%).

Species-level taxonomy. Original descriptions were used as the primary reference for the identification of species. The features examined were shell shape and sculpture, digestive system (radulae, gizzard plates and jaws) and male reproductive system. Specimens were dissected and hard structures (shells, jaws, radulae and gizzard plates) were examined by scanning electron microscopy (SEM). The buccal mass, gizzard and male reproductive system were extracted from the dissected organisms. Radulae were soaked in sodium hypochlorite solution (household bleach) diluted to obtain a concentration of approximately 20% for about 20–40 minutes at room temperature, rinsed in distilled water and flattened with a glass cover-slip. Radulae were mounted for SEM and left to dry overnight. Photographs were taken in several orientations in order to obtain best coverage of the entire structure. Jaws were isolated, cleaned in bleach for about 5–10 mins, followed by cleaning with distilled water. They were then mounted and observed by SEM. The gizzards were opened dorsally and the gizzard plates were extracted and soaked in bleach for 5–10 mins, followed by cleaning with a paintbrush and distilled water, then mounted for SEM. Shells were mounted on SEM stubs to study their microsculpture. All the material prepared for SEM was coated with gold-palladium. An auto-montage imaging system was used to take photographs of the shells before dissection and of gizzard plates after dissection. The male reproductive system was separated from the body, studied and drawn under a dissection microscope with camera lucida.

Preliminary molecular phylogenetic analyses including various representatives of Haminoeidae were performed in parallel to this morphological study. The results of these analyses are part of a master thesis (Too 2011), have been recently presented at an international meeting (Malaquias *et al.* 2013), and will be published elsewhere. These phylogenetic results were used in part to aid on the generic assignment of the species studied here. The molecular and phylogenetic work followed the methods and protocols described by Malaquias *et al.* (2009).

Results

Eleven species were recognized; two of them are described as new to Science.

Family Haminoeidae Pilsbry, 1895

Genus *Aliculastrum* Pilsbry, 1896

Type species: *Bulla cylindrica* Helbling, 1779

The genus *Aliculastrum* was introduced by Pilsbry (1896) as a replacement name for *Alicula* Ehrenberg, 1831. The latter name was preoccupied by *Alicula* Eichwald, 1830 in reference to another group of marine gastropods with a projecting spire and based on a fossil placed in the family Scaphandridae (Bouchet 2010). The type species, *Aliculastrum cylindricum* was originally ascribed to the genus *Bulla* (Helbling 1779) and has been arbitrarily attributed to the genera *Atys* (Sowerby 1870; Gosliner *et al*. 2008) and *Aliculastrum* (Habe 1952; Lin 1997; Qi 2004). There is very limited literature documenting the characters that define the genus *Aliculastrum*. According to Lin (1997), this genus includes species that possess a cylindrical elongated shell, with spiral grooves at both ends and no umbilicus. *Aliculastrum cylindricum* was described as umbilicated (Helbling 1779; Adams 1850). However, Chemnitz (1788) mentioned that this is simply a depression that looks very much like an umbilicus. Species ascribed to this genus in the tropical West Pacific include *A. cylindricum* (Helbling, 1779), *A. debilis* (Pease, 1860) and *A. parallelum* (Gould, 1846) (Pilsbry 1896; Habe 1952; Lin 1997; Carlson & Hoff 2003; Qi 2004) (Tab. 1).

Aliculastrum cylindricum (Helbling, 1779)

Bulla cylindrica Helbling, 1779: 122, pl. 2, figs 30, 31. Chemnitz 1788: 113, pl. 146, figs 1356, 1357. Adams 1850: 585, pl. 125, fig. 114. (Type untraceable).
Alicula cylindrica—Ehrenberg 1831; Gray 1847: 161. Vayssière 1906: 11, fig. 17.
Aliculastrum cylindricum—Habe 1952: 138, fig. 1. Lin 1997: 99, pl. 8, fig. 1. Qi 2004: 145, pl. 83, fig. C.
Atys cylindrica—Sowerby 1870: pl. 2, sp. 7a, b. Smith 1872: 344. Brazier 1878: 85. Smith 1878: 819. Martens 1880: 303. Watson 1886: 639.
Atys (Alicula) cylindrica—Pilsbry 1895: 265, pl. 33, figs 60-64. Schepman 1913: 469.
Atys (Aliculastrum) cylindrica—Pilsbry 1896: 237; Hatai 1941: 48, 158, pl. 1, figs 7, 8. Kuroda 1947: 1086, fig. 3077. Macnae 1962: 185, fig. 1.
Atys cylindricus—Gosliner *et al*. 2008: 22.
Bulla solida Dillwyn, 1817: 496. Lamarck 1819: 36. Bruguière 1832: 374. Adams 1850: 585, pl. 124, figs 112, 113.
Atys solida—Sowerby 1870: pl. 1, sp. 4. Issel 1869: 168. Brazier 1878: 85.
Bulla elongata Adams, 1850: 587, pl. 125, fig. 121.
Atys elongata—Sowerby 1870: pl. 2, sp. 8a, b. Brazier 1878: 85.
Atys succisa—Sowerby, 1870: pl. 2. sp. 10.
Atys (Alicula) succisa—Pilsbry 1895: 267.

Type locality. Tropical Indo-West Pacific (Not specified in the original description)

Material examined. New Caledonia, 1 specimen (spc.) dissected, MNHN, Paris, H (shell height) = 13.7 mm; the Philippines, 1 spc. dissected, MNHN, Paris (S3/ OT236), H = 22 mm.

Animal (Fig. 1A): Body whitish, dark dots densely all over body, darker along edge of parapodial and cephalic lobes; darker bands visible through shell; eyes visible.

Shell (Figs 2A, B, 4A, B): Maximum height 30 mm; milky white under yellow or orange periostracum; thick and robust, opaque, subcylindrical, widest part between middle-line and apex, anterior end semi-circular; spire sunken, outer lip elevated above the apex, slightly sinuous posteriorly, body whorl fairly convex, columella short and thick; spiral grooves at both ends only (anterior = 16–18, posterior = 14), which become closer towards the ends, growth lines indistinct.

Jaws (Fig. 4C): Present, crescent shape, jaw rodlets with 6–8 denticles.

Radula (Figs 4D–F): Radular formula at mid-point 30–42 x 10–9.2.1.2.9–10; median tooth with broad base, sharp triangular central cusp with pseudo-triangular lateral cusp on both sides; inner lateral teeth hook-shaped,

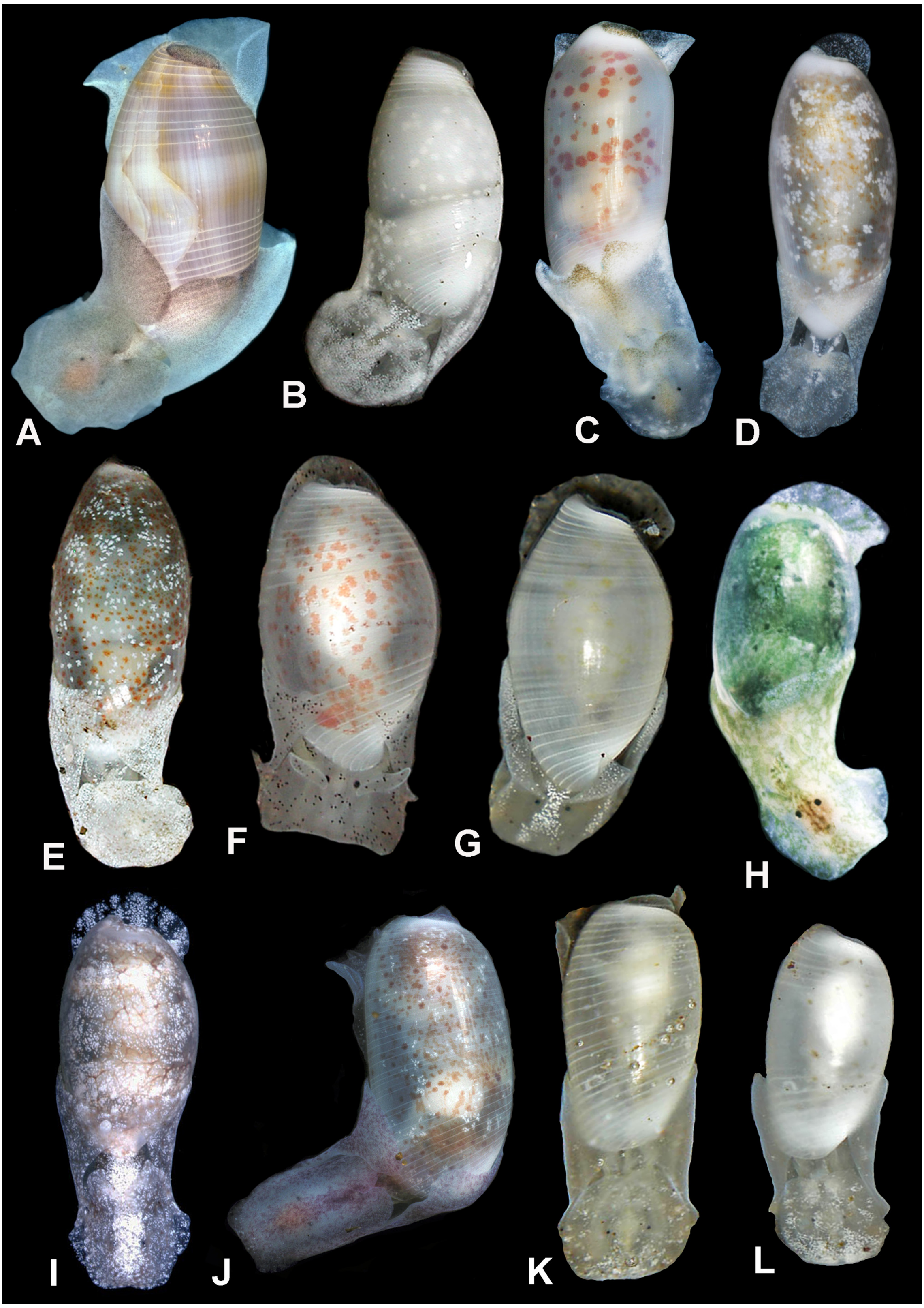

FIGURE 1. Live images. A. *Aliculastrum cylindricum* (Koumac, northern New Caledonia; H = 28 mm, MNHN, Paris), B. *Aliculastrum debilis* (Maui, Hawaii; ZMBN 81658; H = 9 mm), C. *Aliculastrum parallelum* (Guam; UF 374138; H = 19 mm), D. *Atys multistriatus* (Guam; UF 374136; H = 7 mm), E. *Atys pittmani* **nov. sp.** (Maui, Hawaii; ZMBN 81673; H = 10 mm), F. *Atys semistriatus* (Maui, Hawaii; ZMBN 81656; H = 6 mm), G. *Atys ukulele* **nov. sp.** (Maui, Hawaii; ZMBN 89710; H = 5.4 mm), H. *Diniatys dentifer* (Guam; UF 374130; H = 9 mm), I. *Diniatys dubia* (Guam; UF 299907; H = 12.7 mm), J. *Liloa curta* (Guam; UF 374131; H = 15 mm), K. *Liloa porcellana* (Maui, Hawaii; ZMBN 89712; H = 4.2 mm); L. *Liloa porcellana* (Maui, Hawaii; ZMBN 89712; H = 2.8 mm). Image A, courtesy of W. B. Rudman; Images B, E–G, K, L, courtesy of C. Pittman.

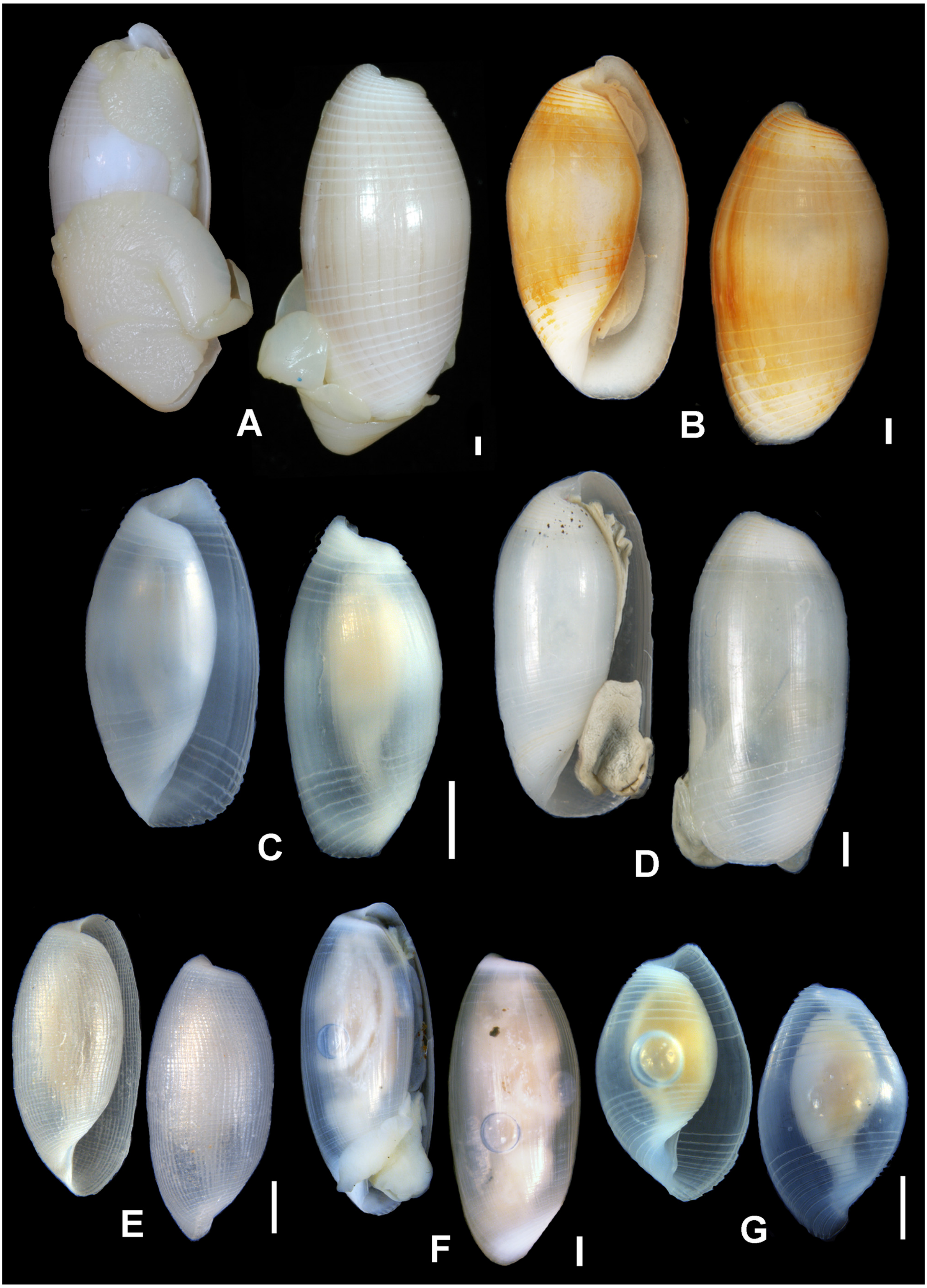

FIGURE 2. Shells. A. *Aliculastrum cylindricum* (the Philippines; MNHN, Paris (S3/ OT236); H = 22 mm), B. *Aliculastrum cylindricum* (New Caledonia; MNHN, Paris; H = 13.7 mm), C. *Aliculastrum debilis* (the Philippines; MNHN, Paris (OT834); H = 4.5 mm), D. *Aliculastrum parallelum* (Guam; UF 374138; H = 10 mm), E. *Atys multistriatus* (Guam; UF 374136; H = 5.3 mm), F. *Atys pittmani* **nov. sp.** (Maui, Hawaii; ZMBN 81673; H = 10 mm); G. *Atys semistriatus* (Tahiti; ZMBN 87082; H = 4.1 mm). Scale bar: 1 mm.

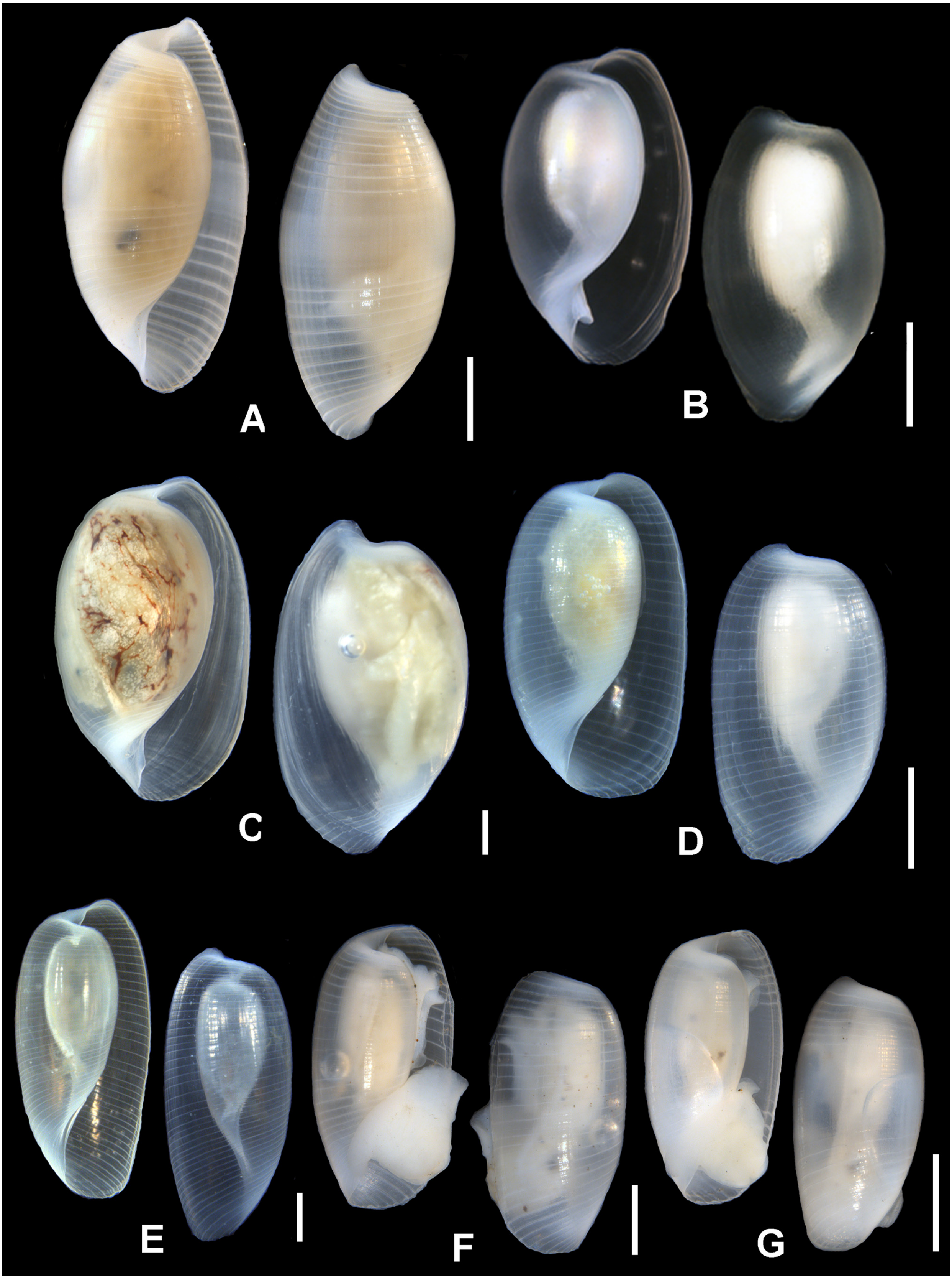

FIGURE 3. Shells. A. *Atys ukulele* **nov. sp.** (Maui, Hawaii; ZMBN 89711; H = 4.6 mm), B. *Diniatys dentifer* (the Philippines, MNHN, Paris (B17/ OT793); H = 3.5 mm), C. *Diniatys dubia* (Guam; UF 299907; H = 7.5 mm), D. *Liloa curta* (the Philippines; MNHN, Paris (S12/ OT575); H = 3.1 mm), E. *Liloa porcellana* (Guam; UF 299895; H = 6.7 mm), F. *Liloa porcellana* (Maui, Hawaii; ZMBN 89712; H = 4.2 mm), G. *Liloa porcellana* (Maui, Hawaii; ZMBN 89712; H = 2.8 mm). Scale bar: 1 mm.

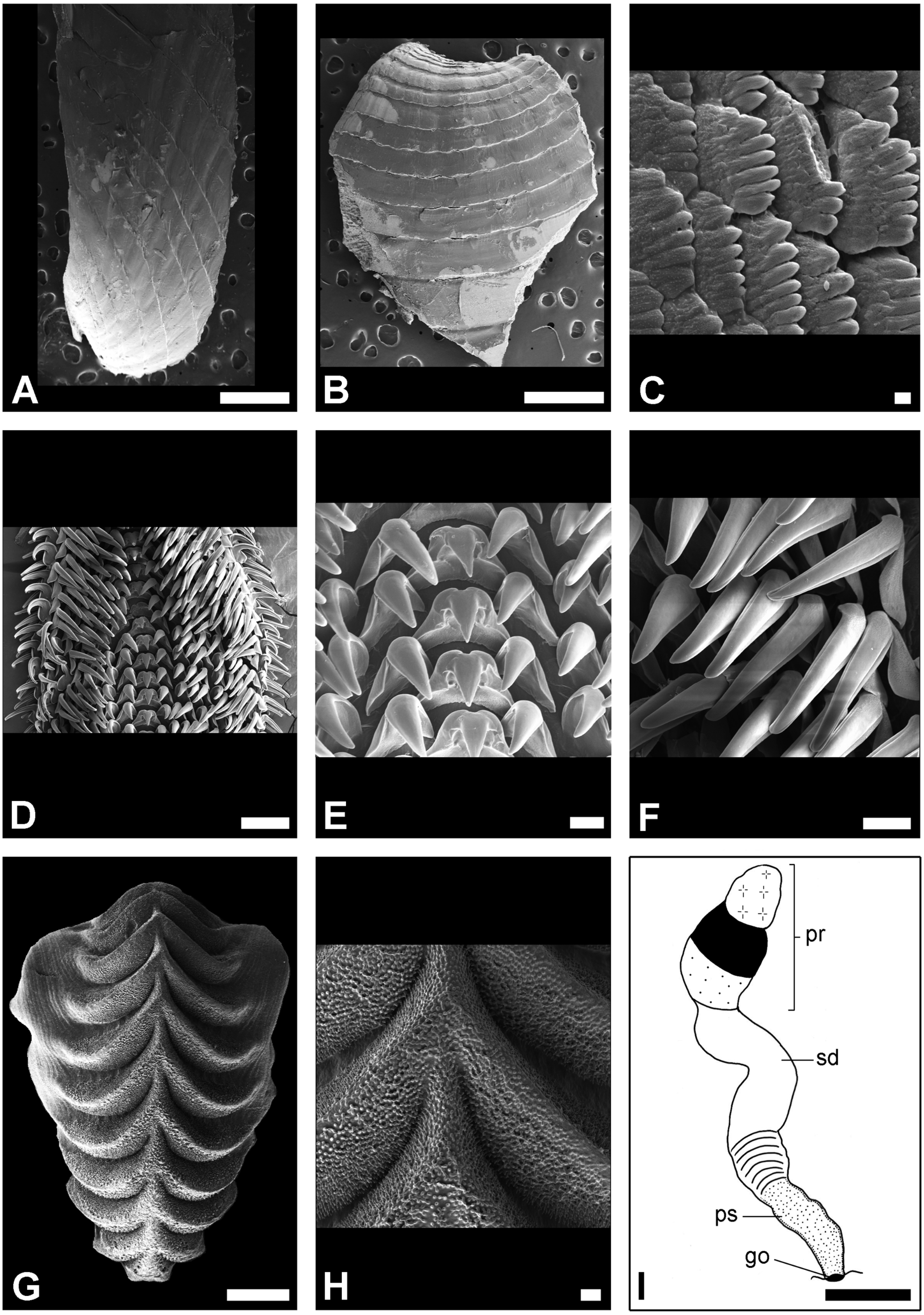

FIGURE 4. Shell and anatomy of *Aliculastrum cylindricum*. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Detail of jaw. D. Front view of middle part of radula. E. Detail of median tooth and inner lateral teeth. F. Detail of outer lateral teeth at left side of radula. G. Top view of gizzard plate. H. Rods on middle ridges of gizzard plate. I. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A, B, I = 1 mm; C = 2 µm; D = 100 µm; E, F, H = 20 µm; G = 200 µm. A–H: MNHN, Paris (S3/ OT236), H = 22 mm; I: MNHN, Paris, H = 13.7 mm.

broader than outer lateral teeth, triangular base with slight semi-circular projection outwardly, groove often presents along outer margin; outer lateral teeth hook-shaped, slender, broad base, with broad semi-circular projection outwardly, grooves along both outer and inner margins, size increases outwardly but outermost tooth smallest.

Gizzard plates (Figs 4G, H): Three gizzard plates; broader at anterior part, narrower posteriorly; 10 transverse ridges with crescent shape on each side of pseudo-rachis; ridges covered by tiny rods with pointed tips, gaps between ridges smooth, high density of rods on ridges throughout plates.

Male reproductive system (Fig. 4I): Total length 5.3 mm (H = 13.7 mm). Formed by three parts: prostate, seminal duct and penial region; prostate elongated, three-lobed, proximal lobe largest and light-brownish, distal lobe orange-coloured, mid-lobe dark brown; broad seminal duct connects prostate and penial region, opaque-yellowish, with striations at anterior end; penial region semi-translucent.

Ecology. Sandy bottom below 15 m depth, reef flat (Gosliner *et al*. 2008; present study).

Geographical distribution. South Africa, Seychelles Island, Mauritius, Andaman Islands, the Philippines, Ryukyu and Amami groups, Kyushu and Honshu in Japan, Guangdong Province, Hainan Province (Xisha Islands) of China, New Caledonia, Fiji, Tahiti (Chemnitz 1788; Pilsbry 1895; Habe 1952; Macnae 1962; Qi 2004; Goslier *et al*. 2008; present study).

Remarks. After attempts to locate Helbling's type material we concluded that his collection seems to have been lost or is at least presently untraceable. *Aliculastrum cylindricum* shows variation in shell morphology; it is usually subcylindrical, and more or less convex (Pilsbry 1895, pl. 33, figs 60, 61; present study, Fig. 2A). There are specimens with more cylindrical and elongated shells and this latter form has been named *Atys elongata* (Pilsbry 1895, pl. 33, fig.62). Shells that are angular above the mid-part have been named *Atys solida* (Pilsbry 1895, pl. 33, figs 63, 64; present study, Fig. 2B). Martens & Langkavel (1871) stated that *Atys alicula* might be a synonym but Pilsbry (1895) rejected this view after examining the type specimen. *Atys alicula* was described as a thin and hyaline shell (Adams 1850) and does not resemble *Aliculastrum cylindricum*. Pilsbry (1895) mentioned that *Atys succisa* could be a juvenile of *Aliculastrum cylindricum* but this was rejected by Martens (1880) without giving sound arguments. *Atys succisa* was described as a thin shell with very fine spiral grooves at both ends (Adams 1850; Sowerby 1870). In addition, Pilsbry (1895) also placed *Atys angustata* described by Smith (1872) as a synonym of *Aliculastrum cylindricum*. However, Smith (1872)'s description as "very narrow species, thinner at both ends, strongly sinuated posteriorly" sounded more similar to *Aliculastrum debilis*.

The shell variability of this species led to taxonomic confusion with several synonyms available but also its generic placement has been contentious. Pilsbry (1896) introduced the name *Aliculastrum,* because of the robust cylindrical shell and thick columella that is neither truncated nor folded; this classification has since being followed by several authors (e.g. Habe 1952; Lin 1997; Qi 2004; Willan & Tagaro 2010) but others include the species in the genus *Atys* (e.g. Gosliner *et al*. 2008). Compared to the type species of *Atys* — *Atys naucum* — which has an ovoid inflated shell and gizzard plates with very fine ridges that are occupied by tiny rods (Carlson & Hoff 1999), *Aliculastrum cylindricum* shows different characters: cylindrical shell and gizzard plates with large crescent-shaped ridges. Moreover, preliminary molecular data (Too 2011) supports the validity and inclusion of this species in the genus *Aliculastrum*.

Several authors referred to this species as umbilicated (e.g. Helbling 1779; Adams 1850; Sowerby 1870), but Chemnitz (1780) showed this to be simply a depression of the posterior part of the shell, which is corroborated by our findings. Descriptions of the radula can vary significantly and this more than reflecting intraspecific variability likely results from authors dealing with more than one species. For example, Vayssière (1906) studied specimens from Borneo and the Philippines and recorded a radula with a formula of 9.1.9, whereas Bergh (1901) founded in specimens from the Red Sea a radular formula of 35–45 x 12.1.12 with denticulated inner lateral teeth. Macnae (1962) reported a formula of 11.1.11 for specimens from South Africa with teeth depicting a fine denticulation along the inner margin.

Aliculastrum debilis (Pease, 1860)

Atys debilis Pease, 1860: 20. Sowerby 1870: pl. 5, sp. 28. Watson 1886: 640. Pilsbry 1917: 217, fig. 7. Kay 1979: 424, fig. 137C. Gosliner *et al*. 2008: 23.

Atys (Alicula) debilis—Pilsbry 1895: 266, pl. 33, figs 69, 70. Kobelt 1896: 22, pl. 6, fig. 15.

Atys (Aliculastrum) debilis—Pilsbry 1896: 267.
Atys angustata—Smith 1872: 346.
Atys cortuna—Kay 1979: 424.

Type locality. Hawaii (Sandwich Islands).

Material examined. Tahiti, 1 shell examined, ZMB unnumbered (paratype), H = 10.13 mm; Maui, Hawaii, ZMBN 81658, H = 9 mm; the Philippines, 1 shell examined, MNHN, Paris (OT834), H = 4.5 mm; the Philippines, 2 spcs dissected, MNHN, Paris (M9/OT802), H = 5.3 mm, 5.9 mm; Tahiti, 1 spc. dissected, ZMBN 87083, H= 5.2 mm; Tahiti, 2 spcs dissected, ZMBN 87084, H = 8.2 mm, 8.4 mm; the Philippines, 2 spcs dissected, MNHN, Paris (OT834), H = 4.6 mm, 5.6 mm.

Animal (Fig. 1B): Body whitish-translucent, white dots scattered over the body, more dense on edges and mid part (between mouth and eyes) of cephalic shield, forming abundant blotches on the mantle and parapodial lobes; eyes visible, inserted in unpigmented periocular areas.

Shell (Figs 2C, 5A, B): Maximum height 15 mm; milky white; slightly robust, slightly thick, semi-opaque, cylindrically ovate, narrowed towards both ends, widest right below the mid-line, anterior end truncated; spire sunken, outer lip elevated above the apex, strongly sinuous at the posterior end, columella short and thick; step-like spiral grooves at both ends only (anterior = 10–18, posterior = 7–13), which become closer towards the ends, axial lines present.

Jaws (Fig. 5C): Present, crescent shape, jaw rodlets with 5-6 denticles.

Radula (Figs 5D–F): Radular formula at mid-point 20-30 x 12–8.1.1.0.8–12; median tooth with broad base, triangular central cusp with thinner membrane-like structure on both sides, pseudo lateral cusps present; inner lateral tooth presents only at right side, hook-shaped, broad base, with semi-circular projection outwardly, broader than outer lateral teeth, strong denticulation presents along outer margin; outer lateral teeth hook-shaped, slender, broad base, with semi-circular projection outwardly, groove along the outer margin, size decreases outwardly.

Gizzard plates (Figs 5G, H, 6A, B): Three gizzard plates; broader at anterior part, narrower posteriorly; 8–11 ridges, pseudo-rachis present; For specimens from Tahiti (Fig. 6A), 8 ridges, rachis absent or faint; ridges covered by rods with pointed tips along top edge, smaller rods with pointed tips densely at both anterior and posterior sides of ridges, gaps between ridges smooth, high density of rods on ridges throughout plates.

Male reproductive system (Fig. 5I): Total length 3.2 mm (H = 8.2 mm). Formed by three parts: prostate, seminal ducts and penial region; prostate elongated, bilobed, proximal lobe larger, opaque-yellowish, distal lobe translucent, striations on entire prostate; two seminal ducts connect prostate and penial region, seminal duct makes two coils right after prostate before branching into two, first seminal duct is narrower than second seminal duct, first seminal duct curls at the posterior end and stretches underneath of second seminal duct towards penial region, both seminal ducts yellowish but turn translucent at anterior end; penial region translucent with broad end, narrower towards genital opening.

Ecology. Sandy bottom or on *Halimeda* beds between depth of 6–18 m (Gosliner *et al*. 2008; present study).

Geographical distribution. Tahiti, Fiji, Hawaii, the Philippines, Guam (Kay 1979; Gosliner *et al*. 2008; present study).

Remarks. This species is often misidentified with *Aliculastrum cylindricum* due to their extreme similarity in shell morphology. Pease (1860) described *Aliculastrum debilis* as having a pellucid and fragile shell. The specimens examined during this study agree in part with this description; they have semi-translucent shells, which are, however, relatively robust. A paratype of this species (see examined material; Fig. 7) from Tahiti has a solid opaque shell, which might indicate that Pease used shells from more than one species to describe *Aliculastrum debilis*. Confusion around the characters to distinguish this species is well patent in the literature. For example, Pilsbry (1917) mentioned that the illustration of *Aliculastrum debilis* in Sowerby (1870: pl. 5, sp. 28a, b) show a projecting point at the posterior end of the columella, although such feature is not referred by Pease (1860). Carpenter (1865) mentioned that *Aliculastrum debilis* is identical to *Atys succisa*, and simply a slender version of *Atys alicula*. Pilsbry (1895) mentioned that *Atys angustata* is a synonym of *Aliculastrum cylindricum* but, his description of the species: “a very narrow shell with both ends thinner and strongly sinuous at the posterior ends”; resembles *Aliculastrum debilis* rather than *Aliculastrum cylindricum*. Similarly, Kay (1979) expressed doubts about a species described by Pilsbry (1917), which he named *Atys cortuna* that only differs from *Aliculastrum debilis* by possessing a wider posterior end; Kay (1979) synonymized both species under the name *Atys debilis*.

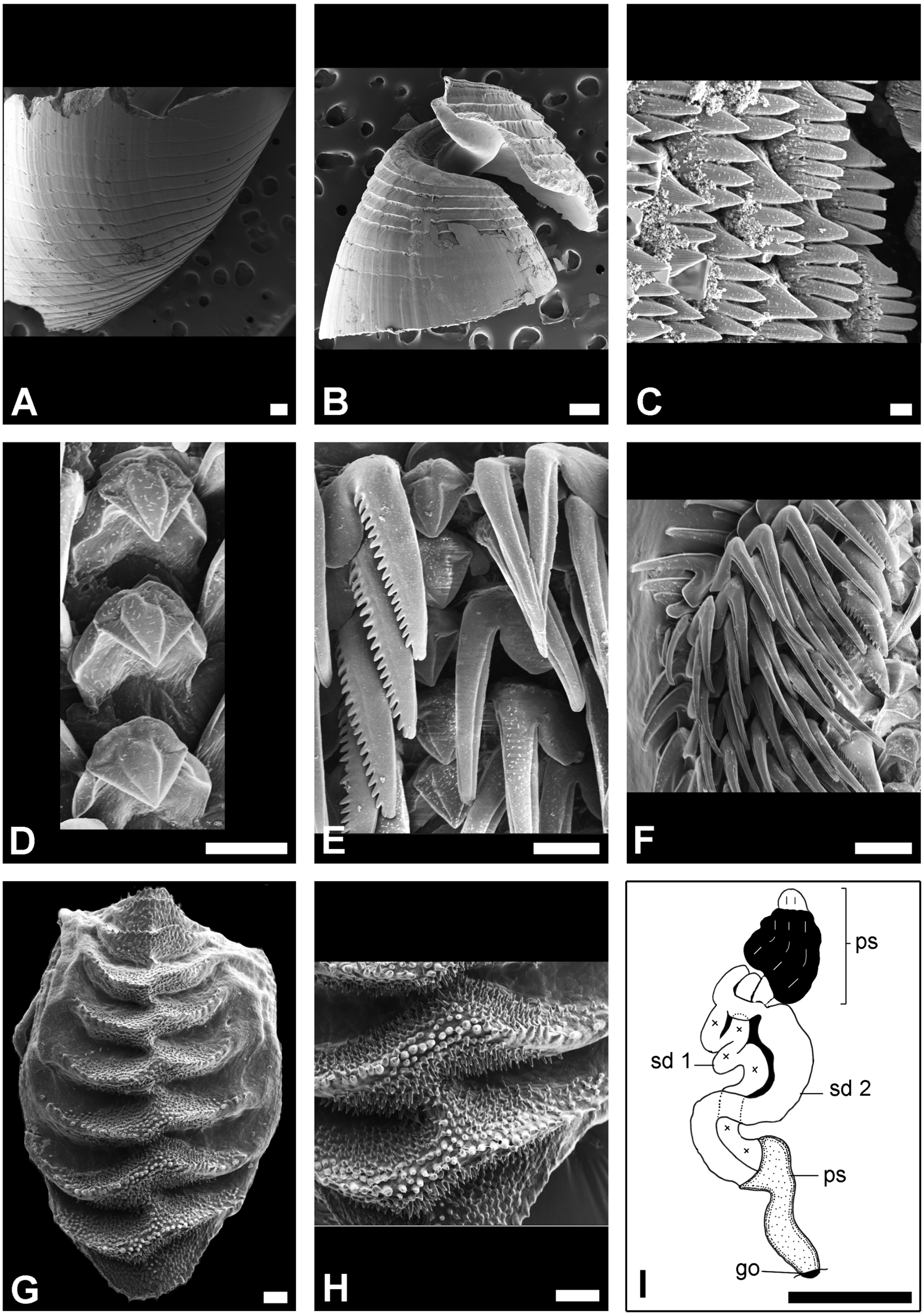

FIGURE 5. Shell and anatomy of *Aliculastrum debilis*. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Detail of jaw. D. Detail of median tooth at the middle of radula. E. Inner lateral tooth with denticulation at the right side of radula. F. Detail of outer lateral teeth at right side of radula. G. Top view of gizzard plate of specimen from the Philippines. H. Rods on ridges at posterior edge of gizzard plate. I. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd 1, first seminal duct; sd 2, second seminal duct. Scale bars: A, B = 200 µm; C = 2 µm; D, E = 10 µm; F, H = 20 µm; I = 1 mm. A, C, D: ZMBN 87084, H = 8.4 mm; B= MNHN, Paris (M9/ OT802), H= 5.3 mm; E–H: MNHN, Paris (M9/ OT802), H = 5.9 mm; I: ZMBN 87084, H = 8.2 mm.

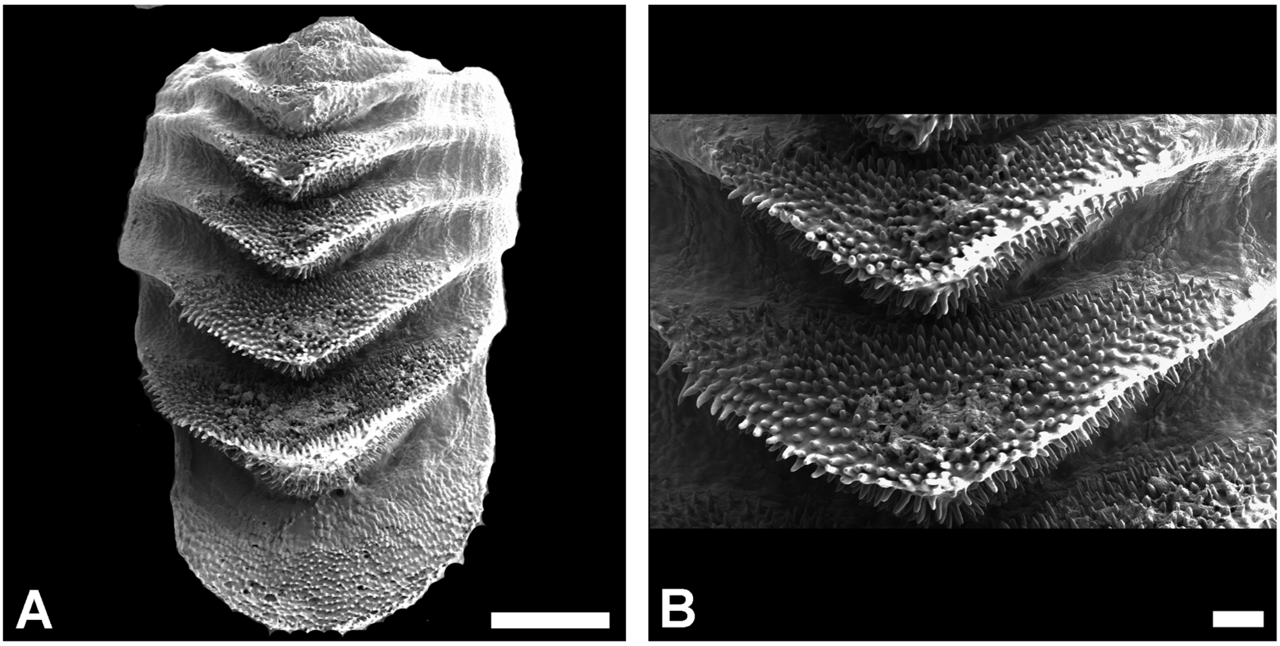

FIGURE 6. Gizzard plate anatomy of specimen *Aliculastrum debilis* from Tahiti. A. Top view of gizzard plate. B. Rods on middle ridges of gizzard plate. Scale bars: A = 100 µm; B = 20 µm. A, B: ZMBN 87084, H = 8.4 mm.

FIGURE 7. Paratype of *Aliculastrum debilis* in Museum für Naturkunde (Berlin, Germany). (H = 10.13 mm).

Aliculastrum debilis has a more elongated semi-translucent shell with deep spiral grooves at both ends, when compared with *Aliculastrum cylindricum*, which has a more inflated opaque shell with shallower spiral grooves at both ends. Besides, the former usually has a narrower shell towards both ends, whereas the latter has a broader anterior end compared to its posterior end. Moreover, these two species can be distinguished easily based on their anatomical features as documented above.

This species has been placed under the genus *Atys* by most authors although it possesses features that are different from the type species *Atys naucum*; for example, a cylindrical shell, gizzard plates with large ridges and complex male reproductive system with two seminal ducts. *Aliculastrum debilis* has an asymmetric radula; the inner lateral tooth with strong denticulation along the outer margin appears only at the right side. This character is found also in another *Aliculastrum* species studied in this work (e.g. *A. parallelum*). Preliminary phylogenetic data (Too 2011) suggest the inclusion of this species in the genus *Aliculastrum*.

Aliculastrum parallelum (Gould, 1846)

Bulla parallela Gould, 1846: 98. Gould 1847: 251. Gould 1852: 220, pl. 15, figs 267, 267a (type lost; USNM 19091).
Cylichna parallela—Adams 1862: 152.
Atys parallela—Sowerby 1870: pl. 4, sp. 21a–c. Watson 1886: 640.
Atys parallelus—Martens & Langkavel 1871: 53.
Atys (Alicula) parallela—Pilsbry 1895: 266, pl.28, figs 21, 22. Kobelt 1896: 21, pl. 6, figs 13, 14.
Atys (Aliculastrum) parallela—Pilsbry 1896: 237.
Aliculastrum parallela—Carlson & Hoff 2003: 281.

Type locality. West Pacific (Not specified in the original description).

Material examined. Mariana Islands, Guam, 4 spcs dissected, UF 374138, H = 6.8–9.6 mm.

Animal (Fig. 1C): Body whitish-translucent, white dots scattered over the body, more dense at pallial lobe edge and ventral areas of parapodial lobes, white blotches scattered over cephalic shield; between eyes, edges of cephalic and parapodial lobes with darker pigmentation; red blotches scattered on the mantle; eyes visible.

Shell (Figs 2D, 8A, B): Maximum height 12.5 mm; milky white; thick, robust, semi-opaque, cylindrical, both sides of body whorl nearly parallel, rounded anteriorly and conical posteriorly, apex imperforate; spire sunken, aperture narrow, widening towards posterior edge, outer lip elevated above the apex; spiral grooves at both ends only (anterior = 17–18, posterior = 14–20), fine longitudinal growth lines present throughout shell; orange-coloured periostracum observed.

Jaws: Present, crescent shape.

Radula (Figs 8C, D): Radular formula at mid-point 27 x 12.1.1.0.12; median tooth with broad base, triangular central cusp with thinner membrane-like structure on both sides, central cusp becomes more pointed posteriorly, pseudo-triangular cusp on both sides; inner lateral tooth presents only at right side, hook-shaped, broader base compared to outer lateral teeth, with semi-circular projection outwardly, broader than outer lateral teeth, strong denticulation along outer margin; outer lateral teeth hook-shaped, slender, with semi-circular projection outwardly, groove along the outer margin, size decreases outwardly.

Gizzard plates (Figs 8E, F): Three gizzard plates; broader at anterior part, narrower towards posterior end; 8–9 ridges, covered by tiny rods with pointed tips at both anterior and posterior sides, density of rods higher at anterior half of gizzard plate; posterior half of gizzard plate lacks rods on posterior side of ridges.

Male reproductive system (Fig. 8G): Total length 3.4 mm (H = 8.54 mm). Formed by three parts: prostate, seminal ducts and penial region; prostate elongated, semi-translucent, faint striations at distal end, division into lobes not evident; two seminal ducts, first seminal duct whitish, narrower than second seminal duct, connects distally at a pouch close to prostate and proximally close to penial sheath, coils around second seminal duct, second seminal duct yellowish, broad, proximal part of both ducts semi-translucent; penial region elongated, semi-translucent.

Ecology. There is hardly any record on the habitat for this species. Materials examined were sampled on shallow areas up to 18 m depth.

Geographical distribution. Japan, Guam, Fiji, Tahiti (Adams, 1862; Martens & Langkavel, 1871; Watson, 1886; present study).

Remarks. *Aliculastrum parallelum* was originally ascribed to the genus *Bulla*, but from very early on, authors like Sowerby (1870), Martens & Langkavel (1871), and Watson (1886) consider this species to belong on the genus *Atys*; later Pilsbry (1921) and Habe (1952) included it in the genus *Aliculastrum.*

Adams (1862), apparently unaware of Gould (1846)'s work, described a similar species as *Cylichna parallela*, which was collected in Tsushima, Japan (Strait of Korea; as Tsu-Sima). Comparison of the original descriptions revealed that these two species are identical and likely synonyms (Gould, 1846; Adams, 1862).

Aliculastrum parallelum does not have an ovoid inflated shell as the type species of the genus *Atys* (*Atys naucum*); moreover, the gizzard plates are also different from those of *A. naucum* with presence of few broad

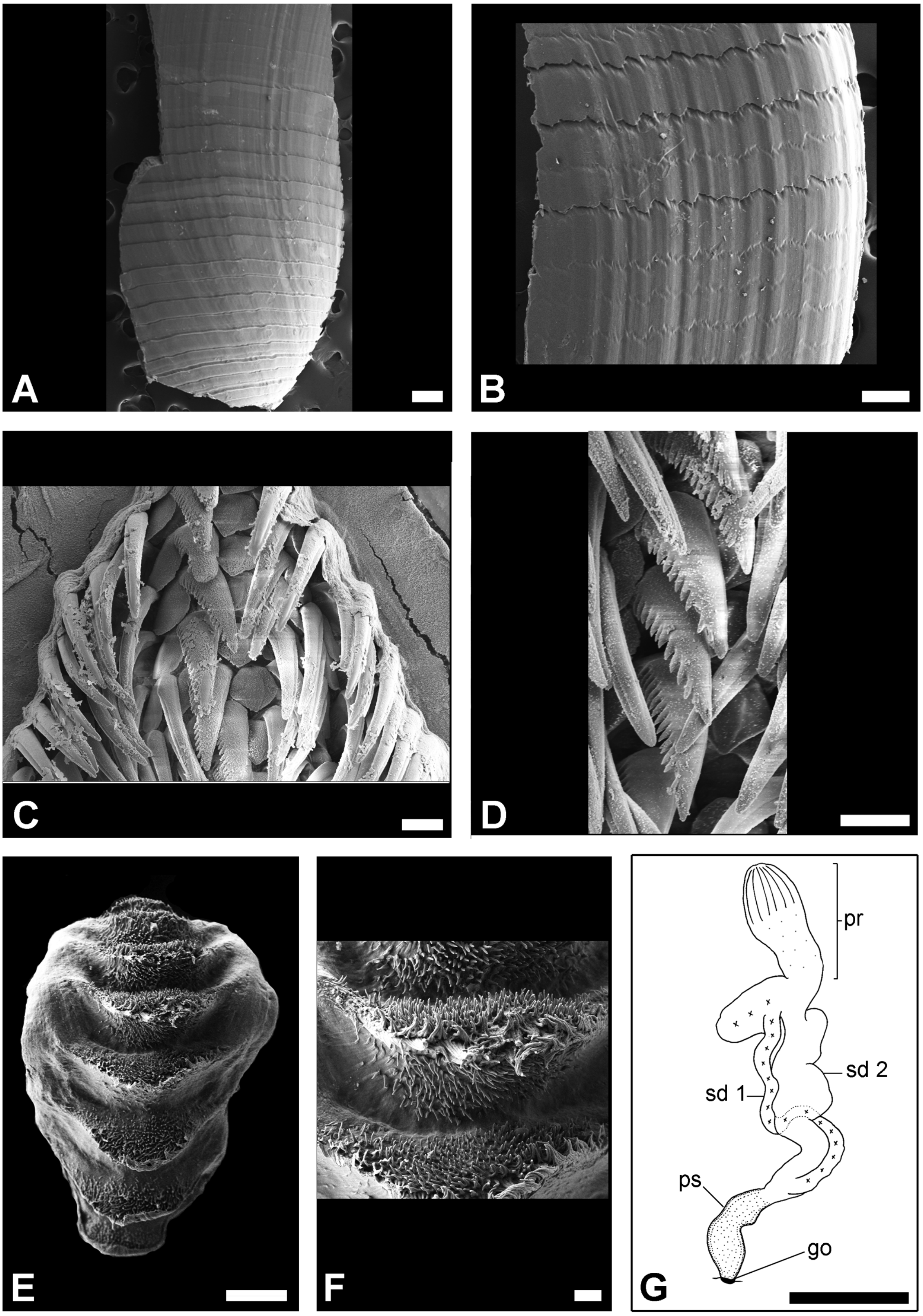

FIGURE 8. Shell and anatomy of *Aliculastrum parallelum*. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Anterior part of radula. D. Inner lateral tooth with denticulation at right side of radula. E. Top view of gizzard plate. F. Rods on middle ridges of gizzard plate. G. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd 1, first seminal duct; sd 2, second seminal duct. Scale bars: A, B = 200 µm; C = 10 µm; D = 2 µm; E = 100 µm; F = 20 µm; G = 1 mm. A: UF 374138, H = 8.7 mm; B, G: UF 374138, H = 8.54 mm; C, D: UF 374138, H= 6.8 mm; E, F: UF 374138, H = 9.6 mm.

ridges (Carlson & Hoff 1999). On the other hand, *Aliculastrum parallelum* shares similarities with the other studied species of *Aliculastrum* by possessing a cylindrical robust shell, and, as in the species *Aliculastrum debilis*, an asymmetric radula with strongly denticulated inner lateral teeth and a male reproductive system with two seminal ducts. Moreover, preliminary phylogenetic data (Too 2011) suggest the inclusion of this species in a clade together with the other two species of *Aliculastrum*.

Genus *Atys* Montfort, 1810

Type species: *Atys naucum* (Linnaeus, 1758)

Type locality. Ambon region, Indonesia (based on Rumphius 1705).

The genus *Atys* was first introduced by Montfort (1810) with type species *Atys cymbulus* Montfort, 1810. This species was considered a synonym of *Bulla naucum* Linnaeus, 1758 by Pilsbry (1895), and apparently even before by Sowerby (1870). Montfort (1810) referred the species to the African coast, although he did not specify the exact locality; though, the author was likely referring to the east coast of Africa, because *A. naucum* is only known in the Indo-West Pacific.

Species have been ascribed to this genus mostly based on shell morphology. The genus is characterized by umbilicate oval-elongate or inflated shells, with spiral grooves. The gizzard plates are covered with tiny rods and the radula has a median tooth (Bergh 1901; Lin 1997; Carlson & Hoff 1999). Species of the genus *Atys* are commonly found on shallow sandy bottoms in tropical and temperate regions and about 50 species have been reported in the Indo-West Pacific (OBIS 2012a) (see Tab. 2 for diagnostic characters of species described here).

Atys multistriatus Schepman, 1913

Atys multistriata Schepman, 1913: 468, pl. 32, fig. 2.
Atys multistriatus—Carlson & Hoff 2000: 170. Gosliner *et al*. 2008: 23.

Type locality. Balabalagan Islands, between Borneo and Sulawesi (Paternoster Islands)

Material examined. Mariana Islands, Guam, 2 spcs dissected, UF 374136, H = 6.27 mm, 6.6 mm.

Animal (Fig. 1D): Body whitish-translucent, white dots scattered all over body, red dots and white blotches on mantle; eyes visible.

Shell (Figs 2E, 9A, B): Maximum height 11.75 mm; whitish; fragile, thin, semi-translucent, elongated, oval, with slightly convex sides, anterior end protruded, posterior end truncated; spire sunken, outer lip elevated slightly above the apex, aperture narrow posteriorly and broader anteriorly, columella short, slightly concave, with a fold at the base; spiral grooves throughout shell but weaken in middle part, conspicuous axial lines present, creating net-like pattern all over the shell but weaken in middle part.

Jaws: Elongated with multiple denticles (Carlson & Hoff 2000).

Radula: Radular formula at mid-point 21–23 x 5–4.1.4–5; median tooth broad, slightly bilobed, with weak denticulation and small lateral cusp; outer lateral teeth hook-shaped, with weak denticulation (Carlson & Hoff 2000). There is no differentiation between inner and outer lateral teeth.

Gizzard plates (Figs 9C–E): Three gizzard plates; broader at anterior part, narrower towards posterior end; 20 ridges, thick, become crescent-shaped towards both ends, middle ridges inverted V-shaped, ridges covered by single rows of tiny rods with pointed tips along top edge, both anterior and posterior sides of ridges smooth.

Male reproductive system (Fig. 9F): Total length 3 mm (H = 6.27 mm). Formed by three parts: prostate, seminal duct and penial region; prostate single-lobed, ovoid, translucent; long seminal duct connects the prostate to penial region, about four times the length of prostate, opaque-yellow; penial region cylindrical-elongated, about half of the length of seminal duct, slightly broader than seminal duct, semi-translucent.

Ecology. Shallow water, reef flat to 21 m depth on sandy bottom (Carlson & Hoff 2000; Gosliner *et al*. 2008).

Geographical distribution. Indonesia, the Philippines, Guam, Palau, Hawaii, Tahiti, Fiji (Kay 1979; Carlson & Hoff 2000; present study).

TABLE 1. Summary of most useful characters for diagnosis of species of *Aliculastrum*.

	***A. cylindricum* (Helbling, 1779)**	***A. debilis* (Pease, 1860)**	***A. parallelum* (Gould, 1846)**
1. Animal	Eyes visible	Eyes visible	Eyes visible
2. Shell			
- Internal/ external	External	External	External
- Shape	Subcylindrical; widest part between apex and middle-line	Cylindrically ovate, narrowed towards both ends; widest part right below middle-line	Cylindrical
- Spire	Sunken	Sunken	Sunken
- Sculpture	Spiral grooves at both ends only (anterior = 16–18, posterior = 14), growth lines indistinct	Step-like spiral grooves at both ends only (anterior = 10–18, posterior = 7–13)	Spiral grooves at both ends only (anterior = 17–18, posterior = 14–20), fine longitudinal growth lines throughout shell
- Umbilicus	Absent	Absent	Absent
3. Jaws	Crescent shape, jaw rodlets with 6–8 denticles	Crescent shape, jaw rodlets with 5–6 denticles	Crescent shape
4. Radula			
- Formula	30–42 x 10–9.2.1.2.9–10	20–30 x 12–8.1.1.0.8–12	27 x 12.1.1.0.12
- Median tooth	Broad base, sharp triangular central cusp, pseudo triangular lateral cusp	Broad base, triangular central cusp with thinner membrane-like structure on both sides, pseudo lateral cusps	Broad base, triangular central cusp with thinner membrane-like structure on both sides, pseudo triangular cusp
- Inner lateral tooth	Hook-shaped, triangular base with slight semi-circular projection outwardly, groove along outer margin	Present only at right side, hook-shaped, broad base with semi-circular projection outwardly, strong denticulation along outer margin	Present only at right side, hook-shaped, broad base with semi-circular projection outwardly, strong denticulation along outer margin
- Outer lateral teeth	Hook-shaped, slender, broad base, broad semi-circular projection outwardly, grooves along both outer and inner margins	Hook-shaped, slender, broad base with semi-circular projection outwardly, groove along the outer margin	Hook-shaped, slender, with semi-circular projection outwardly, groove along the outer margin
5. Gizzard plates			
- Structure	10 transverse ridges on each side of pseudo-rachis, ridges crescent shape	8–11 transverse ridges, pseudo-rachis present, sometimes nearly absent.	8–9 ridges
- Sculpture	Tiny rods with pointed tips	Tiny rods with pointed tips along top edge of ridge, smaller rods with pointed tips at both anterior and posterior sides of ridges	Tiny rods with pointed tips at both anterior and posterior sides of ridges, higher density of rods at anterior half of plate; posterior half lacks rods on posterior side of ridges
- Gaps between ridges	Smooth	Smooth	Smooth
6. Male reproductive system			
- Prostate	Elongated, three-lobed	Elongated, bilobed, striation present	Elongated, semi-translucent, faint striations at distal end, division into lobes not evident
- Seminal duct	One; broad	Two; coiled distally nearly prostate	Two; first seminal duct originates distally at a pouch close to prostate
- Penial region	Semi-translucent	Translucent	Elongated, semi-translucent
7. Ecology	Sandy bottom below 15 m deep; reef flat	Sandy bottom and *Halimeda* beds between 6–18 m deep	Shallow areas up to 18 m deep
8. Key references	Pilsbry (1895)	Pease (1868)	Pilsbry (1895)

Remarks. This species has a conspicuous reticulated sculpture on the shell, which is uncommon among haminoeids species. This feature can also be seen in Schepman's (1913: pl. 32, fig. 2a, b) illustration of the holotype. Jaws and radula could not be successful prepared for SEM and descriptions are based on Carlson & Hoff (2000). According to the latter authors, this species possesses a bilobed median tooth with fine denticulation. This feature is known in the Mediterranean and eastern Atlantic species *Atys macandrewii* (Martinez & Ortea, 1998) and was found in the new species here described and named *Atys pittmani*. The shell of *Atys multistriatus* and its anatomy differs from the type species *Atys naucum*. The disparity of shell shapes and anatomies across *Atys* species hints that the genus may not be monophyletic. Preliminary molecular phylogenetic results (Too 2011) point in this direction, but a generic splitting of *Atys* will require the use of a broader taxon sampling; therefore, we refrain to do it at this stage.

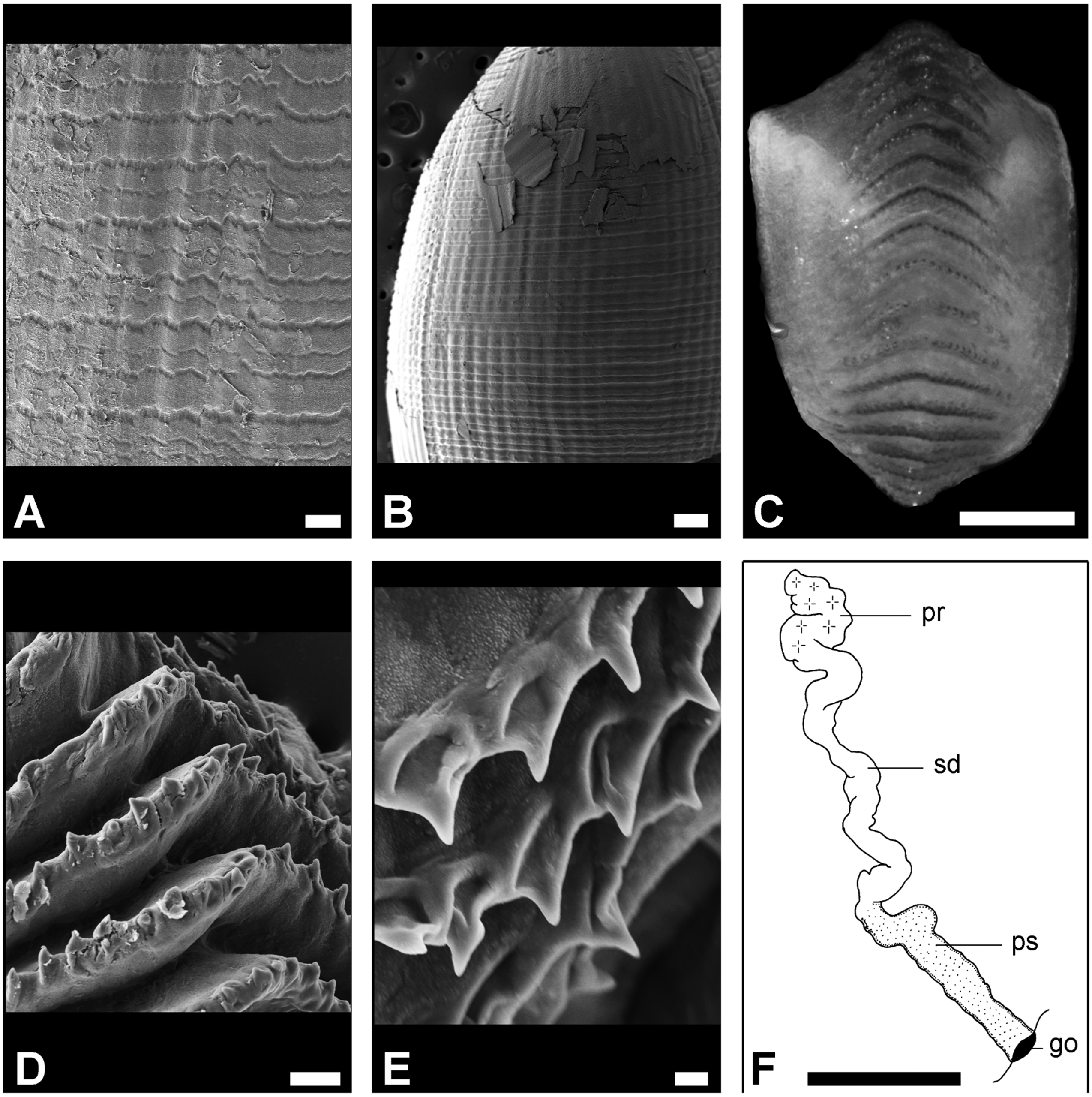

FIGURE 9. Shell and anatomy of *Atys multistriatus*. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Top view of gizzard plate. D. Middle ridges on gizzard plate. E. Rods on middle ridges of gizzard plate. F. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A, C = 100 µm; B = 200 µm; D = 10 µm; E = 2 µm; F = 1 mm. A, C–F: UF 374136, H = 6.27 mm; B: UF 374136, H = 6.6 mm.

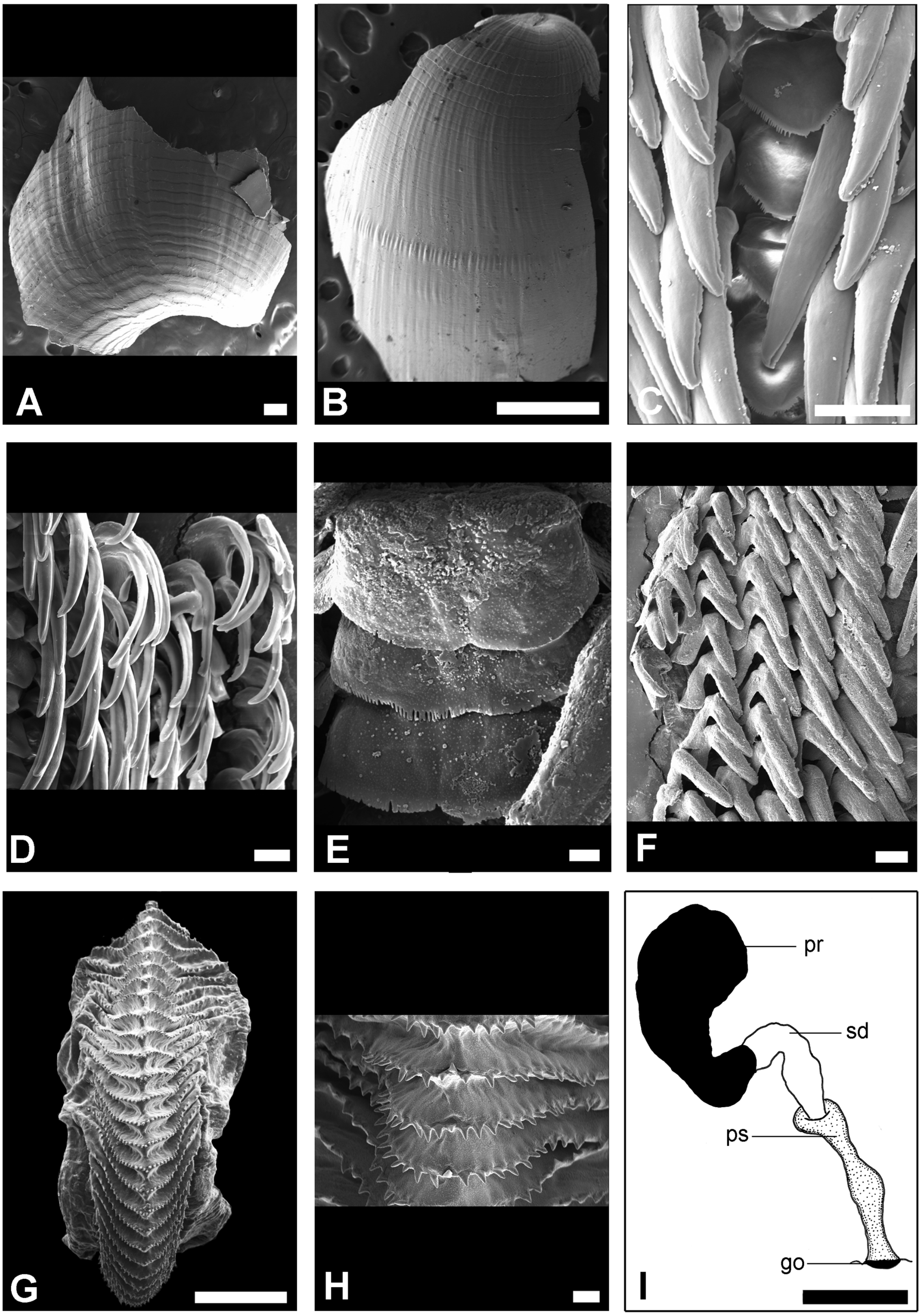

FIGURE 10. Shell and anatomy of *Atys pittmani* **nov. sp.**. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Detail of semi-circular median tooth at anterior part of radula. D. Detail of outer lateral teeth at left side of radula. E. Detail of bilobed median tooth at the middle part of radula. F. Detail of outer lateral teeth at right side of radula. G. Top view of gizzard plate. H. Rods on middle ridges of gizzard plate. I. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A = 200 µm; B = 1 mm; C, D, F, H = 10 µm; E = 2 µm; G = 100 µm; I = 0.5 mm. A, B, E, F: MNHN, Paris (S18/ OT756), H = 4.9 mm; C, D, G–I: ZMBN 81673, H = 10 mm.

Atys pittmani nov. sp.

Type locality. Black Rock, Maui Island, Hawaii.

Etymology. We name this species after Cory Pittman, a chief collaborator and provider of specimens from the Hawaiian Islands. This also intends to honour his brilliant and dedicated work on the taxonomy and diversity of heterobranch gastropods of Hawaii.

Material examined. Maui, Hawaii, 1 spc. dissected and sequenced, ZMBN 81673, H = 10 mm; Black Rock, Maui, Hawaii, 2 spcs studied (holotype and paratype), ZMBN 92894, H = 6 (paratype), 8 (holotype) mm; the Philippines, 1 spc. dissected, MNHN, Paris (S18/ OT756), H = 4.9 mm.

Animal (Fig. 1E): Body whitish-opaque, whitish pigmentation densely covering cephalic shield and parapodial lobes; white and red blotches on the mantle; eyes visible.

Barcode: GenBank Accession No KF735657 (ZMBN 81673).

Shell (Figs 2F, 10A, B): Maximum height 10 mm; whitish; fragile, thin, semi-translucent, ovo-cylindrical, elongated, anterior end protruded, posterior end truncated; spire sunken, outer lip elevated slightly above the apex, aperture narrow posteriorly and slightly broader anteriorly, strongly calcified callus at the end of columella but does not form tooth-like projection; spiral grooves at both ends (anterior = 14–18, posterior = 5–9), light axial lines present.

Jaws: Present, crescent shape.

Radula (Figs 10C–F): Radular formula at mid-point 27–32 x 7–4.1.4–7; median tooth rounded-triangular to bilobed, denticulation present along edge; outer lateral teeth hook-shaped, slender, size decreases outwardly. There is no differentiation between inner and outer lateral teeth.

Gizzard plates (Figs 10G, H): Three gizzard plates; long and narrow; 22–28 ridges, semi-circular, pseudo-rachis presents, ridges covered by single rows of tiny rods with pointed tips along top margin, both anterior and posterior sides of ridges smooth.

Male reproductive system (Fig. 10I): Total length 2 mm (H = 10 mm). Formed by three parts: prostate, seminal duct and penial region; prostate elongated-pyriform, single-lobed, opaque-yellow, broad posteriorly, narrower towards seminal duct; seminal duct shorter and narrower than prostate, creamy-white; penial region cylindrical-elongated, translucent.

Ecology. Mud flat or on algae *Halimeda*; up to 10 m deep.

Geographical distribution. the Philippines and Maui, Hawaii (present study).

Remarks. Shells of this species have spiral grooves at both ends interconnected with light axial lines throughout shell, a feature also found in *Atys multistriatus* (here studied), *Atys dactylus* and *Atys jeffreysi*, the latter two species from the Atlantic Ocean. Live animals of both *Atys multistriatus* and *Atys pittmani* are highly similar. Whereas in *Atys multistriatus* the white dots visible through the shell in the dorsal part of the mantle form compact clusters, in *Atys pittmani* those are separated and sparse apart intermingled with red dots. Also the reticulated pattern in the shell is conspicuous in *Atys multistriatus* whereas in *Atys pitttmani* is very light almost inconspicuous. Anatomically they possess distinct male reproductive systems; *Atys pittmani* has an elongated and distally broader prostate and shorter seminal duct. Additionally, we have evidence from preliminary molecular phylogenetic analyses that confirm the different identities of these two species (Too 2011).

Both specimens examined of *Atys pittmani* have identical gizzard plates and male reproductive systems, but the radula showed some variability; the specimen from Hawaii had rounded-triangular rachidian teeth whereas, the specimen from the Philippines has broader bilobed rachidian teeth. In both specimens the rachidian teeth were denticulate along the top edge.

Atys semistriatus Pease, 1860

Atys semistriata Pease, 1860: 20. Sowerby 1870: pl. 5, sp. 27. Smith 1872: 345. Pilsbry 1917: 217, fig. 5. Kay 1979: 426, figs 134A, B, 136A, 137A.
Atys (Alicula) semistriata—Pilsbry 1895: 267, pl. 28, fig. 30. Kobelt 1896: 20, pl. 6, fig. 11.
Atys semistriatus—Gosliner *et al*. 2008: 23.

Type locality. Hawaii.

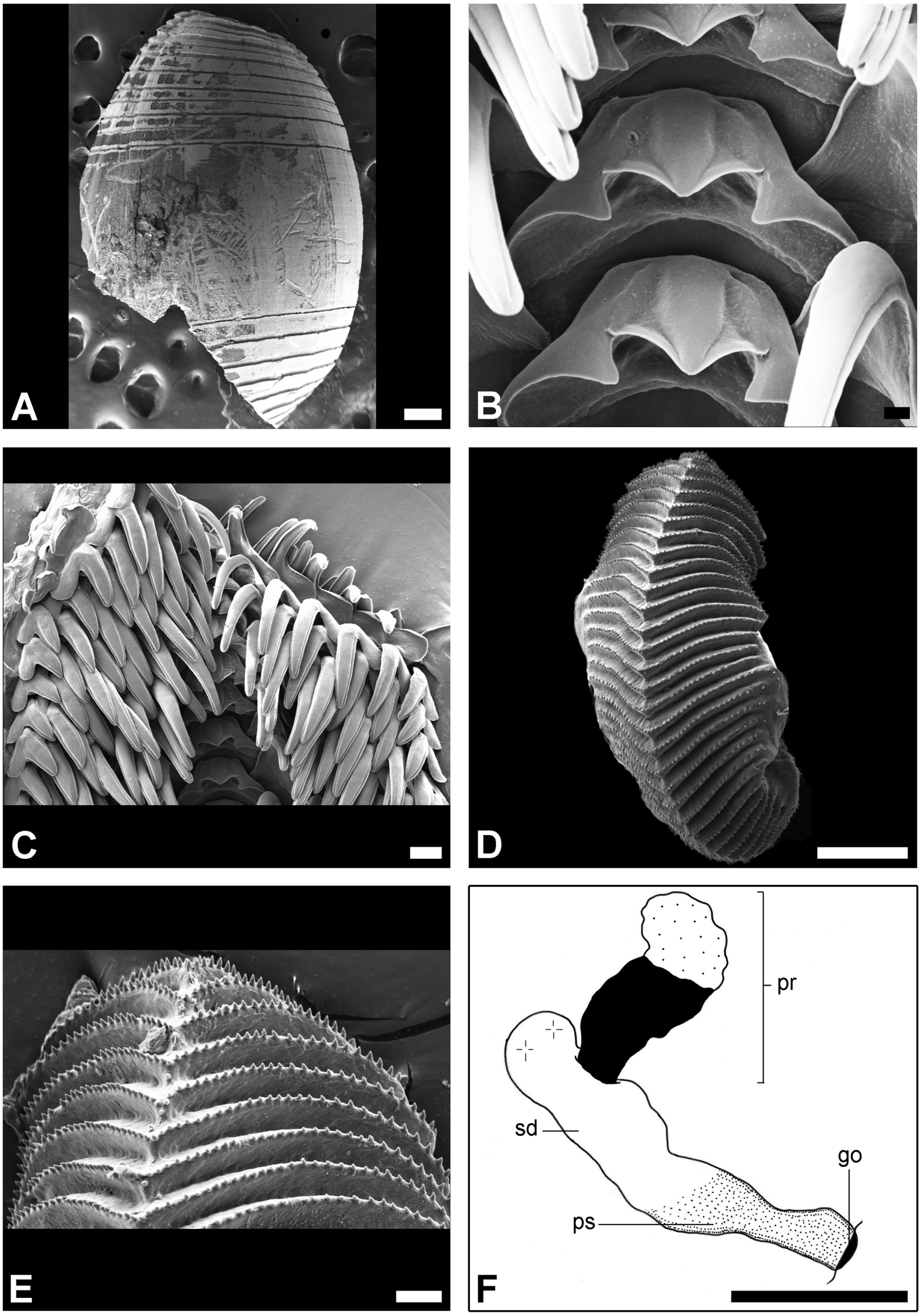

FIGURE 11. Shell and anatomy of *Atys semistriatus*. A. Detail of shell. B. Detail of median tooth at the middle part of radula. C. Detail of outer lateral teeth at the anterior part of radula. D. Top view of gizzard plate. E. Rods on middle ridges of gizzard plate. F. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A = 200 µm; B = 2 µm; C = 10 µm; D = 100 µm; E = 20 µm; F = 0.5 mm. A: MNHN, Paris (B31/ OT1042), H= 4.5 mm; B–E: ZMBN 87082, H = 4.9 mm; F: MNHN, Paris (B31/ OT1042), H = 6.4 mm.

Material examined. Hawaii, 1 shell examined, ZMB Moll 112.677 (paratype; see Fig. 12), H = 9.45 mm; Maui, Hawaii, live image taken, ZMBN 81656, H = 6 mm; Tahiti, 1 shell examined, ZMBN 87082, H = 4.1 mm; Tahiti, 1 spc. dissected, ZMBN 87082, H = 4.9 mm; the Philippines, 2 spcs dissected, MNHN, Paris (B31/OT1042), H = 4.5 mm, 6.4 mm.

Animal (Fig. 1F): Body whitish-opaque, dark dots scattered over the body, abundant red blotches on the mantle; eyes visible.

Shell (Figs 2G, 11A): Maximum height 14 mm; whitish; thick, translucent, barrel-shape, oval, inflated, conspicuously wider at the centre, narrower posteriorly; anterior end protruded, posterior end truncated, apex perforate; spire sunken, umbilicated, aperture narrow posteriorly and broader anteriorly; spiral grooves at both ends only (anterior = 11–20, posterior = 11–16), which become closer towards the ends, spiral grooves deeper towards both ends forming step-like grooves, faint axial lines present.

Jaws: Present, crescent shape.

Radula (Figs 11B, C): Radular formula at mid-point 25–28 x 7–6.1.6–7; median tooth with broad base, triangular central cusp with membrane-like structure on both sides, shorter triangular lateral cusps present; outer lateral teeth hook-shaped, base with rectangular projection outwardly, grooves along both outer and inner margins, size decreases outwardly. There is no differentiation between inner and outer lateral teeth.

Gizzard plates (Figs 11D, E): Three gizzard plates; long and narrow; 21–31 ridges on each side of pseudo-rachis, V-shaped, ridges covered by single rows of tiny rods with pointed tips along top edge of ridge, both anterior and posterior sides of ridges smooth.

Male reproductive system (Fig. 11F): Total length 1.5 mm (H = 6.4 mm). Formed by three parts: prostate, seminal duct and penial region; prostate elongated-ovoid, bilobed, proximal lobe larger and opaque-yellowish, striations on proximal lobe sometimes present, distal lobe semi-translucent, creamy-white; prostate inserts laterally at the beginning of posterior part of seminal duct, seminal duct broad, anterior part semi-translucent, posterior part opaque-yellowish; penial region elongated, translucent, about same length as seminal duct, slightly narrower than seminal duct.

Ecology. Sandy bottom or on *Halimeda* beds between depth of 3–15 m (Gosliner *et al*. 2008; present study).

Geographical distribution. Madagascar, Indonesia, Malaysia, Japan, the Philippines, Papua New Guinea, New Caledonia, Guam, Tahiti, Hawaii (Kuroda & Habe 1952; Gosliner *et al*. 2008; present study).

Remarks. Shells of this species vary from thin and fragile (Pease 1860) to slightly thick but always semi-translucent. Pilsbry (1895) mentioned that *Atys semistriatus* is identical to *Atys ehrenbergi* Issel, 1869, which is a fossil found in the Red Sea. The con-specificity of these species remains to be confirmed. This species possesses an ovoid inflated shell, a feature shared with the type species *Atys naucum*, but its gizzard plates, radula and male reproductive system have different structure and arrangement (Bergh 1901; Lin 1997; Carlson & Hoff 1999).

FIGURE 12. Paratype of *Atys semistriatus* in Museum für Naturkunde (Berlin, Germany; ZMB Moll 112.677; H = 9.45 mm).

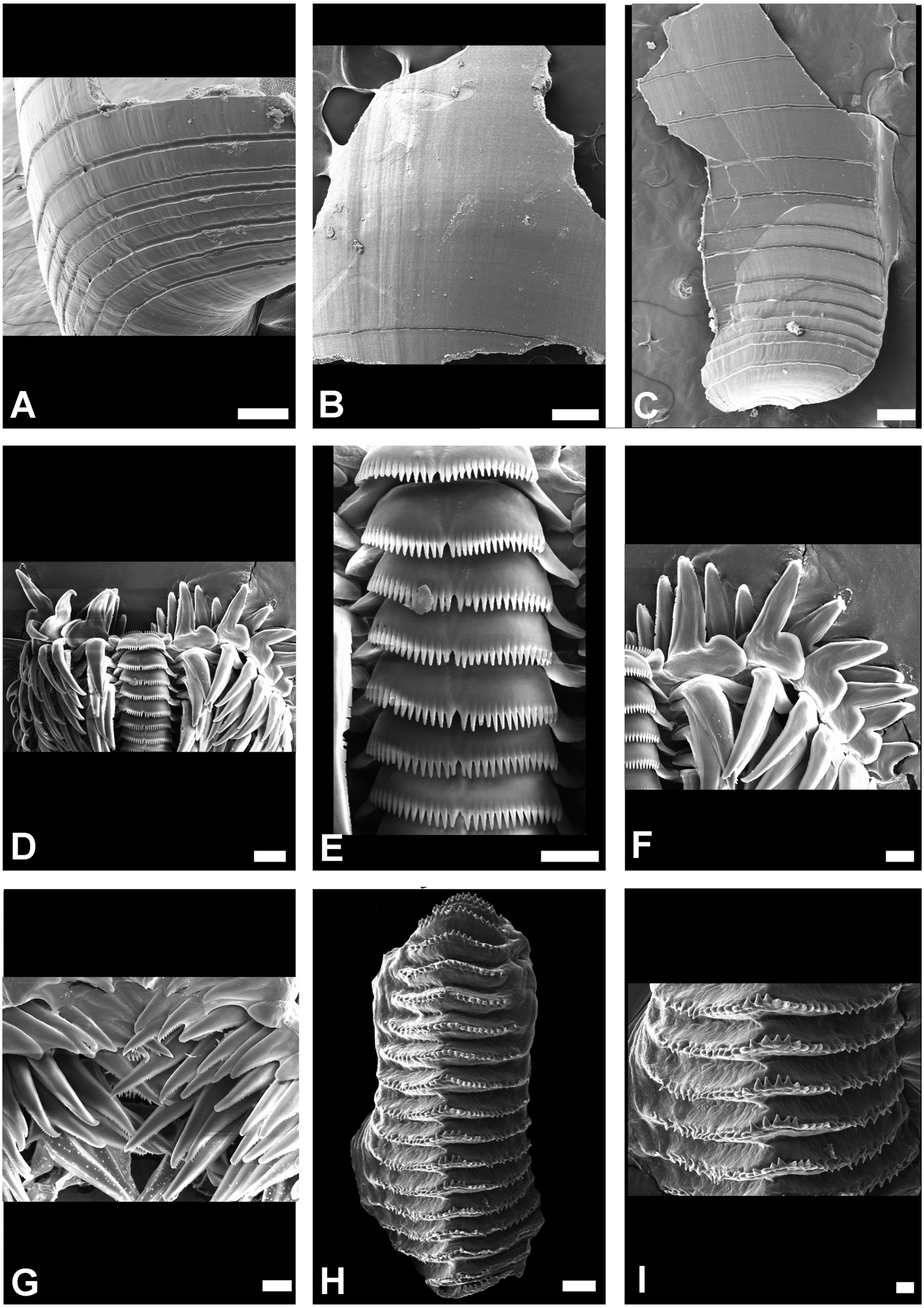

FIGURE 13. Shell and anatomy of *Atys ukulele* **nov. sp.**. A. Detail of anterior part of shell. B. Detail of middle part of shell. C. Detail of posterior part of shell. D. Anterior part of radula. E. Detail of median tooth at the anterior part of radula. F. Detail of outer lateral teeth at left side of radula. G. Weak denticulation along the outer margin of lateral teeth at the posterior of radula. H. Top view of gizzard plate. I. Rods on middle ridges of gizzard plate. Scale bars: A–C = 200 µm; D = 20 µm; E–G, I = 10 µm; H = 30 µm. A–I: ZMBN 89710.

TABLE 2. Summary of most useful characters for diagnosis of species of *Atys*.

	A. multistriatus **Schepman, 1913**	***A. pittmani*** **Too, Carlson, Hoff, and Malaquias, 2014**	***A. semistriatus*** **Pease, 1860**	***A. ukulele*** **Too, Carlson, Hoff, and Malaquias, 2014**
1. Animal	Eyes visible	Eyes visible	Eyes visible	Eyes visible
2. Shell				
- Internal/ external	External	External	External	External
- Shape	Elongated, oval	Ovo-cylindrical, elongated	Barrel-shape, oval, inflated; widest bellow middle-line, posterior end narrower	Barrel-shape, elongated; widest bellow middle-line, narrowing towards both ends
- Spire	Sunken	Sunken	Sunken	Sunken
- Sculpture	Spiral grooves throughout shell but weaken in middle part, conspicuous axial lines creating net-like pattern throughout shell but weaken in middle part	Spiral grooves at both ends (anterior = 14–18, posterior = 5–9), light axial lines present	Spiral grooves at both ends only (anterior = 11–20, posterior = 11–16)	Step-like spiral grooves at both ends (anterior = 11, posterior = 11), faint whitish band at middle part
- Umbilicus	?	?	Present	Present
3. Jaws	Elongate; jaw rodlets with multiple denticles	Crescent shape	Crescent shape	Crescent shape
4. Radula				
- Formula	21–23 x 5–4.1.4–5	27–32 x 7–4.1.4–7	25–28 x 7–6.1.6–7	23 x 6.1.6
- Median tooth	Broad, slightly bilobed, weak denticulation, small lateral cusp	Rounded-triangular to bilobed, denticulation present along the edge	Broad base, triangular central cusp with membrane-like structure on both sides, shorter triangular lateral cusps	Bilobed with broad base, and conspicuous denticulation along edge, shorter triangular lateral cusps
- Inner lateral tooth	Not distinct	Not distinct	Not distinct	Not distinct
- Outer lateral teeth	Hook-shaped, weak denticulation	Hook-shaped, slender	Hook-shaped, base with rectangular projection outwardly, grooves along both outer and inner margins	Hook-shaped, broad base with semi-circular projection outwardly, groove along inner margin, weak denticulation along outer margin
5. Gizzard plates				
- Structure	20 ridges, thick, become crescent-shaped towards both ends, middle ridges inverted V-shaped	22–28 ridges, semi-circular, pseudo-rachis present	21–31 ridges on each side of pseudo-rachis, V-shaped	18 ridges on each side of pseudo-rachis
- Sculpture	Single rows of tiny rods with pointed tips along top edge of ridges	Single rows of tiny rods with pointed tips along top edge of ridges	Single rows of tiny rods with pointed tips along top edge of ridges	Single rows of tiny rods with pointed tips along top edge of ridges
- Gaps between ridges	Smooth	Smooth	Smooth	Smooth
6. Male reproductive system				
- Prostate	Single-lobed, ovoid, translucent	Elongated-pyriform, single-lobed, opaque-yellow	Elongated-ovoid, bilobed, inserts laterally at the beginning of posterior part of seminal duct	?
- Seminal duct	Long, opaque-yellow	Shorter and narrower than prostate, creamy-white	Broad, anterior part semi-translucent, posterior part opaque-yellowish	?
- Penial region	Cylindrical-elongated, semi-translucent	Cylindrical-elongated, translucent	Elongated, translucent	?
7. Ecology	Shallow water, reef flat to 21 m deep on sandy bottom	Mud flat or on algae *Halimeda*; up to 10 m deep	Sandy bottom or on *Halimeda* beds between 3–15 m deep	Sandy bottom between 6–17 m deep
8. Key references	Carlson & Hoff (2000)	Present study	Sowerby (1870)	Present study

Atys ukulele nov. sp.

Type locality. Black Rock, Maui Island, Hawaii

Etymology. This species is only known from Hawaii and we named it after a traditional musical instrument of these islands, the ukulele guitar, a "derived form" of the Portuguese "cavaquinho" guitar introduced in Hawaii during the 19^{th} century by Portuguese immigrants.

Material examined. Maui, Hawaii, 1 spc. dissected, ZMBN 89710, H = 5.4 mm. Black Rock, Maui, Hawaii, 1 spc. sequenced, ZMBN 89707 (holotype), H = 3.5 mm. Black Rock, Maui, Hawaii, 1 spc., ZMBN 89708 (paratype), H = 4.2 mm. Black Rock, Maui, Hawaii, 1 spc., ZMBN 89709 (paratype), H = 3.1 mm.

Animal (Fig. 1G): Body whitish-translucent, white dots scattered over the body, more dense on edges and mid part (between mouth and eyes) of cephalic shield, forming light yellowish blotches on the mantle, dark dots scattered over the parapodial lobes; eyes visible, inserted on unpigmented periocular areas.

Barcode: GenBank Accession No KF735658 (ZMBN 89707).

Shell (Figs 3A, 13A, B): Maximum height 5.4 mm; whitish; fragile, semi-translucent, barrel-shape, elongated, widest right below the mid-line, anterior end protruded, posterior end truncated; spire sunken, outer lip elevated above the apex, aperture narrow posteriorly and slightly broader anteriorly, umbilicus present; step-like spiral grooves at both ends (anterior = 11, posterior = 11), which become closer towards the ends, faint bands at the middle part.

Jaws: Present, crescent shape.

Radula (Figs 13D–G): Radular formula at mid-point 23 x 6.1.6; median tooth bilobed with broad base, and conspicuous denticulation along edge, shorter triangular lateral cusps present; outer lateral teeth hook-shaped, broad base with semi-circular projection outwardly, groove along inner margin, weak denticulation along outer margin, size decreases outwardly. There is no differentiation between inner and outer lateral teeth.

Gizzard plates (Figs 13H, I): Three gizzard plates; long and narrow; 18 ridges on each side of pseudo-rachis, ridges covered by single rows of tiny rods with pointed tips along top edge of ridges, both anterior and posterior sides of ridges smooth.

Male reproductive system: Unknown.

Ecology. Sandy bottom between 6–17 m deep (present study).

Geographical distribution. Maui, Hawaii (present study).

Remarks. This species has a bulloid shell more elongated than *Atys semistriatus*. The colour patterns of *Atys semistriatus* and *Atys ukulele* **nov. sp.** are distinct. The former has large conspicuous red blotches in the mantle and dark spots scattered over the cephalic shield, whereas *Atys ukulele* has a mantle pigmented with faint, almost inconspicuous yellowish blotches and a cephalic shield with white dots along the edges and between the eyes. Moreover, *Atys ukulele* has a distinct radular median tooth, slightly bilobed with the presence of conspicuous denticulation along the margin. The reproductive system was damaged during dissection hindering comparison with *Atys semistriatus*.

Genus *Diniatys* Iredale, 1936

Type species: *Bulla dentifera* Adams, 1850

This genus was originally named *Dinia* by H. and A. Adams (1854) as a subgenus of *Atys*. It has been placed as a subgenus of *Cylichna* in Scaphandridae (Thiele 1931; Maes 1967), or as a genus of Scaphandridae (Pilsbry 1921) and Haminoeidae (Habe 1952; Burn 1978). Since *Dinia* was preoccupied by a group of lepidopteran insects (Walker 1854), Iredale (1936) introduced the new generic name *Diniatys* with the type species *Diniatys dentifer*, which was originally described as *Bulla dentifera* (Adams 1850).

The traditional diagnostic character of the genus is the tooth-like projection at the end of columella. Shells are usually ovoid and broad with fine spiral grooves and without umbilicus (Burn 1978). Three species were described in the Indo-West Pacific: *D. dentifer* (Adams, 1850), *D. monodonta* (Adams, 1850) and *D. truncatula* (Schepman, 1913) (Burn 1978; Carlson & Hoff 2003; Qi 2004; Gosliner *et al.* 2008). According to Schepman (1913), *D. truncatula* was found at a depth of 522 m in the Sulu Sea off the Philippines (see Tab. 3 for diagnostic characters of species described here).

Diniatys dentifer (Adams, 1850)

Bulla dentifera Adams, 1850: 588, pl. 115, fig. 124.
Atys dentifera—Sowerby 1870: pl. 3, sp. 13. Schepman 1913: 470.
Atys (Dinia) dentifer—Martens 1880: 303.
Atys (Dinia) dentifera—H. & A. Adams 1854: 21. Watson 1886: 641. Pilsbry 1895: 276, pl. 27, fig. 81. Kobelt 1896: 27, pl. 8, fig. 15.
Diniatys dentifer—Iredale 1936: 329. Habe 1952: 141, pl. 20, fig. 12. Gosliner *et al*. 2008: 28.

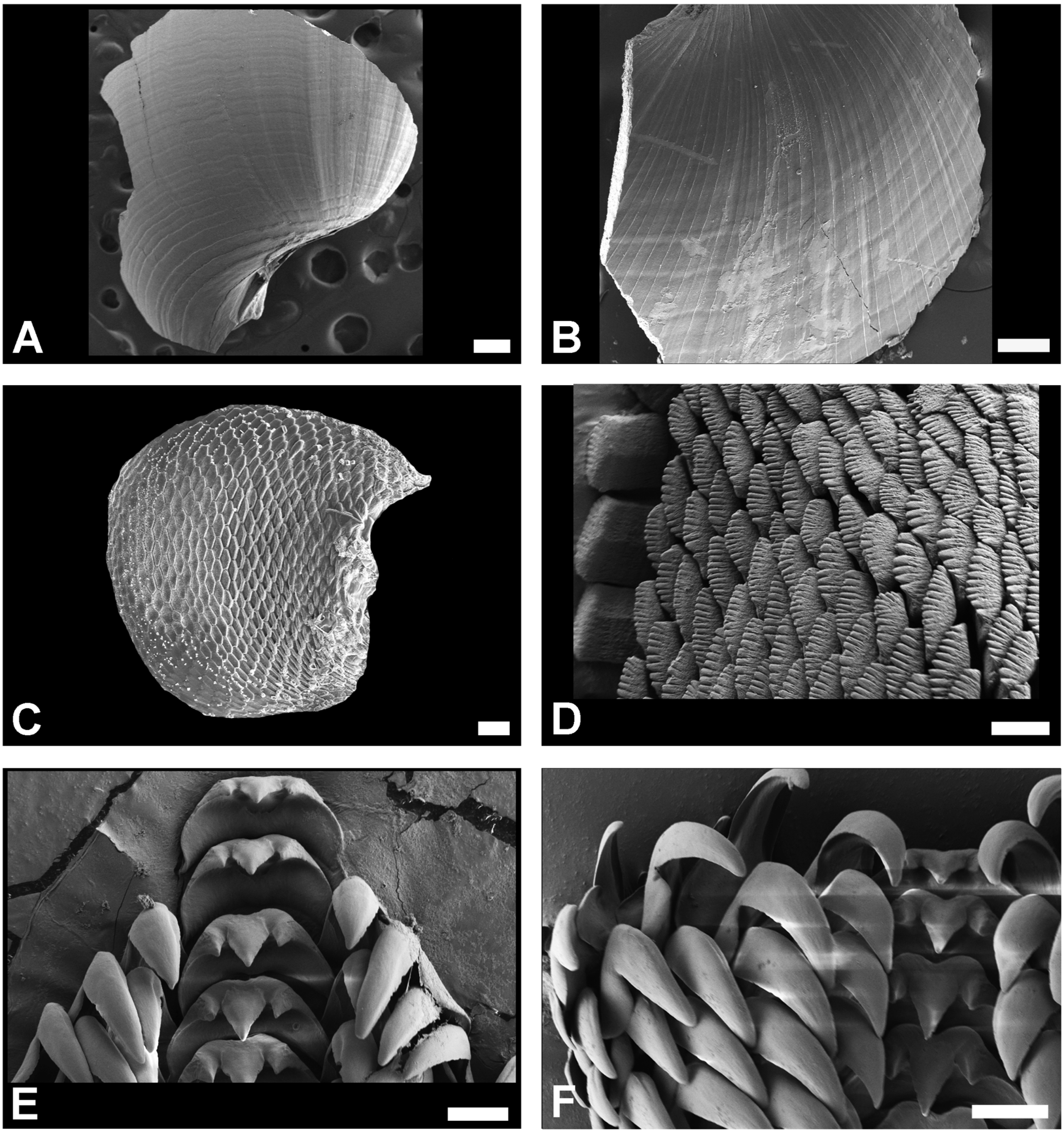

FIGURE 14. Shell and anatomy of *Diniatys dentifer*. A. Detail of anterior part of shell. B. Detail of posterior part of shell. C. Top view of jaw. D. Detail of jaw. E. Detail of median tooth at the anterior part of radula. F. Detail of outer lateral teeth at right side of radula. Scale bars: A = 200 µm; B = 100 µm; C, E–F = 20 µm, D = 10 µm. A, B, E, F: UF 374130, H = 4.4 mm; C, D: UF 374130, H = 4.3 mm.

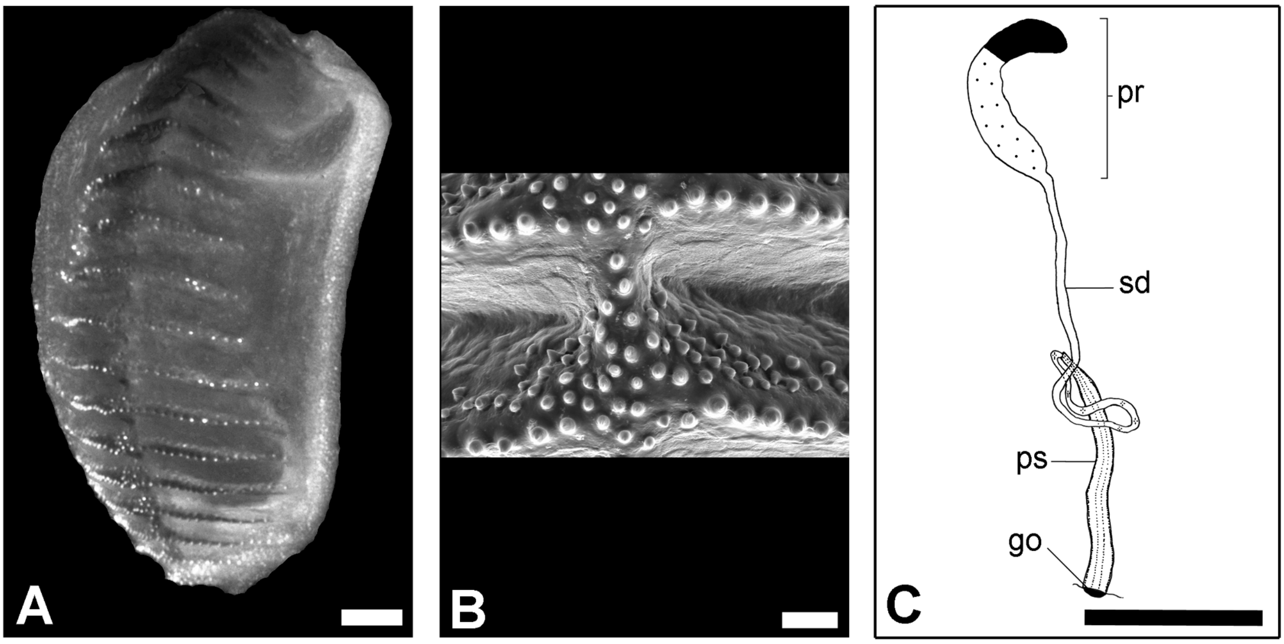

FIGURE 15. Anatomy of *Diniatys dentifer*. A. Top view of gizzard plate. B. Rods on middle ridges of gizzard plate. C. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A = 20 µm; B = 10 µm; C = 1 mm. A, B: ZMBN 81706, H = 4 mm; C: MNHN, Paris (B17/OT793), H = 3.5 mm.

Type locality. Marutea Atoll, French Polynesia (Lord Hood's Island).

Material examined. the Philippines, 1 shell examined, MNHN, Paris (B17/OT793), H = 3.5 mm; Mariana Islands, Guam, 5 spcs dissected, UF 374130, H = 3.1–4.6 mm; Maui, Hawaii, 1 spc. dissected, ZMBN 81706, H = 4 mm; the Philippines, 1 spc. dissected, MNHN, Paris (B17/OT793), H = 3.8 mm.

Animal (Fig. 1H): Whitish and greenish pigmentation abundant all over body; dark blotches present on mantle; eyes visible.

Shell (Figs 3B, 14A, B): Maximum height 12 mm; whitish; fragile, translucent, ovoid, narrower towards both ends, posterior part broader than anterior part, anterior end protruded, posterior end truncated; spire sunken, columella ends in tooth-like projection; spiral grooves at both ends only (anterior = 12–13, posterior = 15), inconspicuous axial lines present throughout shell.

Jaws (Figs 14C, D): Present, crescent shape, jaw rodlets with 9–11 denticles.

Radula (Figs 14E, F): Radular formula at mid-point 16–22 x 6.1.6; median tooth with broad base, sharp triangular central cusp, small triangular lateral cusp; outer lateral teeth hook-shaped, broad base with semi-circular projection outwardly, size decreases outwardly.

Gizzard plates (Figs 15A, B): Three gizzard plates; broad, almost equal size from anterior to posterior, 11–13 ridges, rachis conspicuous, single rows of rods with pointed tips along top edge of ridges, anterior side of ridges and top side of rachis covered by tiny rods with pointed tips, posterior side of ridges smooth, density of rods increases posteriorly.

Male reproductive system (Fig. 15C): Total length 4.6 mm (H = 3.5 mm). Formed by three parts: prostate, seminal duct and penial region; prostate elongated, bilobed, proximal lobe larger, semi-translucent, distal lobe opaque-yellowish; long and thin seminal duct connects prostate and penial region, anterior part of seminal duct narrower and translucent, coils into a loop before inserting penial region; penial region elongated, semi-translucent, about half of length of seminal duct, a narrower duct is observed within.

Ecology. Associated with cyanobacteria, particularly *Lyngbya*, on rock reef flats and beds of *Halimeda* spp. at the depth of up to 21 m (Gosliner *et al*. 2008; present study).

Geographical distribution. Madagascar, the Philippines, Japan, Indonesia, Papua New Guinea, Guam, Hawaii, French Polynesia (Watson 1886; Kay 1979; Gosliner *et al*. 2008; present study).

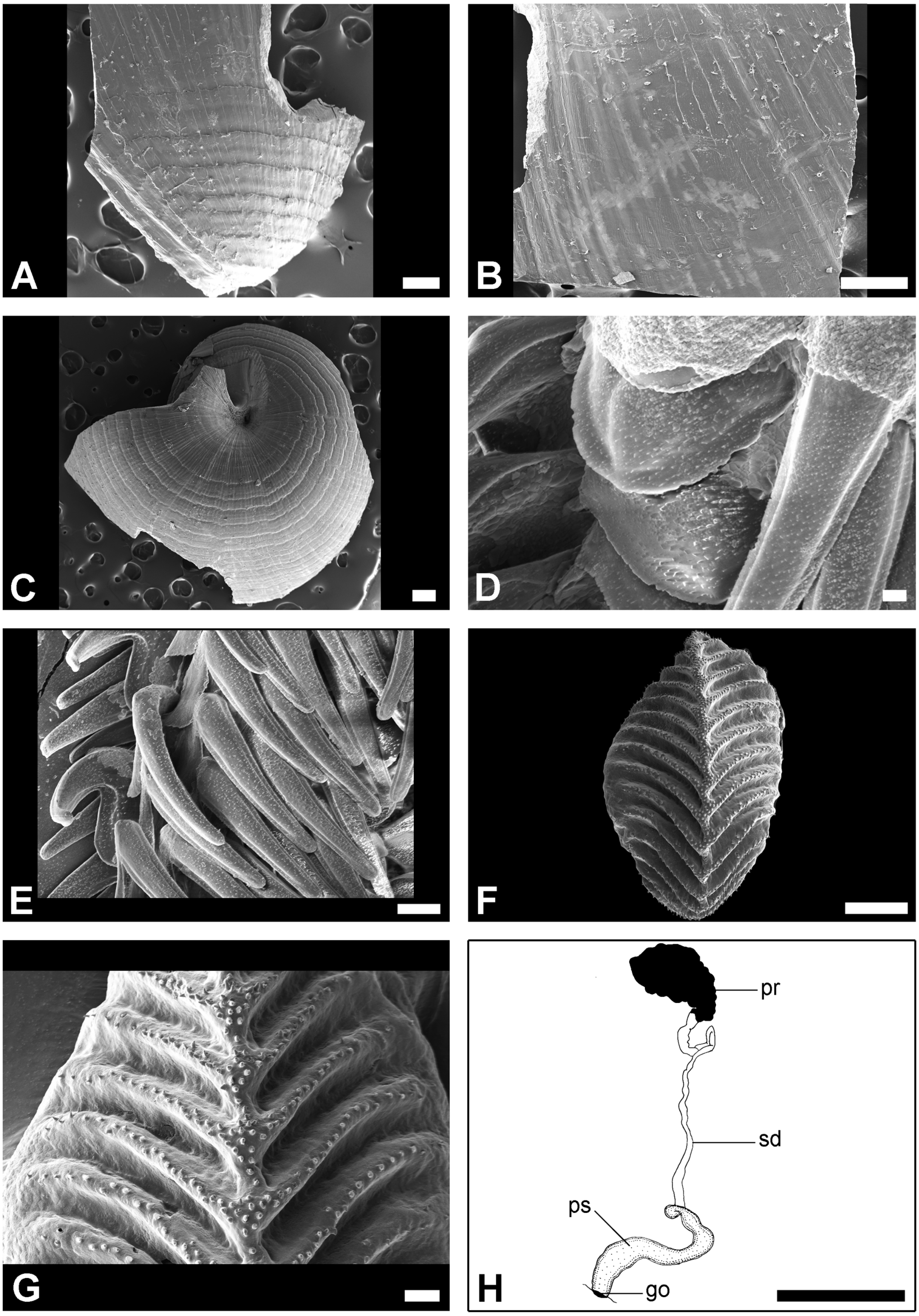

FIGURE 16. Shell and anatomy of *Diniatys dubia*. A. Detail of anterior part of shell. B. Axial lines in the middle part of shell. C. Detail of posterior part of shell and sunken spire. D. Detail of median tooth at the anterior part of radula. E. Detail of outer lateral teeth at right side of radula. F. Top view of gizzard plate. G. Rods on ridges of gizzard plate. H. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd, seminal duct. Scale bars: A, G = 20 µm; B, C = 200 µm; D = 2 µm; E = 10 µm; F = 100 µm; H = 1 mm. A–C, F-H: UF 299907, H= 6.1 mm; D, E: UF 299907, H = 6.3 mm.

TABLE 3. Summary of most useful characters for diagnosis of species of *Diniatys*.

	D. dentifer **(Adams, 1850)**	***D. dubia*** **(Schepman, 1913)**
1. Animal	Eyes visible	Eyes visible
2. Shell		
- Internal/ external	External	External
- Shape	Ovoid	Ovoid
- Spire	Sunken	Sunken
- Sculpture	Spiral grooves at both ends only (anterior = 16–18, posterior = 14), growth lines indistinct	Step-like spiral grooves at both ends only (anterior = 10–18, posterior = 7–13)
- Columella	Ends in tooth-like projection	Strongly calcified, folded outwardly, becoming thicker but not forming a tooth-like projection
- Umbilicus	?	?
3. Jaws	Crescent shape, jaw rodlets with 9–11 denticles	Crescent shape
4. Radula		
- Formula	16–22 x 6.1.6	30–36 x 8–6.1.6–8
- Median tooth	Broad base, sharp triangular central cusp, small triangular lateral cusps	Semi-circular at anterior part of radula, and more pointed at posterior part
- Inner lateral tooth	Not distinct	Not distinct
- Outer lateral teeth	Hook-shaped, broad base with semi-circular projection outwardly	Hook-shaped, grooves along both outer and inner margins
5. Gizzard plates		
- Structure	11–13 ridges, rachis conspicuous	14–15 ridges, V-shaped, rachis conspicuous
- Sculpture	Single rows of rods with pointed tips along top edge of ridges, anterior side of ridges and top of rachis covered by tiny rods with pointed tips, posterior side of horizontal ridges smooth	Tiny rods with pointed tips on top edge of ridges and rachis
- Gaps between ridges	Smooth	Smooth
6. Male reproductive system		
- Prostate	Bilobed, elongated	Single-lobed, elongated, opaque-yellow
- Seminal duct	Long and thin, anterior part narrower and translucent, coils into a loop before inserting in penial region	Long and thin, translucent, slightly coiled at both ends
- Penial region	Elongated, semi-translucent, with a narrower duct observed within	Elongated, light-yellowish
7. Ecology	Associated with cyanobacteria, particularly *Lyngbya*, on rocky reef flats and beds of *Halimeda* spp. down to 21 m deep	Sandy bottom where it feeds upon cyanobacterium *Microcoleus* down to 27 m deep
8. Key references	Schepman (1913)	Schepman (1913)

Diniatys dubia (Schepman, 1913)

Haminea dubia Schepman, 1913: 474, pl. 32, figs 8, 9.
Diniatys? *dubia*—Carlson & Hoff 2003.
Haminoea sp. 2—Gosliner *et al*. 2008: 27.

Type locality. Balabalagan Islands located between Borneo and Sulawesi (Paternoster Islands).

Material examined. Mariana Islands, Guam, 2 spcs dissected, UF 299907, H = 6.1, 6.3 mm.

Animal (Fig. 1I): Body whitish-translucent, whitish dots abundant over the body, densely organized between eyes and around edge of cephalic shield; mantle with dark brownish network of lines and whitish blotches throughout; eyes visible.

Shell (Figs 3C, 16A–C): Maximum height 12 mm; whitish; fragile, thin, translucent, ovoid, narrower towards both ends, posterior part broader than anterior part, anterior end protruded, posterior end truncated; spire sunken, columella end semi-translucent, strongly calcified, folded outwardly, becoming thicker but not forming a tooth-like projection; spiral grooves at both ends only (anterior = 8–10, posterior = 5–6), inconspicuous axial lines present throughout shell.

Jaws: Present, crescent shape.

Radula (Figs 16D, E): Radular formula at mid-point 30–36 x 8–6.1.6–8; median tooth at anterior part of radula semi-circular and more pointed at posterior part; outer lateral teeth hook-shaped, grooves along both outer and inner margins, size increases outwardly but outermost tooth smallest.

Gizzard plates (Figs 16F, G): Three gizzard plates; widest in the middle, narrower towards both ends, 14–15 ridges, V-shaped, rachis conspicuous, top edge of ridges and rachis covered by tiny rods with pointed tips, both anterior and posterior sides of ridges smooth.

Male reproductive system (Fig. 16H): Total length 4 mm (H = 6.1 mm). Formed by three parts: prostate, seminal duct and penial region; prostate single-lobed, elongated, opaque-yellow; long and thin seminal duct connects prostate and penial region, translucent, slightly coils at both ends; penial region elongated, light-yellowish, about half of length of seminal duct.

Ecology. Sandy bottom where it feeds upon cyanobacterium *Microcoleus*, between 12–27 m deep (Gosliner *et al*. 2008, present study).

Geographical distribution. the Philippines, Indonesia, Papua New Guinea, Guam, Hawaii (Gosliner *et al.* 2008; present study).

Remarks. This species has been subjected to taxonomic confusion. Schepman (1913) named it *Haminoea dubia* based on features of the gizzard plates and outer lateral teeth. Carlson & Hoff (2003) placed it provisionally in the genus *Diniatys* and Gosliner *et al*. (2008) named this species *Haminoea* sp. 2. Shells of this species displayed a strongly calcified callus at the end of the columella folding outwardly, which is distinct from the tooth-like projection at the end of columella in *Diniatys dentifer.* In addition, this species also shows differences in the gizzard plates and radula compared to *Diniatys dentifer.* The median tooth in *D. dubia* is semi-circular, whereas in *D. dentifer* it has a sharp triangular central cusp with smaller triangular cusps at both sides. Gizzard plates of this species display single rows of tiny rods along the top edge of ridges, whereas the latter possesses tiny rods on both top edge and anterior side of ridges. On the other hand, both species possess male reproductive systems with long and fine seminal duct and elongated narrow penial region. Preliminary molecular phylogenetic analyses (Too 2011) further support the inclusion of this species in the genus *Diniatys*.

Genus *Liloa* Pilsbry, 1921

Type species: *Bulla curta* Adams, 1850

Pilsbry (1921) introduced *Liloa* as a subgenus of Haminoeidae with type species *Haminoea curta tomaculum* Pilsbry, 1917. According to Pilsbry (1917), this species has a narrower shell compared to *Bulla curta* described by Adams (1850). Habe (1952) considered both species to be synonyms and gave *Liloa* genus status in the family Haminoeidae. Pilsbry (1921) stated that species of the genus *Liloa* possess narrow shells with spiral grooves throughout but some authors claimed that some species only have spiral grooves at the ends of the shell (Habe

1952; Lin 1997; Rudman 1998a; Qi 2004). Species recognized in the Indo-West Pacific include *L. curta* (Adams, 1850), *L. brevis* (Quoy & Gaimard, 1833), *L. porcellana* (Gould, 1859), *L. translucens* (Adams, 1862), *L. incisula* Yokoyama, 1928 and *L. nipponensis* (Nomura & Hatai, 1940) (Burn 1978; Lin 1997; Gosliner *et al*. 2008; OBIS 2012b) (see Tab. 4 for diagnostic characters of species described here).

Liloa curta (Adams, 1850)

Bulla curta Adams, 1850: 582, pl. 124, fig. 100.
Haminea curta—Pilsbry 1895: 368, pl. 40, figs 84, 85.
Haminea curta tomaculum Pilsbry, 1917: 219, fig. 10.
Haminoea curta—Pilsbry 1921: 369, fig. 8a. Kay 1979: 427: fig. 137 I.
Haminoea tomaculum—Pilsbry, 1921: 370.
Haminoea (Liloa) curta—Pilsbry 1921: 369, fig. 8a.
Liloa curta—Habe 1952: 151, pl. 21, fig. 19. Qi 2004: 147, pl. 83, fig. N.
Atys curta—Gosliner *et al*. 2008: 23.

Type locality. Indo-Pacific (not specified in the original description).

Material examined. Guam, UF 374131, H = 15 mm; the Philippines, 1 shell examined, MNHN, Paris (S12/ OT575), H = 3.1 mm; the Philippines, 5 spcs dissected, MNHN, Paris (S12/ OT575), H = 3.4–7.5 mm; the Philippines, 2 spcs dissected, MNHN, Paris (S5/ OT392), H = 5.4 mm, 6 mm.

Animal (Fig. 1J): Body whitish-translucent, pinkish dots scattered over the body, more dense between eyes and mid part (between mouth and eyes) of cephalic shield; white and red blotches scattered on mantle; eyes visible.

Shell (Figs 3D, 17A–C): Maximum height 18 mm; whitish; thin and fragile, translucent, cylindrically oval, sides slightly convex only, anterior end slightly rounded, posterior end truncated; spire sunken, aperture broad, outer lip thin, base semi-circular; spiral grooves covering entire shell, distance between spiral grooves almost equal, faint irregular axial lines present.

Jaws (Fig. 17D): Present, crescent shape, jaw rodlets with 7–10 denticles.

Radula (Figs 17E, F): Radular formula at mid-point 19–25 x 8–7.1.7–8; median tooth with broad base, large triangular central cusp, small triangular lateral cusps; outer lateral teeth hook-shaped, slender, base with semi-circular projection outwardly, groove along the outer margin, size decreases outwardly. Inner-lateral teeth not distinct.

Gizzard plates (Figs 17G, H): Three gizzard plates; widest in the middle, narrower towards both ends, 27–42 ridges, single rows of rods with pointed tips along top edge of ridges, both anterior and posterior sides of ridges covered densely by tiny rods with pointed tips.

Male reproductive system (Fig. 17I): Total length 2.5 mm (H = 7.5 mm). Formed by three parts: prostate, seminal ducts and penial region; prostate oval-rounded, bilobed, proximal lobe narrower, opaque-yellowish, faint striations sometimes present, distal lobe light-brownish; translucent pouch connects to the prostate, light-yellowish mass observed within, pouch opens to two seminal ducts, first seminal duct translucent, with hook-like posterior end, second seminal duct broad and short, translucent, connects to the penial region; penial region elongated, translucent, with opaque inner duct visible.

Ecology. Sandy bottom in shallow water (Qi 2004; Gosliner *et al*. 2008; present study).

Geographical distribution. Red Sea, Malaysia, the Philippines, China, Japan, Papua New Guinea, Guam, New Caledonia, Hawaii (Habe 1952; Qi 2004; Gosliner *et al*. 2008; present study).

Remarks. Pilsbry (1917) named a shell that was identical but narrower than *Liloa curta* as *Haminea curta tomaculum*. Later, Pilsbry (1921) considered that both "*curta*" and "*tomaculum*" deserved species status. Additionally, Pilsbry (1921) described *Haminea olopana*, based on a shell that was more convex than *Haminea curta* and *Haminea tomaculum* and with spiral grooves more distantly spaced at the centre and placed all three species in the new subgenus *Liloa*. Kay (1979) synonymised these species under the name *Haminoea curta*. However, the original description of *H. olopana* fits *Liloa porcellana* (Gould, 1859), which possess a cylindrical and translucent shell, with spiral grooves more visible at both ends, arched callus at the end of columella and the anterior end of the shell subtruncated.

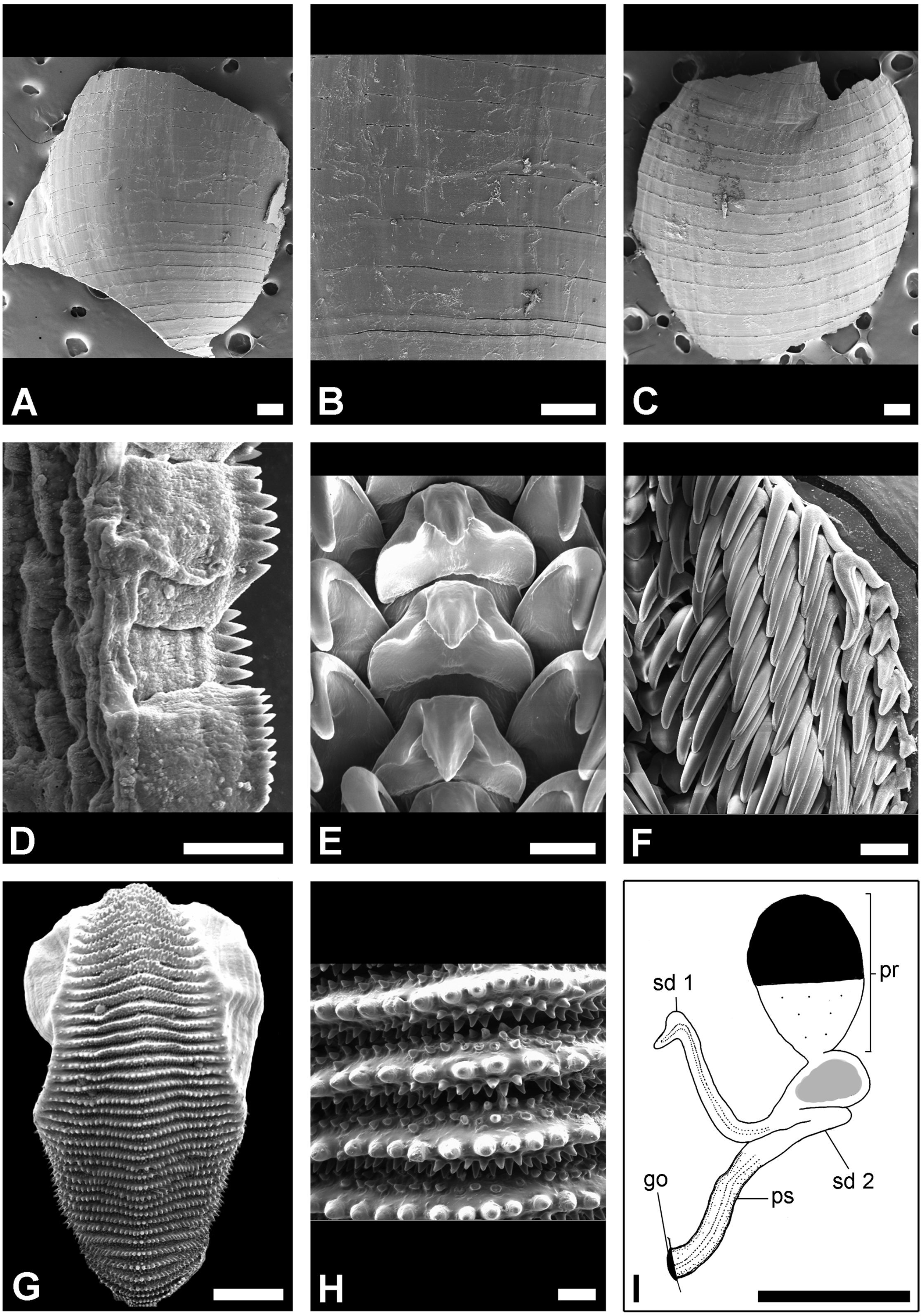

FIGURE 17. Shell and anatomy of *Liloa curta*. A. Detail of anterior part of shell. B. Detail of middle part of shell C. Detail of posterior part of shell. D. Detail of jaw. E. Detail of median tooth at the middle part of radula. F. Detail of outer lateral teeth at left side of radula. G. Top view of gizzard plate. H. Rods on middle ridges of gizzard plate. I. Male reproductive system. go, genital opening; pr, prostate; ps, penial sheath; sd 1, first seminal duct; sd 2, second seminal duct. Scale bars: A–C = 200 µm; D, H = 10 µm; E, F = 20 µm; G = 100 µm; I = 1 mm. A, B, D: MNHN, Paris (S5/ OT392), H = 6 mm; C, E-I: MNHN, Paris (S12/ OT575), H = 7.5 mm.

The species *Liloa curta* has been either ascribed to the genus *Liloa* (e.g. Habe 1952; Qi 2004) or to the genus *Atys* (e.g. Gosliner *et al*. 2008). However, this species possesses both shell and anatomical features that are different from the type species *Atys naucum*. *Liloa curta* has unique gizzard plates, which have 27–42 ridges, with pointed rods along the top edge and smaller pointed rods densely covering both anterior and posterior sides of ridges. The male reproductive system of this species is also different from other haminoeids. It possesses two seminal ducts interconnected at the entrance of a translucent pouch showing a yellowish mass content. The first seminal duct has a hook-like posterior end, which might be a synapomorphy of the genus *Liloa*.

Liloa porcellana (Gould, 1859)

Atys porcellana Gould, 1859: 138. Sowerby 1870: pl. 5, sp. 30. Johnson 1964: 130, pl. 12, fig. 13.
Atys (Alicula) porcellana—Pilsbry 1895: 268, pl. 28, fig. 23. Kobelt 1896: 26, pl. 8, fig. 11.
Haminoea olopana Pilsbry, 1921: 369, fig. 8b.
Liloa porcellana—Habe 1952: 151, pl. 21, figs 20, 22, 25. Lin 1997: 106, pl. 10, fig. 3. Qi 2004: 147, pl. 83, fig. O.

Type locality. Kagoshima Bay, Japan.

Material examined. Kagoshima, Japan, 1 shell examined (holotype), USNM 1357, H = 12 mm. Mariana Islands, Guam, 3 spcs dissected, UF 299895, H = 9.7–10 mm; the Philippines, 1 spc. dissected, MNHN, Paris (S6/OT926), H = 7.8 mm. Maui, Hawaii, 1 spc dissected, ZMBN 89712, H = 4.2 mm. Maui, Hawaii, 1 shell examined, ZMBN 89712, H = 2.8 mm.

Animal (Figs 1K, L): Body whitish-translucent, white dots scattered over the body, more dense at cephalic shield; eyes visible.

Shell (Fig. 3E–G, 18A): Maximum height 19 mm; whitish translucent; fragile, thin, elongated-cylindrical, both anterior and posterior ends truncated, anterior end narrower; spire sunken, outer lip thin; spiral grooves covering entire shell in adults (which become closer towards the ends) and only visible at shell ends in juveniles; faint axial lines present irregularly.

Jaws (Fig. 18B): Present, crescent shape, jaw rodlets with 6-10 denticles.

Radula (Figs 18C–F): Radular formula at mid-point 18–20 x 7–4.1.1.1.4–7; median tooth with broad base, triangular central cusp prominent, small triangular lateral cusp; inner lateral tooth hook-shaped, base with semi-circular projection outwardly, groove along outer margin, weak denticulation along groove; outer lateral teeth hook-shaped, base with semi-circular projection outwardly, weak groove along outer margin, size decreases outwardly.

Gizzard plates (Figs 19A, B): Three gizzard plates; almost equal size from anterior to posterior, 10–11 ridges, covered by rods with pointed tips along top edge of ridges, dense tiny rods with pointed tips on both anterior and posterior sides of ridges, gaps between ridges smooth.

Male reproductive system (Fig. 19C): Total length 4.2 mm (H = 10 mm). Formed by three parts: prostate, seminal ducts and penial region; prostate oval, bilobed, proximal lobe smaller, opaque-brownish, distal lobe light-yellowish; translucent duct connects prostate to creamy-yellowish striated (?)glandular region, which opens distally to first seminal duct that possesses hook-like posterior end, and proximally opens to second seminal duct, translucent, coils twice before connecting to penial region; penial region oval, translucent, with convoluted opaque-yellowish inner glandular duct connecting to genital opening.

Ecology. Sandy bottom below 29 m deep (Lin, 1997; present study).

Geographical distribution. Japan, China, Taiwan, the Philippines, Guam, Big Island, Maui, Oahu and French Frigate Shoals of Hawaii (Qi 2004; present study).

Remarks. There are a few conflicting features about the description of this species. Some authors referred to *Liloa porcellana* with spiral grooves only at both ends of shell (Pilsbry 1895; Habe 1952; Lin 1997). However, the original description states that spiral grooves are more visible at both ends, which does not imply that the middle part of the shell is smooth (Gould 1859). The study of the holotype (USNM 1357) confirmed the presence of spiral grooves throughout the shell but they are in fact faint in the middle part of the shell. Larger specimens that we examined (H $\geq$ 4.2 mm) have spiral grooves along the entire shell, with distance between grooves decreasing towards both ends; whereas the small specimen (H = 2.8 mm) have spiral grooves only at both ends of the shell (Figs 1K–L, 2E–G). The holotype of *Liloa porcellana* has a narrower posterior end compared to its anterior end.

However, this was not exactly the case for the shells examined during this study, but differences in shell height may explain this phenotypic difference, since none of our specimens was as large as the holotype (H = 12 mm). The anatomical features of our specimens match those described by Habe (1952).

This species can be distinguished from *Liloa curta* by a slender-elongated shell shape and spiral grooves that become closer towards the ends of the shell, although the latter feature may vary ontogenetically. Also, *Liloa porcellana* only has spiral grooves in the mid-region of the shell in adult specimens; in juveniles, those can be faint or absent. Both species have similar radula. The gizzard plates of *Liloa porcellana* have fewer and far apart ridges than *Liloa curta* where the ridges are numerous and tight together. Moreover, the male reproductive system of *Liloa porcellana* has a longer and twisted secondary seminal duct (Fig. 19C, sd 2) and a conspicuous duct connecting the prostate to a globose glandular region whereas in *Liloa curta* the prostate almost sits on top of the globose glandular region.

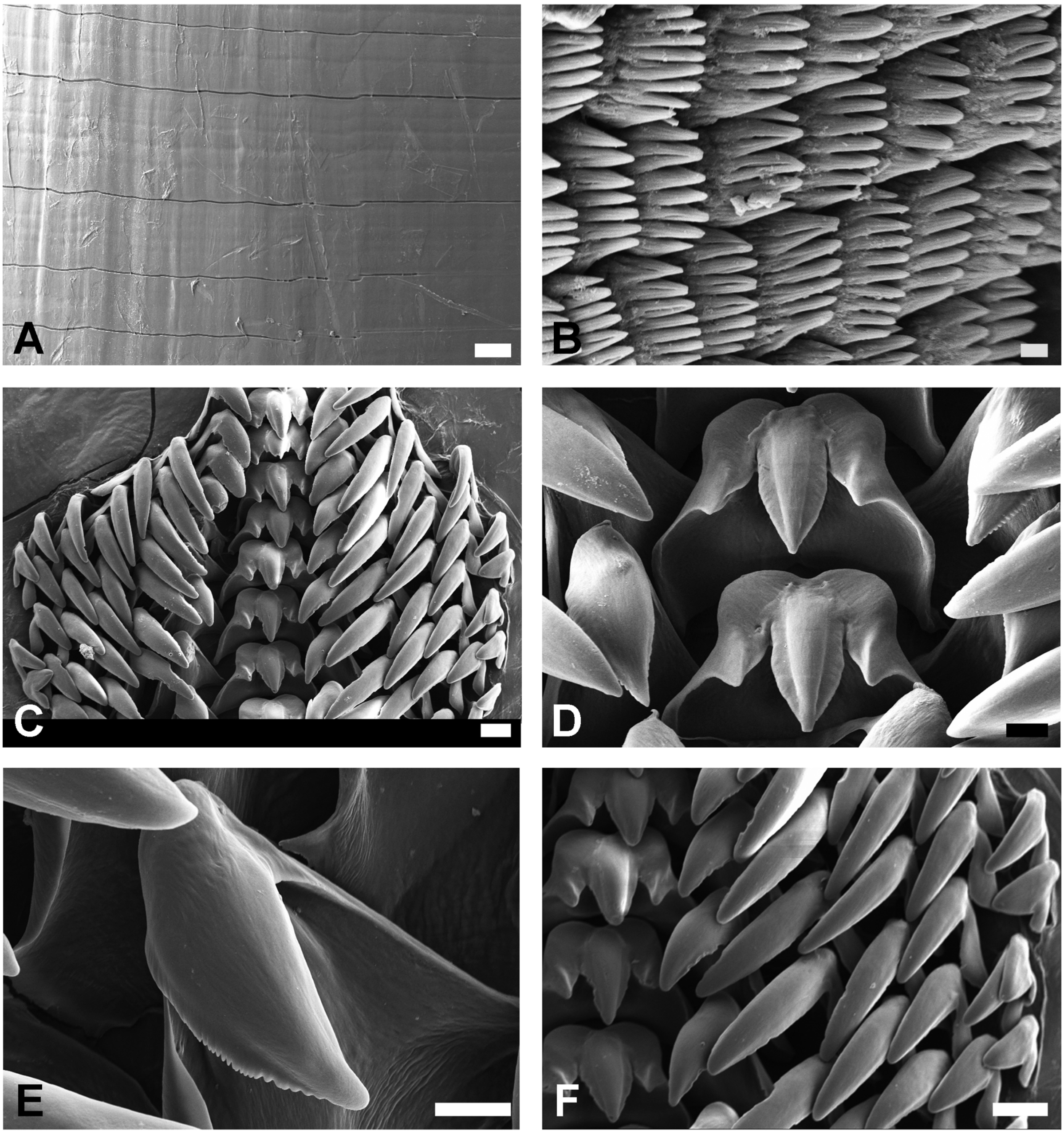

FIGURE 18. Shell and anatomy of *Liloa porcellana*. A. Detail of middle part of shell. B. Detail of jaw. C. Front view of anterior part of radula. D. Detail of median tooth at the middle part of radula. E. Denticulation on inner lateral tooth at right side of radula. F. Detail of outer lateral teeth at left side of radula. Scale bars: A = 100 µm; B = 2 µm; C, F = 20 µm; D, E = 20 µm. A, B: UF 299895, H = 9.8 mm; C–F: UF 299895, H = 10 mm.

TABLE 4. Summary of most useful characters for diagnosis of species of *Liloa*.

	L. curta **(Adams, 1850)**	***L. porcellana*** **(Gould, 1859)**
1. Animal	Eyes visible	Eyes visible
2. Shell		
- Internal/ external	External	External
- Shape	Cylindrically oval; slighthly convex sides	Elongated-cylindrical; anterior end narrower
- Spire	Sunken	Sunken
- Sculpture	Spiral grooves covering entire shell, faint irregular axial lines present	Spiral grooves covering entire shell in adults (which become closer towards the ends) and only at shell ends in juveniles; faint axial lines present irregularly
- Umbilicus	?	?
3. Jaws	Crescent shape, jaw rodlets with 7–10 denticles	Crescent shape, jaw rodlets with 6–10 denticles
4. Radula		
- Formula	19–25 x 8–7.1.7–8	18–20 x 7–4.1.1.1.4–7
- Median tooth	Broad base, large triangular central cusp, small triangular lateral cusps	Broad base, triangular central cusp prominent, small triangular lateral cusp
- Inner lateral tooth	Not distinct	Hook-shaped, base with semi-circular projection outwardly, groove along outer margin, weak denticulation along groove
- Outer lateral teeth	Hook-shaped, slender, base with semi-circular projection outwardly, groove along outer margin	Hook-shaped, base with semi-circular projection outwardly, weak groove along outer margin
5. Gizzard plates		
- Structure	27–42 ridges	10–11 ridges
- Sculpture	Single rows of rods with pointed tips along top edge of ridges, both anterior and posterior sides of ridges covered densely by tiny rods with pointed tips	Rods with pointed tips along top edge of ridges, dense tiny rods with pointed tips on both anterior and posterior sides of ridges
- Gaps between ridges	Smooth	Smooth
6. Male reproductive system		
- Prostate	Bilobed, oval-rounded, translucent pouch connects to the prostate, light-yellowish mass observed within	Bilobed, oval, translucent duct connects prostate to creamy-yellowish striated (?)glandular region, which opens distally to first seminal duct
- Seminal duct	Two seminal ducts; first seminal duct translucent, with hook-like posterior end; second seminal duct broad and short, translucent, connects to the penial region	Two seminal ducts; first seminal duct with hook-like posterior end; proximally opens to second seminal duct, translucent, coils twice before connecting to penial region
- Penial region	Elongated, translucent, with opaque inner duct visible	Oval, translucent, with convoluted opaque-yellowish inner glandular duct
7. Ecology	Sandy bottom in shallow water	Sandy bottom below 29 m deep
8. Key references	Qi (2004)	Lin (1997)

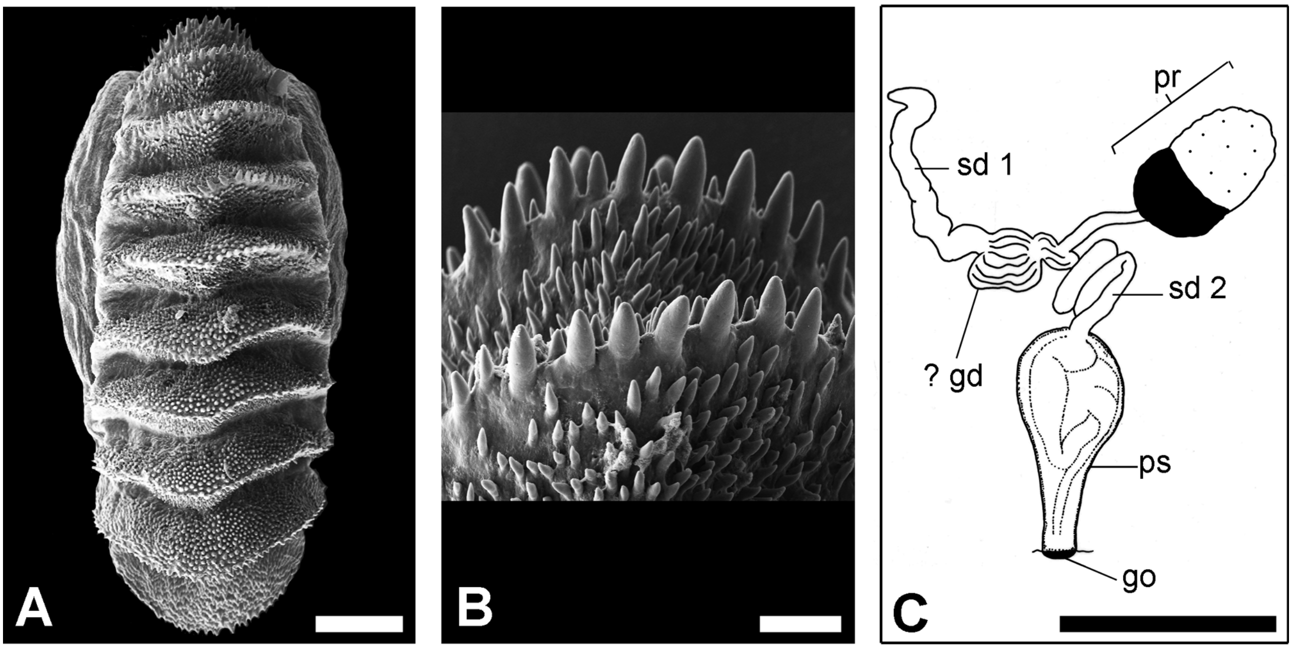

FIGURE 19. Anatomy of *Liloa porcellana*. A. Top view of gizzard plate. B. Rods on middle ridges of gizzard plate. C. Male reproductive system. go, genital opening; (?) gd, (?) glandular duct; pr, prostate; ps, penial sheath; sd 1, first seminal duct; sd 2, second seminal duct. Scale bars: A = 100 µm; B = 20 µm; C = 1 mm. A–C: UF 299895, H = 10 mm.

Discussion

The generic classification of the family Haminoeidae has been hindered by taxonomic uncertainty. Authors had ascribed species to various genera with questionable reasons or strict criteria as documented in the Results section of this work. Also species descriptions have been hampered by the lack of use of anatomical data and details of the morphology and colouration of live animals. Though some authors considered morpho-anatomical features (e.g. Rudman 1971, 1972a, b; Gosliner 1979, 1989), the use of conchological features has traditionally dominated the taxonomy of cephalaspids worldwide (discussed in Malaquias and Reid 2008). In the tropical Indo-West Pacific the situation is no different and the problem has been acknowledged by several authors (e.g. Pease 1868; Carlson & Hoff 2000; Malaquias and Reid 2008).

Based on the combined study of live animals, external morphology, anatomy and shells, and in part aided by molecular phylogenetic data (Too 2011) we here provide new insights into the diversity of four genera of haminoeids gastropods inhabiting the tropical West Pacific and attempt to recognize morpho-anatomical synapomorphies:

Aliculastrum—Species in this genus have cylindrical robust shells with spiral grooves at both ends and a thick columella. The combination of these features seems to be diagnostic of the genus. No anatomical synapomorphy could be established; *A. debilis* and *A. parallelum* share the possession of an asymmetric radula and male reproductive system with two seminal ducts, but none of these characters were found in the type species *A. cylindricum*. On the other hand, *A. cylindricum* and *A. debilis* are fairly identical in shell morphology, which led authors to misidentify these two species (Watson 1886; Pilsbry 1895). *Aliculastrum debilis* has been recently placed under the genus *Atys* (see Remarks section), but preliminary molecular phylogenetic analysis suggests its inclusion in the genus *Aliculastrum* (Too 2011).

Atys—The definition of this genus has been a matter of ongoing debate. Pilsbry (1895) expressed doubts about the taxonomic arrangement of the group and mentioned that at least two to three genera could be created based upon differences of shell morphology. Rudman (1998b) questioned the systematic arrangement of *Atys* and Malaquias *et al.* (2009b) claimed *Atys* to be monophyletic but only *Atys curta* (= *Liloa*) and *Atys cylindricus* (=*Aliculastrum*) were included in their phylogenetic analyses.

There are more than 50 species described under the genus *Atys* in the Indo-West Pacific, although most of them do not possess ovoid inflated robust shells as the type species *A. naucum*, but instead elongated and fragile shells. Unfortunately, specimens of the type species *A. naucum* were not available for anatomical dissection but this species has been extensively studied before (e.g. Bergh 1901; Lin 1997; Carlson & Hoff 1999). According to Bergh (1901), *A. naucum* possesses a radula with 70 rows of teeth with a triangular median tooth. While documenting similar median tooth character, Lin (1997) referred to the presence of smaller triangular cusps at both sides of the median tooth. Both Bergh (1901) and Carlson & Hoff (1999) referred that gizzard plates have a high number of fine ridges, and the latter authors mentioned the presence of tiny rods on top of ridges.

Clarification of the generic status of species traditionally included in the genus *Atys* would require a broader study encompassing species from all biogeographic regions. However, preliminary molecular phylogenetic data (Too 2011) rendered traditional *Atys* paraphyletic. Until a sound phylogenetic framework is available for the relationships of haminoeidae gastropods we suggest using *Atys* in its traditional sense (*sensu* Burn & Thompson 1998).

Diniatys—Species of this genus have a strongly calcified callus at the end of columella folding outwardly that can resemble a tooth-like projection. This seems to be a synapomorphy of the genus. Anatomically, species of *Diniatys* have a male reproductive system with a fine and long seminal duct that is at least twice as long as the elongated penial region. This is unique among haminoeidae gastropods and can also be considered a synapomorphic trait of the genus.

Liloa—Recognized synapomorphies of the genus are the presence of spiral grooves covering the translucent shells more or less regularly spaced throughout; gizzard plates lacking rachis with ridges organized parallel to each other with pointed rods densely arranged on both anterior and posterior sides and a single row of larger pointed rods along the top margin; presence of two seminal ducts in the male reproductive system, one of them having a hook-like posterior end.

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Disclaim: Codes and numbers between parenthesis after the acronym of the Muséum National d'Histoire Naturelle, Paris (MNHN, Paris) are not official voucher numbers but only our own author codes.

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