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Glossing over cryptic species: Descriptions of four new species of *Glossodoris* and three new species of *Doriprismatica* (Nudibranchia: Chromodorididae)

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Zoobank Registrations:
***Glossodoris buko* sp. nov.** urn:lsid:zoobank.org:act:8D5F6679-9741-45B2-8951-3D171044DC83
***Glossodoris bonwanga* sp. nov.** urn:lsid:zoobank.org:act:1FEDEB09-90CA-45F2-8D07-AAB689CB3305
***Glossodoris andersonae* sp. nov.** urn:lsid:zoobank.org:act:07CAA0DA-EB28-4AFF-B019-2314D11C9DB9
***Glossodoris acosti* sp. nov.** urn:lsid:zoobank.org:act:D5A04090-4080-49EA-962A-43585B65F86D
***Doriprismatica balut* sp. nov.** urn:lsid:zoobank.org:act:4BE3E979-326C-44DF-8C62-B0227157C850
***Doriprismatica rossi* sp. nov.** urn:lsid:zoobank.org:act:A4E09CED-5D33-476A-B094-92C5BE4F51D7
***Doriprismatica marinae* sp. nov.** urn:lsid:zoobank.org:act:FB55BFD1-FC47-48FE-9BC3-62C3EDA1E0C6

Abstract

Advances in molecular systematics have led to a rapid increase in the identification of cryptic and pseudocryptic species in organisms exhibiting diverse and complex coloration with complicated taxonomic histories. A recent molecular phylogenetic analysis of nudibranchs in the genus *Glossodoris* (Mollusca: Gastropoda: Heterobranchia: Chromodorididae) and related genera identifies multiple cryptic and pseudocryptic species complexes, one within *Glossodoris pallida* and three within *Glossodoris cincta*, and support for three new species of *Doriprismatica*. Morphological analyses of color pattern, radular structure, buccal mass, and reproductive system support these identifications. Descriptions for ***Glossodoris buko* sp. nov.**, ***Glossodoris bonwanga* sp. nov.**, ***Glossodoris andersonae* sp. nov.**, ***Glossodoris acosti* sp. nov.**, and what will retain the name *Glossodoris sp. cf. cincta* are provided here, in addition to descriptions for new species ***Doriprismatica balut* sp. nov.**, ***Doriprismatica rossi* sp. nov.**, and ***Doriprismatica marinae* sp. nov.**. *Glossodoris pallida* and *G. buko* exhibit extreme differences in radular structure in addition to a clear biogeographic split in range. *Glossodoris bonwanga*, *G. andersonae*, *G. acosti* and *G.* sp. cf. *cincta*, share morphological and geographic differences but these are not as pronounced as in *G. pallida* and *G. buko*. More detailed study of the *G. cincta* complex is necessary to resolve some remaining systematic challenges. *Doriprismatica balut* is clearly distinct from all other congeners based on molecular and morphological characters. In contrast, *D. rossi* and *D. marinae* are not strongly divergent genetically, but have major morphological divergences that clearly distinguish them.

Key words: Mollusca, Nudibranch, sea slug, biodiversity, biogeography

Introduction

Chromodorid nudibranchs are tropical sea slugs characterized by an elongate body and oftentimes a brightly colored, undulate mantle. While most species are easily recognizable based on distinctive color patterns, an increasing number of cryptic and pseudocryptic species are being identified by molecular and morphological analyses (Johnson & Gosliner 2012; Almada *et al.* 2016; Furfaro *et al.* 2016; Padula *et al.* 2016; Matsuda & Gosliner 2017). Some of these studies (Almada *et al.* 2016; Padula *et al.* 2016) show that remarkable polymorphism may be present in some species and that color patterns may converge within distinct lineages, thus masking the diversity present at a given locality. Other studies on chromodorid nudibranchs (Hoover *et al.* 2017) show that color patterns and morphological differences are not as profound as previously thought and that in

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eastern Pacific *Felimare* there is actually less diversity than previously determined. Recent studies show several examples of polymorphism in nudibranch color pattern and in some cases, this has a strong biogeographical component (Almada *et al*. 2016). Other species of heterobranchs seemingly have little variation in their color patterns (Hoover *et al*. 2015; Lindsay & Valdes 2016; Ong & Gosliner 2016; Uribe *et al*. 2017). Thus, additional studies are needed to establish more generalized patterns of color variation and polymorphism in a diversity of chromodorids and other heterobranchs.

The distinction between cryptic and pseudocryptic species has been widely explored for other heterobranch gastropods (e.g., Churchill *et al*. 2014; Hoover *et al*. 2015; Lindsay & Valdes 2016; Uribe *et al*. 2017) and will not be repeated here. Matsuda & Gosliner's (2017) recent molecular phylogeny of the genus *Glossodoris* and related genera presents evidence for multiple cryptic and pseudocryptic species in *Glossodoris* and identifies three new species of *Doriprismatica*. Here we provide morphological support and species descriptions for these new species.

Rudman (1986) identified three main color morphs within *Glossodoris cincta* (=*Casella cincta* (Bergh 1888)), that correspond to three geographic areas: East Africa, northern Australia, and Indonesia/Philippines. The most observed differences were in the colored bands that lined the mantle and the mantle coloration itself, with little to no difference in the reproductive systems and only slight differences in the radula noted. Consistent in all three of Rudman's color groups was the presence of a yellow marginal band. Rudman noted a potential fourth color group from the Red Sea, but without enough material, did not designate it (Rudman 1986). The earliest collected specimen of *Casella cincta,* from which the species description was based, was found off of Mauritius (Bergh 1888). The color plate depicts a long orange body covered with cream-white speckling that suggests a textured appearance. Dark blue bands on the mantle surround a whitish-blue marginal band, and a blue band appears to line the edge of the foot. No yellow band is present. In Bergh's (1888, pl. 77, fig. 9) illustration, the base of the rhinophores are orange and the lamellae are blue and white with a white line on the anterior side of the rachis. The gills form an arc around the anus and curve inward at the ends to form two small spirals with shorter lamellae. The gills are cream colored with a dark line running up the middle and expanding slightly at the tips. This color pattern differs slightly from the variants described by Rudman.

Glossodoris pallida (= *Doris pallida* (Rüppell & Leuckart 1830)) is the type species of *Glossodoris*, which was originally described from a specimen from the Red Sea. Rudman's (1984) dissection of the holotype (= *Doris xantholeuca* (Ehrenberg 1831)) observed a radular formula of 80(+2) x 24.0.24. In his description of *G. pallida*, Rudman (1984) analyzed scanning electron micrographs of the radula of a 15 mm (alive) Red Sea specimen (108(+4) x 39.1.39) and the jaws of a Tanzanian specimen (bicuspid). The radular formula for a 9 mm Australian specimen with a broken ribbon (23.1.23) exhibited a very different number of lateral teeth, however no images of this specimen were provided. In a later manuscript that described external morphology, Rudman (1990) described the color pattern for specimens from the Red Sea, Tanzania and Australia as being generally similar, with the major differences only in the rhinophore and gill color (yellow in Australia, the Red Sea and Reunion Island; white in Tanzania and Sudan).

The genus *Doriprismatica* shares some morphological similarities to *Glossodoris.* The body is elongate with the mantle high on the foot and they have characteristic semi-permanent undulations of the mantle, which is ringed by a series of mantle bands. Johnson & Gosliner's (2012) mitochondrial phylogeny of the Chromodorididae drastically changed the classification of the genera. *Glossodoris* was one of nine genera whose name was maintained, while *Doriprismatica* was one of five older names reinstated. Matsuda & Gosliner's (2017) phylogeny included 48 individual specimens of *Glossodoris* and *Doriprismatica*, along with taxa that had previously fallen under the classification *Glossodoris* prior to Johnson & Gosliner (2012). The resulting phylogenies increased species-level resolution and identified cryptic and pseudocryptic species nestled within *Glossodoris cincta*, a cryptic species complex within *Glossodoris pallida*, and identified three new species of *Doriprismatica*. The focus of the present paper is to formally describe seven of the cryptic and pseudocryptic species illuminated by the molecular data and analyses from Matsuda and Gosliner (2017) and integrated with additional morphological differences recognized by the present investigation. The integration of these data provides a basis for differentiating distinct lineages and formally naming them as distinct species. We name distinct lineages that are supported by the species delimitation analysis and augmented by morphological characters that support these lineages.

Methods

Specimens in this study are housed in the wet collections at the California Academy of Sciences (CAS), except for one specimen from the South African Museum that prior to this study had its radula and jaws removed and prepared for scanning electron microscopy. The specimens are contained in 95% ethanol, and were originally fixed in 75% or 95% ethanol or Bouin's solution. Specimens were dissected at CAS, and some have previously had a small amount of tissue extracted from the foot for molecular analyses.

The radula and jaws were removed and the surrounding tissue was dissolved with a 10% NaOH solution and rinsed with diH2O before being mounted on stubs. Scanning electron micrographs were taken on a LEO/Zeiss 1450 VP scanning electron microscope. The buccal mass from specimens of *G. pallida* and *Glossodoris buko* **sp. nov.** were dissected and illustrated. Reproductive systems for all of the species described here were dissected and drawn by hand and imaged on the automontage workstation at CAS. Photographs of living and preserved specimens were examined for color pattern. Additional specimens from sister species were dissected for comparison to determine whether closely related species identified by molecular techniques could be recognized morphologically.

Species descriptions

Family: Chromodorididae

Genus: *Glossodoris* Ehrenberg 1831

Type species: *Doris xantholeuca* Ehrenberg 1831=*Glossodoris pallida* (Rüppell & Leuckart 1830), by monotypy, Red Sea

Diagnosis: Chromodorid nudibranchs with a broad body and semi-permanent series of undulations around mantle margin. Oral tentacles short. Gill often forming double spirally arranged branches. Jaw rodlets unifid or bifid. Radular teeth with small denticles or entirely lacking denticles. Reproductive system with bursa copulatrix and receptaculum seminis of equal size. Receptaculum inserting directly into bursa rather than vagina. Prostate and ejaculatory portions of vas deferens elongate. Penis unarmed.

Glossodoris buko, Matsuda & Gosliner sp. nov.

Figures (1A–C, 2A, 3A–E, 4C–D)

Glossodoris pallida (Rüppell & Leuckart 1830), misidentification, Rudman 1990: figs. 9c, 10e–f; Gosliner *et al.* 2008: 240, third photo; Turner & Wilson 2008; Gosliner *et al.* 2015: 237, upper right photo.
Glossodoris xantholeuca Ehrenberg 1831: 92; Rudman 1984.
Glossodoris sp. A Matsuda & Gosliner 2017.

Type Material. *Holotype*: CASIZ-223284 (ex CASIZ-191102B) 4 mm preserved, Papua New Guinea, Madang Province, Bilbil Island, coll: V. Knutson, 10 November 2012, orig. fixative 95% EtOH, GenBank: KT600713 (COI).

Paratypes: CASIZ-191102A, 13 specimens,1 dissected, 3–8 mm, same collection data as holotype. CASIZ-086381, 6 specimens, 1 dissected, 6.5–11 mm, Papua New Guinea, North Coast, North of Madang, approx. 1 km South of Cape Croisilles, South side of The Quarry, coll: T.M. Gosliner, 13 June 1992, orig. fixative Bouin's solution. CASIZ-181594, one specimen 6 mm preserved, Philippines, Bohol Island, Panglao, Pontog Lagoon I, reef wall with small caves, coll: T.M. Gosliner, Y. Camacho, J. Templado, M. Malaquias, M. Poddubetskaia, 2 Jul 2004, Panglao Expedition 2004, 17–25 meters, orig. fixative 95% EtOH. CASIZ-177264, one specimen, Philippines, Luzon Island, Batangas Province, Tingloy, Caban Island, Layaglayag, coll: T. Gosliner, A. Valdés, M. Pola, L. Witzel, B. Moore, A. Alejandrino, 16 Mar 2008.

Comparative material of Glossodoris pallida (Figs. 1D–1E): CASIZ-173393, one specimen, dissected, 9 mm preserved, Madagascar, Iles Radama, Nosy Valiha, W of Nosy Valiha, coll: T.M. Gosliner, 20 Oct 2005, 12–13 m, orig. fixative Bouin's solution. CASIZ-173395, one specimen, dissected, 9 mm preserved, Madagascar, Iles Radama, Nosy Kalakajoro, West of Nosy Kalakajoro and Nosy Beratia, coll: T.M. Gosliner, 19 Oct 2005, 13–15 m, orig. fixative Bouin's solution. CASIZ-176997, one specimen, 14.5 mm preserved, Mozambique, Inhambane Province, Jangamo, Pandane Beach, coll: M. Pola and J. Reis, 6 Feb 2008, 1.5 meters, orig. fixative 95% EtOH. CASIZ-175548, one specimen 4 mm preserved (large portion missing from tissue sample), Madagascar, Iles Radama, Nosy Kalakajoro, coll: S. Fahey and T. M. Gosliner, 13 Oct 2005, CAS-WCS Radama Islands Expedition, 15-20 meters, orig. fixative 95% EtOH. CASIZ-194338, one specimen, dissected, 6 mm preserved, Madagascar, South Madagascar, "Pointe Evatra, crique fond rocheux et gazon d'algues", coll. South Madagascar Expedition, 30 Apr 2006–May 2010, 3–8 meters, orig. fixative 95% EtOH. CASIZ-175554, one specimen, dissected, 2 mm preserved, Madagascar, Iles Radama, Nosy Faly, NW of Nosy Faly, coll: S. Fahey and T.M. Gosliner, CAS-WCS Radama Islands Expedition, 13–16 meters, orig. fixative 95% EtOH.

FIGURE 1. A–C, *Glossodoris buko* **sp. nov.** A. CASIZ-191102 (i. large, ii. small) Papua New Guinea. B. CASIZ-181594 Philippines. C. CASIZ-086381 (A, B) Papua New Guinea. D–F, *Glossodoris pallida*: D. CASIZ-194338 Madagascar. E. CASIZ-175548 Madagascar. F. CASIZ-175554 Madagascar. Photos: T.M. Gosliner.

Etymology. The name *Glossodoris buko* comes from buko (young coconut) owing to the resemblance of this species to the cream-colored coconut meat from the Philippines, where this species is found.

Geographical Distribution. Specimens identified by Matsuda & Gosliner (2017) range from the Philippines to Papua New Guinea and Australia (Turner & Wilson 2008).

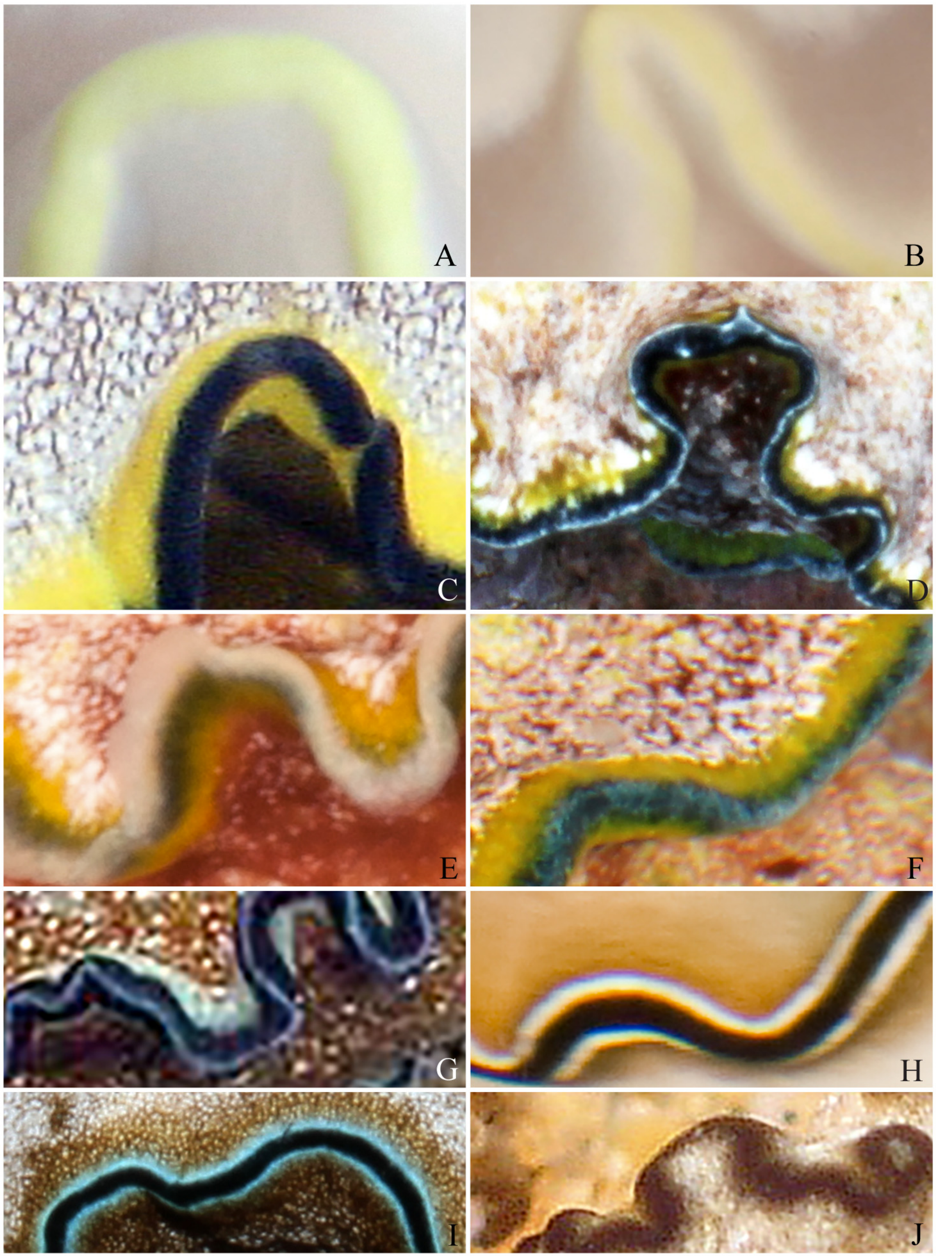

FIGURE 2. Mantle margins. A. *Glossodoris buko* **sp. nov.**, CASIZ-222107. B. *Glossodoris pallida* (Cuvier, 1804), CASIZ-175554. C. *Glossodoris bowanga* **sp. nov.**, CASIZ-194204, photo by Marina Poddubetskaia. D. *Glossodoris andersonae* **sp. nov.**, CASIZ-192288. E. *Glossodoris acosti* **sp. nov.**, CASIZ 191352, photo by Vanessa Knutson. F. *Glossodoris* sp. cf. *cincta*, CASIZ-199204. G. *Glossodoris cincta* Bergh, 1888, from Reunion, photo only, photo by Philibert Bidgrain. H. *Doriprismatica balut* **sp. nov.**, CASIZ-182787. I. *Doriprismatica rossi* **sp. nov.** CASIZ-192281. J. *Doriprismatica marinae* **sp. nov.** CASIZ-194050, Marina Poddubetskaia, all other photos by. T. Gosliner.

External Morphology. *Glossodoris buko* has a long and slender body that is transparent white in color (Fig. 1A–C). There is an opaque white band that starts anteriorly on the mantle, narrows between the rhinophores and then widens again and narrows between the two major folds in the middle of the mantle, and ends circling the gills (Fig. 2A). In most specimens, the band is continuous, however there was a break in the band posterior to the rhinophores in some. A white opaque band runs the length of the foot on both sides and connects posteriorly. The mantle edge is rippled with the semi-permanent undulations that are characteristic of all *Glossodoris.* One primary pair of undulations midway on the mantle is identifiable by an indentation of the white dorsal band. A thin, light yellow marginal band runs the length of the outer edge of the mantle and opaque white mantle dermal formations that appear as a thick white band that lies partly under the yellow band. The degree and number of the smaller semi-permanent undulations varies between individuals, but larger specimens have more pronounced undulations. A yellow band borders the foot, however no white band is visible due to the absence of mantle dermal formations. The rhinophores are elongate and conical with 11–12 lamellae. The bases of the rhinophores are white and the tips are yellow. The gill forms a semicircle surrounding the anus opening posteriorly, consisting of approximately 5–8 unipinnate branches. The lamellae are white with yellow tips and are shorter at the ends of the arc. The genital pore is located on the right side of the body below the mantle and behind the rhinophores.

Internal Anatomy. *Radula and buccal armature* (Fig. 3A–E). The radular ribbon (Fig. 3E) is short and wide with a radula formula for a preserved specimen of 3 mm of approximately 28 x 14.1.14 (CASIZ-191102A) and 13.1.13 for a 6.5 mm preserved specimen (CASIZ-086381). The rachidian tooth (Fig. 3A) is very reduced and quasi-triangular. The first lateral tooth is almost bilaterally symmetrical. It is wide and has a relatively short triangular pointed central cusp. There are approximately five well-defined denticles, each about half the length of the central cusp, that point down and outward on the inner and outer sides of the central cusp. The mid-lateral teeth (Fig. 3B) are longer and have a shorter central cusp with approximately 6–8 loosely packed and well defined denticles solely on the outer edge. Unlike the first lateral, the central cusp on the mid-laterals is almost indistinguishable from the denticles next to it. The denticles in the mid-laterals are almost indistinguishable in size and shape from the central cusp, and maintain this shape and their size integrity to the edge of the ribbon (Fig. 3C). The jaw rodlets are short and well-spaced with distinct gaps between rodlets. They are predominantly bifid (Fig. 3D) with a few trifid rodlets. The ventral side of the buccal mass has a glandular sheath covering the oral tube that contains numerous densely packed white opaque glands (Fig. 4D).

Reproductive system (Fig. 4C). The penial bulb is long and folded and leads to a coiled vas deferens followed by an approximately equal in length prostate gland. The receptaculum seminis duct and the vagina are relatively short. The receptaculum seminis is slightly smaller than the bursa copulatrix, and they are found adjacent to each other rather than being aligned linearly.

Remarks. At first glance, *G. buko* and *G. pallida* could be easily confused, as there are few external morphological differences (Fig. 1; Rudman 1984: fig 1b; Gosliner *et al*. 2015: 237, upper right fig.; Matsuda & Gosliner 2017: fig. 1). The holotype of *G. pallida* was collected from the Red Sea and subsequently examined by Rudman (1984) together with a specimen from Tanzania. Both specimens share the same color pattern, radular structure and reproductive system morphology as the five specimens of *G. pallida* we comparatively examined here from Madagascar and Mozambique (Figs. 1D–F, 3F–J). In Rudman's (1990) *G. pallida* description, he noted that specimens from East Australia have yellow gills and rhinophores, which are consistent with *G. buko*, whereas his Tanzania and Sudan specimens, the rhinophores and gills are white. However, he further remarks that yellow tips were reported from specimens in the Red Sea and Reunion Island, indicating that yellow tips may not be a consistent identifier for *G. buko.* The rhinophores and gills of our *G. pallida* specimens from Madagascar and Mozambique all have frosted yellow tips, although the yellow is not as bright as in the *G. buko* specimens.

The most striking differences between the two species are found in the radula, jaws and buccal mass. The radular ribbon of G. pallida (Fig. 3J) is elongate (~85 x 23.1.23 CASIZ-173395), whereas it is short and squat in G. buko (Fig. 3E) (~ 28 x 14.1.14) for specimens of comparable size. This is confirmed in Rudman's *G. pallida* specimen from the Red Sea (type locality), which has a radular formula of 108(+4) x 39.1.39 (15 mm specimen alive) and 23.1.23 for his Australian specimen (9 mm preserved) (Rudman 1984), and while no length was reported, the number of lateral teeth and presence of a rachidian tooth suggest that this specimen is likely *G. buko. Glossodoris pallida* has a more prominent and pointed rachidian tooth (Fig. 3F), whereas the rachidians are significantly reduced and amorphous in *G. buko*. There are also significant dissimilarities in the lateral teeth. The East African *G. pallida* specimens examined here share the same lateral tooth structure as Rudman's Red Sea specimen (1984), with a long narrow hook-shaped central cusp with well-defined short denticles resting flat against the outer edge (Fig. 3G, H). *Glossodoris buko* has a lateral tooth that is broad and concave with a central cusp that is almost indistinguishable from the denticles in size and shape that shares no similarities with *G. pallida.* These differences are also visible in the jaw. *Glossodoris pallida*'s rodlets are long, curved, and tightly packed with bifid tips where one of the points protrudes from slightly below the adjacent rodlet (Fig. 3I). *Glossodoris buko* has short and loosely packed rodlets that are less consistent in shape (Fig. 3D). Finally, the large glandular sheath on the ventral side of the buccal mass in *G. buko* (Fig. 4D) is not present in *G. pallida* (Fig. 4B).

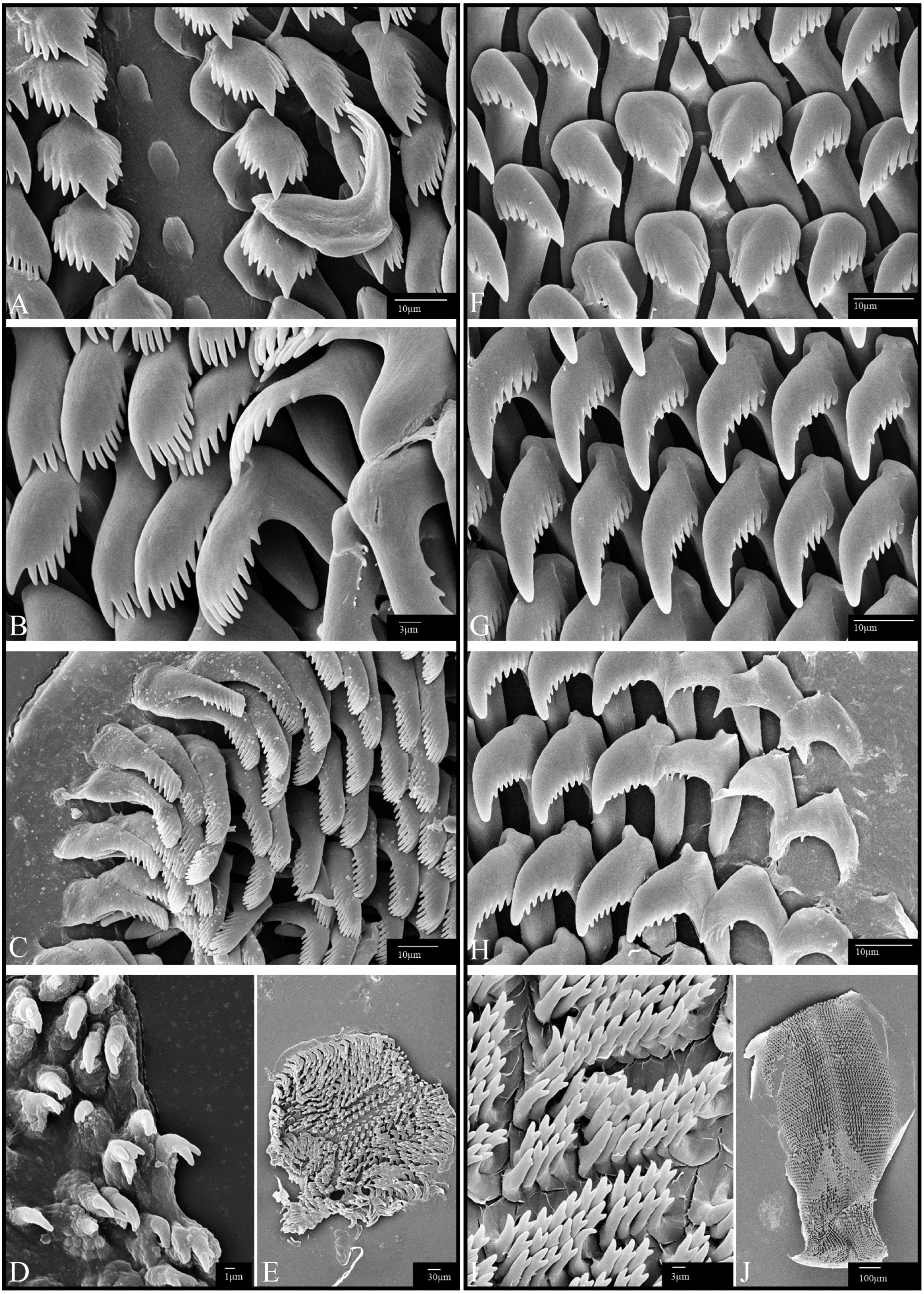

FIGURE 3. Scanning electron micrographs. Left column (A–E) *Glossodoris buko* **sp. nov.**, CASIZ-086381A Papua New Guinea, A. Rachis B. Mid-laterals. CASIZ-191102A Papua New Guinea, C. Outer laterals. D. Jaws. E. Radular ribbon. Right column (F–J) *Glossodoris pallida*, CASIZ-173395 Madagascar: F. Rachis. G. Mid-laterals. H. Outer laterals. I. Jaws. J. Radular ribbon.

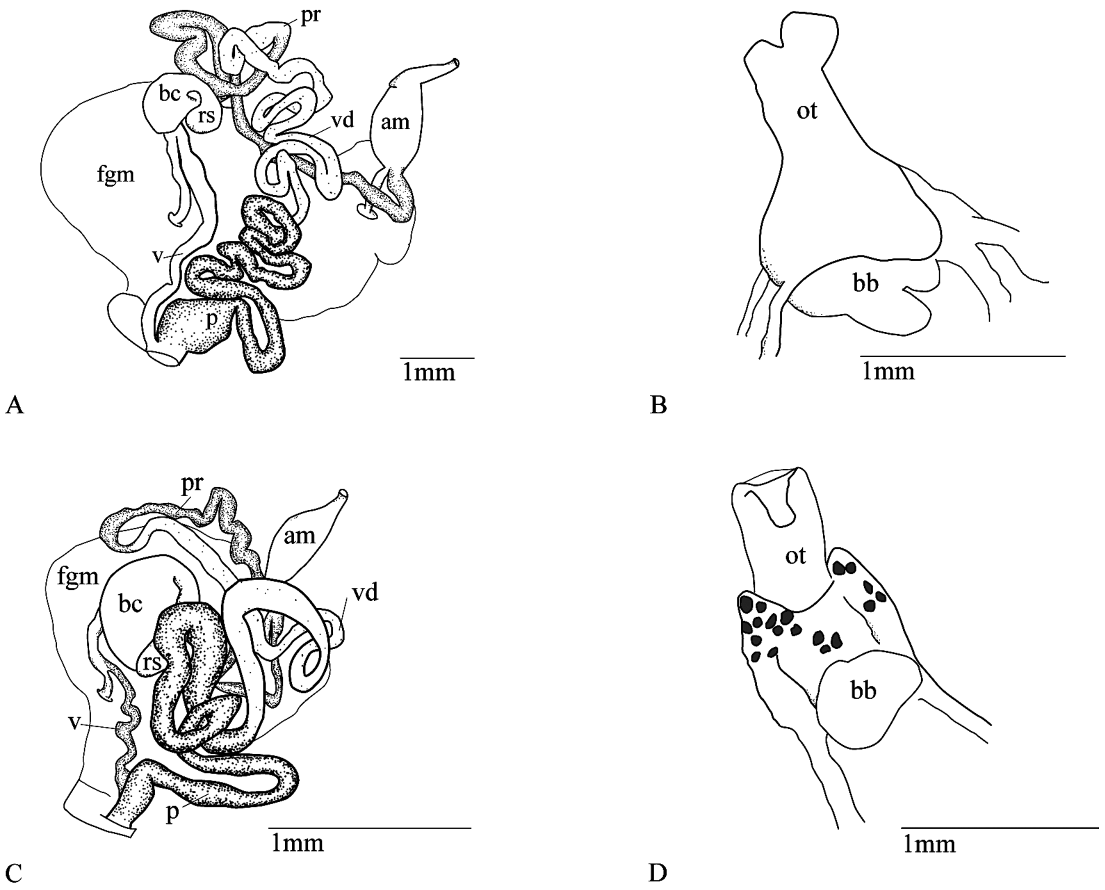

FIGURE 4. *Glossodoris pallida,* CASIZ-173395: (A) Reproductive system (B) Buccal mass, ventral side has no glands. *Glossodoris buko* **sp. nov.**, CASIZ-086381A: (C) Reproductive system (D) Buccal mass, ventral side with glandular sheath. Abbreviations: p, penis; vd, vas deferens; pr, prostate; v, vaginal duct; rs, receptaculum seminis; bc, bursa copulatrix; am, ampulla; fgm, female gland mass; ot, oral tube, bb, buccal bulb.

The reproductive system appears similar to the description by Rudman (1983) for *G. pallida* from Tanzania and the Red Sea and examined here from Madagascar (Fig. 4A). The only noteworthy distinction in the reproductive systems of the two species is that the ejaculatory portion of the vas deferens of *G. pallida* (Fig. 4A) contains many more convolutions than does that of *G. buko* (Fig. 4C).

Glossodoris buko is distinct from *G. pallida* in both internal morphology as shown here, and based on molecular analyses (Matsuda & Gosliner 2017). This distinction is also maintained geographically. *Glossodoris pallida* has only been recorded off the coast of eastern Africa and the Red Sea, and *G. buko* is solely from the western Pacific. Matsuda & Gosliner's (2017) phylogeny of *Glossodoris* provides support for the splitting of the previously hypothesized *Glossodoris pallida* into two distinct species. This is further supported through p-distance values (Matsuda & Gosliner 2017). Within *G. buko*, a grade and one clade are supported (a grade from the Philippines and a clade from Australia and Papua New Guinea). However, there were no observed morphological differences and only a 5–6% p-distance between them and these were not recovered as distinct lineages in the ABGD analysis conducted by Matsuda and Gosliner (Fig. 5). This strongly supports that the western Pacific specimens represent a single species distinct from the Indian Ocean specimens (Matsuda & Gosliner 2017).

***Glossodoris bonwanga,* Matsuda & Gosliner sp. nov.**

Figures (2C, 6A, 7A–D, 8A–B)

Glossodoris cincta (Bergh 1888), Rudman 1986 in part, misidentification: 149, figs, 30B, 32, 33C.
Glossodoris sp. 2 Gosliner 1987: 84, middle photo.

Glossodoris sp. 5 Gosliner *et al*. 2008: 236, upper photo.
Glossodoris sp. 3 Gosliner *et al*. 2015: 236, upper right photo.
Glossodoris sp. B Matsuda & Gosliner 2017.

Type Material. *Holotype*: CASIZ-194018, one specimen 8 mm preserved (hardened), Madagascar, "Pointe Evatra, crique fond rocheux et gazon d'algues", 30 April–6 May 2010, South Madagascar Expedition, 3–8 meters, orig. fixative 95% EtOH. Tissue sampled (foot) for molecular analysis by Matsuda & Gosliner (2017), GenBank: KT600695 (COI).

Paratypes: CASIZ-173433, one specimen, dissected, 13.5 mm preserved, Madagascar, Iles Radama, Nosy Valiha, coll: S. Fahey, 14 Oct 2005, CAS-WCS Radama Islands Expedition, 16 meters, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for molecular analysis by Johnson & Gosliner (2012) and reanalyzed by Matsuda & Gosliner (2017). SAM A35516 (South African Museum), one specimen, dissected, 12 mm preserved, South Africa Kwazulu Natal, Sodwana Bay, 2 mile Reef KZ11, coll: T.M. Gosliner, 13 May 1981, orig. fixative 95% EtOH.

Etymology. The first specimen of *Glossodoris bonwanga* was collected in South Africa, and the species is named after the Zulu word for "unseen", owing to its confusion with *G. cincta* (Rudman 1986).

Distribution. Madagascar to the northeast coast of South Africa.

External morphology. *Glossodoris bonwanga* has an elongate oval-shaped mantle that is elevated from the sides of the body above the foot (Fig. 6A). The mantle edge is made up of a series of permanent primary undulations with additional semi-permanent folding. There is one large distinguished pair of primary folds midway on the mantle. The mantle and foot are a light brick red color that is covered in a dusting of white speckles denser at the edge of the mantle giving the nudibranch an overall lighter appearance. A bright yellow band followed by a thinner black band (Fig. 2C) surrounds the outermost edge of the mantle and foot. On the inner edge of the black band there appears to be a fine band of a translucent white. The gill forms an arc around the anus and the 16–24 unipinnate branches are shorter in length at both ends of the arc to form two smaller spirals. The branches are a light brick red and cream color with two thin black lines that run along the edge beginning midway up and joining at the tip. The rhinophores have about 24 lamellae and are the same color as the body or darker. They are covered with opaque white speckling arranged in rows along the lamellae and have black tips. Posterior to each rhinophore are two spots on the mantle that do not have white spots and therefore appear as dark circles, this becomes more evident once the specimen is preserved. The genital pore is located on the right side of the body, under the mantle behind the rhinophores.

Internal Anatomy. *Radular structure*. (Fig. 7A–D). The radular ribbon is long and wide (Fig. 7D), characteristic of the genus. The rachidian tooth (Fig. 7A) is elongate and triangular at the tip and approximately two-thirds the length of the innermost lateral tooth. The innermost lateral tooth has a long narrow central cusp that is slightly curved with approximately seven denticles on the outer edge and a well-defined ridge with no denticles on the inner edge. The inner lateral teeth have a similar shape with a slightly longer cusp and no inner ridge or denticles. They have a well-defined peen (an extension on top of the primary cusp similar to the ball peen of a hammer), and approximately 5–6 small denticles on the outer edge of the inner lateral teeth and 10–12 on the outer edge of the mid-laterals (Fig. 7B). The outer lateral teeth (Fig. 7C) are reduced in size and have no peen or denticles. The scanning electron micrograph of radula had been made twenty years ago and no image was available of the entire ribbon, but from the SEM images and the remainder of the radular ribbon mounted on a microscope slide, we estimate the radular formula to be approximately 41.1.41.

Reproductive system (Figs. 8A, B). The vagina is long and coiled and branches off from the short receptaculum seminis duct just below the bursa copulatrix and receptaculum seminis. The penial bulb is thick and long with folds before joining the muscular vas deferens and prostate gland, both of which are long and convoluted. The prostate joins the ampulla before entering the albumen gland.

Remarks. The color pattern on *Glossodoris bonwanga* appears similar to Rudman's description of the *Glossodoris cincta* East African color form, except for the lack of a "diffuse yellow tinge surrounding the central region of the mantle" (Rudman 1986), but this could certainly be due to individual variation. The black and bright yellow marginal bands distinguish this species from the other cryptic and pseudocryptic *G. cincta* species, which each have three easily distinguishable marginal bands. However, in his description, Rudman (1986) also identifies a transparent band on the outer edge of the black band. The white speckling that blankets the mantle and foot give it a smoother appearance and each dot is distinguishable, also separating it from members of the other clades within the *G. cincta* complex. The striking difference between the light coloration of the stalk of the lamellae on the gills against the black-bordered tips is also a defining characteristic.

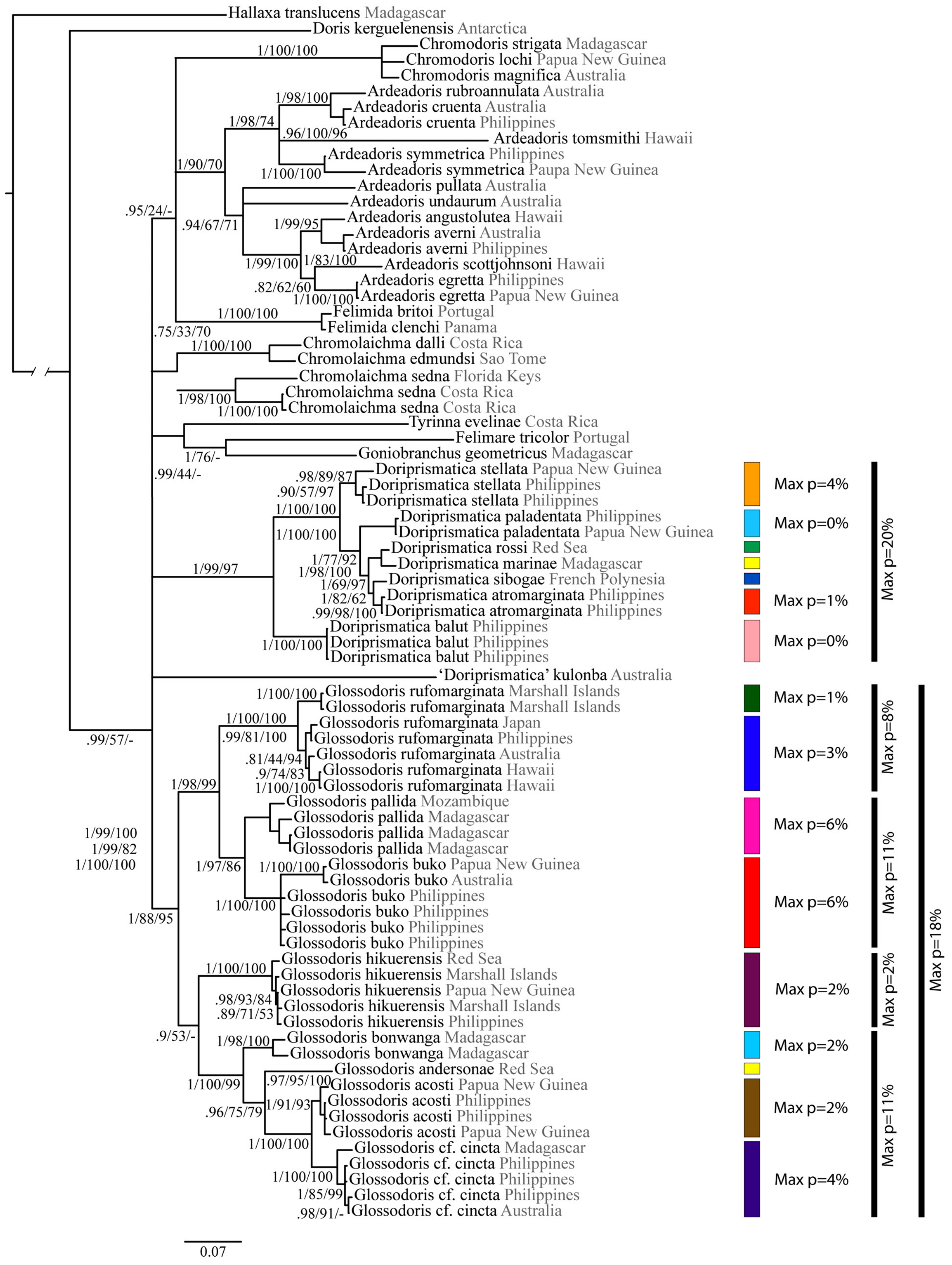

FIGURE 5. Phylogenetic tree (Matsuda & Gosliner 2017) with ABGD partitions (colored bars) and p-distances. Values listed are Bayesian Inference posterior probabilities/Maximum Likelihood bootstraps/Maximum Parsimony bootstraps.

The presence of an outer black marginal band with an inner broad yellow band clearly distinguishes *G. bonwanga* from all other members of the *G. cincta* clade. Additionally, it is the only member of this clade with a conspicuous black line along the rachis of each branchial rachis.

There are only subtle differences in the radular structure between all the species in the *G. cincta* complex. The lack of denticles on the inner edge of the first lateral tooth sets *G. bonwanga* apart from other members of this complex. Its denticles are also more well-defined. The rachidian tooth is pointed, which is similar to *Glossodoris acosti* and *G.* sp. cf. *cincta,* but not *Glossodoris andersonae*. The jaw rodlets for members of all four clades are similarly unicuspid and curved. The radula is similar to what Rudman (1986) described, however he noted denticles on the inner edge of the first lateral tooth, whereas here there were none. The penis of *G. bonwanga* is far less convoluted than in other members of this species complex (Fig. 8) and curves simply over the female glands prior to becoming a highly convoluted ejaculatory vas deferens (Fig. 8A, B). This difference is also evident in the figure of the Tanzanian specimen illustrated by Rudman (1986: fig. 33C).

Molecular data place *Glossodoris bonwanga* as sister to the rest of the species in the *Glossodoris cincta* species complex (Matsuda & Gosliner 2017) and the ABGD analysis clearly places this lineage as a distinct species (Fig. 5). The intraspecific p-distance is 2, whereas a p-distance of ≤9 separates this species from *G. andersonae* **sp. nov.**, *G. acosti* **sp. nov.**, and *G.* sp. cf. *cincta* (Matsuda & Gosliner 2017).

Glossodoris andersonae **Matsuda & Gosliner sp. nov.**

Figures (2D, 6B, 7E–I, 8C, D)

Glossodoris sp. 1 Gosliner *et al*. 2015: 235, upper right photo.
Glossodoris sp. C Matsuda & Gosliner 2017.

Type material. *Holotype*: CASIZ-192288, one specimen, dissected, 12 mm preserved, Saudi Arabia, Red Sea, "Abu Lad" [Abulad Islands], coll: T.M. Gosliner, 10 Mar 2013, Red Sea Biodiversity Cruise 2013, 7 meters, orig. fixative 95% EtOH. A tissue sample from the foot was taken for molecular analyses (Matsuda & Gosliner 2017), GenBank: KT600694. No other specimens from this location have been collected at this time.

Etymology. *Glossodoris andersonae* is named after Jennifer Anderson, retired lecturer in the Environmental Studies Department at the University of California Santa Cruz, who is a longtime friend and mentor of the first author.

Distribution. Known only from the Saudi Arabian Red Sea (Gosliner *et al*. 2015; present study).

External morphology. *Glossodoris andersonae* has an elongate oval mantle that is elevated from the sides of the body above the foot (Fig. 6B). The mantle and foot are both a rust-orange color covered almost entirely with white blotches that become denser towards the outer edge, giving it a textured appearance. The mantle edge is characterized by a series of small permanent and semi-permanent undulations with a pair of large permanent folds midway on the mantle that correspond to the only location where the thick white splotching crosses over the top of the mantle. There are three marginal mantle bands; the outermost is a thin white, followed by a navy blue and then greenish-yellow that contains irregular opaque white spots (Fig. 2D). These same colors similarly border the base of the foot though appear slightly less intense. The gill sits on the posterior third of the body and forms a semicircle around the anus. The approximately 19 unipinnate gill branches curve inwards at both ends into small spirals where the branches are shorter. Each branch has a single tip and shares the same color pattern as the mantle at the base, with the white spots becoming denser towards the dark blue-green tips. The rhinophores have approximately 18 lamellae and are almost entirely covered in soft white spots with a few darker spots around the base and the tips. Most notable are two dark blackish-blue circles with a diameter approximately double that of the rhinophores on the mantle directly behind each rhinophore. The genital pore is located on the right side of the body just under the mantle skirt posterior to the rhinophores.

Internal anatomy. *Radula* (Figs. 7E–I). The radular ribbon is long and wide (Fig. 7H) (12 mm preserved specimen, with a formula of 88 x 68.1.68). The rachidian tooth (Fig. 7E) is approximately two-thirds the length of the adjacent lateral teeth, and each rachidian tooth ends in a narrow but blunt tip. The first lateral tooth is long, curved and narrow with nine well-defined denticles on the outer edge and five distinct denticles on the inner face. The denticles are small and do not protrude out from the main body of the tooth. The inner and mid-laterals (Fig. 7F) have well defined denticles on the outer edge (~11 and ~12–14 respectively), and a well-defined peen. The outer laterals (Fig. 7G) are reduced in size, have no peen, however retain their denticles, though reduced, until almost the very edge. The jaws contain densely packed unicuspid, curved rodlets (Fig. 7I).

Reproductive system (Fig. 8C, D). The bursa copulatrix is almost double the size of the receptaculum seminis, and the receptaculum duct itself is short. The penial bulb is long and convoluted, leading to the vas deferens and the prostate gland, which are both long and folded. The ampulla and prostate gland do not join before entering the albumen gland.

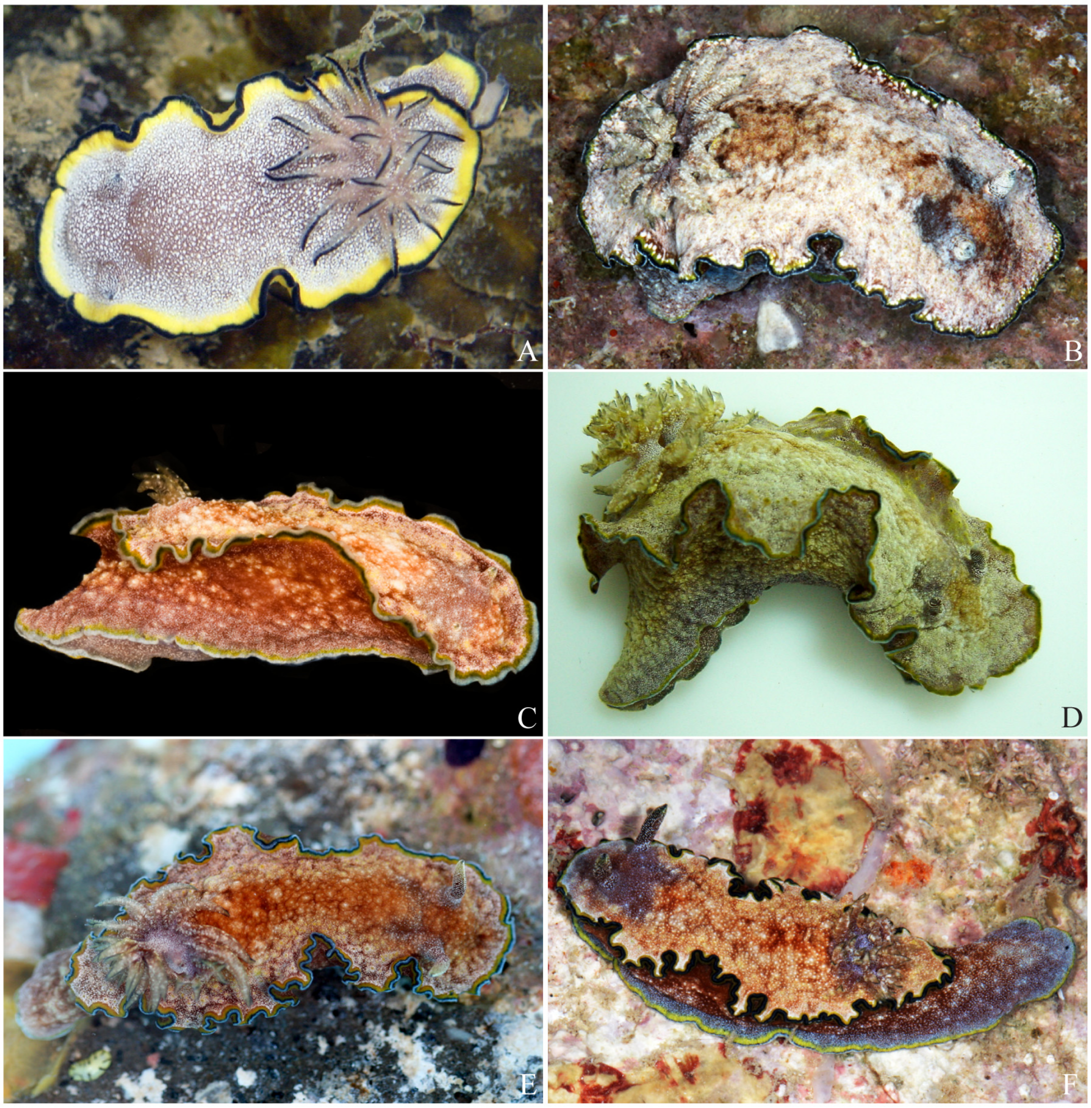

FIGURE 6. A. *Glossodoris bonwanga* **sp. nov.**, CASIZ-194018 Madagascar, Photo: Marina Poddubetskaia. B. *Glossodoris andersonae* **sp. nov.**, CASIZ-192288 Saudi Arabia, Red Sea, Photo: T.M. Gosliner. C. *Glossodoris acosti* **sp. nov.**, CASIZ-191352 Papua New Guinea, Photo: V. Knutson. D. *Glossodoris acosti* **sp. nov.**, CASIZ-175327 Philippines, Photo: T.M. Gosliner. E. *Glossodoris* sp. cf. *cincta*, CASIZ-173394 Madagascar, Photo: T.M. Gosliner. F. *Glossodoris* sp. cf. *cincta*, CASIZ-177257 Philippines, Photo: T.M. Gosliner.

Remarks. *Glossodoris andersonae* shares similarities in color pattern with some members of the *Glossodoris cincta* clade. Rudman (1986) did not specifically mention any Red Sea specimens as belonging to the *Glossodoris cincta* color group. However, he did list two species documented from the Red Sea as synonyms of *G. cincta*: *Casella foxi* (O'Donoghue 1929) and a species identified as *Casella obsoleta* (Rüppell & Leuckart 1828) by Gohar & Soliman (1967). The specimen they illustrated is clearly distinct from *Doris obsoleta* Rüppell & Leuckart, 1928, which has orange and black marginal bands, is currently classified as a species of *Goniobranchus* (Gosliner *et al.* 2015). *Casella foxi*, based on its radula teeth with small denticles and permanently undulating mantle margin, is most likely a *Glossodoris* as is the species misidentified by Gohar & Soliman. However, both of these species differ from *G. andersonae*, described here in having an outer yellow (yellowish green in "*Casella obsoleta*") marginal band that is followed by a middle cobalt blue band and a second band of yellow. In *G. andersonae*, the outer band is white to blue, followed by a dark blue to black band and greenish yellow band with numerous opaque white spots. The colored bands that surround the mantle are distinctive, as are the dark blackish-blue spots behind the rhinophores. The white blotches covering the mantle and foot are more textured and dense than in other members of the *G. cincta* clade. In *G. foxi* and "*Casella obsoleta*" the gill branches are held erectly away from the body surface whereas they are curved inward in *G. andersonae* and are appressed against the mantle surface. The rachidian teeth in *G. andersonae* are almost two thirds the height of the adjacent laterals, have a broad base and a narrower outer portion, whereas they are much shorter and more uniformly triangular in *G. foxi* and "*Casella obsoleta*". The rachidian tooth is elongate but rounded apically in *G. andersonae*, a trait that separates it from *G. bonwanga*, and *G.* sp. cf. *cincta*, which have acutely pointed apices, and *G. acosti*, which is blunt. *Glossodoris andersonae* has a much shorter vagina than G. *bonwanga* and *G. acosti* and only slightly shorter than *G.* sp. cf. *cincta*.

Molecular and morphological data support this as independent and distinct (Matsuda & Gosliner 2017). A p-distance >9% separates *G. andersonae* from the other closely related species (Matsuda & Gosliner 2017) and the ABGD analysis from this study clearly differentiates this as a distinct species (Fig. 5).

Glossodoris acosti **Matsuda and Gosliner, sp. nov.**

Figures (2E, 6C, D, 8E, F, 9A–E)

Glossodoris cincta (Bergh, 1888), (Rudman 1986 in part, misidentification: 155, figs, 30C, 33B, 35).
Glossodoris sp. D Matsuda & Gosliner 2017.

Type Material. *Holotype*: CASIZ-191352, one specimen, dissected, 18 mm preserved, Papua New Guinea, Madang Province, Rempi, coll: D. Uyeno, 20 November 2012, Papua New Guinea Biodiversity Expedition 2012, orig. fixative 95% EtOH. Tissue sample was removed from the foot for DNA sequencing in Matsuda & Gosliner (2017), GenBank: KT600698 (COI).

Paratypes: CASIZ-191109, one specimen, 6 mm preserved, Papua New Guinea, Madang Province, coll: Expedition by vacuum, 10 Nov 2012, Papua New Guinea Biodiversity Expedition 2012, orig. fixative 98% EtOH. Tissue sample was removed from the foot for DNA sequencing in Matsuda & Gosliner (2017). CASIZ-158809, one specimen, dissected, 31 mm preserved, Philippines, Luzon, Batangas Province, Mabini (Calumpan Peninsula), Maricaban Strait, Arthur's Rock, coll: B. Castillo, 7 May 2001, 10 meters, orig. fixative Bouin's solution. A tissue sample was removed from the foot for DNA sequencing by Johnson & Gosliner (2012) and the extraction was additionally used in Matsuda & Gosliner (2017). CASIZ-175327, one specimen 42mm preserved, Philippines, Bohol Island, Panglao, Sungcolan Bay, fringe mangrove, sand and seagrass, coll: T.M. Gosliner, Y. Camacho, J. Templado, M. Malaquias, M. Poddubetskaia, 9 June 2004, Panglao Expedition 2004, 1–5 meters, orig. fixative Bouin's solution or 10% formalin.

Etymology. *Glossodoris acosti* is named after Robert Acosta, a longtime friend and mentor of the first author.

Distribution. Specimens identified in Philippines and Papua New Guinea (present study) and possibly Christmas Island (Indian Ocean) (Rudman 1986).

External morphology. *Glossodoris acosti* have an elongate oval mantle that sits high on the well-elevated sides of the body (Fig. 6C, D). The mantle edge consists of small permanent and semi-permanent undulations with a larger fold on both sides at the midpoint of the mantle. The coloration of the mantle and foot range from brick red to brown, which is covered with small white spots that are denser closer to the edge of the mantle giving it a textured appearance. Three marginal bands run along the outer edge of the mantle and foot, the outermost light blue, followed by dark green and then a lighter yellow-green (Fig. 2E). The color bands on the mantle are more intense than on the foot. The gill forms an arch around the anus that opens posterior, and the gills at both ends of the arc curl inwards. The posterior gill branches form two spirals that are found dorsal to the anterior branches. The gill is large and extends all the way to the mantle margins when fully extended. The lamellae are covered in small white spots with dark colored tips, and while the majority are forked, some are not. In one specimen, the lamellae at the middle of the arc had a notably long fork. The base of the rhinophores are the same color as the mantle that become increasingly whiter approaching the dark tips. The genital pore is located on the right side of the body below the mantle and posterior to the rhinophores.

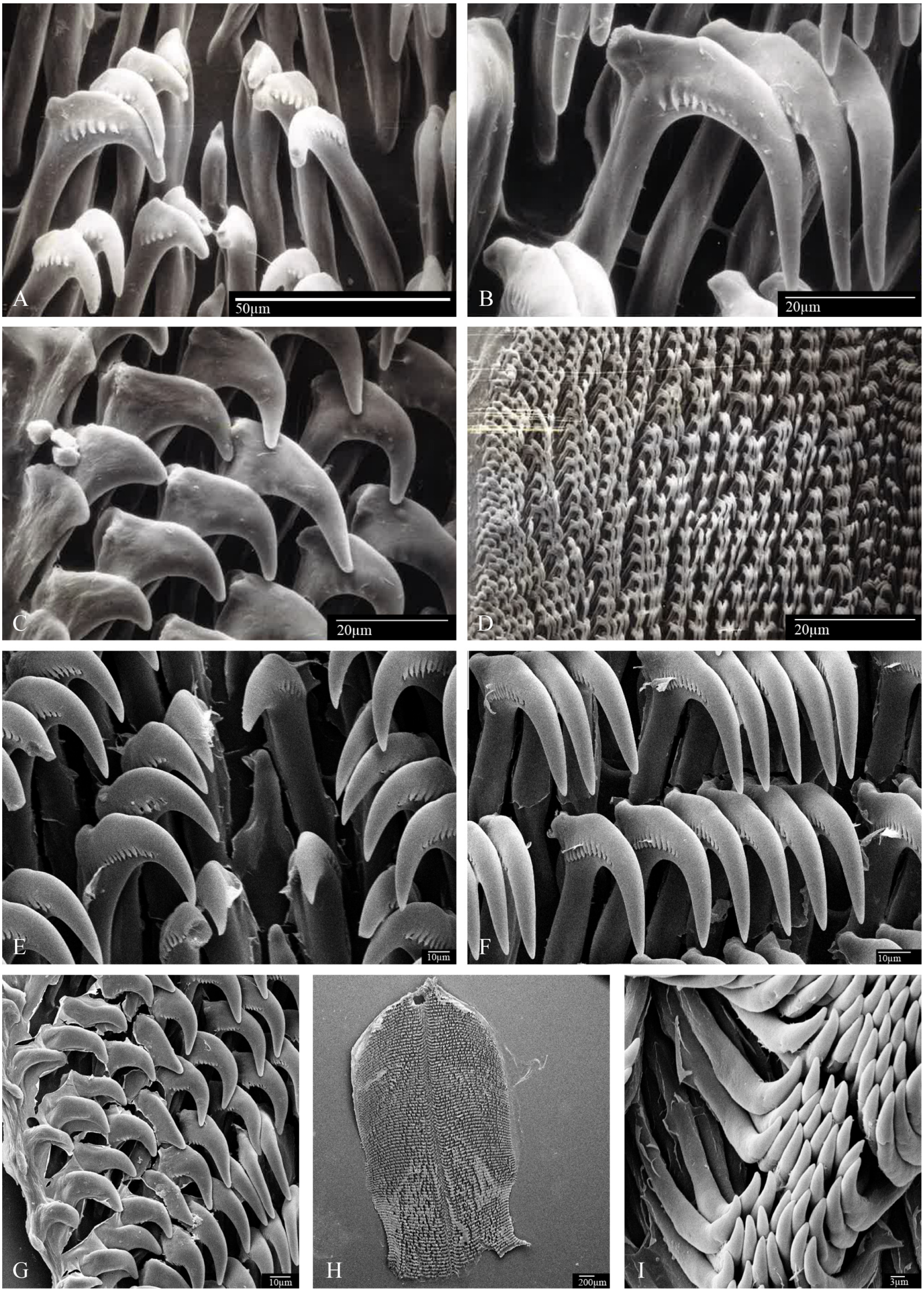

FIGURE 7. Scanning electron micrographs. A–D, *Glossodoris bonwanga* **sp. nov.**, A35516 South Africa: A. Rachis. B. Mid laterals. C. Outer laterals. D. Radula ribbon. E–I, *Glossodoris andersonae* **sp. nov.**, CASIZ-192288 Saudi Arabia, Red Sea: E. Rachis. F. Mid laterals. G. Outer laterals. H. Radular ribbon. I. Jaws.

Internal morphology. *Radular structure* (Fig. 9A–E). The radular ribbon is long and wide (Fig. 9D) (radular formula for an 18 mm preserved specimen CASIZ-191352 is approximately 106 x 65.1.65). The rachidian tooth (Fig. 9A) is two-thirds of the length of the first lateral tooth and narrows to a dull point. The first lateral tooth has a long central cusp with six well-defined small denticles on each side of the tooth. The inner edges of the first laterals have a thicker ridge behind the denticles. The cusps of the inner laterals are slightly longer and there are approximately 12–15 denticles only on the outer edge. The mid-laterals (Fig. 9B) have a more pronounced peen than the inner teeth, and have 8–10 denticles on the outer edge. The outer laterals (Fig. 9C) are reduced with a shorter central cusp, a reduced peen, and only small indentations where the denticles are on the inner and mid-laterals. The outer three teeth entirely lack any trace of denticles. The jaw rodlets have a unicuspid tip and are slightly curved (Fig. 9E).

Reproductive system (Fig. 8E, F). The vagina is very long and folded and the bursa copulatrix is of comparable size to the receptaculum seminis sac. The bursa and receptaculum have a common insertion. The penial sac is long and twisted and wraps around the more distal part of the penis. The muscular vas deferens and glandular prostatic portion are also highly convoluted.

Remarks. The color pattern is distinctly different than *G. bonwanga* and *G. andersonae*, however closely resembles that of *G.* sp. cf. *cincta*. In *G. bonwanga*, there are only two marginal bands of color (outer black and inner yellow) compared to the three bands of *G. acosti* (outer light blue, middle dark green and outer yellowish green). Similarly, *G. andersonae* has a white to light blue outer band, followed by a middle band of dark blue and a yellowish green band that contains numerous opaque white markings. There appear to be subtle, but consistent differences in the external morphology between *G. acosti* and *G.* sp. cf. *cincta*. In *G. acosti*, the marginal bands are much wider and more subdued than in *G.* sp. cf. *cincta*. When fully extended, the gill of *G. acosti* is much larger (extending to the outer margins of the mantle) and has two distinct spirals found above the lower gill branches (Fig. 6D), whereas the gill of *G.* sp. cf. *cincta* is smaller and has all branches at one level. *Glossodoris acosti* closely matches the description of Rudman's (1986) Philippines-Indonesia color group. This is especially evident in the light blue mantle band noted in Rudman's Philippines specimen (Fig. 5). It also shares similarities to Rudman's (1986: figs. 33B, 35) Christmas Island specimen in its reproductive system structure and radular morphology.

The radula in *G. acosti* and *G.* sp. cf. *cincta* are also very similar, however the rachidian tooth in *G. acosti* (Fig. 9A) is less pointed than in *G.* sp. cf. *cincta* (Fig. 9F) and lacks the bulbous swelling below the apex. The outer laterals in *G. acosti* have faint indentations where the denticles would be, whereas in *G.* sp. cf. *cincta* the outer denticles are completely smooth in the Philippines and Papua New Guinea specimens, although the Madagascar specimen has well-defined denticles all the way to the edge. Further study is needed to determine the range of variation of these radular characters.

The vagina of *G. acosti* is very long and convoluted, which is similar to *G. bonwanga*, however it is significantly longer than in *G. andersonae* and *G.* sp. cf. *cincta*. Similarly, the penial papilla of *G. acosti* (Fig. 8E, F) is elongate and twists around the distal portion of the penis, where as it is much shorter and evenly curved in *G.* sp. cf. *cincta* (Fig. 8G, I).

The ABGD analysis clearly separates *G. acosti* from other members of the *G. cincta* clade. The intraspecific p-distances are less than or equal to 2, and interspecific p-distances ≥7 (Matsuda & Gosliner 2017) (Fig. 5).

***Glossodoris* sp. cf. *cincta* (Bergh 1888)**

Figures (2F, 6E, F, 8G–I, 9F–J)

Glossodoris cincta Bergh, 1888; (Rudman 1986 in part: 155, figs, 30A).
Glossodoris sp. E Matsuda & Gosliner 2017.

Material. *Material examined*: CASIZ-173394, one specimen, dissected, 17 mm preserved, Madagascar, Iles Radama, West of Nosy Valiha, coll: F. Ramahatragra, 20 October 2005, CAS-WCS Radama Islands, 12–13 meters, orig. fixative Bouin's solution. This specimen was tissue sampled (foot) for DNA analysis in Johnson & Gosliner (2012) and Matsuda & Gosliner (2017). CASIZ-199204, one specimen, dissected, 21 mm preserved, Philippines, Luzon Island, Batangas Province, Calatagan, Verde Island Passage coast, "Talisay North", coll: T.M. Gosliner, 18 May 2014, 2014 Verde Island Passage Expedition, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017). CASIZ-177257, one specimen 35mm preserved, Philippines, Batangas Province, Maricaban Island, Caban Island, Layag Layag, coll: T.M. Gosliner, A. Valdes, M. Pola, L. Witzel, B. Moore, A. Alejandrino, 16 Mar 2008, Philippines Expedition March 2008, 14.2 meters, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017). CASIZ-120737A, two specimens (A) 12 mm preserved (B) 10 mm preserved, Pacific Ocean, Marshall Islands, Enewetak Atoll, Cement Ship Pinnacle, on dead coral, coll: L. Boucher, 18 Jun 1981, 6-10 meters, orig. fixative 75% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017). CASIZ-199187, one specimen 19mm preserved, Philippines, Luzon Island, Batangas Province, Calatagan, Verde Island Passage Coast, Caritunan Reef, coll: S. Cohen, 10 May 2014, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017).

Distribution. The Philippines to Papua New Guinea, and Madagascar.

External morphology. *Glossodoris* sp. cf. *cincta* has an elongated mantle that sits high on the sides of the body above the foot (Figs. 6E, F). The body is a brick-rust color with white spots that are more concentrated towards the outer edge. Some specimens exhibit a slight yellow hue on the mantle. The mantle edge is a series of small to medium sized permanent and semi-permanent undulations, which include the large central fold on both sides of the mantle midway between the gill and rhinophores. The mantle edge and foot are surrounded by three vividly colored marginal bands: the outermost is thread-thin and light (almost white) blue, the middle ranges from light to dark blue, and the inner a bold yellow (Fig. 2F). The bands on the foot are paler, and the outer two bands are much thinner leaving the inner yellow band more visually dominant. The gill is located on the posterior third of the body and forms a semicircle around the anus with the ends spiraling inward and opening posteriorly. The lamellae are the same color as the body and the tips (unifid with some bifid) are outlined in dark blue and are smaller in size at the ends of the arc. In the Madagascar specimen, a single tri-tipped lamella is present between the anus and the top of the arc that is not present in the Pacific specimens. The rhinophores match the coloration of the body at the base and fade to yellow and then blue at the tip. There is a white line that runs down the front of each rhinophore. The genital pore opens on the right side of the body under the mantle and behind the rhinophores.

Internal anatomy. *Radular structure* (Figs. 9F–J). The muscular portion of the buccal mass is about the same size and the glandular portion of the oral tube (Fig. 8H). The radular ribbon is long and wide (Fig. 9I) (17 mm specimen 102 x 50.1.50, 21 mm specimen 124 x 75.1.75). The rachidian tooth (Fig. 9F) is approximately two-thirds the length of the first inner lateral and is slightly rounded with a bulbous area below the apex before coming to an acute point at the apex. The first inner lateral tooth has a long central cusp with 5–6 well defined small denticles on both sides. The inner edge also has a thick ridge. The denticles on the first lateral of the Madagascar specimen are more well defined. The inner lateral teeth have a longer central cusp and only denticles on the outer edge (10–12), and a peen. The central cusp on the mid-laterals (Fig. 9G) is longer and although has poorly defined denticles on the outer edge. Specimens from the Philippines and Papua New Guinea have smooth outer laterals with reduced central cusp and peen. The outer laterals (Fig. 9H) of the Madagascar specimen have reduced but denticles all the way to the outer edge. The jaws are unicuspid, long, and curved (Fig. 9I) in specimens from all localities studied.

Reproductive system (Fig. 8G, I). The reproductive systems of both the Madagascar specimen and the Philippines specimen are similar. The vagina is of short to medium length and the receptaculum seminis sac and bursa copulatrix are similar in size. The penial bulb is relatively long and convoluted, as are the muscular vas deferens and prostate gland.

Remarks. *Glossodoris* sp. cf. *cincta* is similar to Rudman's (1986) North Australia color group and to the animal depicted in fig. 30A, however the yellow tinge he reports as missing, is present in some of the Philippines specimens (Matsuda & Gosliner 2017). The innermost yellow line is clearly visible, followed by a dark blue (Rudman's black) line and a white to light blue line (Rudman's translucent). In Rudman's account and in the specimens in this study, the dark yellow and dark blue lines are not present on the foot, instead only the outermost band appears, a trait that appears to separate *G.* sp. cf. *cincta* from the others in the species complex.

The Philippines specimens of *G.* sp. cf. *cincta* have faint inner denticles on first inner lateral, which is similar to *G. acosti*, although in the later the denticles are more clearly defined. Rudman's (1986) N. Australian color group also lacks inner denticles on the inner lateral. Unlike the other Madagascar specimens of *G. bonwanga,* which have faint denticles on the outer laterals, the *G.* sp. cf. *cincta* specimen from Madagascar has well defined denticles all the way to the outer edge. The degree of variation of these radular characters needs to be assessed more fully with larger populations of all species across a broad geographical range.

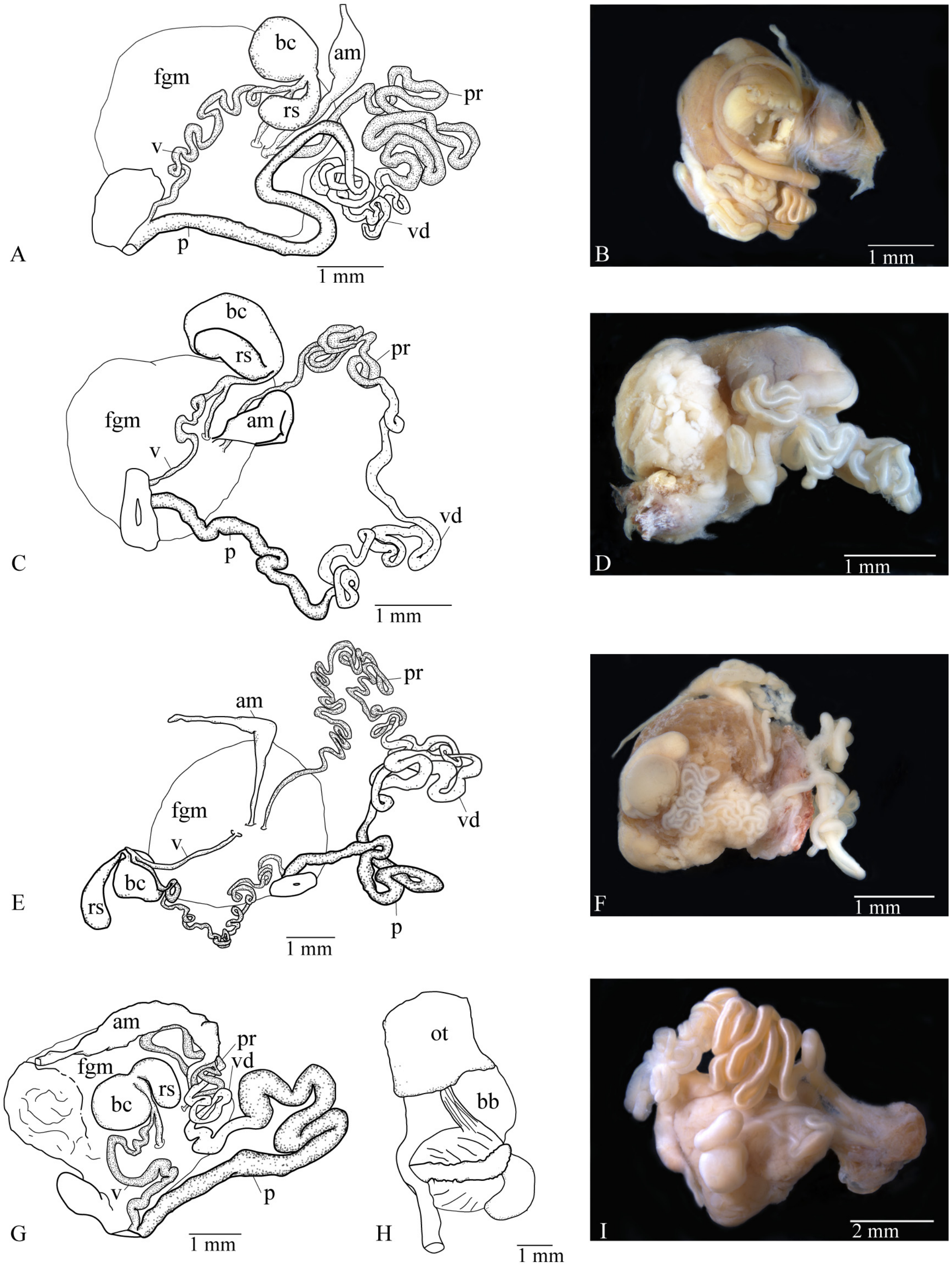

FIGURE 8. Reproductive systems, drawing (left)/photograph (right). A, B. *Glossodoris bonwanga* **sp. nov.**, A35516 South Africa. C, D. *Glossodoris andersonae* CASIZ-192288 Saudi Arabia, Red Sea. E, F. *Glossodoris acosti* **sp. nov.**, CASIZ-191352 Papua New Guinea. G, H (buccal bulb), I. *Glossodoris* sp. cf. *cincta* CASIZ-177257 Philippines.

The ABGD analysis clearly shows that the specimens here called *G.* sp. cf. *cincta* all represent a single species distinct from the other members of the *G. cincta* clade studied here (Fig. 5). The p-distances reported by Matsuda & Gosliner (2017) within *G.* sp. cf. *cincta* are <1% between the Philippines and Australian specimens, and ≤4% when including the Madagascar specimen (Fig. 5). The p-distances separating *G.* sp. cf. *cincta* from *G. bonwanga*, *G. andersonae*, and *G. acosti* are 7–10% (Matsuda & Gosliner 2017).

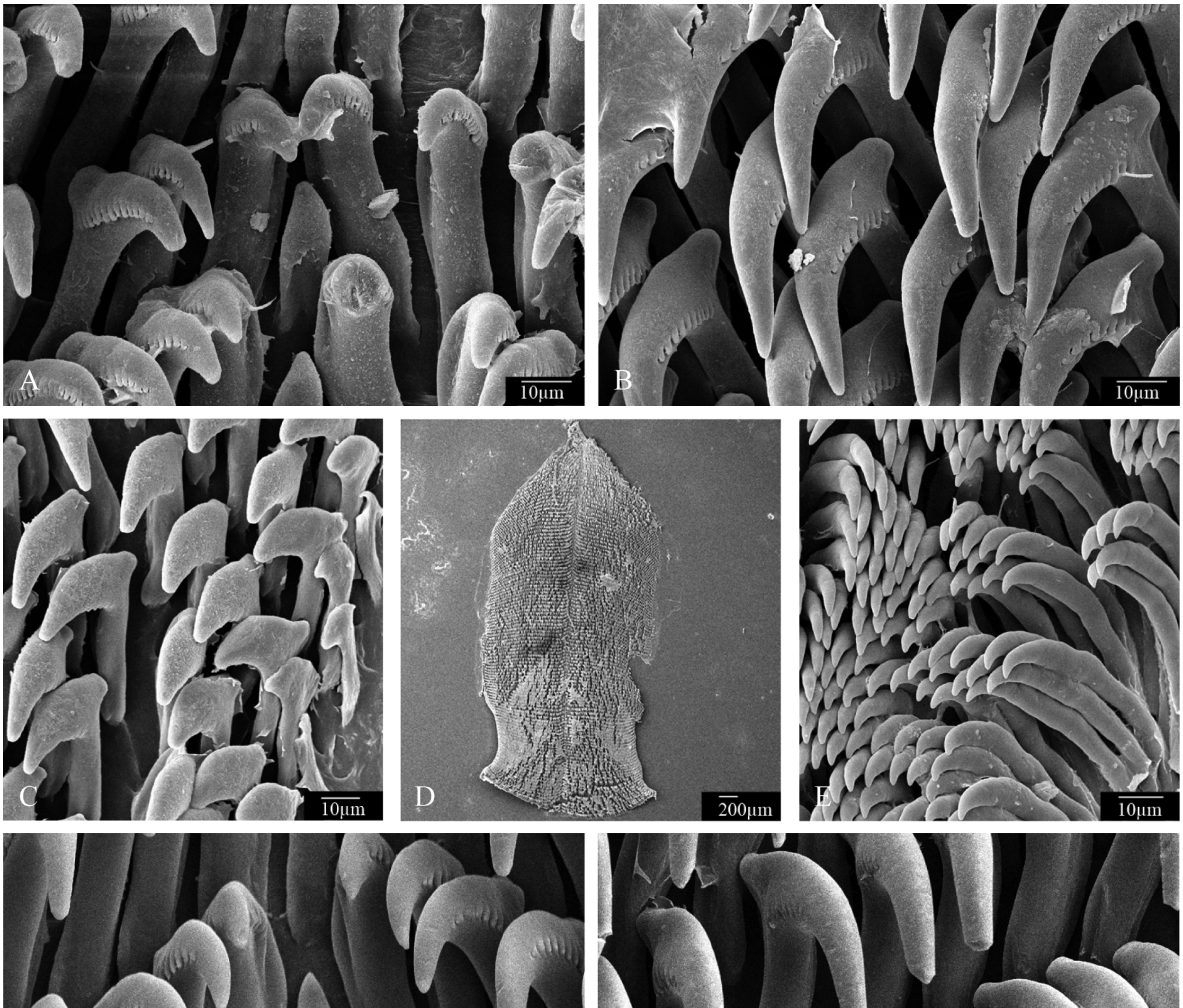

FIGURE 9. Scanning electron micrographs. A–E. *Glossodoris acosti* **sp. nov.**, CASIZ-191352, Papua New Guinea: A. Rachis. B. Mid laterals. C. Outer laterals. D. Radula ribbon. E. Jaws. F–J. *Glossodoris* sp. cf. *cincta* CASIZ-173394, Madagascar: F. Rachis. G. Mid laterals. H. Outer laterals. I. Radula ribbon. J. Jaws.

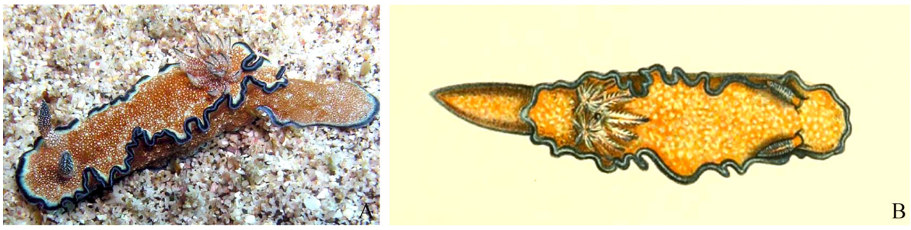

FIGURE 10. A. Photograph of *Glossodoris cincta* from Reunion Island (Photo: Philibert Bidgrain). B. Original Plate drawing of *Cassella cincta* Bergh, 1888.

The doubt as to whether this species represents the true *Glossodoris cincta* stems from the fact that the type locality for *G. cincta* is Mauritius. It is important to note that we were unable to obtain specimens of *G. cincta* from Mauritius (type locality). We noted that none of the color patterns of any of the cryptic and pseudocryptic species in the *Glossodoris cincta* species complex studied here matched the original plate figured by Bergh (1888: pl.77, fig. g) (reproduced in Fig. 10B) exactly. The figure depicts an orange and cream-colored mantle and foot that both are surrounded by colored bands (blue and white). However, we obtained photographs of what is currently being referred to as "*Glossodoris* cf. *cincta*" from Mauritius (Fig. 10A), and there is an uncanny resemblance to Bergh's illustration. We therefore think there is a high probability that the species we have retained the name "*Glossodoris* sp. cf. *cincta*" for currently, is something else. The collection of specimens of *G. cincta* from Mauritius for molecular and morphological analyses is imperative for further resolving the systematics of the *Glossodoris cincta* species complex.

Family: Chromodorididae

Genus: *Doriprismatica* d'Orbigny, 1839

Type species*: Doris atromarginata* Cuvier, 1804, by monotypy, no locality recorded.

Diagnosis: Chromodorid nudibranchs with a narrow body and permanent series of undulations around mantle margin. Oral tentacles elongate. Gill often forming double spirally arranged branches. Jaw rodlets unifid or bifid. Radular teeth with large denticles equaling size of primary cusp. Reproductive system with bursa copulatrix and receptaculum seminis of equal size. Receptaculum inserting directly into bursa rather than vagina. Prostate and ejaculatory portions of vas deferens elongate. Penis unarmed.

Doriprismatica balut Matsuda and Gosliner, sp. nov.

Figures (2H, 11A, B, 12, 13A–C)

Glossodoris sp. 1 Gosliner *et al*. 2008: p. 234, upper middle photo.
Doriprismatica sp. 1 Gosliner *et al*. 2015: p. 239, left middle photo.
Doriprismatica sp. A Matsuda & Gosliner 2017.

Type Material. *Holotype*: NMP 041278 (ex CASIZ-186096), one specimen 12 mm preserved, Philippines, Luzon, Batangas Province, Mabini (Calumpan Peninsula), Maricaban Strait, Murals dive site, coll: T.M. Gosliner, 3 May 2011, Hearst Philippine Biodiversity Expedition 2011, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017), GenBank: KT600688 (COI).

Paratypes: CASIZ-186095, one specimen, dissected, 10 mm preserved, Philippines, Batangas Province, Maricaban Island, Sepok Point, coll: M. Burke, 25 May 2011, Hearst Philippine Biodiversity Expedition 2011, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017). CASIZ-105745A and 105745B, two specimens, dissected, (A) 13 mm preserved (B) 10.5 mm preserved, Philippines, Mindoro Island, North side of the island, mouth of the northwest passage, coll: R. McPeak, 28

February 1995, orig. fixative Bouin's solution. CASIZ-182787, one specimen 8 mm preserved, Philippines, Batangas Province, Maricaban Island, Caban Island, Layag Layag, coll: T.M. Gosliner, 18 May 2010, Philippines Expedition 2010, orig. fixative 95% EtOH. CASIZ-208500, two specimens, Philippines, Mindoro: Oriental Mindoro Province, Puerto Galera, Palangan Point, coll: T.M. Gosliner, 07 April 2015, 2015 Verde Island Passage Expedition, orig. fixative 95% EtOH.

Etymology. *Doriprismatica balut* is named after the Filipino food, "balut", which is a boiled duck egg that contains a developed embryo, to represent the presumed direct development of *D. balut*, based on its large egg size (Fig. 11B).

Distribution. Specimens analyzed here have only been identified in the Philippines, although it has also been recorded from Indonesia (Gosliner *et al*. 2008).

External morphology. *Doriprismatica balut* has an elongate body with a light caramel colored mantle that is slightly darker near the edge (Figs. 11A, B). The mantle is surrounded by permanent and smaller semi-permanent undulations, and a series of marginal bands: a thin white inner band, followed by a thicker black one (Fig. 2H). A second inner white band is found on the ventral surface of the mantle. The caramel color is present on the underside of the mantle, but the foot itself is semi-transparent white. The gill has 12–14 unipinnate lamellae arranged in a semicircle. A few gill branches are bifid near the apices. The gill sits a little more than half way back on the top of the mantle and surrounds the anus in an arc that opens posteriorly. The gill lamellae are the same color as the mantle on the underside and fades to a cream color facing inwards. The tips are outlined in black. The rhinophores are cream and caramel colors with a black vertical line running up the anterior and posterior sides. The rhinophores have 10–12 crowded lamellae. The genital opening is on the right side located slightly behind the rhinophores.

Internal anatomy. *Radular structure* (Fig 12). The muscular portion of the buccal mass is slightly longer than the oral tube (Fig. 13C). The radula ribbon is long and wide (Fig. 12D) (13 mm specimen 119 x 30.1.30, 10 mm specimen 136 x 30.1.30). The rachidian tooth (Fig. 12A) is reduced and is approximately a quarter of the length of the first lateral tooth. The first lateral tooth has 3–6 well defined large denticles flat against both sides of a longer central cusp. The remaining inner laterals are similar in appearance but do not have denticles on the inner side. The mid-laterals (Fig. 12B) have a longer central cusp and the outer laterals are reduced and smooth (Fig. 12C). The jaw rodlets are curved with a bifid tip (Fig. 12E).

Reproductive system (Figs. 13A, B). The vagina is short and connects to the receptaculum seminis duct just below the bursa copulatrix and receptaculum seminis sac, which is significantly smaller than the bursa copulatrix. The penial bulb is of medium length and connects to a short muscular vas deferens and long and folded prostate gland that is pressed to the female gland mass. The ampulla connects to the prostate gland before connecting to the female gland mass. The egg mass is translucent and laid in a spiral with bright yellow eggs, the size of which suggests this species may have direct development (Fig. 11B).

Remarks. *Doriprismatica balut* is morphologically and molecularly distinct from the other *Doriprismatica*. *Doriprismatica balut* shares similarities with *D. atromarginata* (Cuvier 1804) in its shape and body color, however *D. balut* is easily distinguished by the thick continuous black line around the mantle edge, where *D. atromarginata's* black mantle band has multiple breaks. *Doriprismatica balut* also has an inner white line that is absent in *D. atromarginata*. The gill and rhinophores of *D. atromarginata* are black, whereas in *D. balut* they are the same color as the mantle and rhinophores and only have black bands running up the anterior and posterior edge. *Doriprismatica balut* also has a rachidian tooth, which is lacking in *D. rossi* sp. nov., *D. atromarginata*, *Doriprismatica sibogae* (Bergh 1905), and *Doriprismatica paladentata* (Rudman 1986). In D. *paledentata*, the inner lateral tooth is much broader whereas the remaining lateral teeth are narrow and elongate (Rudman 1986: fig. 9). *Doriprismatica stellata* (Rudman 1986) has a rachidian tooth, however the denticles are much larger and well-defined (Rudman 1986: fig. 12) than in *D. balut*. *Dorioprismatica marinae* also has a rachidian row of teeth, but they are broad rather than triangular and have many denticles (Fig. 124).

There are also differences in internal anatomy. The vagina of *D. balut* is closer in length to *Doriprismatica rossi* and *D. marinae*, and shorter than *D. atromarginata*.

Doriprismatica balut is sister to the clade containing other *Doriprismatica.* Our ABGD analysis clearly shows the distinctness of this species, with no genetic variation found in the COI sequences in the three Philippine specimens examined by Matsuda & Gosliner (2017) (Fig. 5). The interspecific p-distances range from 11–16% between g *D. balut* and the other *Doriprismatica* that were studied.

FIGURE 11. A. *Doriprismatica balut* **sp. nov.**, CASIZ-186096 Philippines. B. *Doriprismatica balut* **sp. nov.**, with egg mass, CASIZ-208500 Philippines. C. *Doriprismatica rossi* **sp. nov.**, CASIZ-192281 Saudi Arabia, Red Sea. D. *Doriprismatica marinae* **sp. nov.**, CASIZ-194050 Madagascar, photo by Marina Poddubetskaia. All other photos: T.M. Gosliner.

Doriprismatica rossi **Matsuda and Gosliner, sp. nov.**

Figures (2I, 11C, 13D, E, 14A–E)

Doriprismatica sp. 5 Gosliner *et al.* 2015: p. 240, upper left photo.
Doriprismatica sp. B Matsuda & Gosliner 2017.

Type material. *Holotype*: CASIZ-192281, one specimen, dissected, 31 mm preserved, Saudi Arabia, Red Sea, West Manghar Island, night dive, 8 March 2013, T. Gosliner, Red Sea Biodiversity Cruise 2013, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017), GenBank: KT600690 (COI).

Etymology. *Doriprismatica rossi* is named after the first author's brother, Ross Kyo Matsuda.

Distribution. Known only from the Saudi Arabian Red Sea.

External morphology. The mantle of *Doriprismatica rossi* sits high on the sides of the body above the foot and tapers posteriorly (Fig. 11C). The mantle has small conical tubercles over its entire surface. The mantle edge has the characteristic semi-permanent undulations, including two sets of permanent large folds, the first slightly behind the rhinophores and the second anterior to the gill. The mantle and foot are a burgundy-charcoal color that is covered with small white spots that are denser towards the edge of the mantle. Larger burgundy spots speckle the mantle over the white. A black band runs the edge of the mantle and is bordered on both sides first by thin electric blue bands and then followed by thicker mustard colored bands (Fig. 2I). The gill is two-thirds of the way back on the mantle and consists of approximately 14 unipinnate lamellae arranged in a spiral and forming an arc that opens posteriorly around the anus. Some of the lamellae have branching tips of up to four prongs while others are single and they become shorter at the ends of the arch. All of the gill branches are held close to the surface of the mantle. The gill stalk is a greener mustard color that fades to white, and two dark lines run up the inward and outward facing sides midway-up that join at the tip. The base of the rhinophores are a cream and mustard color and the rhinophores are dark charcoal that is dusted with white that gives them a frosted appearance. The rhinophores have approximately 15 closely packed lamellae. Behind the rhinophores are two burgundy-charcoal patches on the mantle that are not covered in white dots. The genital opening is on the right side of the body below the mantle and behind the rhinophores.

Internal anatomy. *Radular structure* (Fig. 14A–E). The oral tube is approximately three times as long as the buccal bulb (Fig. 13E). The radular ribbon is long and of medium width (Fig. 14D) (radular formula for 35 mm preserved specimen is approximately 165 x 25.0.25). A row of rachidian teeth is absent (Fig. 14A). The first lateral tooth has a long central cusp with three to four, large, well-defined downward-pointing denticles on both sides. The inner and mid-lateral teeth (Fig. 14B) have a longer central cusp with the same number of denticles on the outer edge, however with no denticles on the inner edge. The outer teeth (Fig. 14C) are only slightly reduced and have only one denticle on the outer edge. The jaw plates are composed of long bifid rodlets that are slightly curved (Fig. 14E).

Reproductive system (Fig. 13D). The vagina is of medium length and narrow and connects with the receptaculum seminis duct before reaching the receptaculum seminis sac and bursa copulatrix. The penial bulb is long and convoluted leading to a shorter muscular vas deferens. A long, twisted prostate gland connects to the base of the ampulla adjacent to the albumen gland.

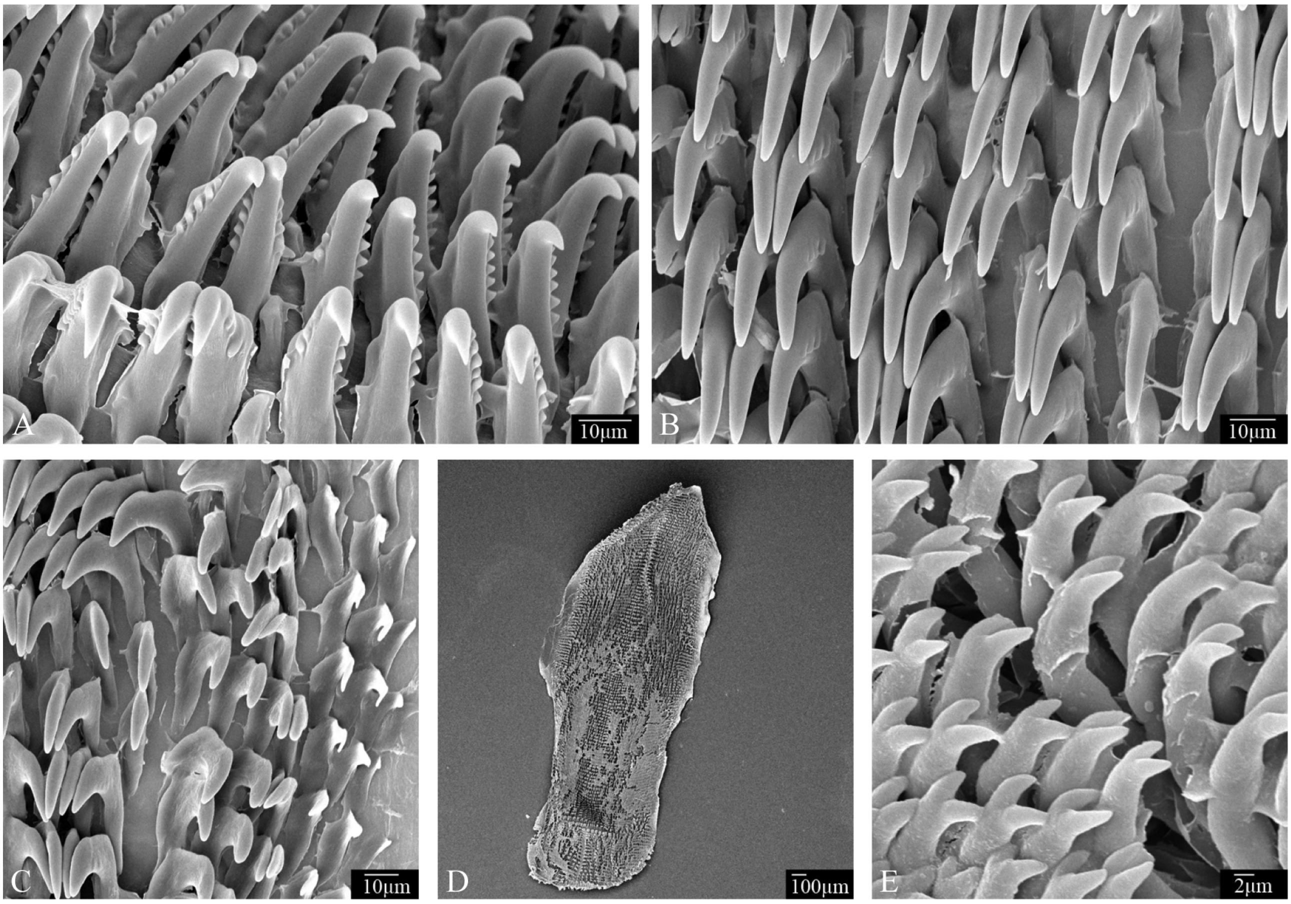

FIGURE 12. Scanning electron micrographs. A–E. *Doriprismatica balut* **sp. nov.**, CASIZ-186095 Philippines: A. Rachis. B. Mid-laterals. C. Outer laterals. D. Radula ribbon. E. Jaws.

Remarks. *Doriprismatica rossi* is sister to *Doriprismatica marinae* **sp. nov.**, and together they are sister to the clade containing *D. atromarginata* and *D. sibogae. Doriprismatica rossi* has its own unique color pattern and together with *D. paledentata* is the only species in the genus with three distinct marginal bands. These two species are unique in having mantle tubercles. The mantle of *D. rossi* is more oval that *D. atromarginata* and *D. sibogae*. The mantle bands are continuous, unlike in *D. atromarginata* and *D. sibogae* whose mantle bands include areas with slight interruptions. The mantle bands are similar in color to *D. paladentata*, however the bands on *D. paladentata* are much lighter and the body is teardrop-shaped with a broader anterior. The mantle of *D. paladentata* is covered with white spots, however the overall color of the mantle is a very light cream. The rhinophores and gills of *D. paladentata*, *D. atromarginata* and *D. sibogae* all stand out dark against the body, which is not the case for *D. rossi*. The radula for *D. rossi* differs from that of *D. atromarginata* by having a slightly longer central cusp, and resemble more closely those of *D. sibogae* (Rudman 1986, fig. 6, specimen from Fiji).

The ABGD analysis supports *D. rossi* as a distinct species (Fig. 5). The p-distance values between *D. rossi* and *D. marinae* is 2%, which while seemingly small, is consistent with the p-distances between and within other species of *Doriprismatica* (Matsuda & Gosliner 2017) (Fig. 5). Their general body form is markedly different. The p-distances between individuals of *D. atromarginata* is 1% and between specimens of *D. paladentata* is 0, and the p-distances that separate *D. atromarginata* and *D. sibogae* is 3%.

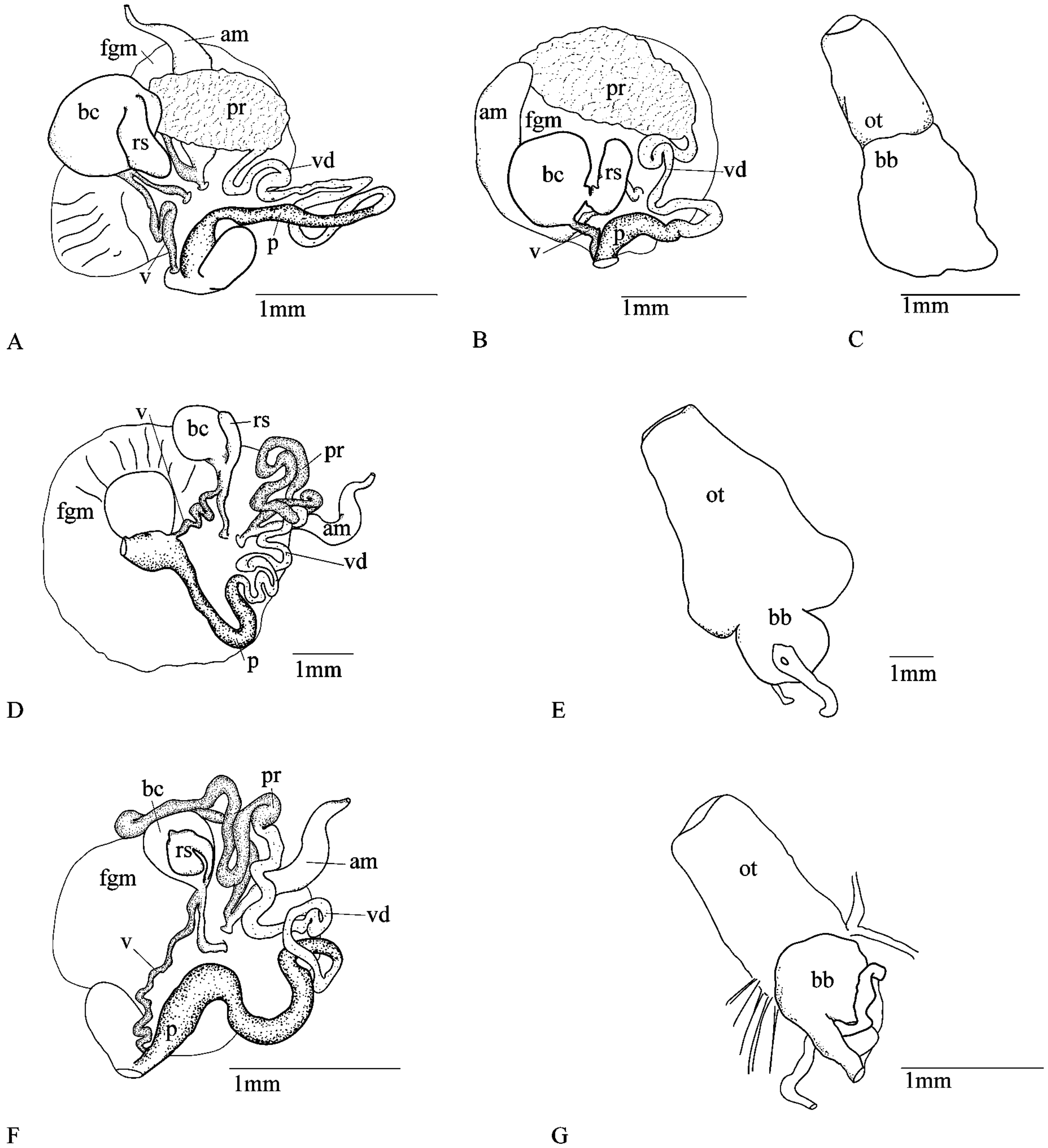

FIGURE 13. A–C, *Doriprismatica balut* **sp. nov.**: A. CASIZ-105745 Philippines, Reproductive system. B–C, CASIZ-186095 Philippines, B. Reproductive system. C. Buccal mass. D–E, *Doriprismatica rossi* **sp. nov.**, CASIZ-192281 Saudi Arabia, Red Sea: D. Reproductive system. E. Buccal mass. F–G, *Doriprismatica marinae* **sp. nov.**, CASIZ-194050 Madagascar: F. Reproductive system. G. Buccal mass. Abbreviations: p, penis; vd, vas deferans; pr, prostate; v, vaginal duct; rs, receptaculum seminis; bc, bursa copulatrix; am, ampulla; fgm, female gland mass; ot, oral tube, bb, buccal bulb.

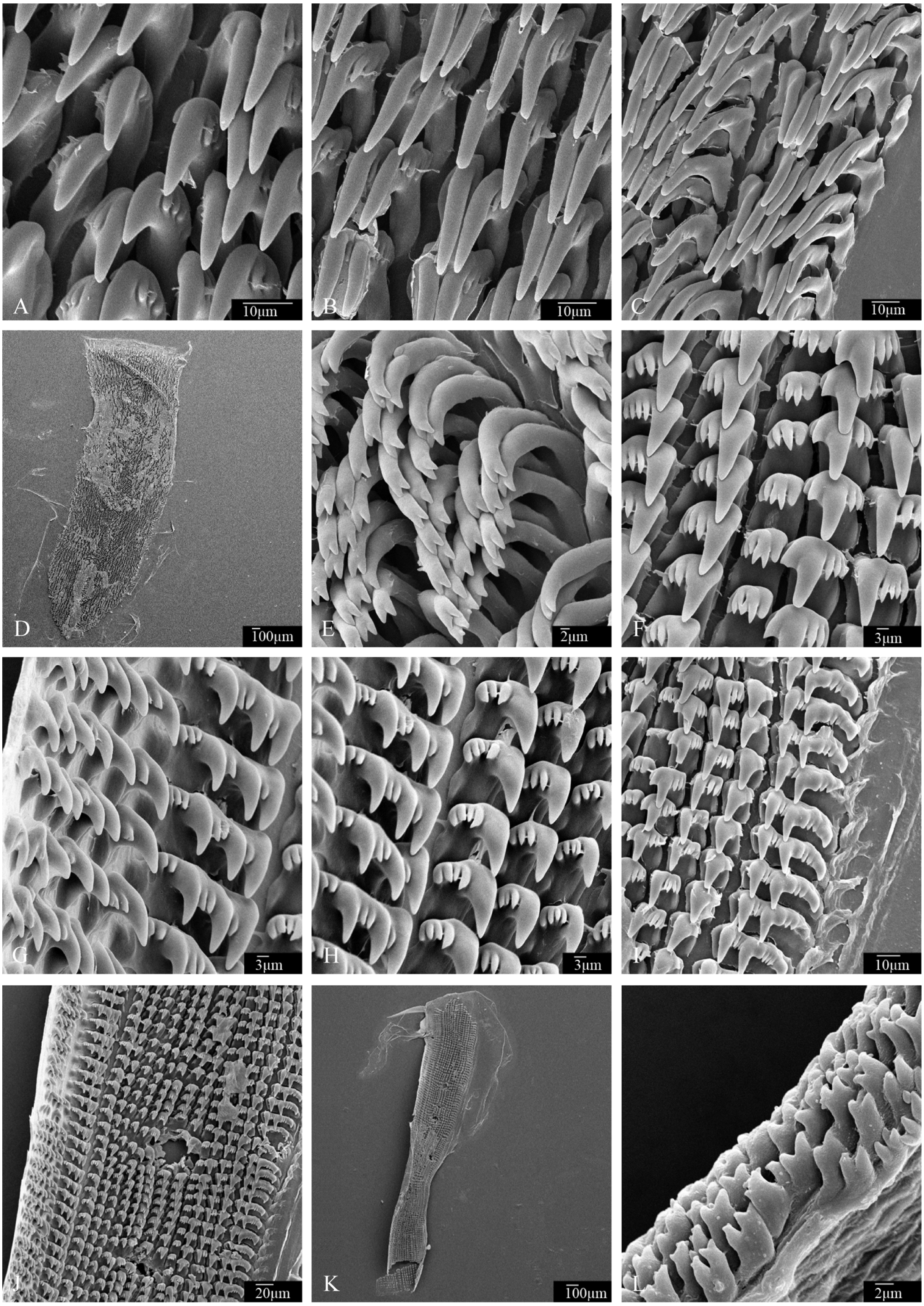

FIGURE 14. Scanning electron micrographs. A–E. *Doriprismatica rossi* **sp. nov.,** CASIZ-19228 Saudi Arabia, Red Sea: A. Rachis. B. Mid-laterals. C. Outer laterals. D. Radula ribbon. E. Jaws. F–L. *Doriprismatica marinae* **sp. nov.**, CASIZ-194050 Madagascar: F. Rachis. G. Outer laterals (right). H. Mid-laterals. I. Outer laterals (left). J. Ribbon. K. Whole radular ribbon. L. Jaws.

Doriprismatica marinae **Matsuda and Gosliner sp. nov.**

Figures (2J, 11D, 13F, G, 14F–L)

Doriprismatica sp. 6 Gosliner *et al*. 2015: p. 240, upper right photo.
Doriprismatica sp. C Matsuda & Gosliner 2017.

Type material. *Holotype*: CASIZ-194050, one specimen, dissected, 7.5 mm preserved, Madagascar, South Madagascar, "Pointe Evatra, crique fond rocheux et gazon d'algues", 30 April and 6 May 2010, Expedition Atimo Vatae-South Madagascar Expedition 2010, 3-8 meters, orig. fixative 95% EtOH. This specimen was tissue sampled (foot) for DNA analysis in Matsuda & Gosliner (2017), GenBank: KT600691 (COI).

Etymology. *Doriprismatica marinae* is named after Marina Poddubetskaia, who found and collected the type specimen.

Distribution. Madagascar.

External morphology. *Doriprismatica marinae* has a long mantle that tapers posteriorly (Fig. 11D) and terminates gradually above the posterior end of the foot. The mantle is a warm brown color that is covered in white dots that are denser towards the edge of the mantle. The mantle is thrown into permanent and semi-permanent undulations that are outlined by one brown marginal mantle band (Fig. 2J). There are two pairs of permanent folds, that are equally spaced between the rhinophores and the gills. The gill forms an arch around the anus opening posteriorly. The 10 lamellae are unipinnate and unifid apically and a cream color with two thin brown bands running up the outer edge and joining at the tip. The base of the rhinophores are a cream color and the rhinophores themselves are the same color brown as the mantle band with 12 white lamellae. The short, rounded oral tentacle is visible in Fig. 11D. The genital opening is on the right side of the body just behind the rhinophores.

Internal anatomy. *Radular structure* (Fig. 14F–L). The buccal mass is about twice as long as oral tube (Fig. 13G). The radular ribbon is long and narrow (Fig. 14K) and there are more teeth on the left side of the rachidian tooth (Fig. 14J) (135x 17.1.5). The rachidian tooth (Fig. 14F) is short and stubby with a short central cusp that is bifid in some cases. It has one denticle on the right side, and 2–4 denticles on the left that are all similar in length to the rachis. The mid-laterals on the left (Fig. 14H) have a long and pointed curved central cusp that has 3–4 short well-defined denticles on the outer edge and none on the inner. The denticles are similar in size to the central cusp of the rachis, and are packed next to each other adding girth to each tooth. The outer denticles on the left side (Fig. 14G) begin to fuse together to form a single tooth that has three long curved central cusps with denticles packed between them. The first lateral tooth on the right side of the rachis has a long curved central cusp with one denticle on the inner edge and 3–4 on the outer edge. These denticles are similar in shape and size to the denticles on the left side. The next two inner lateral teeth only have denticles on the outer edge (Fig. 14I), the third lateral has only one denticle on the outer edge, and the fifth lateral (also the outermost tooth) is fused. This outer lateral has two central cusps with 2–3 denticles in between them, and an undeveloped third central cusp on the outermost edge with 2–3 denticles between it and the middle central cusp. The jaw rodlets are short and stubby and are bifid with some instances where two bifid tips fuse before connecting to the jaw plate (Fig. 14L).

Reproductive system (Fig. 13F). The bursa copulatrix is approximately double the size of the receptaculum seminis sac. The vagina is medium in length and connects with the receptaculum seminis duct before reaching the bursa copulatrix and sperm sac. The penial bulb is long and convoluted leading to a shorter muscular vas deferens. A long, twisted prostate gland connects to the base of the ampulla adjacent to the albumen gland.

Remarks. *Doriprismatica marinae* is distinct morphologically and molecularly from the other *Doriprismatica.* A detailed comparison of *D. marinae* with its sister taxon *D. rossi* is warranted. The general body color is similar in that both species have opaque white spots, but *D. marinae* has only a single mantle band whereas the others, *D. rossi* and *D. paledentata*, have three distinct bands. *Doriprismatica rossi* also lacks the black pigment on the gill rachis that is evident in *D. marinae*. Also, the rhinophore color distinguishes these two species. The gill branches of *D. marinae* are held vertically, whereas those of *D. rossi* are horizontal to the mantle surface and include secondary branches at the tips of some of the larger gill branches. The long body shape that starts with a rounded anterior that tapers posteriorly is similar to *D. atromarginata*, and differs from *D. rossi*, which has a well-rounded, distinct posterior end of the mantle rather than one that gradually merges with the posterior end of the foot. The buccal bulb to oral tube ratio is less in *D. marinae*. The jaws of *D. marinae* bear short bifid rodlets in contrast to the uniformly elongate rodlets of *D. rossi.* The radula of *D. marinae* is markedly asymmetrical with far more teeth on the left side of the radula and a rachidian row of teeth is present. In contrast, *D. rossi* lacks rachidian teeth and has a symmetrical radula. In *D. marinae*, the radular teeth all have a very short primary cusp whereas *D. rossi* has far more elongate cusps on all of its teeth. Although the reproductive systems of these two species are quite similar, *D. marinae* has a longer vagina than does *D. rossi*. More specimens, beyond the single specimens of *D. marinae* and *D. rossi* studied here, are needed to more fully understand the range of variation in jaw, radular structure, and reproductive anatomy, but the differences observed above are consistent with species-specific differences found in other clearly distinct species of *Doriprismatica* and are not likely to reflect intraspecific variation. The fact that these differences span, external coloration, body shape, gill morphology, buccal armature and reproductive anatomy strongly suggests that these two species are distinct. The ABGD analysis as outlined in Matsuda & Gosliner (2017) also supports the distinctness of *D. marinae* and *D. rossi*, despite the relatively low genetic divergence of 2% for the COI gene (Fig. 5).

Discussion and conclusion

Scanning electron microscopy of the radular ribbon and dissections of the reproductive systems confirm the new, cryptic, and pseudocryptic species identified in the molecular phylogenies and ABGD analysis presented by Matsuda & Gosliner (2017). Other novel characters such as the presence of an envelope of distinct oral glands were found to differentiate closely related species such as *Glossodoris buko* from *G. pallida*. In some instances, small numbers of individuals prevent exploration of the full range of morphological variability. In three cases, only a single individual of the new species described here have been found. In these three instances, all singletons were sequenced for molecular data and the anatomy was completely described. No other records are known for these species, despite considerable exploration of the remote localities where they were found. This is not an atypical situation for novel species encountered in the Coral Triangle megadiversity region (Jörger & Schrödl 2013). Bouchet (2009) found that of the 714 species of pyramidellid gastropods found during the Panglao Philippine expedition, 205 species (28.7%) were known from only a single specimen. We are of the opinion that it is better to describe unknown diversity from remote places to document the existence of those taxa and to be able to have that increased diversity known to conservation biologists, government officials and policy makers rather than await the discovery of additional individuals, which might require decades of additional exploration. Also, from a scientific point of view, description of a new taxon generates a hypothesis that can be tested by discovery of additional individuals in the future.

Traditional morphological characters such as color patterns, especially the number and arrangement of marginal color bands appears to be a strong differentiator between species. Another set of external morphological characters, the shape of the gill, the mantle edge and general body shape appear to be consistently correlated with the molecular species delimitation characters obtained here. Radular morphology, particularly the presence or absence and shape of a rachidian tooth appears to be strongly supported as providing diagnostic tools for differentiating species within *Glossodoris* and *Doriprismatica*. The shape of jaw rodlets also appears to be a good differentiator between closely related species such as the sister species pairs of *Glossodoris buko* and *G. pallida* and *Doriprismatica rossi* and *D. marinae*. With regard to reproductive anatomy, the relative lengths of the penis, muscular portion of the vas deferens and the prostatic portion of vas deferens and length of the vagina are strongly correlated with the molecular data.

While the newly described *Doriprismatica* species were previously unidentified, the *Glossodoris* species complexes represent a growing trend of cryptic and pseudocryptic nudibranch species identification by molecular analyses and subsequent confirmation through morphological examination (Pola *et al*. 2012; Hoover *et al*. 2015, 2017; Lindsay & Valdés 2016; Churchill *et al*. 2013). Previous morphological studies describing the taxonomy of *Glossodoris* and sister genera have commented on the likelihood of crypsis due to color variations, but lacked the molecular technology for confirmation (Rudman 1986).

Some recent studies of chromodorid nudibranchs (Almada *et al*. 2016; Fufaro *et al*. 2016; Padula *et al*. 2016) have shown that species of Atlantic chromodorids in the genera *Felimare* and *Felimida* are polymorphic for color variation and that color is generally more highly varied that previously thought. Layton *et al.* (in 2018) have found that species of *Chromodoris* in the Indo-Pacific have some highly divergent color morphs in distinct geographical areas that likely represent patterns of local mimicry. Another recent study of Indo-Pacific *Hypselodoris* (Epstein *et al.* in press) has shown divergent color patterns with little local polymorphism and strong convergence in color patterns between species occurring sympatrically. The present study on *Glossodoris* and *Doriprismatica* shows that subtle, but consistent, color pattern differences can be useful in detecting pseudocryptic species. The importance of subtle but differing color patterns being good differentiators of recently diverged pseudocryptic species is similar to the findings of Hoover *et al*. (2015), Lindsay & Valdés (2016) and Uribe *et al*. (2017). Clearly, considerable variation in plasticity of color pattern exists in nudibranchs and the degree of polymorphism can be extremely limited or highly variable. The same can also be said for morphological variation of traditional characters such as radular morphology and anatomy of the reproductive system. In this study, there are strong examples such as characteristics of the radula, jaws and buccal secretory glands that clearly differentiate closely related species such as *Glossodoris buko* and *G. pallida*. The fact that these characters are more variable in some species and more consistent in others does not mean that they diminish in their taxonomic value. It simply means they should be examined more carefully to fully understand the range of variability and how this variation correlates with geographical and ecological factors. Further studies are needed to focus on the evolutionary drivers of this variation.

Lack of comparative material of *Glossodoris cincta* from the type locality hampers our ability to fully resolve the taxonomic status of some of the members of this species complex. This is especially true, given that differences in marginal bands of the mantle once thought to be an artifact of Bergh's original drawing of this species has now been confirmed by photographs of living animals from the Mascarene Islands (Bidgrain 2017, present study). Further study is needed to resolve these remaining issues within this species complex.

Nudibranchs in the family Chromodorididae are prime candidates for exploring cryptic species diversity. The newly described species that emerged from *Glossodoris* and *Doriprismatica*, a group that is widely recognized by recreational divers and coveted for natural products research, is yet another example of the likelihood that current biodiversity estimates are erroneously low. This is not solely for a lack of new exploration—a rising number of new, cryptic, and pseudocryptic species are being identified or confirmed from the vast collections housed in the world's museums (for example, Stiller *et al*. 2015; Brannoch & Svenson 2016; Lengger *et al*. 2016). The new, cryptic, and pseudocryptic nudibranch species described here are significant in systematic, evolution and chemical studies, and are an example of the need for integrative approaches in the pursuit of understanding the biodiversity and systematics of life on earth.

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