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A New Species of *Marionia* (Gastropoda: Nudibranchia) from the Caroline Islands

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A new species of tritoniid nudibranch is described from the western Caroline Islands. *Marionia bathycarolinensis* is known only from its type location of Palau. This animal exceeds 10 cm in length, is reddish in color and is the second record from the Indo-Pacific region of a tritoniid with more than 20 pairs of branchial plumes. Internally, it is distinguished from other Indo-Pacific tritoniids by jaws with masticatory borders composed of multiple rows of rodlets, a broad radula with elongate and distinctively shaped rachidian teeth, and a proportionally long esophagus. A muscular band carries approximately 50 chitinous plates arranged so their distal edges face the lumen of the stomach. Analysis of stomach contents shows that the holotype was feeding on octocorals of the genus *Paracis*. This is the first record of a nudibranch feeding on this genus. Placement of the new species in the genus *Marionia* is discussed in the light of taxonomic problems brought about by the treatment of the group by Odhner (1963).

The current state of knowledge of the tritoniid nudibranchs from the Indo-Pacific region leaves workers with a difficult set of taxonomic and nomenclatural problems to overcome as they attempt to sort out the relationships within this diverse family. Descriptions from the early 1800's through the mid 1900's lack consistency and are based primarily on external morphology, with only scattered references to important anatomical details. Subsequently, many species names have been synonomized, and other species have not been recorded since their original description. In some cases this may be due to the relative rarity of the taxa, in others the descriptions are insufficient to convince modern workers of their validity. Initial taxonomy was established by and expanded upon by Odhner (1936, 1963) but other workers still find difficulties with the most recent system (Willan 1988). Odhner proposed three plate bearing genera: *Marionia*, *Marioniopsis* and *Paratritonia*. His division was based primarily on characters of the digestive gland (liver), jaws and radula. *Marionia* was defined as having a digestive gland in two masses leaving the stomach uncovered, a jaw with 3 to 6 rows of fine denticles and a radula possessing tricuspid central teeth and differentiated first lateral teeth. *Marioniopsis* was defined by a digestive gland in a single mass covering the upper and left side of the stomach, jaws with a single row of strong denticles and a radula as in *Marionia*. In his 1963 key, Odhner defined *Paratritonia* as having a radula with unicuspidate central teeth and undifferentiated first laterals. This does not agree with the original description (Baba 1949), which stated that the first lateral teeth differ from the outer laterals. Baba also describes the jaw as having up to 10 rows of fine denticles, and a digestive gland in a single mass.

Odhner's classification scheme relies heavily on the morphology of the digestive gland, which he felt was of utmost importance in dividing the genera. This presents problems on more than one

level. Firstly, the progression of the nudibranch digestive gland from a compact single mass to a divided state and then to a diffuse distribution is on a continuum, is not composed of discrete steps, and appears in multiple lineages. Secondly, detailed dissections of numerous tritoniids by the senior author have not always yielded results in agreement with published descriptions (e.g., Odhner 1963). In addition, there have been descriptions of new animals (e.g., Willan 1988) that do not fit well into any of the current genera, including the present study. Accordingly, the authors feel that it is most prudent for all new species of plate-bearing tritoniids to be placed in the genus *Marionia,* which precedes the more controversial genera *Paratritonia* and *Marioniopsis.*

Nudibranchs of the family Tritoniidae are thus far known to feed exclusively on soft corals, sea pens, and gorgonians, but exact feeding patterns are unknown for many species (McDonald and Nybakken 1999). The gut contents of *Marionia bathycarolinensis* sp. nov. contained skeletal elements of an undescribed octocoral of the genus *Paracis* Kükenthal, 1919; Family Plexauridae Gray, 1859. This is the first record of a nudibranch feeding on this genus of octocoral.

Methods

Dissection was performed by a ventral incision through the length of the sole of the foot and around the genital and anal openings, allowing the removal of the entire visceral mass in one piece. The jaws and radula were freed from the buccal mass by partially dissolving tissues in 10% KOH solution. They were then rinsed in deionized water, air dried, mounted and coated for electron microscopy. Scanning electron micrographs (SEMs) were produced with a Hitachi S-520 or Leo 1450VP scanning electron microscope. Digestive contents were treated with undiluted household bleach to dissolve the tissue from the octocoral skeletal elements. After multiple rinses in water and 75% EtOH, sclerites and axial samples were mounted, dried and coated for electron microscopy. Slides of sclerites were also prepared for optical microscopy.

Species Description

Suborder Dendronotacea Odhner, 1934
Family Tritoniidae Lamarck, 1809

Genus *Marionia* Vayssière, 1877

Type species: *Marionia berghi* Vayssière, 1877

***Marionia bathycarolinensis* Smith and Gosliner, sp. nov.**
(Figs. 1–9)

Type material.— All material examined was collected by the Coral Reef Research Foundation (CRRF) and has been deposited at California Academy of Sciences Department of Invertebrate Zoology (CASIZ). Holotype: CASIZ 156081, one specimen collected at 191.4 m depth, on rock, Mutremdiu 3, Palau, Caroline Islands, 07°16.27′N, 134°34.37′E, 18 March, 2001, L.J. Bell aboard the Deep Worker Submarine, dissected. Paratype: CASIZ 156082, buccal mass only, remainder of body not sent, Mutremdiu 3, Palau, Caroline Islands, 07°16.27′N, 134°34.37′E, 25 March, 2001, P.L. Colin aboard the Deep Worker Submarine, 222.5 m depth, on rock, dissected.

External Anatomy.— The size of the living paratype specimen was approximately 118 mm in length. Only the buccal mass of this specimen was sent. The color of the living animal (Fig. 1a) is brick red, with scattered patches of lighter red and greenish-red on the notum. There are also small white flecks, patches, and short linear white markings on the body. The sheaths and shafts of

the rhinophores are brick red, with the apical portions a contrasting dark greenish-red color. The preserved holotype specimen is 155 mm in length, and 65 mm wide by 40 mm high in its largest section. The size of this animal alive was not recorded. The notum is a dull red color, with patches of a greenish tinge. The sides are of a more even red color. The foot, rhinophores and branchial plumes all have a greenish tinge. The body is elongate, subquadrilateral in cross section, with the largest section at about ⅔ of the way to the posterior end of the foot. The tapering posterior of the notum overhangs the posterior end of the foot by about 20 mm. The broad oral veil is slightly incised at midpoint and extends about 5 mm beyond the front of the body. There are 12 velar papillae on each side of the veil. The relatively short velar papillae are arranged in multifid groups, with blunt rounded apices. The grooved oral tentacles usually associated with the tritoniids are present but are not distinctly demarcated, instead being incorporated as the outer margins of the veil. The body is finely granular all over, except for the smooth sole of the foot, with some development of low rounded tubercles on the notum and sides. The broad foot is rounded anteriorly. From the narrowly overhanging margin of the notum are produced the rhinophores and branchial plumes. In the holotype, the rhinophoral shafts are completely retracted into widely spaced, 6 mm-long sheaths. The photograph of the living animal (Fig. 1a) shows a typical tritoniid arrangement, with a central clavus surrounded by a series of pinnate projections. The branchial plumes are relatively short, the largest being slightly greater in length than the extended rhinophores in the photograph. The anterior 8 or so plumes are discrete and easy to count, whereas the more posterior plumes tend to run together, making an exact count difficult. There are approximately 22 plumes per side, with the largest in the middle third of the body. The branchial plumes are divided into three or four main branches, which then subdivide one or two more times. The gonopore is located on the right side, at about midline below and between the 4th and 5th branchial plume. It has the three-valve appearance of some tri-

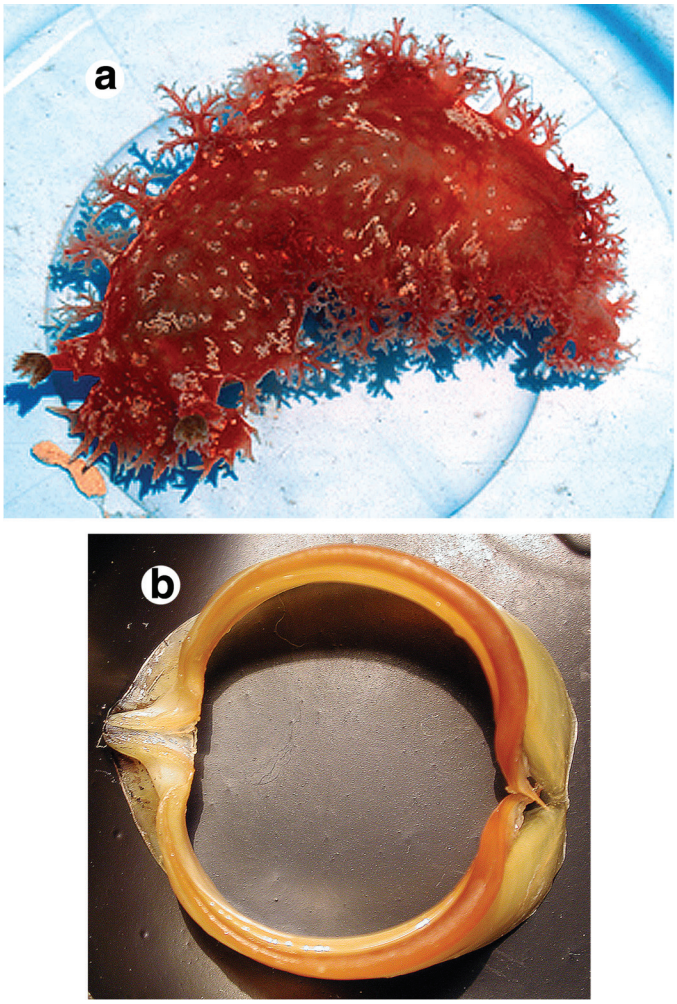

FIGURE 1. *Marionia bathycarolinensis* sp. nov., digital photographs. (a). Photo of living animal provided by CRRF. (b). Jaws of paratype, 35 mm in length.

toniids, and the tip of the penial papilla was visible. A floret of distended tissue surrounds the large opening of the anus, which is situated close to the notal margin below the 10th and 11th branchial plume on the right. The nephroproct opens between the 8th and 9th plume, just anterior to the anus.

DIGESTIVE SYSTEM.— The jaws are yellowish brown in color, with a darker, thickened reddish brown masticatory margin slightly overhanging the length of the base (Fig. 1b). The masticatory margin appears smooth to the naked eye, but scanning electron microscopy reveals the presence of 25 or more rows of jaw rodlets visible in approximately the distal 5 mm of the half jaw examined (Figs. 2–3). The jaw rodlets exhibit a complex ultrastructure, with multiple vertical elements encased in an outer layer showing horizontal sculpture. The radula of the paratype is large compared with other tritoniids, with a formula of 72 (142.1.1.142) at its broadest point (Figs. 4a-d, 5a–b). The base of the rachidian is roughly rectangular, and is wider than it is long. The upper margin of the base (as oriented in the figures) is incised in the shape of a 'V'. The central cusp arises as a sturdy wedge-shaped process oriented nearly 90º from the plane of the base. The top of the wedge flattens and forms a long, emarginate, blade-shaped triangular denticle. Behind the base of this denticle the top of the wedge forms two projecting ridges that follow the 'V' shape of the margin. The rows of teeth are arranged very closely together, so that the projecting wedge of the central cusp fits neatly into the 'V' shaped margin and ridges of the next tooth, with the apex of the flat blade extending over the top. At the base of each wedge-shaped ridge is a small, flattened, emarginate denticle, considered here as accessory. The two outer cusps of the rachidian are shorter than the median, and are formed from the thickened outer margins of the base. Their surface and that of the accessory denticles bears a pattern of folds or ridges resembling the veins on a leaf. The

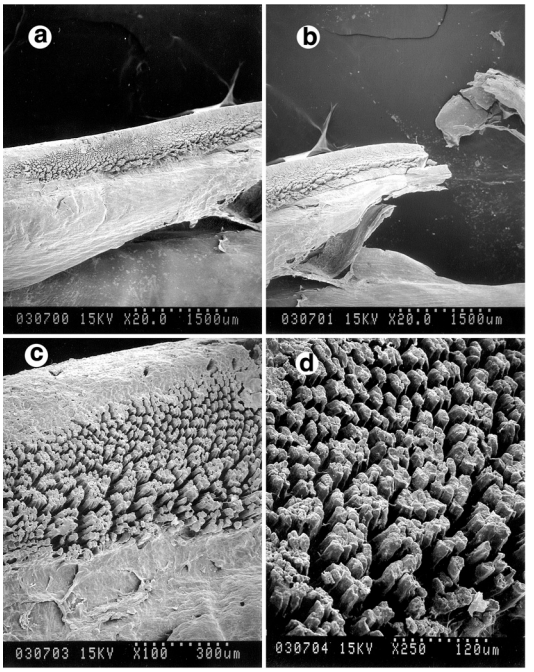

FIGURE 2. SEMs of jaw of paratype. (a). Proximal portion of masticatory border showing eruption of jaw rodlets. (b). Distal portion of masticatory border, showing part of overhang broken off in preparation. (c). Higher magnification view of proximal masticatory border. (d). Close up of rodlets in proximal masticatory border.

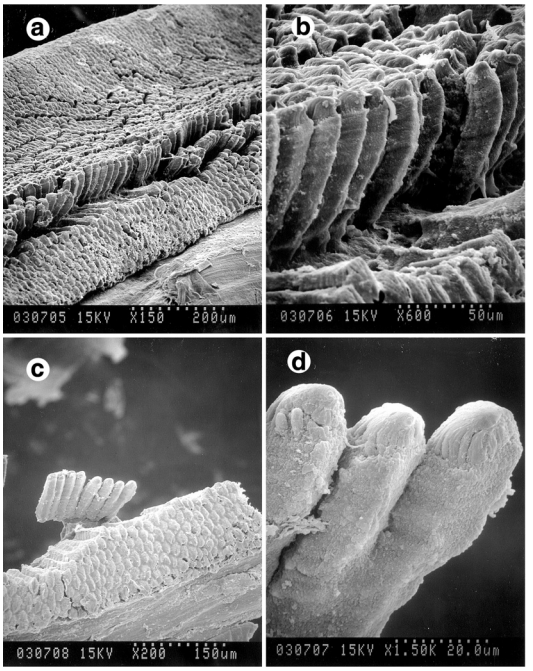

FIGURE 3. SEMs of jaw of paratype. (a). View of rodlets near distal end of masticatory border. (b). Detail of rodlets from same area. (c). View of rodlets at distal end of masticatory border. (d). Detail of rodlets seen in Figure 3c.

first lateral teeth are differentiated from the remaining laterals, being more heavily constructed with a short, hooked, chisel-shaped denticle fitting closely with the edges of the outer cusps of the rachidian. The remaining laterals are straight to slightly curved, and relatively broad and stout (Figs. 5 a–b). A pair of floccose salivary glands extended backwards from the proximal portion of the buccal mass, with attachments to the buccal mass on either side of the esophagus. The preserved salivary glands exhibit a greenish coloration. The esophagus extends about 8 cm from the median posterior buccal mass as a long straight tube, widening into a distended sac-like portion before turning and entering the stomach on the ventral side (Fig. 5c). A large bolus of gorgonian food material was present in the proximal esophagus, and will be described and discussed in a later section. The stomach is relatively small, 2 cm in diameter, with a muscular girdle visible in the proximal portion (Fig. 5c). Inside the stomach are approximately 50 stout, dark brown plates arranged so that the bases are attached to the muscular girdle and the plates point to the lumen of the stomach (Figs. 6a–b). The plates are roughly rectangular, with the exposed corners rounded, and most are about 7 mm long by 3mm high. A pair of larger, thicker and higher plates surrounds the typhlosole that continues through the stomach from the esophagus and into the intestine. There are also some thinner plates and some plates that are only 4 mm long interspersed in no discernable pattern. The intestine (Fig. 5c) exits the stomach from the anterior left portion, curving up and around the anterior portion of the digestive gland towards the right, becoming wider for a portion before narrowing again to terminate at the anus. The compact digestive gland is divided into two lobes, each with a duct leading into the stomach. The large, spheroid posterior portion has an anterior hollow that fits around the posterior stomach, leaving the top exposed. The smaller anterior

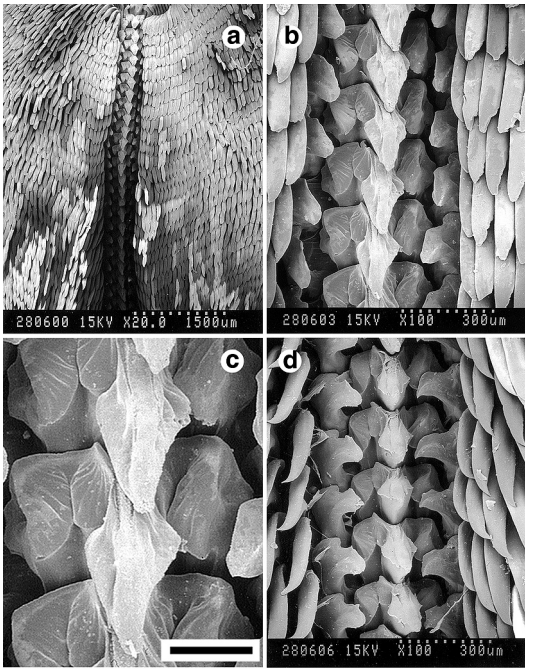

FIGURE 4. SEMs of radula of paratype. (a). Low magnification view of radula, older portion. (b). Rachidian teeth, first and inner lateral teeth at older portion. (c). Detailed view of rachidian at area shown in Figure 4b. Scale bar = 300 µm. (d). Rachidian teeth, first and inner lateral teeth at newer portion.

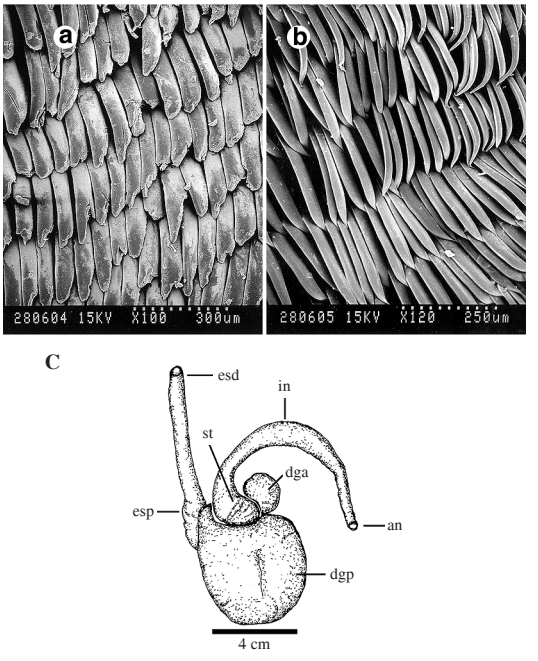

FIGURE 5. SEMs from paratype, drawing from holotype. (a). Middle latteral teeth from older portion of radula. (b). Outer laterals from newer portion of radula. (c). Visceral mass (from holotype). an = anus; dga = anterior digestive gland; dgp = posterior digestive gland; esd = distal esophagus; esp = proximal esophagus; in = intestine; st = stomach.

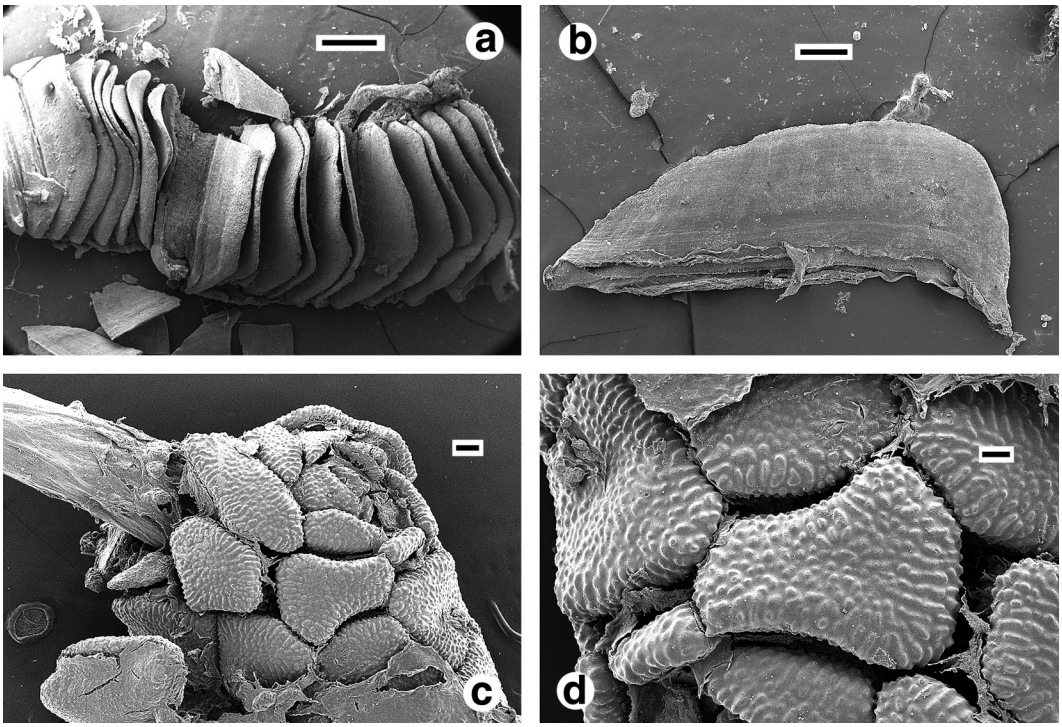

FIGURE 6. SEMs from holotype. (a). Portion of band of stomach plates, showing typhlosole area. Scale = 1 mm. (b). Isolated plate. Scale = 400 µm. (c). Portion of gut contents, showing overview of characteristic plates and 'woody' stem. Scale = 200 µm. (d). Closer view of plates. Scale = 100 µm.

lobe abuts the right anterior portion of the stomach, and is loosely connected to the posterior digestive gland (Fig. 5c).

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic. The diffuse ovotestis covers much of the surface of the digestive glands. A narrow hermaphroditic duct connects to the narrow end of the ampulla (Fig. 7a). The ampulla is muscular and convoluted, its wide end encased within the compact female gland mass. The smaller albumen gland is easily discernable from the larger membrane and mucos glands. The proximal vas deferens emerges from the female gland mass as a thin, relatively straight tube for about 10 mm, becoming thickened and sinuous in its median portion. The distal portion then extends, thinning slightly before entering the base of the conical unarmed penis, lying near the gonopore. The muscular bursa copulatrix is an inflated oval 18 mm long. The vaginal duct is approximately equal to the bursa in length, widening at the vaginal atrium. The oviduct exits the female gland mass and opens to the vaginal atrium.

NERVOUS SYSTEM.— The ganglia of the central nervous system sit on the dorsal esophagus, just behind the buccal mass (Fig. 7c). A thin transparent membrane not apparent in dissections of other tritoniids covers the ganglia and large nerves. The paired cerebral and pleural ganglia are distinct but somewhat fused, and the pairs are joined by a short connective. The pedal ganglia are on either side of the cerebropleurals, joined to them by short connectives, and to each other by the circum-esophageal nerve ring, which also contains commisures joining the cerebropleurals. A pair of buccal ganglia is present on the ventral esophagus, just anterior to the nerve ring. These are joined by a short connective (Fig 7c). The central nervous system and buccal ganglia are distinctly asym-

metrical and 'lumpy' in appearance, with irregular nodules and distinct giant nerve cells scattered about. The darkly pigmented eyes are small, connected to the central nervous system by long nerves.

Gut Contents.— The contents of the digestive system contained both free sclerites and large pieces consisting of a "woody" appearing axis which is covered by distinctive large plates (Figs. 6c–d; 8a–d; 9a–b). The exposed sides of the plates have a pearly appearance, the bumpy surface giving the impression of sclerites immersed in a smooth nacreous coating. There is a distinct transition between the smooth exposed side and the rougher surface of the attached side. A crack in the membrane of the attached side shows a few sclerite-like objects imbedded in a matrix. Although it is not possible to know with any certainty the origin or exact identity of the octocoral from which the free sclerites were derived, the larger pieces are consistent with the genus *Paracis* Kükenthal, 1919, Family Plexauridae Gray, 1859 and appear to belong to an undetermined species (G.C. Williams, pers. commun.). Further references to octocoral information and biology can be found in Smith and Gosliner (2003).

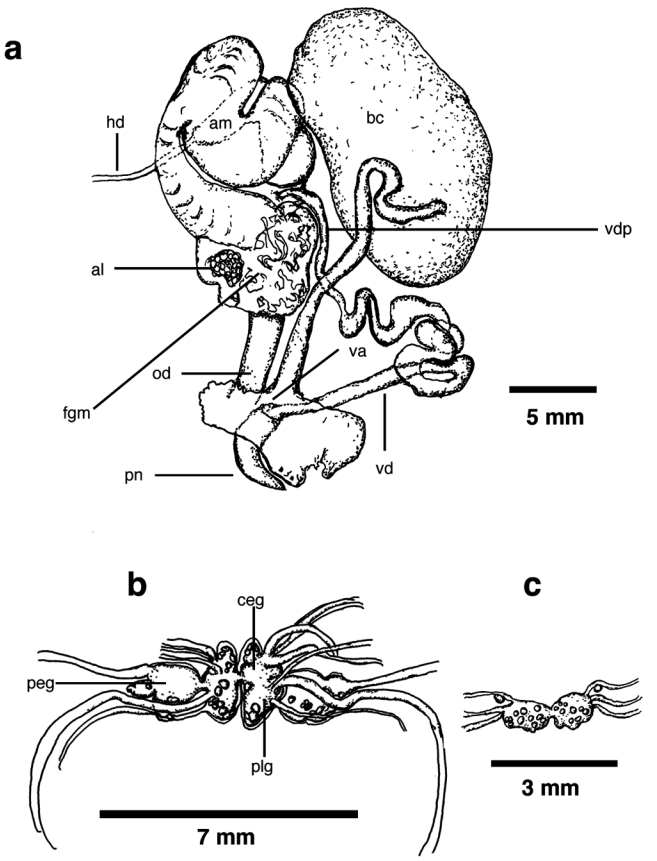

Figure 7. Drawings from holotype. (a). Reproductive system. Al = albumin gland; am = ampulla; bc = bursa copulatrix; fgm = female gland mass; hd = hermaphroditic duct; od = oviduct; pn = penis; va = vaginal atrium; vd = distal portion of vas deferens; vdp = proximal portion of vas deferens. (b). Central nervous system. ceg = cerebral ganglia; peg = pedal ganglia; plg = pleural ganglia. (c) Buccal ganglia. Scale bars as indicated.

Distribution.— *Marionia bathycarolinensis* sp. nov. is known only from the type locality of Palau, in the Caroline Islands.

Etymology.— The first part of the specific name is derived from the Greek, *bathys* (deep); the latter part refers to the type locality in the western-most fringe of the Caroline Islands.

Discussion

In two recent papers (Avila et al. 1999; Jensen 1994), the anatomical and morphological characters of plate-bearing tritoniids have been tabulated. Avila et al. compared characteristics of species of the genus *Marioniopsis*, and included eight other species along with their newly described species. Jensen compared anatomical characters of species of *Marionia* and *Marioniopsis,* listing 17 species plus her newly described species. The combined species discussed

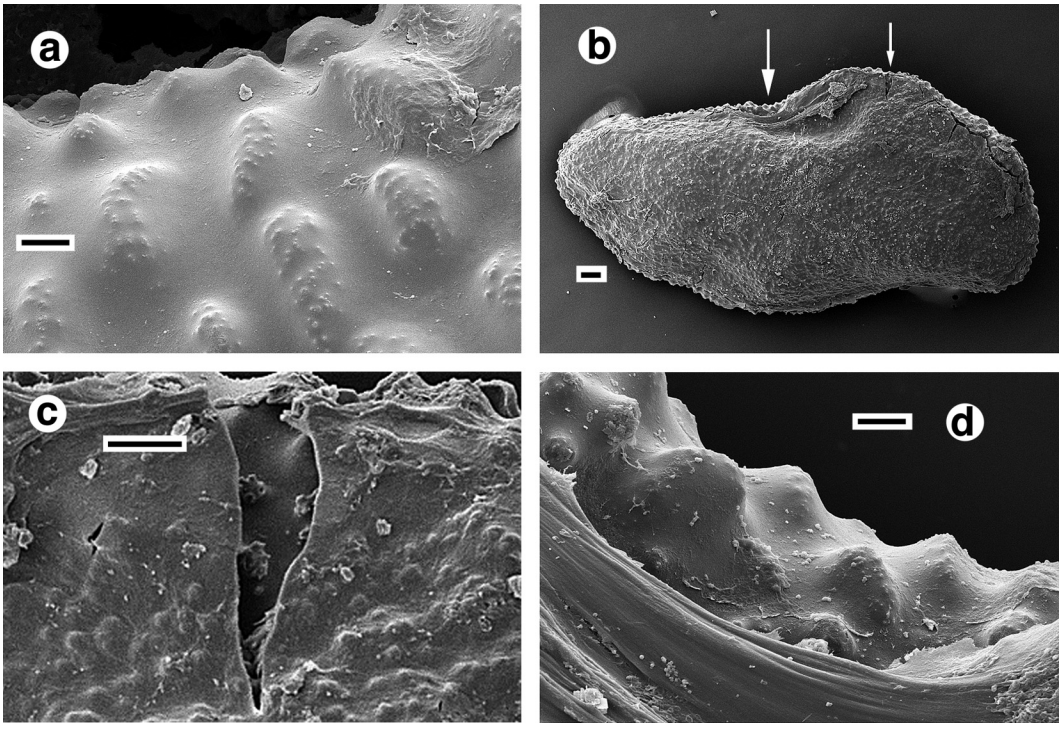

FIGURE 8. Detailed view of detached octocoral plate. (a). Close up view of exposed (front) side. Scale bar = 20 µm (b). A single detached plate, viewed from the attachment (back) side. Scale bar = 100 µm. Small arrow indicates area detailed in 8c, large arrow indicates area detailed in 8d. (c). Detailed view of area indicated by smaller arrow in 8b. Scale bar = 100 µm. (d). Detailed view of area indicated by larger arrow in 8b. Scale bar = 20 µm.

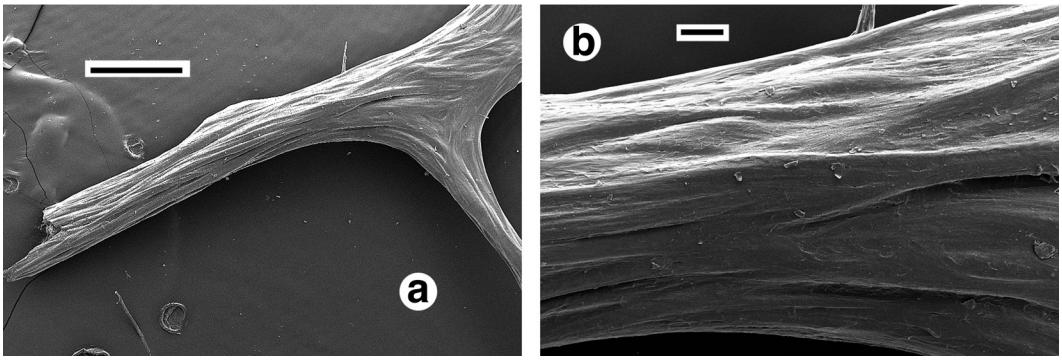

FIGURE 9. A Portion of the 'woody' axis of the octocoral. (a). Scale bar = 1 mm. (b). Scale bar = 100 µm.

in both papers are summarized in Table 1, along with *Paratritonia lutea* Baba, 1949, and *Marionia bathycarolinensis* sp. nov.

There are two external characters that differentiate all other plate-bearing tritoniids from *Marionia bathycarolinensis* sp. nov.: the number of branchial plumes and the number of velar papillae. *Marionia bathycarolinensis* sp. nov. has 22 pairs of branchial plumes and 12 pairs of compound velar papillae. All other species listed have 16 or fewer branchial plumes, with the excep-

TABLE 1. Comparison of Indo-Pacific species of the genus *Marionia*

Species	*Branchial plumes*	*Velar papillae*	*Jaws*	*½ row of radula teeth*	*Stomach plates*
M. albotuberculata	9 pairs	5 pairs, some compound	1 row of teeth, trace of second	95	>100
M. babai	7 pairs	6 pairs, compound	> 100 teeth, number of rows not stated	25	present
M. blainvillea	10–12 pairs	7 pairs	2–4 rows of teeth	15–21	ca 40
M. chloanthes	9+ pairs	4 pairs, some compound	5–6 rows of teeth	22	70
M. cucullata	12–16 pairs	7–11 pairs	6 rows of teeth	58	30–40
M. cyanobranchiata	9–13 pairs	4–7 pairs, simple	1 row of teeth, trace of second	15–50	100–120
M. dakini	13 pairs	6–7 pairs, compound	1 row of 45 teeth	135	present
M. echinomuriceae	10–14 pairs	6–8 pairs	1 row of teeth, indistinct	65	28
M. fulvicola	7–9 pairs	3–4 pairs, most simple	4–5 rows,>100 teeth	38–42	22–32
M. granularis	13–14 pairs	6 pairs	unknown	50	present
M. levis	9–10 pairs	3–5 pairs, compound	1–3 rows, 14-30 teeth	80–130	ca 150
M. pambanensis	12 pairs	6 pairs	unknown	43	present
M. pellucida	13 pairs	6 pairs	unknown	22	70
M. platyctena	100 pairs	5–7 pairs, simple	10 rows of teeth	71–103	30–35
M. putulasa	15 pairs	6 pairs	unknown	112	25
M. rubra	10–12 pairs	6 pairs, compound	1 row of 100-120 teeth	50–55	present
M. tessellata	13 pairs	7 pairs	3 rows of teeth	unknown	present
M. bathycarolinensis	22 pairs	12 pairs, compound	25–100 rows of rodlets	142	50
M. viridescens	10 pairs	7 pairs, some compound	single row of teeth	90	25
M. olivacea	9–15 pairs	7 pairs, some compound	3–7 row of teeth	70–80	50–60
Paratritonia lutea	6–7 pairs	3–4 pairs	3–10 rows of teeth	110	25

tion of *M. platyctena*, which has 100. However, this animal is recorded as having a jaw with 10 rows of teeth, a velum with 5–7 pairs of simple papillae, a radular half-row of up to 103 lateral teeth and a maximum of 35 stomach plates. This is in contrast with *M. bathycarolinensis* sp. nov., which has a jaw armed with rodlets, a velum with 12 pairs of compound papillae, a radula with a half-row of 143 lateral teeth, and 50 stomach plates. Only *M. cucullata* (which may be a synonym for *M. blainvillea)* has a recorded number of velar papillae approaching that of the new species. However, *M. cucullata* does not match our new species in any of the other characters discussed, differing in the number of branchial plumes, jaw morphology, radular formula and number of stomach plates.

Internally, the principal apomorphy of *Marionia bathycarolinensis* sp. nov. is a jaw armed with

multiple rows of rodlets. This type of denticulation has not been recorded for any other species of tritoniid nudibranch.

The basic form of the tritoniid radula is, with few exceptions, consistent throughout the genera, consisting of a tricuspid central tooth flanked by a pair of first lateral teeth differentiated from the remaining curved outer laterals. The species described here does not differ from the basic form, but is distinctive in the appearance of the central tooth. The median cusp is elongate, overlapping the next row when the radula is contracted. The leaf-like shape of this flattened central cusp has not been recorded for any other species of tritoniid.

The remaining distinguishing characters are more general: large size and a relatively compact visceral mass with an elongate esophagus. Body lengths of over 10 cm are at the large end of the tritoniid size continuum, mostly occurring in temperate species without stomach plates. Both specimens described here are of this large size. Figure 5b illustrates the long straight esophagus and relatively compact visceral mass, which contrasts with published drawings of other tritoniids (Odhner 1936) and the personal observations of the present authors.

Acknowledgements

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