

Bayerotrochus belauensis, a new species of pleurotomariid from the Palau Islands, western Pacific (Gastropoda: Pleurotomariidae)

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ABSTRACT

A new pleurotomariid species, *Bayerotrochus belauensis* new species, collected from the Palau Islands, western Pacific, is described and illustrated. This new species is most similar in shell morphology to *B. teramachii* (Kuroda, 1955), from which it may be distinguished by its thinner, lighter shell with a taller, more stepped spire and lack of pronounced spiral sculpture along the shell base. Molecular data (COI) show *B. belauensis* new species to be more closely related to *B. boucheti* from New Caledonia and *B. delicatus* from Yap, than to *B. teramachii*. *Bayerotrochus boucheti* (Anseeuw and Poppe, 2001) differs in having a broader, more conical spire, a more depressed aperture, and a more darkly pigmented shell with spiral sculpture on the shell base. The recently described *B. delicatus* S.-P. Zhang, S.Q. Zhang, and Wei, 2016 is easily distinguished by its much smaller size and distinctive shell profile.

Additional Keywords: Slit shell, COI, phylogeny, ecology.

INTRODUCTION

Bayerotrochus Harasewych, 2002 is the most widely distributed of the Recent pleurotomariid genera. It includes 12 living species, two inhabiting bathyal depths of the temperate and tropical western Atlantic, and ten from similar depths along the margins of the Indian and western Pacific Oceans. Ongoing sampling of deep-sea biota using dredges and trawls, as well as manned and remotely operated research submersibles, in addition to analyses of relationships among samples using molecular techniques, continue to expand and refine our knowledge and understanding of the biodiversity and biogeography of the deep oceans and their faunas.

Two samples of living *Bayerotrochus* were first observed and collected off Palau at depths around 200 m by the Japanese research submersible HAKUYO in

October of 1996 (Okutani and Kurata, 1998). They were provisionally identified as *Perotrochus africanus teramachii* (Kuroda, 1955) based on shell morphology. During subsequent explorations at similar depths in Palau in 2001 using the research submersible DEEPWORKER 2000, Coral Reef Research Foundation (CRRF) was able to observe, photograph, and collect additional specimens of that species of *Bayerotrochus*. Shells and tissues of several of these samples were deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). Most recently, Zhang et al. (2016) described *Bayerotrochus delicatus* from Yap Seamount (8°51' N, 137°47' E), SE of Yap near Nguluu Atoll, collected at slightly greater depths (255–289 m). A phylogenetic analysis based on partial COI sequence data that was included in their description showed that *B. delicatus* was more closely related to one of the specimens from Palau (USNM 905395) than to *B. teramachii*.

These results prompted our re-examination of the Palau specimens, which were compared morphologically against all species of *Bayerotrochus* known from the Indian and Pacific Oceans. Results of these morphological comparisons as well as a phylogenetic analysis of COI sequences derived from three of the Palau specimens and additional *Bayerotrochus* sequences, both published and previously unpublished, indicate that the Palau samples differ from all other species of *Bayerotrochus*, and are here described as a new species.

MATERIALS AND METHODS

Radular Morphology: The radula was dissected from the alcohol-preserved holotype, cleaned in 10% NaOH overnight, rinsed in distilled water, cleaned in an ultrasonic cleaner, air dried, coated with gold, and photographed using a Leica StereoScan 440 Scanning Electron Microscope.

Molecular Procedures: Genomic DNA was extracted from alcohol-preserved tissue samples (c. 25 mg buccal muscle) using the DNeasy Tissue Kit (Qiagen) following

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the manufacturer's animal tissue protocol. A 658 bp portion of the cytochrome c oxidase I gene was amplified using the primers of Folmer et al. (1994). PCR amplifications used the Promega GoTaq hot start master mix (Promega M7132) according to manufacturer's instructions, but modified to reduce the reaction volume to 20 μ L. Cycling parameters: initial denaturation at 95°C for 3 minutes, followed by 45 cycles of denaturation at 94 °C for 30 seconds, annealing at 45°C for 45 seconds and extension at 72 °C for 2 minutes, with final extension at 72°C for 5 minutes. Resulting PCR products were visualized by agarose gel electrophoresis (1.5% garose) and purified with ExoSAP-IT (Affymetrix). Sequencing reactions were performed using 1 μ L of purified PCR product in a 10 μ L reaction containing 0.5 μ L primer, 1.75 μ L Big Dye buffer and 0.5 μ L Fig Dye (Life Technologies). Reactions were run for 30 cycles of 95°C for 30 seconds 50°C for 30 seconds and 60°C for 4 minutes then held at 12°C. Reactions were purified using Millipore Sephadex plates and sequenced on an ABI 3730XL automated DNA analyzer. Sequencher v. 4.7 (Gene Codes) was used to visualize, trim and assemble contigs from forward and reverse sequences. The sequences have been deposited in GenBank (NCBI). Accession numbers are provided in Table 1.

The COI sequences were aligned using MUSCLE within Geneious (v. 9.1.6; <http://www.geneious.com>, Kearse et al., 2012) and trimmed to the 658 bp region

flanked by the Folmer primers. The phylogenetic tree (Figure 28) was produced using the RAxML 7.2.8 (GTR Gamma nucleotide model) plugin in Geneious 9.1.6. Institutional acronyms are listed on Table 1.

SYSTEMATICS

Class Gastropoda Cuvier, 1795

Order Vetigastropoda Salvini-Plawen, 1980

Family Pleurotomariidae Swainson, 1840

Genus *Bayerotrochus* Harasewych, 2002

Type Species: *Perotrochus midas* Bayer, 1965, by original designation.

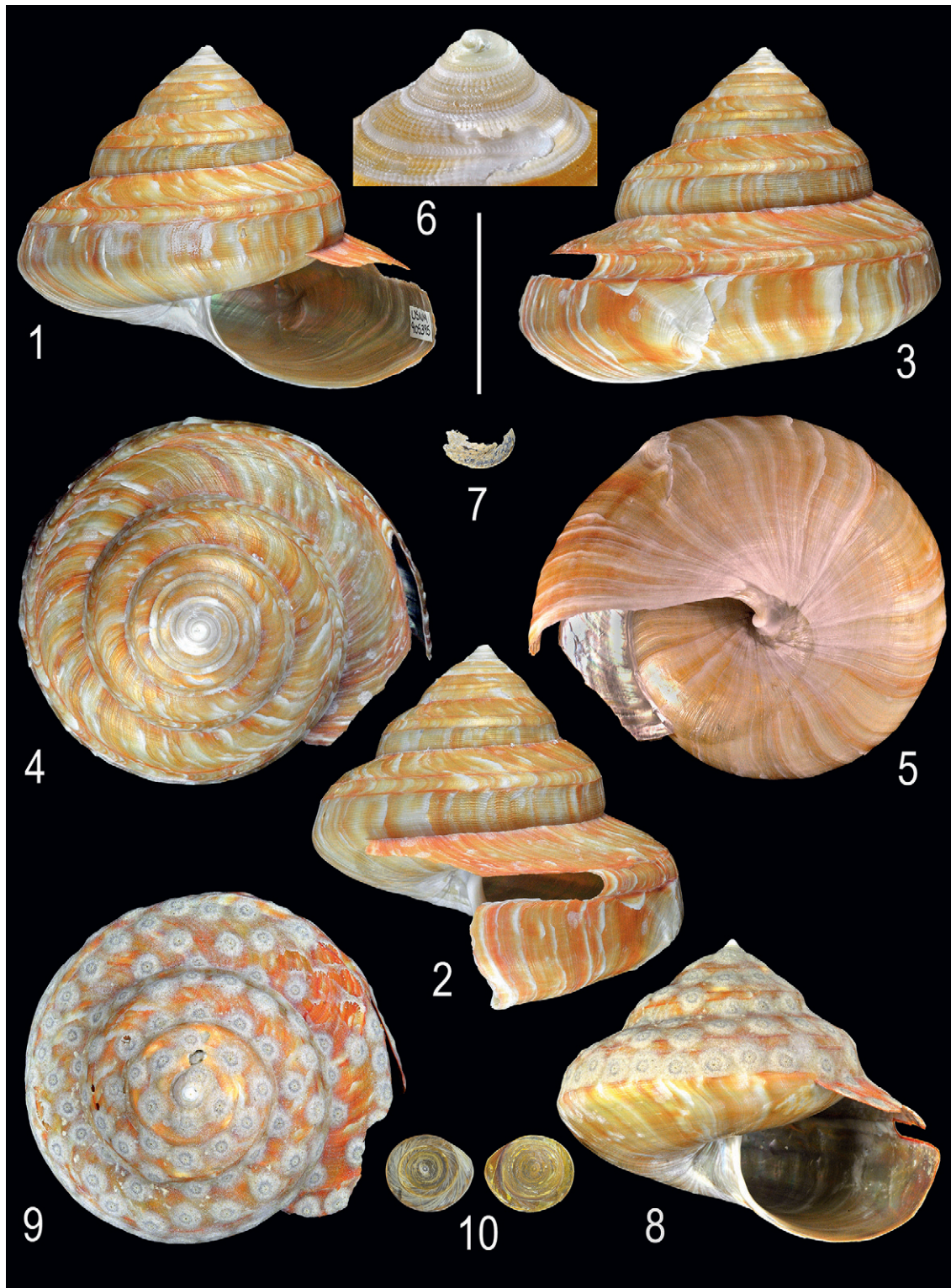
Description: Shell large, thin, turbiniform, lacking an umbilicus, with inflated, rounded whorls. Slit, broad, short (<90°), forming a selenizone slightly below mid whorl. Outer prismatic layer of shell thin, translucent, sculpture usually limited to spiral threads or weak cords and axial riblets that may produce weakly reticulate sculpture on early whorls. Aperture large, ovate. Operculum small relative to aperture.

Remarks: *Bayerotrochus* is easily distinguished from *Entemnotrochus*, which is characterized by having a large, conical shell with a narrow, long (>120°) slit and a deep

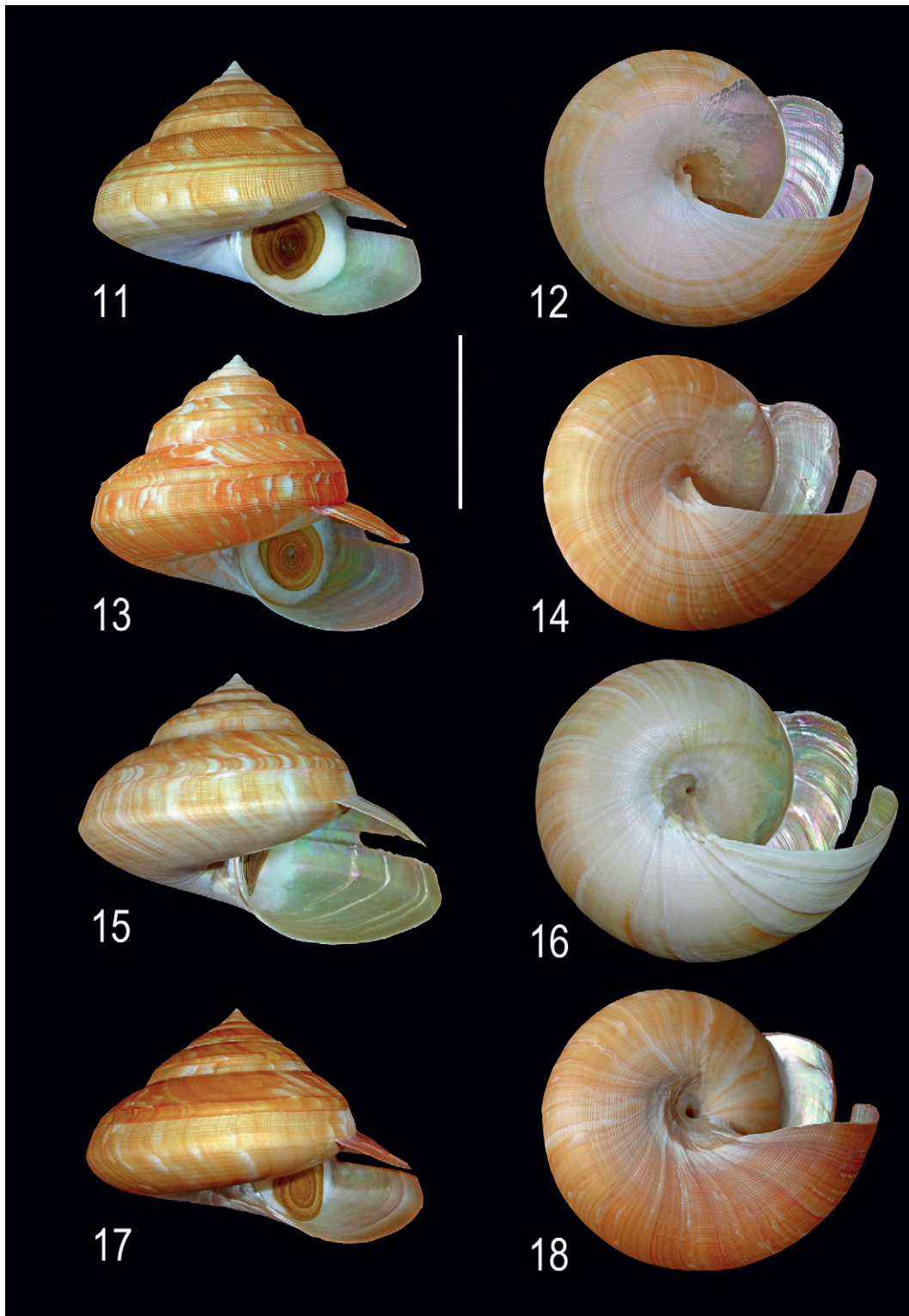
Table 1. Sources for the cytochrome c oxidase I sequence data used to produce the phylogenetic tree in Figure 28.

Taxon	Locality	Voucher	Genbank No.	Reference
<i>Calliostoma torrei</i>	Jacksonville, FL, USA	USNM 1069300	DQ 314293	Harasewych and Sedberry, 2006
<i>Lischkeia imperialis</i>	Guadeloupe	USNM875107	KY426958	This study
<i>Entemnotrochus rumphii</i>	Amami-O-Shima, Japan	USNM888698	L78911	Harasewych et al., 1997
<i>Entemnotrochus adansonianus</i>	Marathon, FL, USA	USNM 1089839	KY432515	This study
<i>Entemnotrochus adansonianus</i>	SW Navassa Is., Haiti	USNM 878151	KY432516	This study
<i>Entemnotrochus adansonianus</i>	Curaçao	USNM 1297226	KY432517	This study
<i>Perotrochus quoyanus</i>	Dominica	USNM 1410044	KY432518	This study
<i>Perotrochus amabilis</i>	Marathon, FL, USA	USNM1080832	KY432519	This study
<i>Perotrochus gotoi</i>	Amami-O-Shima, Japan	Not available	KY432520	This study
<i>Perotrochus caledonicus</i>	New Caledonia	MNHN-IM-2007-36301	KR087190	Anseeuw et al., 2015
<i>Perotrochus deforgesii</i>	Chesterfield Plateau	MNHN-IM-2007-32061	KR087208	Anseeuw et al., 2015
<i>Mikadotrochus beyrichi</i>	Boso Peninsula, Japan	Not available	AM049331	Williams and Ozawa, 2006
<i>Mikadotrochus beyrichi</i>	Boso Peninsula, Japan	Not available	EU530109	Williams et al., 2008
<i>Bayerotrochus midas</i>	Altamaha, Georgia, USA	USNM 1069299	KY432521	This study
<i>Bayerotrochus midas</i>	Great Inagua, Bahamas	USNM 1072411	KY432522	This study
<i>Bayerotrochus midas</i>	Roatan Is., Honduras	USNM 1155020	KY432523	This study
<i>Bayerotrochus teramachii</i>	Okinawa, Japan	Not available	AM049330	Williams and Ozawa, 2006
<i>Bayerotrochus teramachii</i>	Kagoshima, Japan	USNM 869646	KY432524	This study
<i>Bayerotrochus delicatus</i>	SE of Yap, Micronesia	MBM283051	KU759008	Zhang et al., 2016
<i>Bayerotrochus boucheti</i>	New Caledonia	MNHN-IM-2009-7484	KU693173	Anseeuw, 2016
<i>Bayerotrochus boucheti</i>	Chesterfield Plateau	MNHN-IM-2007-34676	KU693174	Anseeuw, 2016
<i>Bayerotrochus boucheti</i>	New Caledonia	MNHN, sta. DW2031	KY432525	This study
<i>Bayerotrochus belauensis</i> HT	N Turtle Cove, Palau	USNM 905395	KY432526	This study
<i>Bayerotrochus belauensis</i>	Mutremdiu 2, Palau	USNM 905393	KY432528	This study
<i>Bayerotrochus belauensis</i>	Mutremdiu 3, Palau	USNM 905397	KY432527	This study

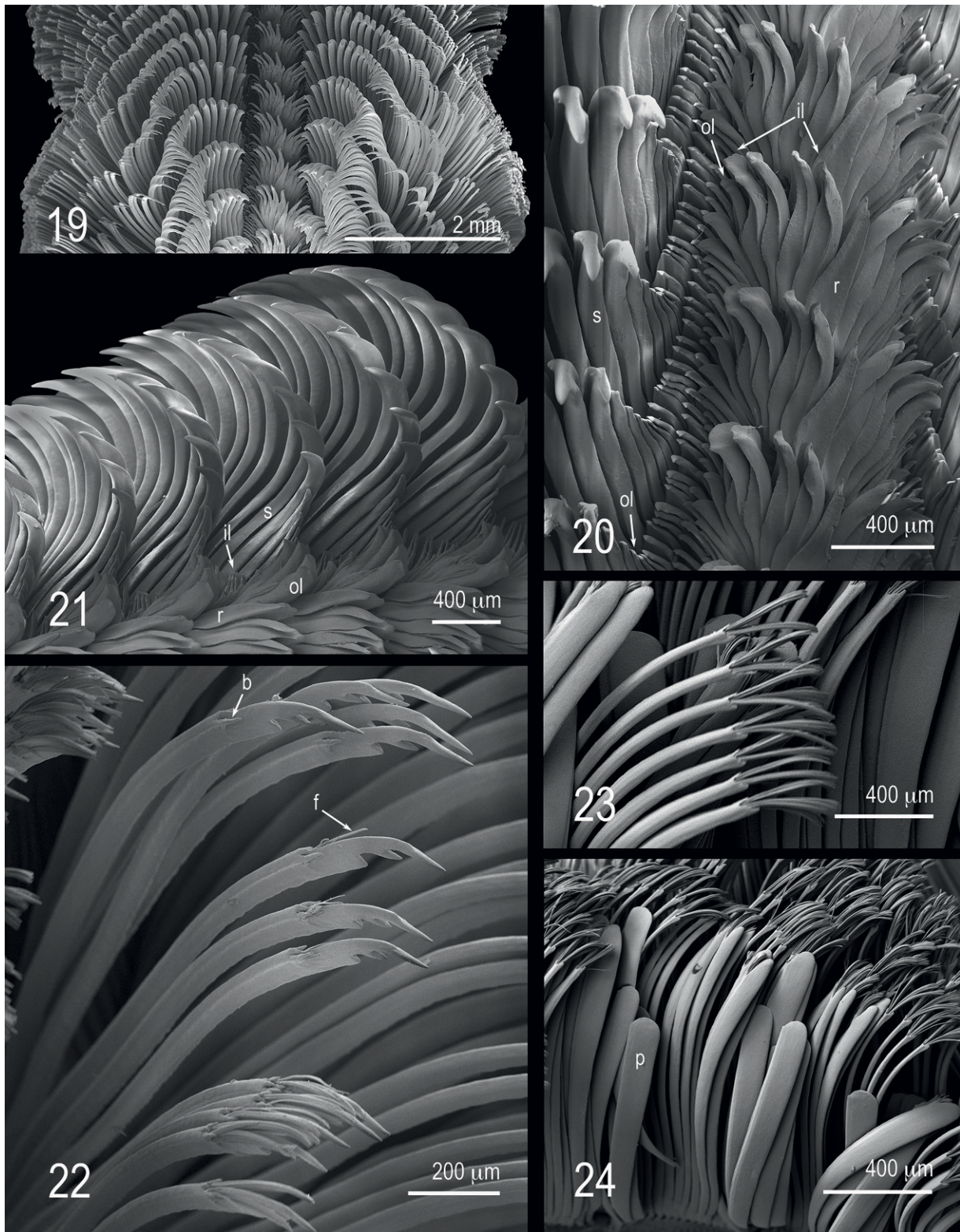
Institutional acronyms: MBM, Marine Biology Museum, Chinese Academy of Sciences, Qingdao; MNHN, Museum national d'Histoire naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington



Figures 1–10. *Bayerotrochus belauensis* new species. **1.** Apertural, **2.** lateral, **3.** dorsal, **4.** apical, and **5.** basal views of holotype (USNM 905395). Palau Islands, North Turtle Cove, 219 m, 26 March 2001. **6.** Detail of early whorls. **7.** Outer surface of damaged operculum of holotype. **8.** Apertural and **9.** apical views of Paratype 1 (USNM 905397). Palau Islands, Mutremdiu 3, in 236 m, March 24, 2001. **10.** Outer and inner surfaces of the operculum of Paratype 1. Scale bar = 5 cm for all shells and opercula, 1 cm for figure 6.



Figures 11–18. Apertural and basal views of: **11–12.** *Bayerotrochus teramachii*, S.W. of Makurazaki, Kagoshima, Japan trawled 350 m, **13–14.** *B. cf. teramachii*, off Panglao, Bohol, Philippines, by native fishermen using tangle nets set at 100 m., **15–16.** *B. westralis*, Rowley Shoals, N.W. Australia, Timor Sea, by shrimp trawler in 580 m. **17–18.** *B. boucheti*, S.E. New Caledonia, trawled in 550 m. Scale bar = 5 cm for all specimens. All specimens in Anseeuw Collection.



Figures 19–24. Radula of holotype of *Bayerotrochus belauensis*, new species. **19.** Extended radula. **20.** Rachidian, inner lateral and outer lateral teeth. Teeth to the left of the rachidian are further anterior than their homologues to the right. **21.** Sickle teeth. **22.** Transition from sickle teeth to filament-tipped teeth marked by onset of bristles. **23.** Detail of distal ends of filament-tipped teeth near the outer margin of the radula. **24.** Paddle-shaped teeth, showing transition from filament-tipped teeth. Abbreviations: **b**, bristle; **f**, filament; **il**, inner lateral teeth; **ol**, outer lateral teeth; **p**, paddle-shaped teeth; **r**, rachidian; **s**, sickle teeth.

umbilicus. It may be distinguished from *Perotrochus* and *Mikadotrochus* by its larger, thinner, more rounded shell. Sequence data from several genes (18S and COI) also readily distinguish among the genera of living Pleurotomariidae (e.g., Harasewych, 2002: 269; Zhang et al., 2016: 258).

***Bayerotrochus belauensis* new species**

(Figures 1–10, 19–27)

Perotrochus africanus teramachii: Okutani and Kurata, 1998: 11, figs. 2, 3. (not of Kuroda, 1955)

Description: Shell (Figures 1–6, 8, 9) large for genus (to 114.6 mm diameter), thin, turbiniform, with conical spire and rounded base, non-umbilicate, consisting of 8+ whorls. Spire coeloconoid (spire angle=87°–99°), with shoulder increasingly pronounced after fifth whorl. Protoconch unknown. Selenizone narrow, situated at mid-whorl in early whorls, becoming broader, descending to just below the shoulder by fifth whorl. Axial sculpture of prosocyrts riblets on early whorls (Figure 6) that form beads at intersections with spiral cords above and below selenizone. Ribs, cords, and beads become reduced above the selenizone by fourth teleoconch whorl. Spiral cords below selenizone remain more pronounced, with 14–16 weak cords persisting onto the last whorl between the selenizone and shell periphery. Selenizone with opisthocyrts ribs on early whorls that transform to spiral cords by fourth whorl and subsequently decrease in prominence. Selenizone on last whorl with coarse, prosocyrts growth striae. Slit broad (to 7.5 mm), short (75°–79° between limit of suture and rear of slit). Suture adpressed. Basal disc strongly and evenly convex, with sigmoidal growth striae more pronounced than weak spiral threads (Figure 5).

Aperture broadly elliptical (w/h=1.3–1.5), deflected from coiling axis by ~81°–85°. Outer lip thin, smooth, portion below slit offset from portion above slit by 36°–51°. Columella spirally coiled, with sigmoidal flexure near the adapical margin. Aperture nacreous, columella porcellaneous. Base color of prismatic layer of shell exterior white, with broad, irregular axial bands of light-orange tan and narrower bands of darker reddish-orange. Shell may appear lustrous to varying degrees, depending on thickness / translucence of the prismatic layer. Operculum (Figure 10) amber-colored, multispiral, corneous, small (spanning 0.5 of minor axis of aperture).

Radula: Radula (Figures 19–24) of holotype (shell=114.6 mm maximum diameter) 97.7 mm long, 6.7 mm wide, asymmetrical, left-skewed, bifid posteriorly, composed of 148 inverted V-shaped teeth rows. Following Hickman's (1984) terminology, each row consists of a single rachidian tooth, 4 inner lateral, 30 outer lateral, 13 sickle, ~58 filament-tipped, and 8–9 paddle-shaped teeth. Transitions between adjacent tooth types are gradual, and may span 2–6 teeth. Tooth morphologies

are similar to those of other species of *Bayerotrochus* and *Perotrochus*.

Type Locality: Palau Islands, Peleliu State, North Turtle Cove, 07°05.12 N, 134°15.61 E, 219 m.

Type Material: Holotype, USNM 905395 (shell and preserved animal) from the type locality, collected 26 March 2001 by Patrick L. Colin; Paratype 1, USNM 905397 (shell and preserved animal), Palau Islands, Koror State, Mutremdiu 3, Uchelbeluu Reef, 07° 16.27 N, 134°31.37 E, in 236 m, collected 24 March 2001 by Patrick L. Colin; Paratype 2 USNM 905396 (preserved animal only), shell in the Patrick Anseeuw Collection, Palau Islands, Koror State, Mutremdiu 3, Uchelbeluu Reef, 07°16.27 N, 134°31.37 E, in 232 m, collected 21 March 2001 by Patrick L. Colin; Paratype 3, USNM 905393 (preserved animal only), shell in the Etpison Museum, Palau Islands, Koror State, Mutremdiu 2, Uchelbeluu Reef, 07°16.41 N, 134°31.43 E, 212 m, collected 12 March 2001, by M.N. Dawson.

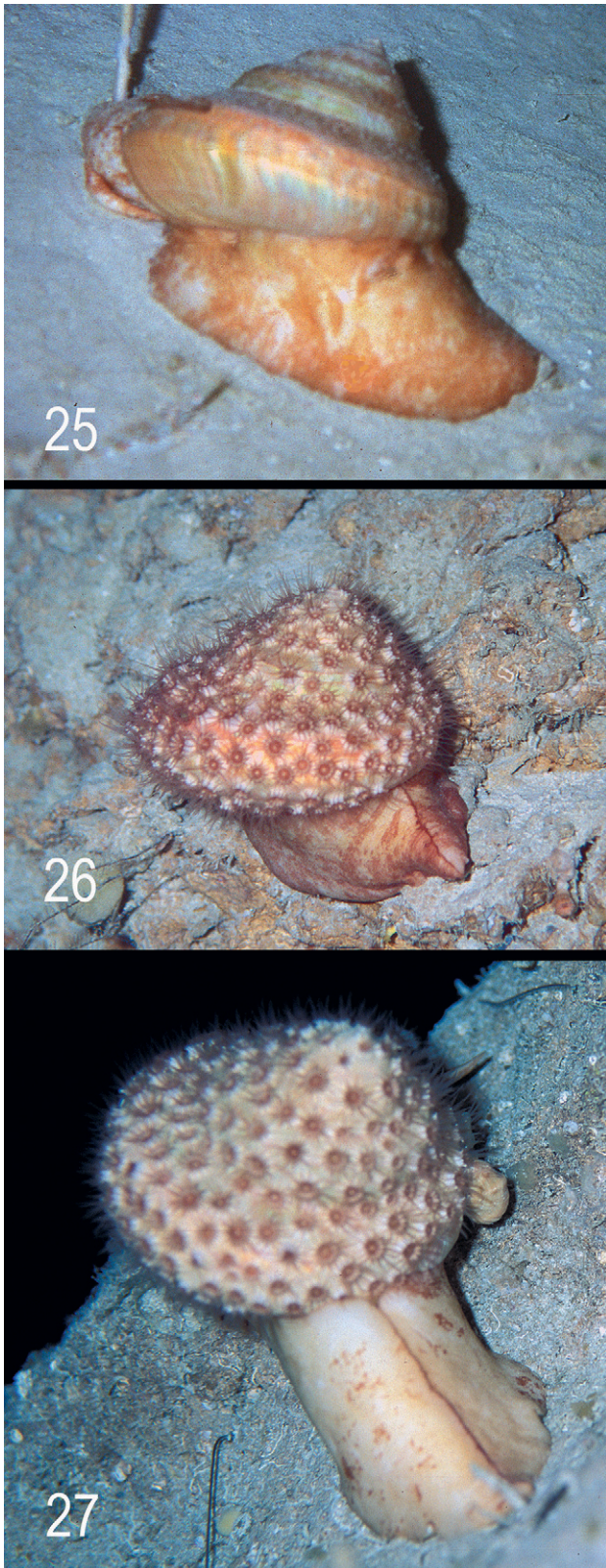
Etymology: *Belau*, the name of the Palau Islands in the Palauan language.

Ecology: In Palau this new slit shell was seen and collected on four out of over 60 submersible dives from both rock and sediment substrates at depths from 210–235 m (Figures 25–27). Submersible operations were conducted for many hours both above and below these depths, but no pleurotomariids were observed outside this depth range. Both of Okutani and Kurata's (1998) specimens were from 200 m, implying perhaps a limited depth range for this species along the outer reef slopes of the Palau Islands.

Downwelling light at these depths was relatively low, although there was still sufficient light to maneuver the submersible around large objects without additional lighting. The water is extremely clear. Temperatures at 200–250 m depth along Palau's outer reefs are generally about 10–13°C.

Overall the outer island slopes in Palau are steep, averaging about 30°–45°. The geomorphology of the outer slope has vertical escarpments, steep rocky slopes and more gentle sediment slopes. No slit shells were seen on any vertical to very steep slopes, although such profiles occurred in the species' depth range. Where seen, observations of slit shells were on both sediment and hard bottoms with slopes from about 25° to 45°.

The new slit shell was observed once apparently feeding on the sea pen *Anthoptilum grandiflorum* at 212 m depth during the day (Figure 25). The snail was on the downslope side of the sea pen with its foot extended and wrapped around the exposed base of the sea pen. Potentially it was digesting tissue around the central pen; the same sea pen has an area slightly above that shows damage, perhaps due to earlier feeding by the mollusk. These fleshy whip-like sea pens occurred only on sediment bottoms in clusters of individuals, their basal bulb buried in the gently sloping bottom.



Figures 25–27. *Bayerotrochus belauensis*, new species, *in situ* photographs. **25.** Paratype 3, station Mutremdiu 2, in 212 m. **26.** Paratype 2, station Mutremdiu 3, in 232 m. **27.** Holotype, station North Turtle Cove, in 220 m.

This sea pen was only observed at depths between 190 and 240m, coinciding with the observed range of the snail.

Comparative Remarks: Morphological similarities among many of the Indo-Pacific species of *Bayerotrochus* have led to the reluctance of some researchers to distinguish populations from throughout the broad range of the genus as separate species (e.g., Abbott and Dance, 1982; Okutani and Goto, 1984; Okutani and Kurata, 1998; Williams and Ozawa, 2006). More recent studies, some based on larger sample sizes and supplemented with molecular data, have led to the recognition of ten Indo-Pacific species within *Bayerotrochus* (Bouchet, 2016).

Among its geographically proximal congeners, *Bayerotrochus belauensis* new species more closely resembles *B. teramachii*, *B. westralis*, and *B. boucheti* than the smaller species *B. poppei*, *B. philpoppei*, and *B. delicatus*, which can be readily distinguished on the basis of size, spire profile, and surface sculpture. This new species is conchologically most similar to the widespread *B. teramachii*, which ranges from Honshu, Japan through the East and South China Seas to the Sulu Sea (Anseeuw & Goto, 1996), and particularly to specimens attributed to this species from Panglao, Bohol, Philippines.

Japanese specimens of *B. teramachii* (Figures 11–12) are similar to *B. belauensis* new species in adult size, but have a less stepped shell profile, thicker and heavier shells that are less lustrous, have more pronounced spiral ribs on the base, and weaker axial growth lines on the apical whorls. Specimens from Panglao that have been provisionally identified as *B. cf. teramachii* (Figures 13–14) more closely resemble *B. belauensis* new species than Japanese *B. teramachii* in spire angle and profile, color and luster of the shell surface and aperture shape. Additional research will be required to more precisely determine the relationships of this population from Panglao.

Bayerotrochus westralis (Figures 15–16) resembles *B. belauensis* new species in adult size and in having a thin, light shell with a short slit and similar sculpture on its early whorls. However, *B. belauensis* new species differs in having a narrower, more stepped spire, a smoother, more lustrous surface and a broader selenizone. *Bayerotrochus boucheti* (Figures 17–18) is also comparable to *B. belauensis* new species in size, but differs in having a more heavily pigmented shell with a more conical, less stepped spire, a more depressed aperture shape, and in having more pronounced spiral sculpture on the basal disk.

Molecular Analysis: Partial sequences of the cytochrome c oxidase I gene spanning 658 bp were obtained from the holotype and two paratypes of *B. belauensis* new species, and a maximum likelihood tree (Figure 28) was produced that included the samples itemized in Table 1. This analysis resulted in a single, fully resolved tree that recovered the monophyly of *Bayerotrochus*, segregated the Atlantic from the Pacific clades, and differentiated the species *B. teramachii*, *B. delicatus*, *B. boucheti*, and

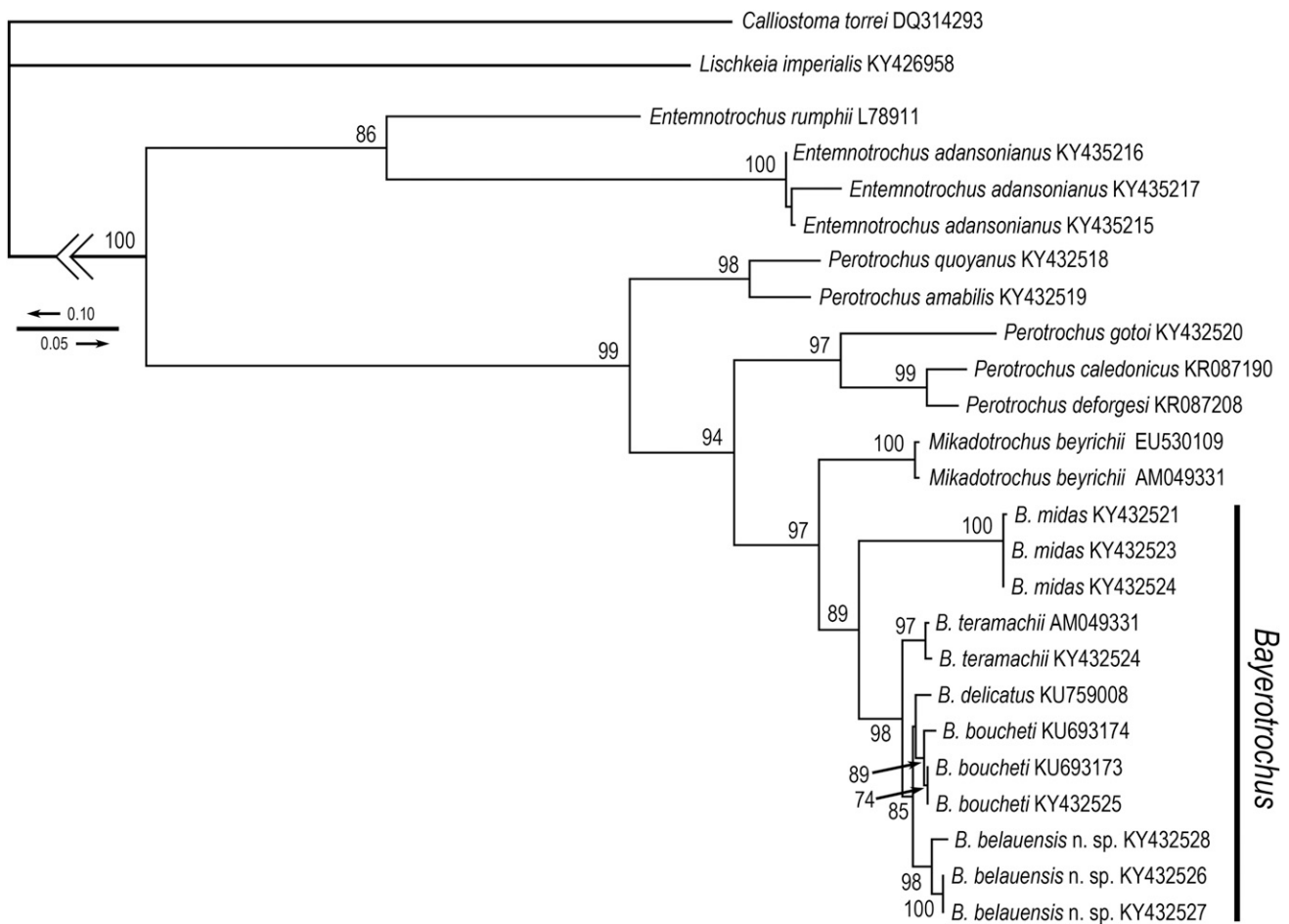


Figure 28. Maximum likelihood (RAxML) analysis of phylogenetic relationships among pleurotomariid taxa based on partial COI sequences. Numbers adjacent to nodes indicate bootstrap values ≥ 50 .

B. belauensis new species, all with high levels of support. These data indicate that *B. belauensis* new species is more closely related to *B. boucheti* and *B. delicatus* than to *B. teramachii*.

DISCUSSION

Based on morphological criteria, specimens of *Bayerotrochus* collected off Palau had been identified as being conspecific with the Japanese species, *B. teramachii* (Okutani and Kurata, 1998). Molecular data from a specimen from this population (USNM 905395, as *Bayerotrochus* sp.) was used in a more recent study describing a new species of *Bayerotrochus* from Yap (Zhang et al., 2016) and revealed that the Palau specimens were not closely related to *B. teramachii* and likely represented a new species. Sequence data from additional Palau specimens as well as from several other Indo-Pacific *Bayerotrochus* confirm that this population from Palau represents a distinct species that is more closely related to

B. boucheti and *B. delicatus* than to Japanese *B. teramachii*.

Specimens from a population of *Bayerotrochus* from Panglao (Figures 13–14) that were previously identified as *B. cf. teramachii*, are morphologically very similar to, and possibly conspecific with the Palau species described here. Additional sampling and molecular studies will be needed to determine the relationships of this population and perhaps revise the range of *B. teramachii*.

Transects along the tropical western Atlantic conducted using submersibles revealed that pleurotomariids species and genera are not sympatric, but inhabit well demarcated, non-overlapping bathymetric zones, each corresponding to a specific bottom topology and habitat (Harasewych, 2002: fig. 12). *Entemnotrochus* species are the shallowest and those of *Bayerotrochus* the deepest dwelling taxa along any transect. Similar data is not yet available for Indo-Pacific species. Although the specimens of *Bayerotrochus belauensis* new species occur at shallower depths than their western Atlantic and most Indo-Pacific congeners (Harasewych, 2002: fig. 12A), their

habitat, including inclination of the slope and the substrate, appear similar.

Three of the four individuals collected had most of the shell covered with an unidentified zoanthid, *Epizoanthus* sp. (Figures 8, 9, 26, 27). The specimen observed feeding on the sea pen lacked zoanthids. Anseeuw and Goto (1996) also report the growth of zoanthids on shells of some species, but attribute no benefit to this relationship, describing it as parasitic growth. Zoanthids are known to possess some of the most potent toxins found in marine organisms and it is likely the covering of toxic zoanthids may provide some protection from predation. Large fishes may be deterred from ingesting whole or crushing the shell by the living sheath of zoanthids. Despite having had an overgrowth of zoanthids (Figure 27), the holotype of *B. belauensis* new species (Figures 1–6) shows evidence of numerous repaired breaks indicating multiple episodes of unsuccessful predation by shell-breaking predators, possibly large crustaceans. Larger sample sizes would help to clarify potential correlations between zoanthid overgrowth and incidence of unsuccessful predation. *Bayerotrochus belauensis* was the largest gastropod found during more than 60 submersible dives off Palau.

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