

## Six New Species of *Philine* (Opisthobranchia: Philinidae) from the Tropical Indo-Pacific

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Six new species of philinid opisthobranchs are described from various localities in the tropical Indo-Pacific. Most were collected from deep waters of the Verde Island Passage, Philippines, while one additional species was collected from relatively shallow water from Panglao, Philippines and the second from shallow water in the Hawaiian Islands.

Morphological characters, including anatomical details of the shell, radular morphology, gizzard plates and male and hermaphroditic reproductive systems are entirely congruent with the molecular differences found. Four of these taxa are members of the *Philine aperta* clade, while two taxa are members of a more basal lineage. *Philine acuticauda* sp. nov. has an elongate body, has a large, smooth shell, lacks gizzard plates and has a radula with two outer lateral teeth, the outer of which is reduced with a blunt cusp. *Philine hearstorum* sp. nov. is also elongate but has a series of clearly defined striations on the shell. It also possesses three small gizzard plates with a distinct crystalline structure, has two outer lateral radular teeth with prominent cusps. *Philine dentiphallus* sp. nov. has residual punctate sculpture lines on the shell, has three equally sized gizzard plates with a prominent medial bar above a single large depression. The radula has a single outer lateral tooth with a prominent cusp. The penis is hammer-shaped with a series of denticles on the outer lobe of the penial papilla. *Philine verdensis* sp. nov. has a large, smooth shell devoid of striation or other obvious sculpture. The gizzard plates are unequal with two larger plates and a single small plate, all with two prominent pores. The penial papilla is hammer-shaped with an unarmed papilla. *Philine pittmani* sp. nov. has unequal gizzard plates where the two longer plates each have only a single pore, *Philine multipapillata* sp. nov., has a smooth shell, devoid of obvious sculpture, has three unequal gizzard plates, all with two large prominent pores. The penis is complex, having a penial papilla densely armed with conical papillae over the entire surface. This study reinforces the view that the diversity of the Indo-Pacific Philinacea still remains incompletely sampled including the *Philine aperta* clade. *Philine acuticauda* and *P. hearstorum* appear to be most closely related to *P. alba* and *P. alboides* and represent the first representatives of this group known from the tropical Indo-Pacific. Both morphological and molecular data support the phylogenetic position of these taxa. The more basal members have small gizzard plates or entirely lack them and have a simple penis, while species in the *Philine aperta* clade have plates with pores or slits and have a complex penis and prostate. In sampling broader outgroup relationships, some members of Philinidae cluster with species of Aglajidae, suggesting that Philinidae as traditionally constructed does not constitute a clade, but represents a paraphyletic assemblage. These relationships need to be further studied with more extensive taxon sampling of philinaceans, but are suggestive that further systematic revision is required to develop a classification consistent with the phylogeny of the Philinacea.

KEYWORDS: Philinidae, Philinacea, Indo-Pacific, new species, biodiversity

Many morphological descriptions of *Philine* species have been undertaken over the past several decades (Marcus 1974; Marcus and Marcus 1966, 1967, 1969; Rudman 1970, 1972a, b; Gosliner 1988), and these studies describe new taxa and review the anatomy of previously identified species. Price et al. (2011) also provided the first morphologically-based phylogenetic study of *Philine*. More recently, Krug et al. (2012) provided a molecular phylogeny based on the 16S mitochondrial gene, that was used primarily to establish the origin of two introduced species of *Philine* now found on the Pacific coast of North America. Ohnheiser and Malaquias (2013) reviewed the North Atlantic *Philine* species, described two additional species from the region and presented a molecular phylogeny of these species based on the COI mitochondrial gene.

The World Register of Marine Species (WORMS: <<http://www.marinespecies.org/aphia.php?p=taxdetails&id=138339>>) lists 117 valid species of *Philine* from throughout the world's oceans. As noted by Price et al. (2011), the majority of these are known only from shells and their identity remains obscure. The Indo-Pacific tropics and adjacent temperate regions support a diversity of philinid opisthobranchs (Gosliner et al., 2008), with 24 described species documented from the region (Price et al. 2011, WORMS). Several relatively recently described species have been added to the Indo-Pacific region since the systematic reviews cited above (Valdés 2008; Price et al. 2011). These include *Philine abyssicola* Valdés, 2008, *P. babai* Valdés, 2008, *P. habei* Valdés, 2008, *P. fenestra* Price, Gosliner and Valdés, 2011, *P. paucipapillata* Price, Gosliner and Valdés, 2011, *P. puka* Price, Gosliner, and Valdés, 2011 and *P. sarcophaga* Price, Gosliner and Valdés, 2011. Krug et al. (2012), illustrated that at least one additional Indo-Pacific species from Australia as unidentified and quite likely undescribed.

Recent biodiversity exploration of deeper waters surrounding the Philippines from the 2004 Panglao International Expedition and the 2011 Hearst Philippine Biodiversity Expedition has produced additional material, which is the focus of the present study. Examination of this material plus specimens of a shallow-water species from the Hawaiian Islands reveals the presence of six additional undescribed species. The description of these species and the examination of their molecular phylogenetic relationships formulate the focus of the present review of the genus *Philine*. In order to compare these species with other species known from the Pacific and Indo-Pacific, our molecular study employs the examination of the 16S gene studied by Krug et al. (2012) rather than using the COI gene used by Ohnheiser and Malaquias (2013) for Atlantic taxa. The intent of the present molecular study is to determine the distinctness of the species described here, as well as further assessing the phylogeny and monophyly of *Philine*.

## MATERIALS AND METHODS

### Morphological Methods

Over the last decade, new specimens of philinds were collected from the Verde Island Passage and Bohol Island, Philippines and the Hawaiian Islands. Specimens collected were preserved in either 10% formalin for proper preservation of anatomical structures, or preserved entirely in 95% ethanol for later molecular study. Prior to preservation of any specimen in formalin, a tissue sample was taken from the animal and preserved in 95% ethanol for later molecular study.

Upon return to the California Academy of Sciences, dissections were completed, and drawings of anatomical structures were accomplished using a Nikon SMZ-U binocular microscope with drawing tube. Buccal mass structures of specimens were dissected and cleaned by placing them in a 10% NaOH solution for 4–10 hours, and then prepared for scanning electron microscopy. The radula was separated and cleaned of any remaining tissue. It was then placed on a glass cover slip, air-dried, and then mounted on a stainless steel stub. The same procedure was followed for exam-

ination of gizzard plates. Specimens of copulatory organs were mounted on stubs and air-dried or were photographed using automontage light microscopy. Hard structures were then coated with gold/palladium using a Denton Desk II vacuum sputter coater. Scanning electron micrographs were produced by a LEO 1450 VP scanning electron microscope. Specimens and dissected structures were deposited at the California Academy of Sciences in the Invertebrate Zoology Department collection (CASIZ).

### Molecular Methods

*Taxon sampling:* Sampling of Philinidae specimens for the molecular study were all preserved in 70% EtOH, making it possible to perform molecular work on the tissue obtain sequences of the mitochondrial gene 16S. New molecular sequence data are provided for 21 specimens of 11 species of *Philine* and outgroup taxa (Table 1). Of the six species described here, five of the species were sequenced. Molecular data were not available for *Philine multipapillata*, since the single specimen was preserved in formalin. The genus *Scaphander* was chosen as an outgroup based on its morphological similarity and apparent close relationship to the genus *Philine*. Additionally, one specimen of *Scaphander mundus* Watson, 1883, was sequenced to test the monophyly of *Philine*. The tissues came from specimens collected from various regions in the Indo-Pacific. The majority of specimens were found from deep waters off the Verde Island Passage, Philippines, but one additional species was collected from relatively shallow water from Panglao, Philippines, and another from shallow water in the Hawaiian Islands. Sequences of the 16S gene from 18 specimens of seven species in *Philine* were obtained from GenBank and were published by Krug et al. (2012) and used in analysis. They are therefore not included in Table 1.

*DNA extraction, amplification and sequencing:* Genomic DNA was extracted from small pieces of foot tissue for most samples using QiagenDNeasy Tissue Kits. Amplification of DNA was conducted on BioRadsMyCycler™Thermocycler (software version 1.065, Bio-Rad Laboratories). Partial sequences of the mitochondrial genes 16S rRNA (485 bp) and 16Sar-L and 16Sbr-H (Palumbiet al. 1991) for one specimen for 16S PCR and sequencing we utilized internal primers developed by V. Knutson (personal communication).

PCR amplifications were carried out in a 25 ml reaction volume including 2.5 ml of 10x PCR buffer, 0.5 ml dNTPs (10 mm stock), 1.0 ml MgCl (25 mm stock), 1.0 ml HotStartTaq (1.25 units/ml)-Apex, 1.0 ml of each primer (25 mm stock), 15 µl H<sub>2</sub>O, and 2 ml of genomic DNA. The partial 16S amplifications followed the following parameters: an initial denaturing step at 94°C for 3 min; 40 cycles of denaturing at 94°C for 30 s, annealing at 48°C for 30 s, amplifying at 72°C; and extension at 72°C for 5 min and 25°C for 5 min.

PCR products were visualized on a 1.0% TBE agarose gel stained with ethidium bromide. PCR products were purified with ExoSAP-IT (USB Scientific) and then EtOH Precipitation. Cycle-sequencing reactions were performed using ABI Prism Big Dye Terminator (Applied Biosystems) (total volume 10 ml) and analyzed using the automated sequencer ABI 3130 Genetic Analyzer (Applied Biosystems) in the Center for Comparative Genomics at the California Academy of Sciences (San Francisco, USA). All new DNA sequences have been deposited in Genbank (Table 1).

*Sequence alignment and analysis:* The authenticity of the sequences was verified by BLAST comparisons. The sequences were edited and aligned using Genious 5.5 (Drummond et al. 2009) and checked by eye.

*Model selection and phylogenetic analyses:* Phylogenetic data were analyzed using Maximum Likelihood with the program RAxML v7.04. RA x ml was employed (Stamatakis, Hoover, and

TABLE I. Specimens examined for new DNA sequences.

Catalog Number	Field Station	Genus	Species	Location	GenBank number
CAS 192085	HEPD 005	<i>Philine</i>	<i>acuticauda</i>	Verde Island Passage, Philippines	KJ411886
CAS 192086	HEPD 005	<i>Philine</i>	<i>acuticauda</i>	Verde Island Passage, Philippines	
CAS 192087	HEPD 019	<i>Philine</i>	<i>acuticauda</i>	Verde Island Passage, Philippines	KJ511781
CAS 189336	HEPD 035	<i>Philine</i>	<i>hearstorum</i>	Verde Island Passage, Philippines	KJ411892
CAS 192088	HEPD 019	<i>Philine</i>	<i>dentiphallus</i>	Verde Island Passage, Philippines	KJ411891
CAS 189337	HEPD 019	<i>Philine</i>	<i>dentiphallus</i>	Verde Island Passage, Philippines	
CAS 192089	HEPD 021	<i>Philine</i>	<i>verdensis</i>	Verde Island Passage, Philippines	KJ411890
CAS 189338	HEPD 021	<i>Philine</i>	<i>verdensis</i>	Verde Island Passage, Philippines	
CAS 192090	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	KJ411910
CAS 185213	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	
CAS 163775	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	
CAS 166768	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	
CAS 118253	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	
CAS 192091	N/A	<i>Philine</i>	<i>pittmani</i>	Black Rock, Maui, HI	
CAS 172841	T-2	<i>Philine</i>	<i>multipapillata</i>	Panglao, Philippines	
CAS 168651	N/A	<i>Philine</i>	<i>auriformis</i>	San Francisco Bay, CA	
CAS 181587	L-42	<i>Philine</i>	<i>orca</i>	Panglao, Philippines	KJ411893
CAS 181478	S-2	<i>Philine</i>	<i>rubrata</i>	Panglao, Philippines	KJ411887
CAS 119036	N/A	<i>Philine</i>	<i>orientalis</i>	San Francisco Bay, CA	
CAS 181565	T-31	<i>Philine</i>	<i>habei</i>	Panglao, Philippines	KJ511780
CAS 171499	T-39	<i>Philine</i>	<i>habei</i>	Panglao, Philippines	
CAS 186467	HEPD 012	<i>Scaphander</i>	<i>mundus</i>	Verde Island Passage, Philippines	
CAS 185778		<i>Philinopsis</i>	sp. 1	Verde Island Passage, Philippines	KJ411888
CAS 185779		<i>Philinopsis</i>	sp. 2	Verde Island Passage, Philippines	KJ411889
CAS 17788	HEPD 026	<i>Philinopsis</i>	<i>ctenophoraphaga</i>	Verde Island Passage, Philippines	KJ411894

Rougemont 2008) random starting trees, using 10,000 rapid bootstraps. The model of analysis was set to GTR + Gamma with *Scaphander mundus* as the outgroup.

*Genetic distances:* In order to compare the genetic distances among specimens of *Philine* from different biogeographic areas, we calculated the mean genetic distances for the molecular marker using PAUP\* 4.0 b 10.0. We followed the criteria applied by Krug et al. (2012) who concluded that mean intraspecific difference for the 16S gene was generally less than 0.5% while intraspecific differences ranged from 1.5%–5.9%. We considered any divergences in the 16S gene exceeding 2% to represent distinct taxa.

## SPECIES DESCRIPTIONS

### **Cephalaspidea Fisher, 1883** **Family Philinidae Gray, 1850**

#### **Genus *Philine* Ascanius, 1772**

Type species: *Bulla aperta* Linnaeus, 1767, by subsequent designation

#### ***Philine acuticauda* Gonzales and Gosliner, sp. nov.**

Figures 1A–B, 2–3

**MATERIAL EXAMINED.**— HOLOTYPE: CASIZ 192085, ST HEPD 05, beam trawl in fine mud, 459–496 m depth, western end of Verde Island Passage, Balayan Bay, Batangas Province, Luzon, Philippines, 13.74833°N, 120.75583°E, 29 May 2011, Hearst Expedition Deep Sea Team. PARATYPES: CASIZ 192086, ST HEPD 05, dissected, beam trawl in fine mud, 459–496 m depth, western end of Verde Island Passage, Balayan Bay, Batangas Province, Luzon, Philippines, 13.74833°N, 120.75583°E, 29 May 2011, Hearst Expedition Deep Sea Team. CASIZ 192087, one specimen, partially dissected, ST HEPD 19, beam trawl in beam trawl in muddy sand with pebbles, 541–636 m depth, western end of Verde Island Passage, southeast end of Golo Island, Batangas Province, Luzon, Philippines, 13.5895°N, 120.4155°E, 1 June 2011, Hearst Expedition Deep Sea Team.

**GEOGRAPHICAL DISTRIBUTION.**— Known only from the Verde Island Passage, southern Luzon, Philippines.

**ETYMOLOGY.**— The name “*acuticauda*” refers to the long tapering posterior end of the body of this species.

**NATURAL HISTORY.**— This species is in mud and sandy mud in 459–636 m.

**DESCRIPTION.**— *External morphology.* The living animals (Figs. 1A, B) are up to 65 mm in length and 20 mm wide. The general body color of the living animal is uniformly white with yellowish pigment on the anterior end of the head and in the mantle cavity on the ventral side. The cephalic shield is shorter than the posterior shield and is slightly indented posteriorly. The parapodia are short, not reaching the cephalic shield, leaving the anterior and posterior shields visible (Fig. 2A). The posterior end of the posterior shield tapers to an acutely pointed posterior terminal.

The gill is simply plicate consisting of 12 primary folds and is situated ventrally on the right posterior end of the animal.

*Shell* (Fig. 2B): The shell is approximately 15 mm long and is relatively thickly calcified and wide. It occupies the majority of the posterior shield. No obvious sculpture is visible on the surface of the shell. The right posterior extreme of the shell has an elongate extension.

*Digestive system* (Figs. 3A–B): The buccal mass is relatively large, occupying the anterior half of the anterior shield. The buccal bulb has a relatively large radula. The radular formula in one paratype specimen (CASIZ 192086) is 16 x 2.1.0.1.2. (Fig. 2C). The inner lateral teeth are large

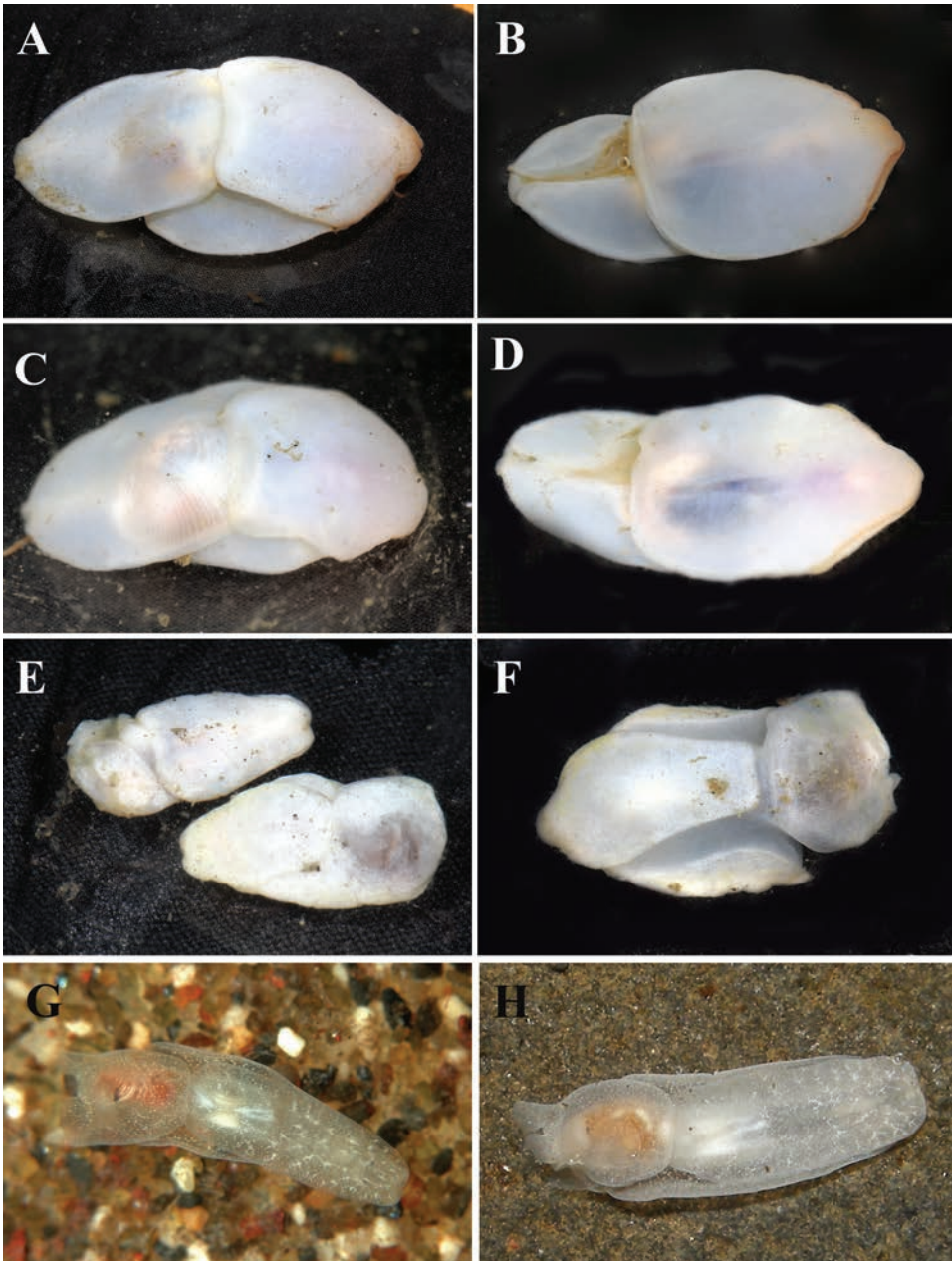


FIGURE 1. Living animals. A. *Philine acuticauda* sp. nov., dorsal view, paratype, CASIZ 192087, Mindoro Occidental, Philippines. B. *Philine acuticauda* sp. nov., ventral view, paratype, CASIZ 192087, Mindoro Occidental, Philippines. C. *Philine hearstorum* sp. nov., dorsal view, holotype, CASIZ 189336, Mindoro Occidental, Philippines. D. *Philine hearstorum* sp. nov., holotype, ventral view, casiz 189336, Mindoro Occidental, Philippines. E. *Philine dentiphallus* sp. nov., holotype and paratype, Mindoro Occidental, Philippines. F. *Philine verdensis* sp. nov., holotype, CASIZ 192089, Mindoro Occidental, Philippines. G. *Philine pittmani* sp. nov., paratype, CASIZ 192091, Makena Landing, Maui, Hawai'i, Photo by Cory Pittman. H. *Philine pittmani* sp. nov., holotype, CASIZ 192090, Black Rock, Maui, Hawai'i, Photo by Cory Pittman. all other photos by T. M. Gosliner.

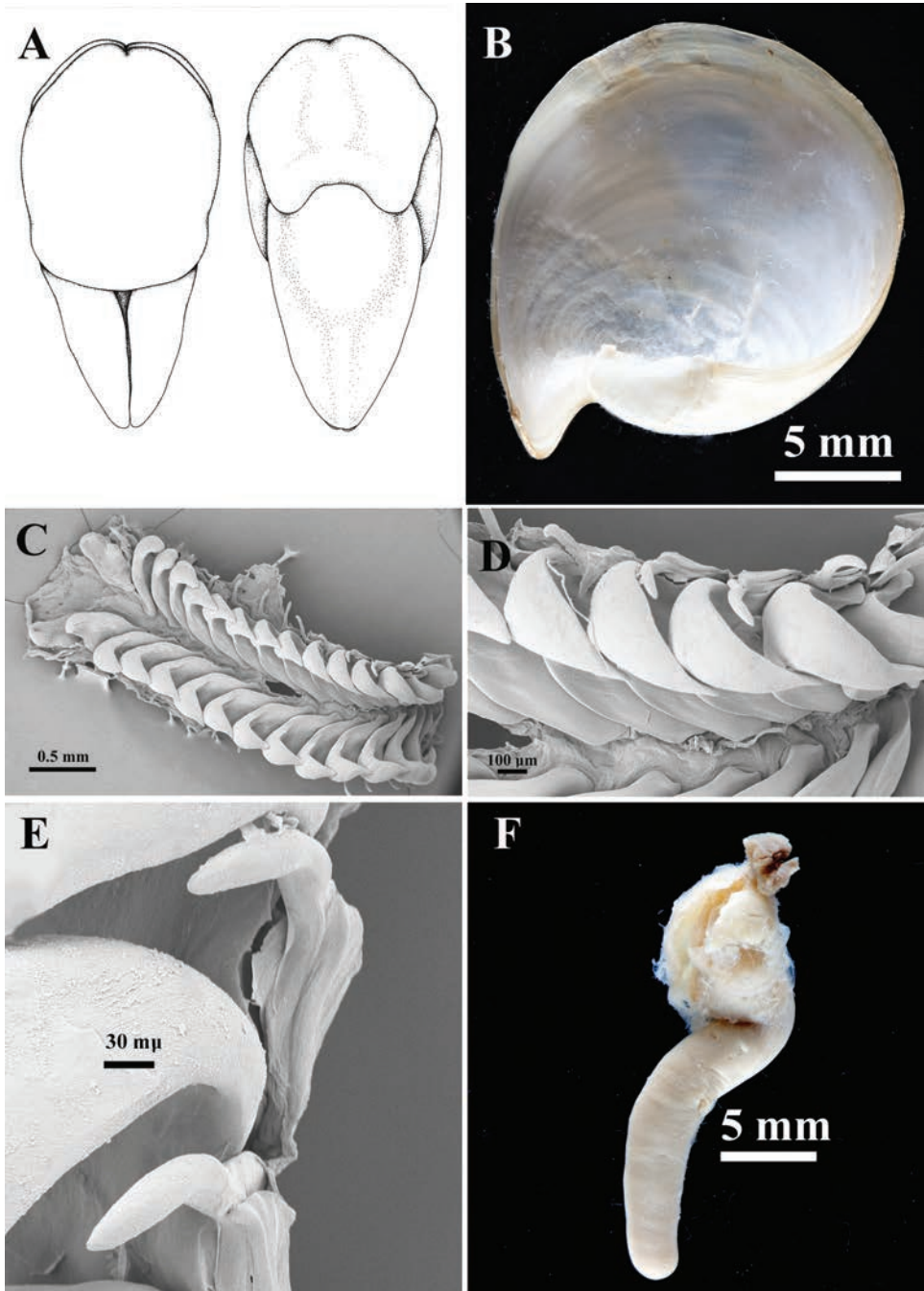


FIGURE 2. Anatomy of *Philine acuticauda* sp. nov. A. Dorsal and ventral views of holotype, CASIZ 192085, drawings by Emily Eng. B. Shell, paratype, CASIZ 192086. C. Scanning electron micrograph of entire radula, paratype, CASIZ 192086. D. Scanning electron micrograph of half-row of radular teeth, paratype, CASIZ 192086. E. Detail of outer lateral teeth illustrating blunt cusp of outermost outer laterals. F. Light micrograph of penis, paratype, CASIZ 192086.

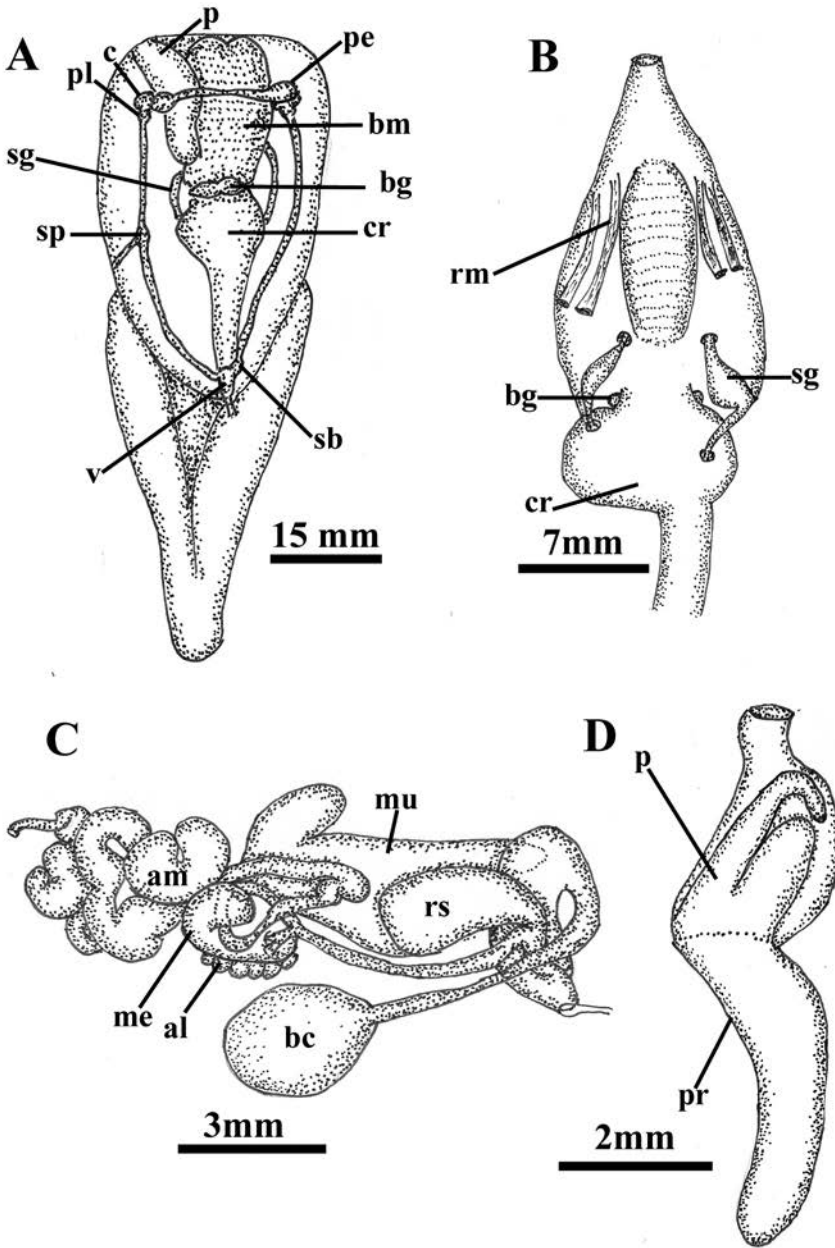


FIGURE 3. Internal anatomy, *Philine acuticauda* sp. nov. of paratype CASIZ 192086. A. Ventral view of preserved animal showing internal anatomy, bg = buccal ganglia, bm = buccal mass, c = cerebral ganglion, cr = crop, p = penis, pe = pedal ganglion, pl, pleural ganglion, sb = subintestinal ganglion, sg = salivary gland, sp = suprainstestinal ganglion v = visceral ganglion. B. Anterior portion of digestive system, bg = buccal ganglion, cr = crop, rm = retractor muscle, sg = salivary gland. C. Posterior reproductive organs, al = albumen gland, am = ampulla, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis. D. Penis and penial papilla, p = penial papilla, pr = prostate.



and broad (Fig. 2D). Their masticatory margin is devoid of denticles. The inner, outer lateral tooth is narrow and elongate with an elongate, curved cusp. The outermost lateral is blunt and curved, lacking an elongate cusp (Fig. 2E). There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands (Fig. 3A, C). The crop is large and saccate, slightly narrower than the buccal bulb. There are no gizzard plates or muscular thickenings in the crop. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 3A): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single suprainestinal ganglion on the right side situated well posterior of the nerve ring. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia, which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop extends posteriorly to the suprainestinal ganglion. The osphradial nerve emerges from suprainestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion (Fig. 3A). From the visceral ganglion is the genital nerve, which does not appear to have a distinct genital ganglion.

*Reproductive System* (Figs. 2F, 3C–D): The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands (Fig. 3C). From the large ovotestis, which is intermingled with the digestive gland, emerges the wide, convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the female glands and enters the short, coiled albumen and membrane glands by means of a single duct. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The hermaphroditic duct is elongate and extends to the genital aperture then joins the short duct of the large, pyriform receptaculum seminis and continues to the genital atrium, where it joins the elongate duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens and curves until its widest portion at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Figs. 2F, 3D) consists of a thick penial sac and an elongate, unbranched, posteriorly directed prostate gland that is joined to the penial sac by a narrowed constriction. Within the penial sac is an elongate, curved penial papilla that is devoid of any armature (Fig. 3D).

**REMARKS.**— Price et al. (2011) described a series of plesiomorphic characteristics found in species of *Philine*. *Philine acuticauda* has several plesiomorphic features including a relatively large radula, more than one outer lateral tooth in the radular ribbon, a suprainestinal ganglion situated posterior to the circumesophageal nerve ring and a simple, unarmed penial papilla with a single unbranched prostate. This species also has several derived attributes including a smooth shell, a lack of gizzard plates and an elongate posterior end of the posterior shield.

*Philine acuticauda* is most similar in its morphology to *P. alba* Mattox, 1958, from the southern California coast and *P. alboides* Price, Gosliner, and Valdés, 2011, from the Gulf of Mexico and Caribbean. These three species have a large body size with a broad body profile and a broad, smooth, flattened shell with an expanded posterior wing. They also have a large radula with a wide inner lateral tooth that either lacks denticles or has greatly reduced denticles. All three species have two outer lateral teeth and a simple penis and prostate. They all have a suprainestinal ganglion located posteriorly to the nerve ring. Despite these similarities, *P. acuticauda* differs significantly from these taxa in several regards. The posterior end of the body of *P. alba* and *P. alboides* is blunt

rather than being acutely tapered as *P. acuticauda*. In *P. acuticauda* and *P. alboides* the inner lateral teeth entirely lack denticles, while in *P. alba*, some of the teeth have minute denticles on the masticatory border, while other teeth in the same radula may entirely lack denticles. In both *P. alba* and *P. alboides* the two outer lateral teeth are similar in shape with evenly curved cusps. In *P. acuticauda*, the inner of these two teeth is similar to those found in the other two species but the outer one has a dramatically reduced cusp. Both *P. alba* and *P. alboides* have three small evenly-sized gizzard plates, while no trace of plates was found in the two specimens of *P. acuticauda* examined. The prostate of *P. acuticauda* is only slightly curved as posteriorly directed while in *P. alba* and *P. alboides*, the prostate is sharply curved, with the posterior end being anteriorly directed.

***Philine hearstorum* Gonzales and Gosliner, sp. nov.**

Figures 1C–D, 4–5

**MATERIAL EXAMINED.**— HOLOTYPE: dissected, CASIZ 189336, ST HEPD 35, beam trawl in fine mud, 397–439 m depth, western end of Verde Island Passage, midway between Ambil Island and Calatagan, Batangas Province, Luzon, Philippines, 13.809°N, 120.46783°E, 4 June 2011, Hearst Expedition Deep Sea Team.

**GEOGRAPHICAL DISTRIBUTION.**— Known only from the Philippines (present study).

**ETYMOLOGY.**— The name “*hearstorum*” honors Will and Margaret Hearst who generously funded the 2011 Hearst Philippine Biodiversity Expedition.

**NATURAL HISTORY.**— This species was found in fine mud. The gizzard contained fragments of tissue that when sequenced were found to be mytilid bivalves.

**DESCRIPTION.**— *External morphology:* The living animal (Figs. 1C–D) was 25 mm in length 17 mm wide. The general body color of the living animal is uniformly white with yellowish pigment on the anterior end of the head and in the mantle cavity on the ventral side. The cephalic shield is shorter than the posterior shield and is slightly indented posteriorly. The parapodia are short, not reaching the cephalic shield, leaving the anterior and posterior shields visible. The posterior end of the posterior shield tapers to an elongate, rounded posterior terminal. The gill is simply plicate consisting of 12 primary folds and is situated ventrally on the right posterior end of the animal.

*Shell* (Fig. 4A): The shell is approximately 15 mm long and is relatively thickly calcified and wide. It occupies the majority of the posterior shield. More than 30 radial bands of obvious sculpture are visible on the surface of the shell. The right posterior extreme of the shell has a short extension.

*Digestive system* (Figs. 4B–E, 5A): The buccal mass is relatively large, occupying the anterior half of the anterior shield (Fig. 5A). The buccal bulb has a relatively large radula. The radular formula of the holotype specimen is 16 x 2.1.0.1.2 (Fig. 4D). The inner lateral teeth are large and broad (Fig. 4E). Their masticatory margin is devoid of denticles. The two outer lateral teeth are narrow and elongate with an elongate, curved cusp. There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, about the same diameter as the buccal bulb. Posteriorly the crop narrows to a slightly muscularized gizzard that contains three symmetrical plates (Figs. 4B–C). The gizzard plates are brown and covered with small rhomboidal crystals. The gizzard narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 5A): The circumesophageal nerve ring consists of paired cere-

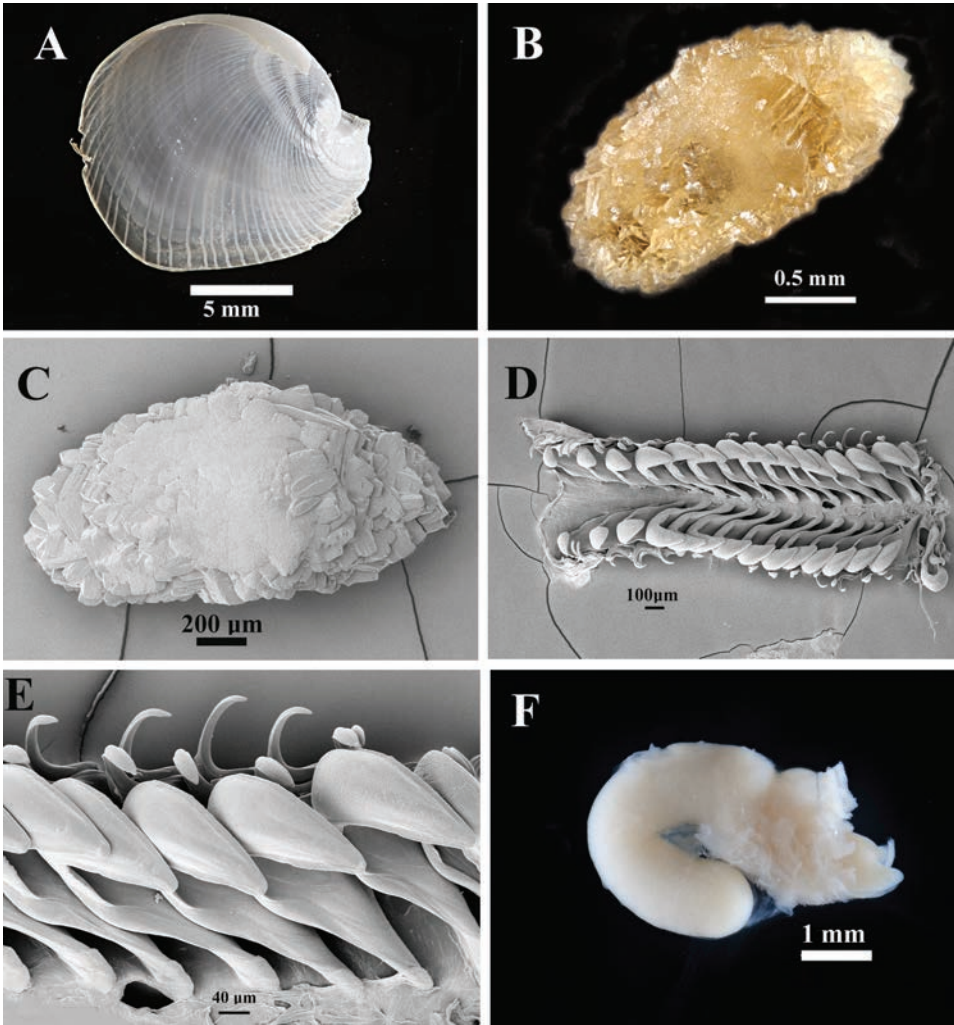


FIGURE 4. Anatomy of *Philine hearstorum* sp. nov., holotype, CASIZ 189336. A. Shell. B. Light micrograph of gizzard plate showing crystalline structure. C. Scanning electron micrograph of gizzard plate. D. Scanning electron micrograph of entire radula. E. Half-row of radular teeth showing two cuspidate rows of outer lateral teeth. F. Light micrograph of penis.

bral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side situated well posterior of the nerve ring. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop extends posteriorly to the supraintestinal ganglion. The osphradial nerve emerges from supraintestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which does not appear to have a distinct genital ganglion.

*Reproductive System* (Fig. 4F, 5B–C): The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to

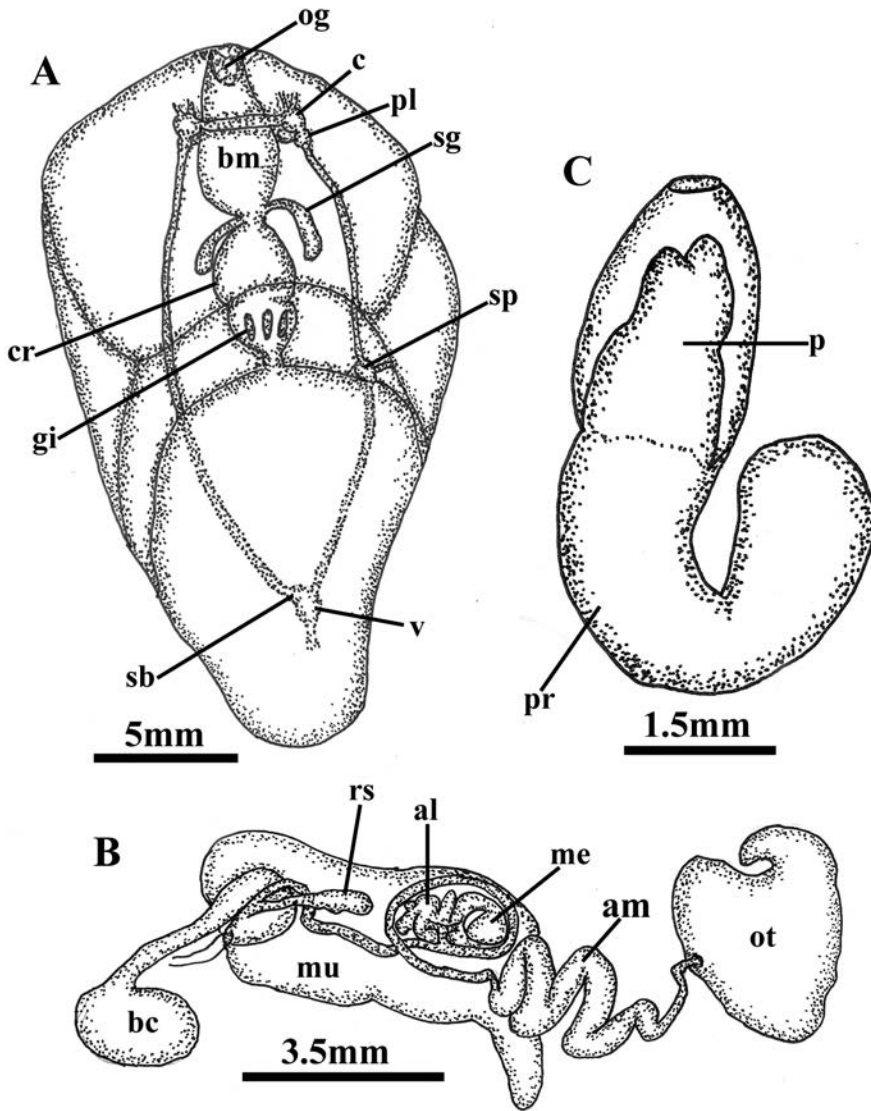


FIGURE 5. Internal anatomy of *Philine hearstorum* sp. nov., holotype, CASIZ 189336. A. Dorsal view of preserved holotype showing internal anatomy, bm = buccal mass, c = cerebral ganglion, cr = crop, gi = gizzard, og = oral gland, p = penis, pe = pedal ganglion, pl = pleural ganglion, sb = subintestinal ganglion, sg = salivary glands, sp = supraintestinal ganglion, v = visceral ganglion. B. Posterior reproductive organs, al = albumen gland, am = ampulla, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, ot = ovotestis, rs = receptaculum seminis. C. Penis and penial papilla, p = penial papilla, pr = prostate.

the albumen and membrane glands (Fig. 5B). From the large ovotestis, which is intermingled with the digestive gland, emerges the wide, convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the female glands and enters the short, coiled albumen and membrane glands by means of a single duct. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The hermaphroditic duct is elongate and extends to the genital aperture then joins the short duct of the narrow, saccate receptaculum seminis and continues to the

genital atrium, where it joins the elongate duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens and curves until its widest portion at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 4F, 5C) consists of a thick penial sac and an elongate, unbranched, anteriorly directed prostate gland that is joined to the penial sac by a narrowed constriction. Within the penial sac is an elongate, lobed penial papilla that is devoid of any armature.

**REMARKS.**— Price et al. (2011) described a series of plesiomorphic characteristics found in species of *Philine*. *Philine hearstorum* has several relatively plesiomorphic features including a relatively large radula, more than one outer lateral tooth in the radular ribbon, a suprainestinal ganglion situated posterior to the circumesophageal nerve ring and a simple, unarmed penial papilla with a single unbranched prostate. This species also has an elongate posterior end of the posterior shield.

*Philine hearstorum* is most similar in its morphology to *P. alba* Mattox, 1958, from the southern California coast, *P. alboides* Price, Gosliner, and Valdés, 2011, from the Gulf of Mexico and Caribbean and *P. acuticauda*, with which *P. hearstorum* is sympatric. No molecular data are available for *P. alba* and *P. alboides*, since all material is either fixed in formalin or the alcohol specimens are very old and there was no amplification of DNA (P. Krug, personal communication). The *p*-distance (Table 2) between *P. acuticauda* and *P. hearstorum* for the 16S gene is 2.7%. This is consistent with the percentages found by Krug et al. (2012) for distinct species of *Philine*. Morphologically, these four species have a large body size with a broad body profile and a broad, smooth, flattened shell with an expanded posterior wing. They also have a large radula with a wide inner lateral tooth that either lacks denticles or has greatly reduced denticles. All four species have two outer lateral teeth and a simple penis and prostate. They all have a suprainestinal ganglion located posteriorly to the nerve ring. Despite these similarities, *P. hearstorum* differs significantly from these taxa in several regards. It is the only species that has distinct sculpture on the shell. The posterior end of the body of *P. alba* and *P. alboides* is blunt rather than being acutely tapered as in *P. hearstorum* and *P. acuticauda*. The posterior end of the body is more acute in *P. acuticauda*. In *P. acuticauda*, *P. hearstorum*, and *P. alboides*, the inner lateral teeth entirely lack denticles, while in *P. alba*, some of the teeth have minute denticles on the masticatory border, while other teeth in the same radula may entirely lack denticles. In *P. hearstorum*, *P. alba*, and *P. alboides*, the two outer lateral teeth are similar in shape with evenly curved cusps. In *P. acuticauda*, the inner of these two teeth is similar to those found in the other two species but the outer one has a dramatically reduced cusp. *Philine hearstorum*, *P. alba*, and *P. alboides* have three small evenly-sized gizzard plates, while no trace of plates was found in the two specimens of *P. acuticauda* examined. The gizzard plates of *P. hearstorum* have rhomboidal crystals on their surface, while those of *P. alba* and *P. alboides* are smooth. The prostate of *P. acuticauda* is only slightly curved and is posteriorly directed, while in *P. hearstorum*, *P. alba*, and *P. alboides*, the prostate is sharply curved, with the posterior end being anteriorly directed. The penial papilla of *P. hearstorum* has a bilobed apex, while the papilla of *P. acuticauda*, *P. alba*, and *P. alboides* is undivided.

***Philine dentiphallus* Gonzales and Gosliner, sp. nov.**

Figures 1E, 6–7

**MATERIAL EXAMINED.**— HOLOTYPE: body wall opened, but not dissected, CASIZ 192088, ST HEPD 19, beam trawl in beam trawl in muddy sand with pebbles, 541–636 m depth, western end of Verde Island Passage, southeast end of Golo Island, Batangas Province, Luzon, Philippines, 13.5895°N, 120.4155°E, 1 June 2011, Hearst Expedition Deep Sea Team. PARATYPE: dissected,

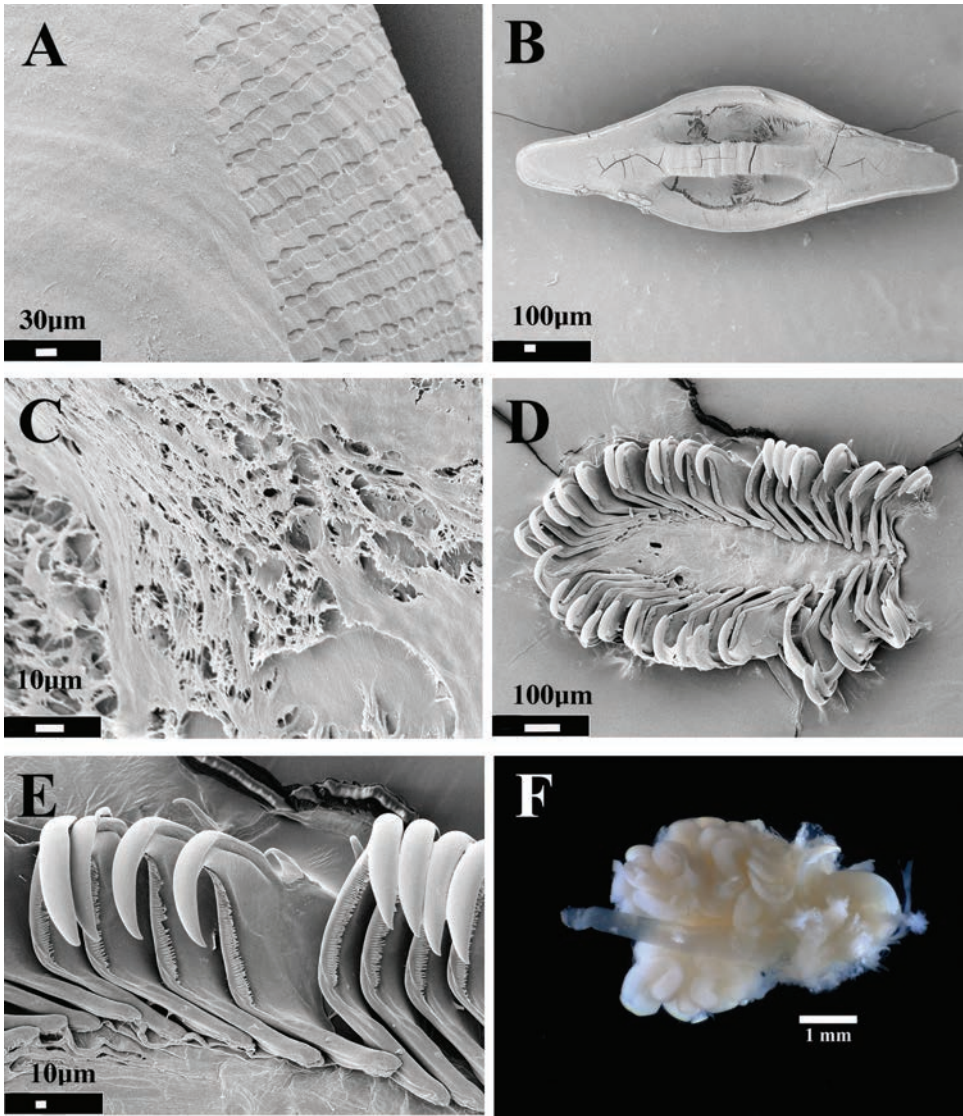


FIGURE 6. Internal anatomy of *Philine dentiphallus* sp. nov., paratype, CASIZ 1893377. A. Scanning electron micrographs of shell sculpture. B. Scanning electron micrograph of gizzard plate. C. Scanning electron micrograph of microsculpture of gizzard plate. D. Scanning electron micrograph of entire radula. E. Scanning electron micrograph of half-row of radular teeth showing inner and outer lateral teeth. F. Light micrograph of penial papilla and complex prostate.

CASIZ 189337, ST HEPD 19, beam trawl in muddy sand with pebbles, 541–636 m depth, western end of Verde Island Passage, southeast end of Golo Island, Batangas Province, Luzon, Philippines, 13.5895°N, 120.4155°E, 1 June 2011, Hearst Expedition Deep Sea Team.

**GEOGRAPHICAL DISTRIBUTION.**— Thus far, this species is known only from the western end of the Verde Island Passage separating southern Luzon and northern Mindoro.

**ETYMOLOGY.**— The name *dentiphallus* refers to the comb-like row of denticles along the lobe of the penial papilla, a characteristic that distinguishes this species from other members of the *Philine aperta* clade (sensu Price et al. 2011).

**NATURAL HISTORY.**— This species has been found in muddy sand with small pebbles. No prey items were found in the gizzard and no other information about its feeding ecology is known.

**DESCRIPTION.**—*External morphology:* The living animals (Fig. 1E) are 8 to 9 mm in length and 5 mm wide. The body color of the living animal is uniformly white with yellowish pigment in the mantle cavity on the ventral side. The roughly trapezoidal cephalic shield is longer than the posterior shield and is not indented posteriorly. The parapodia are relatively short, reaching the cephalic shield, but leaving the anterior and posterior shields almost entirely visible (Fig. 7A). The posterior end of the posterior shield is blunt and has a rounded posterior terminal. The gill is simply plicate consisting of eight primary folds and is situated ventrally on the right posterior end of the animal.

*Shell* (Fig. 6A): The shell was damaged during collection in the trawl and was fragmented. It was quite broad with a relatively low profile, where it occupies the majority of the posterior shield. Most of the shell lacks sculpture but the innermost whorls show remnants of spiral sculpture that is partially covered by a smooth outer layer of additional calcification.

*Digestive system* (Figs. 6B–E, 7B): The buccal mass is relatively small, occupying the anterior quarter of the anterior shield. The buccal bulb has a relatively small radula. The radular formula in the paratype specimen is 20 x 1.1.0.1.1. (Fig. 6D). The inner lateral teeth (Fig. 6E) are large and broad with a curved prominent cusp. Their masticatory margin has a series of up to 64 elongate, closely crowded denticles. The outer lateral tooth is narrow and elongate with an elongate, curved cusp. There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of short salivary glands. The gizzard is large and highly muscular (Fig. 7B), much wider than the buccal bulb. There are three equal-sized gizzard plates (Fig. 6B) that are elongate with rounded apices. The central region contains an elongate, narrow longitudinal bar that occupies the central third of the plate. On the outer sides of bar is a pair of large, deep ovoid depressions. There is no organized pattern of fine microscopic network on the gizzard plates, although a fibrous network is evident (Fig. 6C). The gizzard narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 7C): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single suprainestinal ganglion immediately posterior to the right pleural ganglion. The cerebral and pedal commissures are both somewhat elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop the osphradial nerve extends posteriorly from the suprainestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which does not appear to have a distinct genital ganglion.

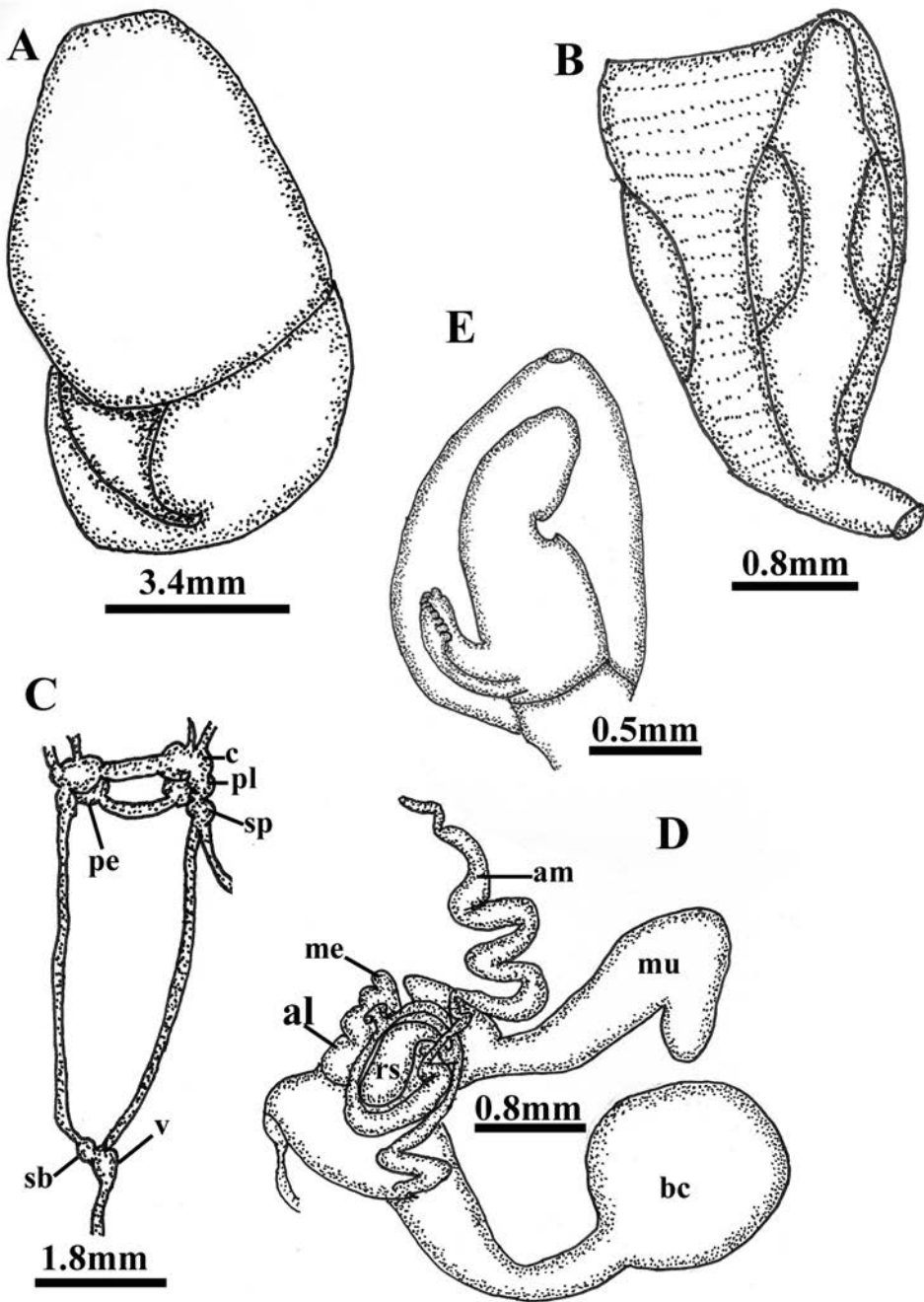


FIGURE 7. Internal anatomy of *Philine dentiphallus* sp. nov., paratype, CASIZ 1893377. A. Ventral view of preserved animal. B. Muscularized gizzard. C. Central nervous system, c = cerebral ganglion, pe = pedal ganglion, pl = pleural ganglion, sb = subintestinal ganglion, sp = supraintestinal ganglion, v = visceral ganglion. D. Posterior reproductive organs, al = albumen gland, am = ampulla, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis. E. Detail of penial sac and penial papilla.



*Reproductive System* (Figs. 6F, 7D–E): The reproductive system is fully mature. The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands (Fig. 7D). From the large ovotestis, which is intermingled with the digestive gland, emerges the wide, convoluted ampulla. The ampulla narrows and appears to have a short proximal receptaculum seminis at the point where the hermaphroditic duct again widens and curves around the large distal receptaculum seminis. The duct again narrows at the point where it enters the albumen and membrane glands. The albumen and membrane glands are small. The larger mucous gland is bilobed with a large primary lobe and small secondary one. After branching to the female glands, the hermaphroditic duct is elongate and narrow and extends to the genital aperture where it then joins the short duct of the large, pyriform distal receptaculum seminis and continues to the genital atrium, where it joins the elongate duct of the bursa copulatrix. The bursa is large and spherical. Its duct is wide throughout its length but is widest at the genital atrium. There are no secondary bursae evident in the specimen dissected. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 6F) consists of a broad penial sac and an elongate, highly branched, posteriorly directed prostate gland and associated ducts that characterize members of the *Philine aperta* clade. There is a large, wide retractor muscle situated on the ventral surface of the penis. Within the penial sac a large bulbous penial papilla with a large lateral flange that terminates in a curved area that has a series of comb-like denticles along its outer surface (Fig. 7E).

**REMARKS.**— This species is most morphologically similar to *Philine auriformis* Suter, 1909, and *P. fenestra* Price, Gosliner and Valdés, 2011. All three of these species have three equal-sized gizzard plates with an elongate central bar, flanked by a pair of depressions. The posterior shield of *P. auriformis* has widely distinct lobes that are widely separated by a distinct notch that is not evident in either *P. dentiphallus* or *P. fenestra*. The shell of *P. dentiphallus* is wide and largely smooth as in *P. auriformis*, whereas that of *P. fenestra* is narrower, with punctate sculpture throughout. All three species have radular teeth with rows of denticulate inner lateral teeth and rows of single outer lateral teeth. In *P. fenestra* (Price et al., 2011), the inner lateral tooth has fewer denticles (35–50) that are more widely spaced than those of *P. dentiphallus*, which has about 64 denticles. In *P. auriformis* there are 30–50 denticles (Gosliner 1995). The outer lateral teeth of *P. fenestra* are narrow but almost as elongate as the inner lateral teeth, whereas in *P. auriformis* and *P. dentiphallus* the outer laterals are much shorter than the inner laterals. The gizzard plates of *P. dentiphallus* and *P. auriformis* have a narrow bar and two relatively lateral depressions that occupy about a third of the length of the plate, whereas in *P. fenestra* the central bar is much broader and the depressions are narrower and far more elongate. In both *P. auriformis* and *P. fenestra* the penial papilla is simple and hammer-shaped, whereas it is bulbous with a lateral denticulate flange in *P. dentiphallus*.

***Philine verdensis* Gonzales and Gosliner, sp. nov.**

Figures 1F, 8–9

**MATERIAL EXAMINED.**— HOLOTYPE: CASIZ 192089, ST HEPD 21, beam trawl in muddy sand, 132–172 m depth, western end of Verde Island Passage, off northwest tip of Lubang Island, Batangas Province, Luzon, Philippines, 13.888167°N, 120.1075°E, 1 June 2011, Hearst Expedition Deep Sea Team. PARATYPE: dissected, CASIZ 189338, ST HEPD 21, beam trawl in muddy sand, 132–172 m depth, western end of Verde Island Passage, off northwest tip of Lubang Island, Batangas Province, Luzon, Philippines, 13.888167°N, 120.1075°E, 1 June 2011, Hearst Expedition Deep Sea Team.

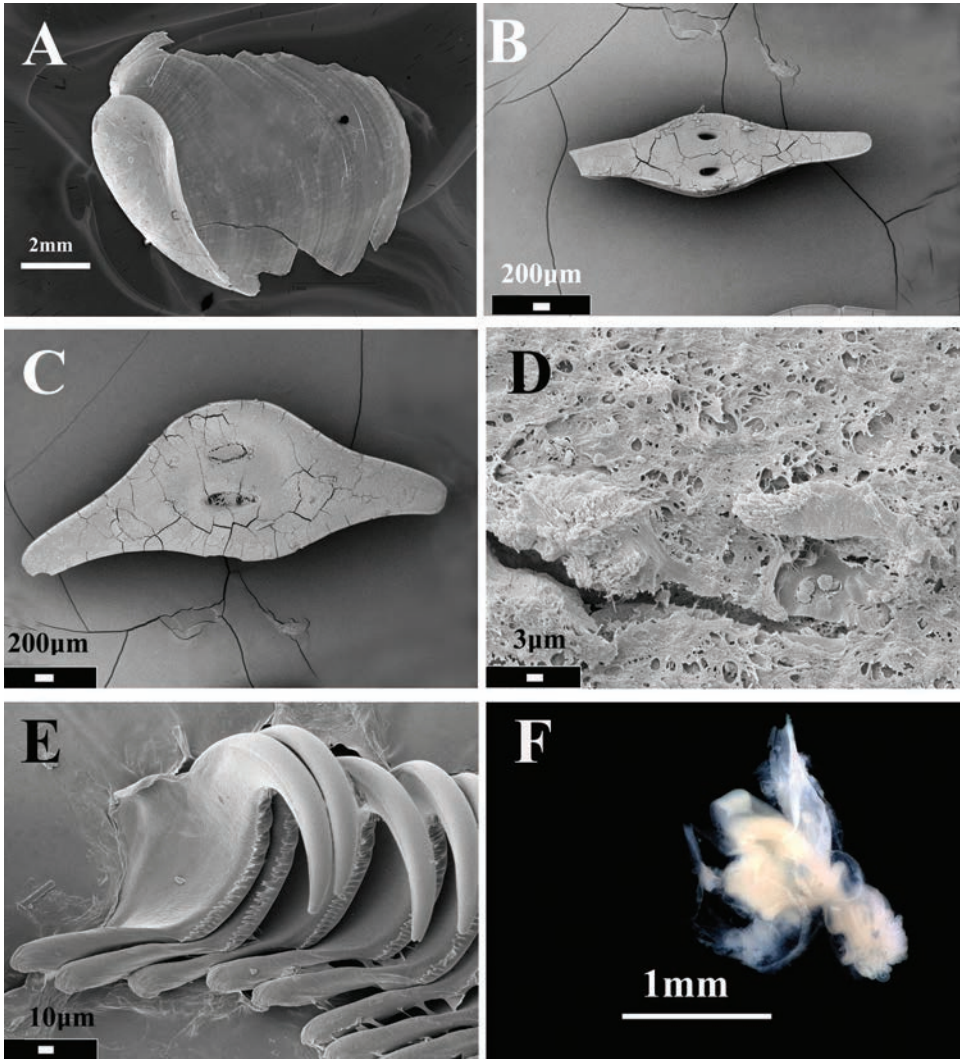


FIGURE 8. Internal anatomy of *Philine verdensis* sp. nov., paratype, CASIZ 1893378. A. Shell. B. Scanning electron micrograph of unpaired gizzard plate. C. Scanning electron micrograph of paired gizzard plate. D. Scanning electron micrograph of gizzard plate microsculpture. E. Radular teeth. F. Light micrograph of penis and prostate.

**GEOGRAPHICAL DISTRIBUTION.**— Thus far, this species is known only from the western end of the Verde Island Passage, separating southern Luzon and northern Mindoro.

**ETYMOLOGY.**— The name *verdensis* refers to the Verde Island Passage, the only locality from which this species is known.

**NATURAL HISTORY.**— This species has been found in muddy sand in 132–172 m depth. No prey items were found in the gizzard and no other information about its feeding ecology is known.

**DESCRIPTION.**— *External morphology.* The living animals (Figs. 1F) are up to 17 mm in length 10 mm wide. The body color of the living animal is uniformly white with yellowish pigment on the anterior end of the cephalic shield and in the mantle cavity on the ventral side. The roughly trapezoidal cephalic shield is longer than the posterior shield and is not indented posteriorly. It is widest anteriorly and tapers to a blunt posterior end. The parapodia are relatively short (Fig. 9A), reaching the cephalic shield, but leaving the anterior and posterior shields almost entirely visible. The posterior end of the posterior shield blunt and has a rounded posterior terminal (Fig. 9B). The gill is simply plicate consisting of eight primary folds and is situated ventrally on the right posterior end of the animal.

*Shell* (Fig. 8A): The shell was slightly damaged during collection in the trawl. It is quite broad with a relatively low profile, where it occupies the majority of the posterior shield.

The shell lacks any obvious sculpture, but spiral growth lines are evident over the shell surface.

*Digestive system* (Figs. 8B–E, 9C): The buccal mass is relatively small, occupying the anterior quarter of the anterior shield. The buccal bulb has a relatively small radula. The radular formula in the paratype is 18 x 1.0.1. The inner lateral teeth are large (Fig. 8E) and broad with a curved prominent cusp. Their masticatory margin has a series of up to 45 elongate, closely-crowded denticles. Outer lateral teeth are absent. There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of short salivary glands. The gizzard is large and highly muscular, much wider than the buccal bulb. There are unequal gizzard plates (Fig. 9C) that are elongate with rounded apices. The unpaired plate is smaller (Fig. 8B) than the paired plates (Fig. 8C) and all plates have paired holes that are large in size. There is not an organized pattern of fine microscopic network on the gizzard plates, although a fibrous network is evident (Fig. 8D). The gizzard narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 9D): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single suprainestinal ganglion immediately posterior to the right pleural ganglion. The cerebral and pedal commissures are both somewhat elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia, which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop the osphradial nerve extends posteriorly from the suprainestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which does not appear to have a distinct genital ganglion.

*Reproductive System* (Figs. 8F, 9E, F): The reproductive system is not fully mature. The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands (Fig. 9E). From the large ovotestis, which is intermingled with the digestive gland, emerges the narrow, convoluted ampulla. The ampulla narrows further at the point where the hermaphroditic duct again

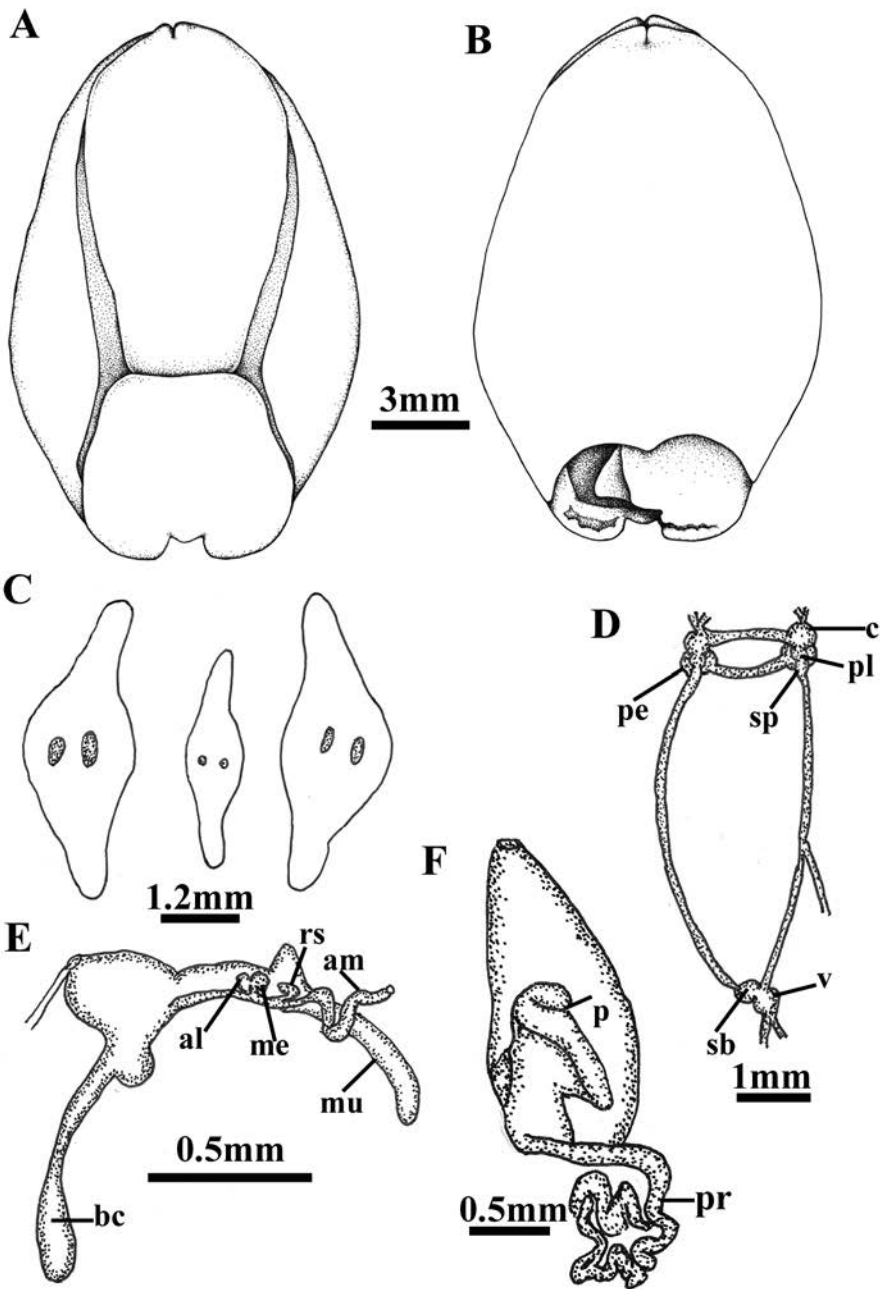


FIGURE 9. Internal anatomy of *Philine verdensis* sp. nov., paratype, CASIZ 1893378. A. Dorsal view of preserved specimen, drawing by Emily Eng. B. Ventral view of preserved specimen, drawing by Emily Eng. C. Gizzard plates. D. Central nervous system, c = cerebral ganglion, pe = pedal ganglion, pl = pleural ganglion, sb = subintestinal ganglion, sp = supraintestinal ganglion, v = visceral ganglion. E. Posterior reproductive organs, al = albumen gland, am = ampulla, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis. F. Penis and penial papilla, p = penial papilla, pr = prostate.

widens and curves around the curved distal receptaculum seminis. The duct again narrows at the point where it enters the albumen and membrane glands. The albumen and membrane glands are small. The larger mucous gland is bilobed with a large primary lobe and small secondary one. After branching to the female glands, the hermaphroditic duct is elongate and narrow and extends to the genital aperture where it then joins the short duct of the small, curved distal receptaculum seminis and continues to the genital atrium, where it joins the elongate duct of the bursa copulatrix. The bursa is small and pyriform. Its duct is wide throughout its length but is widest at the genital atrium. There are no secondary bursae evident in the specimen dissected, but there is a swelling at the base of the bursa duct. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Figs. 8E, 9F) is not fully mature and consists of a broad penial sac and a relatively short, compact, highly branched, posteriorly directed prostate gland and associated ducts that characterize members of the *Philine aperta* clade. Within the penial sac, a large hammer-shaped penial papilla with lobate flap on the anterior side of the lobed papilla (Fig. 9F). The papilla lacks any armature or other ornamentation, but was not entirely mature.

**REMARKS.**—This species is similar externally to other members of the *Philine aperta* clade (Price et al. 2011). Of the species known from deep water in the Indo-Pacific, *P. habeii* Valdés, 2008, *P. rubra* Bergh, 1905, and *P. puka* Price, Gosliner, and Valdés, 2011, have a radula with no outer lateral teeth and have gizzard plates with a pair of relatively large pits on each gizzard plate. *Philine puka* has a narrower body shape than does either *P. habeii* or *P. verdensis*. The body shape of *P. rubra* is unknown. Also, *P. puka* reaches a maximum length of 10 mm (Price et al. 2011) and is entirely sexually mature at that size, while a 17 mm specimen of *P. verdensis* was not fully mature. The inner lateral teeth of *P. habeii* were described as lacking denticles, whereas the inner teeth of both *P. puka* and *P. verdensis* have a large number of denticles on the laterals. One specimen identified here as *P. habeii* (CASIZ 177499) from the Philippines has a radula where most of the older radular teeth appear quite worn with only rudimentary denticles, whereas the newer teeth have strongly pronounced denticles. Rudimentary denticles also appear to be visible in Valdés' figure of *P. habeii* (2008: fig. 64a). Much of the anatomy of *P. rubra* remains undescribed, but the penis is shown as having a distinct vesicle attached to the base of the penial sac that is not evident in the other species. Details of the penial papilla were not described for *P. rubra*, and it is likely that this species will remain unidentifiable owing to the incompleteness of the original description.

Other morphological differences also appear to differentiate *P. verdensis*, *P. habeii*, and *P. puka*. In *P. verdensis*, the pores of the paired gizzard plates are oblong with one of the pores being markedly larger than the other. In *P. puka* and *P. verdensis*, the paired holes are very similar in size. The unpaired gizzard plate of *P. puka* and *P. verdensis* is much smaller than the paired plates whereas in *P. habeii* all three plates are similar in size. The microstructure of the gizzard plates also differs in the three species. In *P. puka*, there is a distinct honey-combed pattern present, whereas in *P. habeii* (present study) there is some organization of a honeycomb pattern, but it is not as highly organized as in *P. puka*. In *P. verdensis*, there is no indication of any organized microstructural pattern. The penial papilla of *P. verdensis* is hammer-shaped with a prominent flap on the anterior lobe, whereas in *P. habeii* the penial papilla is asymmetrical with one lobe larger than the other or more or less equally lobed (present study). The penis of *P. puka* is smaller with markedly unequal lobes and a very short base.

In the molecular phylogenetic analysis (Fig. 14), *P. verdensis* and *P. habeii* are sister species, but have a p-distance of 4.2% in their 16S mitochondrial genes. This strongly supports them being considered as distinct species. Previously, Krug et al. (2012) found that separate species of *Philine* have 16S p values greater than 1.0%, while separate populations of members of the same species had p values between 0.2–0.3%.

***Philine pittmani* Gonzales and Gosliner, sp. nov.**

Figures 1G–H, 10, 11

**MATERIAL EXAMINED.**—HOLOTYPE: CASIZ, 192090, sand sample, 6–17 m, Black Rock, Maui, Hawai'i, 8 April 2011, Cory Pittman. PARATYPES: CASIZ, 185213, dissected, one specimen, sand sample, 6–17 m, Black Rock, Maui, Hawai'i, 8 April 2011, Cory Pittman. CASIZ 163775, one specimen, dissected, in sample of collected sand dwelling *Halimeda*, 10–18 m, Airport Beach, Maui, Hawai'i, 9 October 2000, Cory Pittman. CASIZ 166768, two specimens, *Halimeda incrasita* bed and open sand, 6–11 m depth, Black Rock, Maui, Hawai'i, 14 April 2003, Cory Pittman. CASIZ, 118253, 1 specimen, *Halimeda opuntia* beds, algal wash, Airport Beach, Maui, Hawai'i, 10 May 1999, T.M. Gosliner and P. Fiene. CASIZ 192091, one specimen, algal wash, 3–8 m, Makena Landing, Maui, Hawai'i, 12 August 2002, Cory Pittman.

**GEOGRAPHICAL DISTRIBUTION.**— Thus far, this species is known only from the Maui in the Hawai'ian Islands.

**ETYMOLOGY.**— The name *pittmani* honors Cory Pittman who has been intensely studying the Hawai'ian opisthobranch fauna for nearly two decades and, together with Pauline Fiene, has documented the diversity of this insular fauna. Cory has discovered many new taxa, including the species described here.

**NATURAL HISTORY.**— This species has been found in fine sand basins and burrowed in *Halimeda kanaloana* beds in 3–17 m depth. No prey items were found in the gizzard and no other information about its feeding ecology is known. This species produces a lozenge-shaped to spherical, white egg mass containing a tangled egg string. The mass has a sticky surface and acquires a coating of strongly adherent sand. Hatching of veliger larvae occurs in 5–6 days in the laboratory.

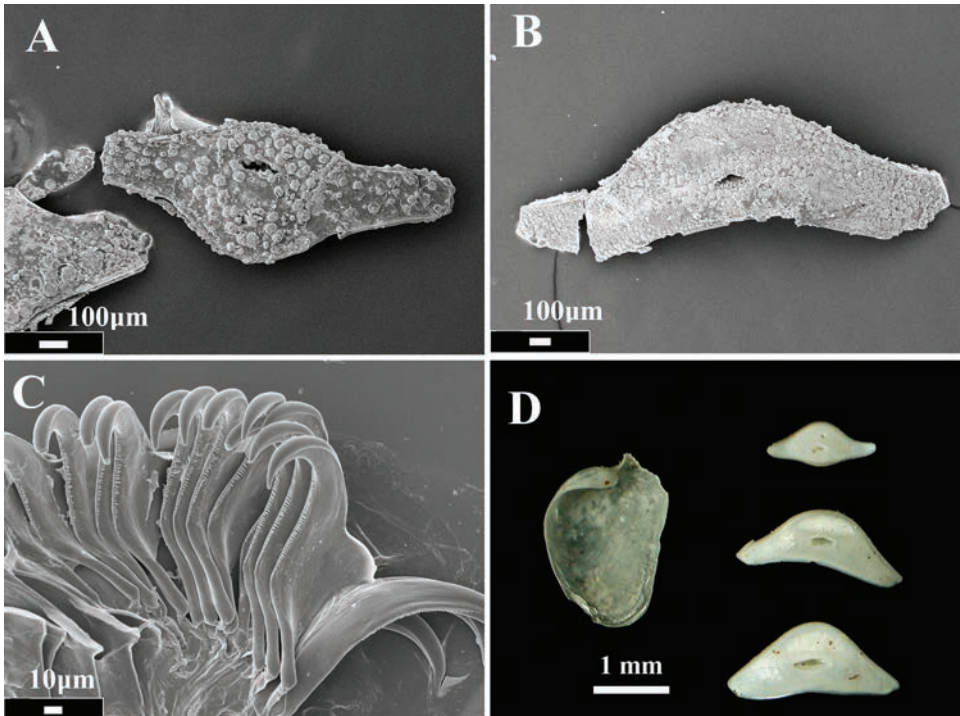


FIGURE 10. Internal anatomy of *Philine pittmani* sp. nov., paratype, CASIZ 163775. A. Scanning electron micrograph of unpaired gizzard plate. B. Scanning electron micrograph of paired gizzard plate. C. Scanning electron micrograph of half-row of radular teeth. D. Shell and gizzard plates, photograph by C. Pittman.

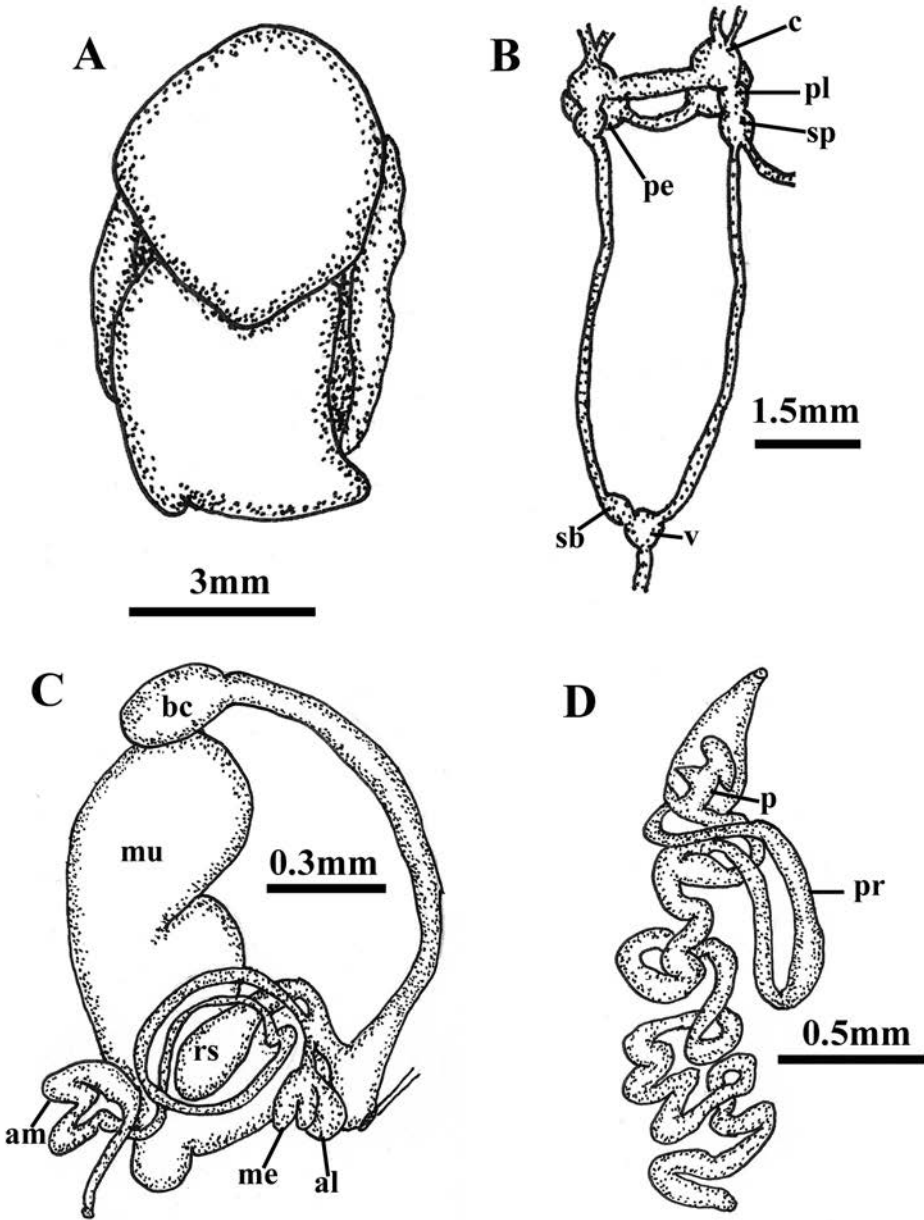


FIGURE 11. Internal anatomy of *Philine pittmani* sp. nov., paratype, CASIZ 163775. A. Dorsal view of preserved animal. B. Central nervous system, c = cerebral ganglion, pe = pedal ganglion, pl = pleural ganglion, sb = subintestinal ganglion, sp = supraintestinal ganglion, v = visceral ganglion. C. Posterior reproductive organs, al = albumen gland, am = ampulla, bc = bursa copulatrix, me = membrane gland, mu = mucous gland large, rs = receptaculum seminis. D. Penis, p = penial papilla, pr = prostate.

**DESCRIPTION.**—*External morphology:* The living animals (Figs. 1G,H) are narrow and elongate, 3 to 13.5 mm in length and about 4 mm wide in the largest specimens. The cephalic shield is two to three times the length of the posterior shield. The parapodia are extremely short (Fig. 11 A), and narrow, barely reaching the cephalic shield, and leaving the anterior and posterior shields entirely visible. The posterior end of the posterior shield is blunt and has a pair of elongate extensions. The gill is simply plicate consisting of five primary folds and is situated ventrally on the right posterior end of the animal.

The body color of the living animal is uniformly translucent white with opaque white speckling over the surface of the animal. The opaque white pigment of the gizzard plates is visible through the translucent body, as is the golden brown pigment of the shell.

*Shell* (Fig. 10D): The shell is wide and open with a thickened posterior margin, where it occupies the majority of the posterior shield.

The shell lacks sculpture but growth lines are evident over its surface. The posterior flange is elongate with a series of irregular denticles along the margin.

*Digestive system* (Fig. 10): The buccal mass is large and elongate, occupying the anterior two-thirds of the anterior shield. The buccal bulb has a relatively small radula. The radular formula in one paratype specimen (CASIZ 163775) is 18–21 x 1.0.1. The inner lateral teeth (Fig. 10C) are large and broad with a curved prominent cusp. Their masticatory margin has a series of up to 52 elongate, closely crowded denticles. Outer lateral teeth are absent. There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of short salivary glands. The gizzard is large and highly muscular, much wider than the buccal bulb. There are three unequally-sized gizzard plates that are elongate with rounded apices. The unpaired plate (Figs. 10A, D) is smaller than the two paired plates (Fig. 10B,D). The central region contains two pores, one that is larger and more elongate and a smaller one that is circular (Fig. 10D). The two paired plates differ in size (Fig. 10D) and each of them has only a single elongate pore. There is organized pattern of fine honeycombed microscopic network on the gizzard plates, although it is not well organized. The gizzard narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 11B): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single suprainestinal ganglion immediately posterior to the right pleural ganglion. The cerebral and pedal commissures are both somewhat elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia, which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop the osphradial nerve extends posteriorly from the suprainestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which does not appear to have a distinct genital ganglion.

*Reproductive System* (Figs. 11C–D): The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands (Fig. 11C). From the large ovotestis, which is intermingled with the digestive gland, emerges the wide, convoluted ampulla. The ampulla narrows considerably. After the hermaphroditic duct crosses over the receptaculum seminis, it widens and curves around the distal surface of the pyriform receptaculum. The duct completes a circle around the receptaculum and branches to the albumen and membrane glands and also receives the duct of the receptaculum.



ulum. The duct widens as it enters the common genital atrium and meets the elongate duct of the bursa copulatrix. The bursa is relatively small and oblong. The genital atrium is relatively wide and somewhat muscular and opens into the ciliated sperm groove. The albumen and membrane glands are small. The larger mucous gland is bilobed with a large primary lobe and small secondary one. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 11D) consists of a narrow penial sac and an elongate, branched, posteriorly directed prostate gland and associated ducts that characterize members of the *Philine aperta* clade. There is a large, wide retractor muscle situated on the ventral surface of the penis. Within the penial sac a small, elongate penial papilla with a narrow hammer-shaped papilla that is rounded apically. Below the papilla is a triangular, acutely pointed lobe

**REMARKS.**— By virtue of its gizzard plates with pores and complex penis and prostate, this species is clearly a member of the *Philine aperta* complex. It is the only member of this complex that has paired gizzard plates with only a single pore. The only other member of this complex with a narrow, elongate body and narrow parapodia is *P. elegans* Bergh, 1905 (Price et al. 2011, fig. 1D).

This species differs markedly from *P. pittmani* in its internal anatomy. The gizzard plates of *P. elegans* have a series elongate fibriate extensions along the lateral margins of the plate (Price et al. 2011, figs. 16A–B). Additionally all gizzard plates of *P. elegans* have two pores, while in *P. pittmani*, the two paired gizzard plates have only a single pore. Also the surface of the gizzard plates of *P. elegans* is tuberculate, while it is smooth in *P. pittmani*. The radula of *P. elegans* also lacks outer lateral teeth but has far fewer denticles (33) than do those of *P. pittmani* (52). The penial papilla of *P. pittmani* has a relatively small penial papilla with equal lobes of the hammer-shaped papilla, while *P. elegans* has a much larger papilla with markedly unequal lobes. Additionally, *P. pittmani* has an acutely pointed appendage below the papilla that is absent in *P. elegans*.

***Philine multipapillata* Gonzales and Gosliner, sp. nov.**

Figures 12–13

**MATERIAL EXAMINED.**— HOLOTYPE: dissected, CASIZ 172841, ST T2, trawl in coarse sand and mud, 150 m depth, south of Alona Kew, Panglao, Bohol, Philippines, 9°32.4'N, 123°47.8'E, 31 May 2004, Panglao Expedition team.

**GEOGRAPHICAL DISTRIBUTION.**— Thus far, this species is known only from the Visayas region of the Philippines from the coast of Bohol.

**ETYMOLOGY.**— The name *multipapillata* refers numerous conical papillae that ornament the surface of the penial papilla.

**NATURAL HISTORY.**— This species has been found in sand and mud in 150 m depth. No prey items were found in the gizzard and no other information about its feeding ecology is known.

**DESCRIPTION.**—*External morphology:* The living animals have not been observed, but the preserved holotype (Fig. 13A) is 9 mm in length 4 mm wide. The cephalic shield is longer than the posterior shield and the parapodia are short and narrow, barely covering the cephalic and posterior shields. The cephalic shield is not indented posteriorly and is blunt and slightly curved. The posterior shield is slightly bilobed posteriorly. The body color of the preserved animal is uniformly white. The posterior shield is not indented posteriorly. The gill is simply plicate consisting of ten primary folds and is situated ventrally on the right posterior end of the animal.

*Shell.* The shell was badly fragmented during collection in the trawl and is not illustrated here. It appears that it was quite broad with a relatively low profile, where it occupies the majority of the posterior shield. The shell lacks sculpture but evidence of growth lines can be found on the remaining fragments.

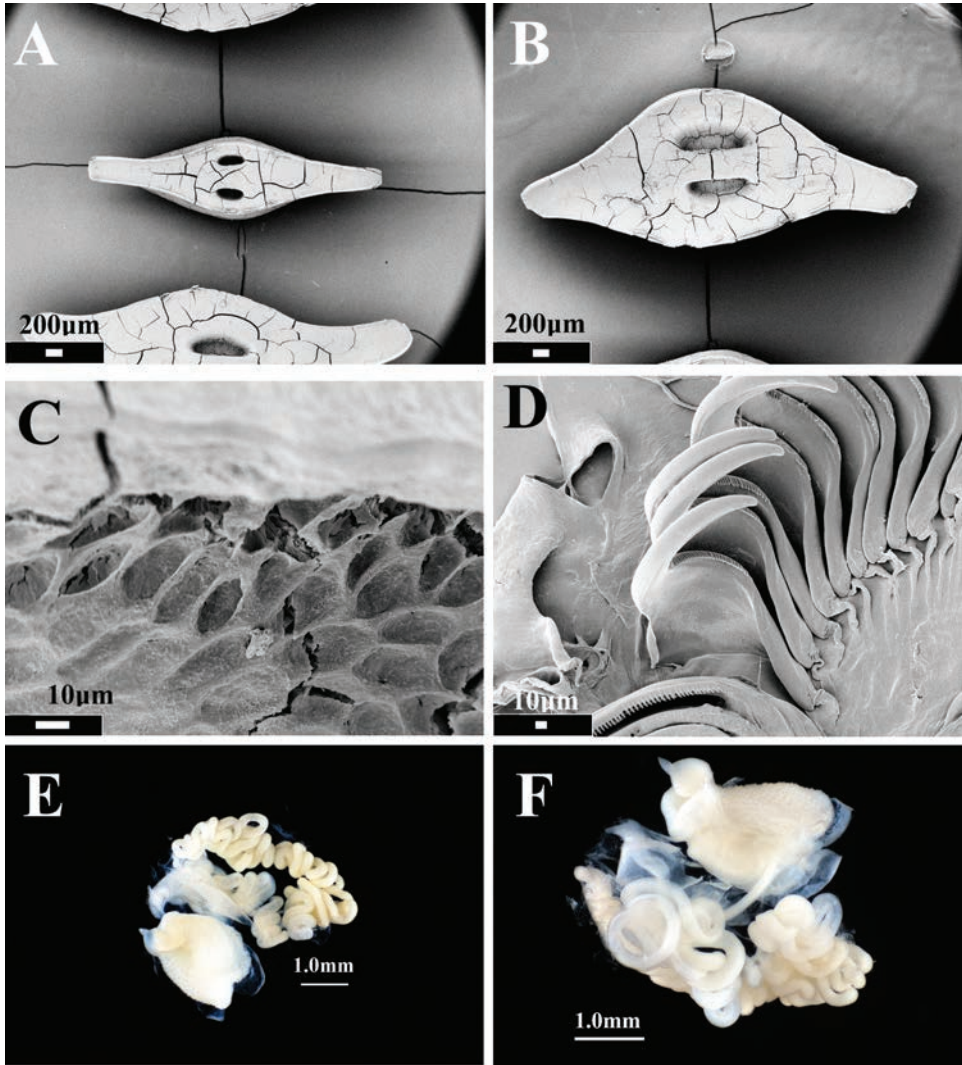


FIGURE 12. Internal anatomy of *Philine multipapillata* sp. nov., holotype, CASIZ 172841. A. Scanning electron micrograph of unpaired gizzard plate. B. Scanning electron micrograph of paired gizzard plate. C. Scanning electron micrograph of gizzard plate microstructure. D. Scanning electron micrograph of half-row of radular teeth. E. Dorsal light micrograph of penis. F. Ventral light micrograph of penis.

**Digestive system** (Fig. 12A-D, 13B): The buccal mass is relatively small, occupying the anterior quarter of the anterior shield. The buccal bulb has a relatively small radula. The radular formula in the holotype is  $20 \times 1.0.1$ . The inner lateral teeth (Fig. 12D) are large and broad with a curved prominent cusp. Their masticatory margin has a series of up to 56 elongate, closely crowded denticles. Outer lateral teeth are absent. There is a large ventral oral gland and small dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of short salivary glands. The gizzard is large and highly muscular, much wider than the buccal bulb. There are unequal gizzard plates (Fig. 13B) that are elongate with rounded apices. The unpaired plate is smaller (Fig. 12A) than the paired plates (Fig. 12B). All plates have paired holes that are elongate and large in size and are relatively equal in size. There is an organized pattern of honeycombed fine

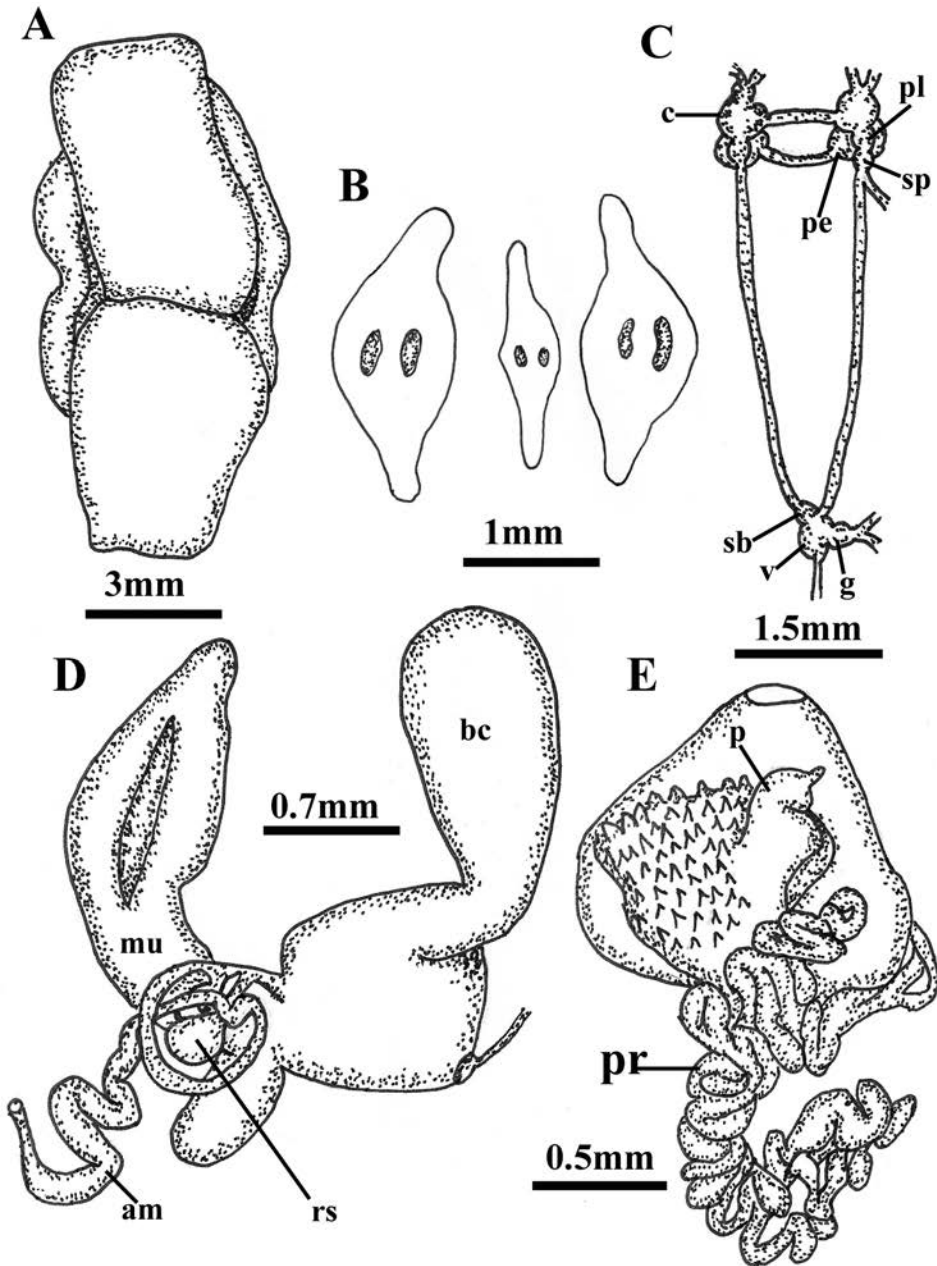


FIGURE 13. Internal anatomy of *Philine multipapillata* sp. nov., holotype, CASIZ 172841. A. Dorsal view of preserved animal. B. Gizzard plates. C. Central nervous system, c = cerebral ganglion, g = genital galion, pe = pedal ganglion, pl = pleural ganglion, sb = subintestinal ganglion, sp = suprainintestinal ganglion, v = visceral ganglion. D. Posterior reproductive organs, am = ampulla, bc = bursa copulatrix, mu = mucous gland, rs = receptaculum seminis. E. Penis showing detailed distribution of papillae, p = penial papilla, pr = prostate.

microscopic network on the gizzard plates, although a fibrous network is evident (Fig. 12C). The gizzard narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

*Central Nervous System* (Fig. 13C): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single suprainestinal ganglion immediately posterior to the right pleural ganglion. The cerebral and pedal commissures are both somewhat elongate with well-separated respective ganglia. On the ventral side of the buccal mass near the entrance of the esophagus are the buccal ganglia, which are immediately adjacent to each other. From the posterior end of the anterior nerve ring the right branch of the visceral loop the osphradial nerve extends posteriorly from the suprainestinal ganglion. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital ganglion which bifurcates into a paired genital nerves.

*Reproductive System* (Figs. 12E–F, 13D–E): The arrangement of reproductive organs is essentially monaulic (Fig. 13D) (as discussed by Gosliner 1994), but with a single branch of the hermaphroditic duct to the albumen and membrane glands. From the large ovotestis, which is intermingled with the digestive gland, emerges the wide, convoluted ampulla. The ampulla narrows considerably. After the hermaphroditic duct crosses over the receptaculum seminis, it widens and curves around the distal surface of the pyriform receptaculum. The duct completes a circle around the receptaculum and branches to the albumen and membrane glands and also receives the duct of the receptaculum. The duct then enters the massive, highly muscularized genital atrium near the wide duct of the bursa copulatrix. The large, ovoid bursa has a thin wall. The entire bursa duct is wide and short and curved. The albumen and membrane glands are small. The larger mucous gland is bilobed with a large primary lobe and small secondary one. There are no secondary bursae evident in the specimen dissected. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 12E–F, 13E) consists of a broad penial sac and an elongate, highly branched, posteriorly directed prostate gland and associated ducts that characterize members of the *Philine aperta* clade. There is a large, wide retractor muscle situated on the ventral surface of the penis. Within the penial sac a large bulbous penial papilla with a curved apex is present. The entire surface of the papilla is ornamented with conical papillae (Figs. 12E–F, 13E).

**REMARKS.**—Morphologically, *Philine multipapillata* is similar to other members of the *Philine aperta* clade in that it has gizzard plates with pores and a penial complex with a highly convoluted and branched prostate. It is the only member of this species complex with a penial papilla ornamented with numerous conical papillae. Like *P. habei*, *P. puka*, *P. rubra*, and *P. verdensis*, it has relatively large pores on the gizzard plates. It is similar to *P. puka*, *P. verdensis*, and *P. rubra*, in that the pores on the gizzard plates are more or less the same size, whereas in *P. habei*, they are markedly unequal. The microstructure of the gizzard plates also differs in the five species. In *P. puka*, there is a distinct honey-combed pattern present, whereas in *P. habei* and *P. multipapillata* (present study) there is some organization of a honeycomb pattern, but it is not as highly organized as in *P. puka*. In *P. verdensis*, there is no indication of any organized microstructural pattern. The microstructure remains unknown for *P. rubra*. All of these species have only inner lateral radular teeth and lack outer laterals. The denticles on the inner laterals of *P. verdensis* are more uneven than those of *P. multipapillata*, *P. puka*, and *P. rubra*. *Philine multipapillata* has more denticles on the inner lateral teeth (56) than do *P. puka* (39–44) or *P. verdensis* (45). The number of denticles was not described for *P. rubra*, but Bergh's figure seems to indicate there are fewer denticles than

in *P. multipapillata*. *Philine multipapillata* has a distinct genital ganglion present on the visceral loop of the central nervous system, whereas it appears to be absent in *P. habei*, *P. puka*, and *P. verdensis*. It has not been described in *P. rubra*. The penial papilla of *P. verdensis* is hammer-shaped with a prominent flap on the anterior lobe, whereas in *P. habei* the penial papilla is asymmetrical with one lobe larger than the other or more or less equally lobed (present study). The penis of *P. puka* is smaller with markedly unequal lobes and a very short base. None of these have a large penial papilla with dense conical papillae found in *P. multipapillata*. The shape of the penial papilla remains unknown for *P. rubra*. Based on these differences, it is clear that *P. multipapillata* is distinct from all other species described within the *P. aperta* clade.

### PHYLOGENETIC ANALYSIS

Our molecular phylogenetic analysis includes five species studied here plus *P. habei*, *P. orca*, and *P. rubrata* and those studied by Krug et al. (2012) and six other taxa from GenBank (Krug et al. 2012). The resulting maximum likelihood tree (using RAxML) molecular phylogeny is depicted in Figure 14.

In our analysis, *Philine verdensis* is most closely related to *P. habei*, but that sister group relationship is not strongly supported. The two species have a *p*-distance of just over 4% (Table 2) for the 16S gene, strongly supporting their distinctness as separate species. Currently, there are no molecular data for *P. puka* and *P. rubra*, the other two species with large pores on the gizzard plates. Together, *P. verdensis* and *P. habei* form a weakly supported sister-group relationship with *P. quadripartita*, *P. aperta*, *P. angasi*, *P. paucipapillata*, and an undescribed species from Australia. *Philine dentiphallus* appears as sister species to *P. auriformis* and *P. pittmani* is sister to both of these species, although these relationships are relatively weakly supported. *Philine acuticauda* is sister to *P. hearstorum* in our analysis and this relationship is strongly supported. Together these species form the sister group to the *Philine aperta* clade, but that relationship is weakly supported. The sister group to these *Philine* species includes seven species of aglajids and *Philine orca* and *P. rubrata*. The relationships within this clade are weakly supported.

TABLE 2. Minimum 16S pairwise uncorrected *p*-distance among *Philine* species described in this paper.

	<i>habei</i>	<i>verdensis</i>	<i>pittmani</i>	<i>dentiphallus</i>	<i>acuticauda</i>	<i>hearstorum</i>
<i>habei</i>	—					
<i>verdensis</i>	0.042	—				
<i>pittmani</i>	0.121	0.116	—			
<i>dentiphallus</i>	0.160	0.122	0.085	—		
<i>acuticauda</i>	0.169	0.147	0.137	0.166	—	
<i>hearstorum</i>	0.168	0.152	0.145	0.178	0.027	—
<i>auriformis</i>	0.105	0.104	0.072	0.067	0.155	0.162

### DISCUSSION

This work includes the description of six new species of *Philine* from the tropical Indo-Pacific. Both morphological and molecular data support the separation of these species. Four of the six species are members of the *Philine aperta* clade, a group that is already been shown to be well represented in the Indo-Pacific tropics (Price et al. 2011). The other two species, *P. acuticauda* and *P. hearstorum*, have the same radular morphology and gizzard plate morphology as *P. alba* Mattox, 1958, from the Pacific coast of California and *P. alboides*, from the Caribbean. The two new species represent the first members of this group known from the tropical Indo-Pacific.

Krug et al. (2012) conducted the first molecular phylogeny of *Philine*, but only included *Phi-*

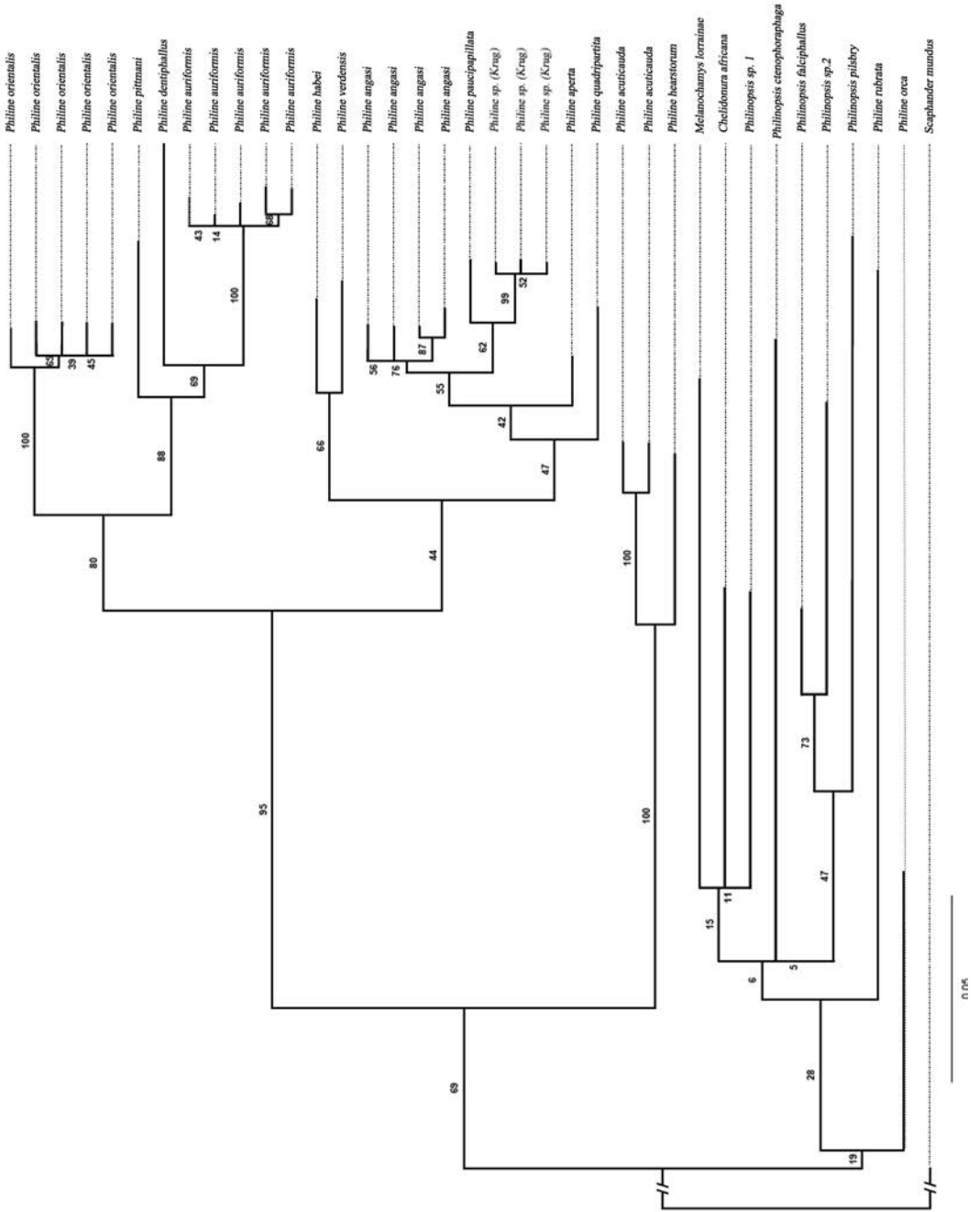


FIGURE 14. Phylogenetic relationships of *Philine* and other Philineacea.

*line aperta* clade members. Our analysis shows strong support for the *Philine aperta* clade, when additional *Philine* are included. A second phylogeny was recently published by Ohnheiser and Malaquias (2013) that focused upon COI sequences from North Atlantic species. Their study also shows strong support for the *Philine aperta* clade, but includes only two members of this group, *P. quadripartita* Ascanius, 1772 and *P. finmarchica* (M. Sars, 1859).

The present molecular study includes four additional species in *Philine aperta* clade: *P. habei*, *P. verdensis*, *P. pittmani* and *P. dentiphallus*. In our analysis, *P. habei* and *P. verdensis* are sister taxa to each other and are collectively the sister taxon to the clade that includes *P. aperta*, *P. quadripartita*, *P. paucipapillata*, *P. sp. 1* (from Australia), and *P. angasi*. These taxa also formed a clade in Krug et al.'s (2012) study, but in our study *P. quadripartita* and *P. aperta* are more basally situated than in the previous study. However, these relationships are weakly supported. The two additional species, *P. pittmani* and *P. dentiphallus*, are most closely related to *P. auriformis*, and collectively these three taxa are sister to *P. orientalis*. In Krug et al. (2012), *P. orientalis* was sister to the clade containing *P. paucipapillata*, *P. sp. 1*, *P. aperta*, *P. quadripartita*, and *P. angasi*. While there are slight variations in the relationships, the same general patterns of relationship persist in the present study, when additional taxa are added. Morphological studies also support the relationship of *P. dentiphallus* with *P. auriformis*, since both of these species, together with *P. fenestra* Price, Gosliner, and Valdés, 2011, are the only members of the *P. aperta* clade with a radula with an outer lateral tooth and gizzard plates with a solid central bar rather than simple paired pores. No molecular data are available for *P. fenestra*. *Philine pittmani* is sister to *P. dentiphallus* and *P. auriformis*. It is unusual for members of this clade in that its paired gizzard plates have only a single pore, but its radula lacks outer lateral teeth, unlike *P. auriformis* and *P. dentiphallus*.

In our analysis, *P. hearstorum* and *P. acuticauda* are sister to each other and collectively are sister to the *P. aperta* clade. As noted above, *P. alba* and *P. alboides* have morphological similarities to *P. hearstorum* and *P. acuticauda*, but no material suitable for molecular sequencing is available for the two former species.

Another weakly supported finding from this study is that *P. orca* Gosliner, 1988 and *P. rubrata* Gosliner, 1988, are both nested at the base of the Aglajidae rather than within the rest of the *Philine* species. It is interesting to note that these species have distinctively pigmented bodies, unlike other *Philine* species, as well as a muscular gizzard that lacks plates. A pigmented body and lack of gizzard plates are also characteristics of the Aglajidae. These features suggest that these species of *Philine* may be more closely related to Aglajidae than to Philinidae. Another species that has a pigmented body, lacks gizzard plates and has a similar radular morphology to *P. orca* and *P. rubrata* is *P. quadrata* (Wood, 1839). *Philine quadrata* was studied by Ohnheiser and Malaquias (2013), but only its COI mitochondrial sequences were studied and no molecular comparisons can be made at this time.

The phylogeny presented here strongly suggests that gizzard plates have been lost at least twice in independent lineages of Philinacea. Within *Philine*, *P. acuticauda* lacks gizzard plates while its sister taxon, *P. hearstorum* still has well-developed plates. The species of *Philine* that are nested with the lineage that also includes the Aglajidae also entirely lack gizzard plates, while the outgroup, *Scaphander*, has well-developed gizzard plates. This suggests a second loss of plates in this lineage, independently from that found in *P. acuticauda*.

The present study presents data that further documents the high species richness of the Indo-Pacific tropics, especially within the deeper waters of the Coral Triangle. The *Philine aperta* clade, appears to be particularly rich in its diversity. Phylogenetically, this clade has been reasonably well studied, but examination of additional genes will hopefully increase the robustness of support for various lineages within the clade as more of its diversity is discovered.

Support values are generally low for most basal relationships, but are still presented here to suggest possible relationships and areas for future study.

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