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Like a bat out of heaven: the phylogeny and diversity of the bat-winged slugs (Heterobranchia: Gastropteridae)

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A molecular phylogeny is presented for 25 newly sequenced specimens of Gastropteridae. The present phylogeny was estimated by analysing the nuclear fragment *28S* and two mitochondrial fragments cytochrome *c* oxidase I (*COI*) and *16S* using maximum likelihood and Bayesian analyses. The distinctness of eight new species of Gastropteridae is supported by the molecular phylogeny and by subsequent Automatic Barcode Gap Discovery (ABGD) analysis. Morphological data also support the distinctness of these species. The following species are described here: ***Gastropteron minutum*** Ong and Gosliner **sp. nov.**, ***Gastropteron multo*** Ong and Gosliner **sp. nov.**, ***Sagaminopteron multimaculatum*** Ong and Gosliner **sp. nov.**, ***Siphopteron vermiculum*** Ong and Gosliner **sp. nov.**, ***Siphopteron flavolineatum*** Ong and Gosliner **sp. nov.**, ***Siphopteron nakakatuwa*** Ong and Gosliner **sp. nov.**, ***Siphopteron makisig*** Ong and Gosliner **sp. nov.** and ***Siphopteron dumbo*** Ong and Gosliner **sp. nov.** All of these species, spanning much of the phylogenetic tree of Gastropteridae, are found in a single, highly diverse region of the Philippines, the Verde Island Passage. These data support the hypothesis that this region is an area of high species richness as well as phyletic diversity. This study also supports strong correlation between morphological characters and the molecular phylogeny within the species of *Siphopteron*. Molecular studies also indicate the distinctness of specimens of *Siphopteron quadrispinosum* from Hawaii and those from the western Pacific. Western Pacific specimens should be regarded as *Siphopteron leah*. *Siphopteron pohnpei* is transferred to *Sagaminopteron* based on the molecular phylogeny. Other species complexes indicating the presence of geographically separated cryptic species indicate that further detailed study of this group is warranted and that hidden diversity is likely to increase with additional study.

ADDITIONAL KEYWORDS: biogeography – Cephalaspidea – coral reefs – Coral Triangle – cryptic species – molecular phylogeny – morphology – new species – species richness.

INTRODUCTION

Gastropteridae is a group of fairly diverse marine snails with 33 described species in four genera (World Register of Marine Species, 2015). Gastropterids are biologically intriguing cephalaspideans that have a reduced internal shell or have lost the shell entirely as adults. They have a shortened body, a relatively small body size (usually <10 mm, but always <35 mm in the largest species). They have large parapodia and are capable of swimming by flapping their parapodia. This behaviour has been the basis for calling these organisms 'bat-winged slugs'. The nervous system is among the most highly cephalized of cephalaspideans and perhaps their elaborate behaviour can be attributed to this level of ganglionic concentration. Ecologically, little is known about the feeding of gastropterids, with the exception that most species of *Sagaminopteron* Tokioka & Baba, 1964 are found and have been observed eating sponges that lack spicules (Carlson & Hoff, 1973; Gosliner, Behrens & Valdés, 2008). Many species of *Siphopteron* Gosliner, 1989 have complex penial morphology, with elaborate rows of spines and more than a single papilla. Lange, Wermkinghausen &

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Anthes (2013) investigated the complex mating behaviour of *Siphopteron* and demonstrated that the elaboration of penial armature in several species was related to the employment of hypodermic insemination.

The overwhelming majority of species are found in the Indo-Pacific tropics or in adjacent temperate regions (Gosliner *et al.*, 2008). While this is a typical pattern of diversity, the extent of distribution of many of these tropical species is poorly understood and there appear to be many undescribed species inhabiting this largest portion of the world's oceans.

The taxonomic history of Gastropteridae clearly indicates that the overwhelming majority of species have been described only in the last 60 years. *Gastropteron* Kosse, 1813 is the only genus that has representative species in both the Atlantic and the Indo-Pacific. While Gastropteridae was established in the early 19th century, only three species had been described up until 1964, when Tokioka & Baba (1964) named four new species of Gastropteridae in the genera *Gastropteron* and *Sagaminopteron*. The following year, Baba & Tokioka (1965) added two additional species of *Gastropteron* to the family. Minichev (1967) described *Enotepteron*, with the monotypic species, *Enotepteron flavum* Minchev, 1967. Carlson & Hoff (1973) described two new species of *Sagaminopteron* from Guam and the following year described one new species of *Sagaminopteron* and three new species of *Gastropteron* that were transferred later to *Siphopteron* (Gosliner, 1989). A decade later, Hoff & Carlson (1983) described *Gastropteron pohnpei* Hoff & Carlson, 1983, which was transferred later to *Siphopteron* (Gosliner, 1989). Gosliner & Armes (1984) described *Gastropteron vespertilium* Gosliner & Armes (1984) from Florida and Gosliner (1984) documented two new species of *Gastropteron* from temperate southern Africa. These two species were later transferred to *Siphopteron* (Gosliner, 1989). In 1988, Gosliner & Williams described *Gastropteron michaeli* Gosliner & Williams, 1988, which was considered later to be a species of *Siphopteron* (Gosliner 1989), while Gosliner (1988) documented *Enotepteron rosewateri* Gosliner, 1988. Gosliner (1989) described the genus *Siphopteron* with three new species of *Siphopteron* and three new species of *Gastropteron*. Brodie, Klussmann-Kolb & Gosliner (2001) erected *Enotepteron heikae* Brodie *et al.*, 2001. Klussmann-Kolb & Klussmann (2003) named *Siphopteron leah* Klussmann-Kolb & Klussmann, 2003. Most recently, Hamatani described two additional species of *Enotepteron*, *Enotepteron hayashii* Hamatani, 2009 and *Enotepteron rubropunctatum* Hamatani, 2013.

Phylogenetic relationships within Gastropteridae have been studied based on anatomy (Gosliner, 1989) and molecular data (Anthes, Schulenburg & Michiels, 2008), and the systematics relationships of these two studies are largely congruent. Most recently, Oskars, Bouchet & Malaquias (2015) revised the phylogeny and systematics of the cephalaspidean heterobranchs and reaffirmed the apparent monophyly of Gastropteridae and suggested its sister relationship with Colpodaspidae Oskars, Bouchet & Malaquias, 2015, another lineage of cephalaspideans with a reduced internal shell.

The Coral Triangle, bordered by the Philippines, Indonesia and Papua New Guinea, has been documented as the area of greatest diversity within the Indo-West Pacific (Roberts *et al.*, 2002) and is also home to many endemic species and clades. Within the Coral Triangle, it has been shown that the Philippine Islands support the highest known diversity for marine shore fishes (Carpenter & Springer, 2005), azooxanthellate corals (Cairns, 2007) and heterobranch mollusks (Gosliner *et al.*, 2008). In order to better understand distribution of marine biodiversity within the Coral Triangle and specifically within the Verde Island Passage of the Philippines, a series of expeditions was undertaken by an international team of systematic experts organized by the California Academy of Sciences to investigate undocumented diversity and patterns of diversification in the region. The 2014 and 2015 Verde Island Passage Expeditions provided an opportunity to collect material of nearly 100 new species of heterobranch gastropods, including what appear to be several new species of Gastropteridae. Based on the examination of the morphology of living material, we estimated that there are likely eight new species of Gastropteridae in three of the four distinct genera. The focus of this study is to examine the molecular phylogeny of these taxa and to determine morphological and molecular boundaries that separate these apparent new species. Also, new taxa will be formally described and differentiated.

MATERIAL AND METHODS

Molecular work

Taxon sampling

Representatives of Cephalaspidea sampled are listed in Table 1, along with their corresponding voucher numbers, GenBank accession numbers and collection sites. The availability of appropriately preserved specimens has limited our ability to undertake molecular phylogenetic studies and many taxa have only been collected once and were not preserved in a manner suitable for molecular study. Previously, sequences from 14 exemplars of Gastropteridae have been published. An additional 25 exemplars, mostly from taxa not previously sequenced, were added in this study. No representatives of *Enotepteron* were available for molecular study, since all specimens were preserved in formalin-based fixatives. *Sagaminopteron* was the most completely sampled genus from Gastropteridae, with five of the six species analysed. *Gastropteron* and *Siphopteron* sampling was less complete. Sampling of *Gastropteron* consisted of five

Table 1. Specimens successfully sequenced. Taxonomy represents new species and classification

Species	Voucher	Locality	GenBank accession numbers		
			16S	*28S*	*COI*
Aglajidae Pilsbry, 1895					
Aglaja tricolorata Renier, 1807	isolate E19	Italy	AM421854	AM421950	AM421902
Aglajidae sp. 1	isolate 9	Queensland, Australia	AM421826	AM421948	AM421878
Chelidonura africana Pruvot-Fol, 1953	BMNH 20030343	Algarve, Portugal		DQ927216	DQ974654
Chelidonura amoena Bergh, 1905	isolate E1	Queensland, Australia	AM421841	AM421962	AM421901
Melanochlamys diomedea (Bergh, 1894)	isolate E14	Washington, USA	AM421825	AM421935	AM421866
Navanax inermis (J. G. Cooper, 1862)	isolate E21	w. Mexico	AM421855		AM421877
Odontoglaja guamensis Rudman, 1978	isolate E23	Queensland, Australia	AM421830		AM421869
Odontoglaja mosaica Gosliner, 2011	CASIZ 175943	nw Madagascar		DQ927218	DQ974655
Philinopsis cyanea (Martens, 1879)	isolate 239	Queensland, Australia	AM421832	AM421951	AM421890
Philinopsis depicta (Renier, 1807)	isolate E17	Mediterranean	AM421831	AM421954	AM421892
Philinidae Gray, 1850 (1815)					
Philine aperta (Linnaeus, 1767)	CASIZ 176332	False Bay, South Africa	JN825128		JN825186
Philine aperta (Linnaeus, 1767)	CASIZ 176345	False Bay, South Africa	JN825129		JN825187
Philine exigua Challis, 1969	ZSM Mol-20080752	Solomon Islands		HQ168438	
Gastropteridae Swainson, 1840					
Gastropteron bicornutum Baba & Tokioka, 1965	CASIZ 186051	Luzon, Philippines	KX551972	KX551996	KX552016
Gastropteron bicornutum Baba & Tokioka, 1965	isolate 231	Queensland, Australia	AM421822	AM421936	
Gastropteron minutum Ong and Gosliner **sp. nov.**	CASIZ 182731	Maui, Hawaii	KX551974		KX552018
Gastropteron minutum Ong and Gosliner **sp. nov.**	CASIZ 199181	Luzon, Philippines	KX551973	KX551997	KX552017
Gastropteron multo Ong and Gosliner **sp. nov.**	CASIZ 186048	Luzon, Philippines	KX551975		KX552019
Gastropteron multo Ong and Gosliner **sp. nov.**	NMP 041181	Luzon, Philippines		KX551998	KX552020
Gastropteron rubrum (Rafinesque, 1814)	isolate E31	Mediterranean	AM422902		AM421865
Sagaminopteron multimaculatum Ong and Gosliner **sp. nov.**	NMP 041182	Luzon, Philippines	KX552012	KX552010	KX552034
Sagaminopteron nigropunctatum Carlson & Hoff, 1973	CASIZ 182870	Luzon, Philippines	KX551976	KX551999	KX552021
Sagaminopteron nigropunctatum Carlson & Hoff, 1973	CASIZ 192431	Red Sea, Saudi Arabia	KX551977	KX552000	KX552022
Sagaminopteron ornatum Tokioka & Baba, 1964	CASIZ 182792	Luzon, Philippines	KX551978	KX552001	KX552023
Sagaminopteron ornatum Tokioka & Baba, 1964	isolate 240	Queensland, Australia	AM421814		AM421857
Sagaminopteron pohnpei (Hoff & Carlson, 1983)	CASIZ 180393	Luzon, Philippines	KX551993		KX552038
Sagaminopteron pohnpei (Hoff & Carlson, 1983)	CASIZ 190655	Luzon, Philippines	KX551983	KX552006	KX552028
Sagaminopteron psychedelicum Carlson & Hoff, 1974	CASIZ 177772	Luzon, Philippines	KX551979	KX552002	KX552024
Sagaminopteron psychedelicum Carlson & Hoff, 1974	CASIZ 191213	Papau New Guinea	KX551980	KX552003	KX552025
Sagaminopteron psychedelicum Carlson & Hoff, 1974	isolate 44	W. Madagascar		DQ927225	DQ974667
Sagaminopteron psychedelicum Carlson & Hoff, 1974	isolate E22	Queensland, Australia	AM421815		AM421856
Sagaminopteron psychedelicum Carlson & Hoff, 1974		Queensland, Australia			AY427478

Table 1. *Continued*

Species	Voucher	Locality	GenBank accession numbers		
			16S	*28S*	*COI*
Sagaminopteron **sp.** cf. *multimaculatum* Ong & Gosliner **sp. nov.**	isolate 7	Queensland, Australia	AM421821		AM421858
Siphopteron brunneomarginatum (Carlson & Hoff, 1974)	CASIZ 177515	Luzon, Philippines	KX551981	KX552004	KX552026
Siphopteron brunneomarginatum (Carlson & Hoff, 1974)	isolate E4	Indonesia	AM421816	AM421939	AM421864
Siphopteron dumbo Ong and Gosliner **sp. nov.**	NMP 041187	Mindoro, Philippines	KX551984		KX552029
Siphopteron flavolineatum Ong and Gosliner **sp. nov.**	CASIZ 204848	Luzon, Philippines	KX552009		KX552031
Siphopteron flavolineatum Ong and Gosliner **sp. nov.**	NMP 041184	Luzon, Philippines	KX551985	KX552007	KX552030
Siphopteron leah Klussmann-Kolb & Klussmann, 2003	isolate 177	Queensland, Australia	AM421818		AM421861
Siphopteron leah Klussmann-Kolb & Klussmann, 2003	isolate 179	Queensland, Australia	AM421819	AM421941	AM421860
Siphopteron leah Klussmann-Kolb & Klussmann, 2003	isolate 5	Queensland, Australia	AM421817		AM421859
Siphopteron makisig Ong and Gosliner **sp. nov.**	NMP 041186	Philippines	KX552010	KX552008	KX552032
Siphopteron michaeli Gosliner & Williams, 1988	CASIZ 188586	Mauritius	KX552011	KX552009	KX552033
Siphopteron nakakatuwa Ong and Gosliner **sp. nov.**	NMP 041185	Luzon,Philippines	KX551990	KX552011	KX552035
Siphopteron nigromarginatum Carlson & Hoff, 1973	CASIZ 182844	Luzon, Philippines	KX551991	KX552012	KX552036
Siphopteron quadrispinosum Gosliner, 1989	CASIZ 180300	Maui, Hawaii	KX551992	KX552013	KX552037
Siphopteron tigrinum Gosliner, 1989	CASIZ 199128	Luzon, Philippines	KX551994	KX552014	KX552039
Siphopteron tigrinum Gosliner, 1989	isolate 45	W. Madagascar	KJ022788	DQ927226	DQ974668
Siphopteron vermiculum Ong and Gosliner **sp. nov.**	CASIZ 199129	Luzon, Philippines	KX551982	KX552005	KX552027
Siphopteron sp.	CASIZ 181575	Panglao, Philippines	KX551971	KX551995	KX552015
Siphopteron sp.	isolate 208	Queensland, Australia		AM421940	AM421862
Siphopteron sp.	isolate 226	Queensland, Australia	AM421820		AM421863

of the 13 species, and *Siphopteron* included ten out of 17 species. No additional exemplars of the remaining species of these genera are available for molecular study. Aglajidae and Philinidae were used as outgroupings due to their hypothesized placement in the Cephalaspidea and relative proximity to Gastropteridae (Vonnemann, *et al.*, 2005). Vouchers and types were deposited at the California Academy of Sciences (CAS) and the National Museum Philippines (NMP).

DNA extraction, sequencing and alignment

Both nDNA (*28S*) and mtDNA [*16S* and cytochrome *c* oxidase I (*COI*)] fragments were utilized to estimate Gastropteridae phylogeny. These molecular markers have been shown to be effective gene markers to infer heterobranch phylogenetic relationships (Dinapoli & Klussmann-Kolb, 2010; Göbbeler & Klussmann-Kolb, 2010; Pola & Gosliner; 2010; Camacho-García *et al.*, 2014; Hallas & Gosliner, 2015; Hallas, Simison & Gosliner, 2016). The DNA was extracted from tissue removed from either the parapodia or foot of the specimen.

Two different extraction methods were utilized, depending on the amount of tissue able to be sampled. For large amounts of tissue, we used the standard Qiagen Dneasy Blood & Tissue extraction kit (Valencia, CA, USA) protocol, and for instances where only small amounts of

tissue was sampled, we used the Qiagen Gentra Puregene Tissue kit (Valencia, CA, USA) 5–10 mg protocol.

Each polymerase chain reaction (PCR) was conducted in 25 µL reactions. Reactions consisted of 2.5 µL of 10× USB buffer, 1.25 µL of $MgCl_2$ (25 mM), 1 µL of each primer (10 µM stock), 1 µL of BSA (10 mg/mL), 0.5 µL of dNTPs (10 mM), 5 µL of betaine (5 M), 1 µL of DMSO, 1 µL of HotStart-IT taq polymerase (1.25 u/µL), 1–4 µL of template DNA and then filled to volume with millipore water. Primers used for sequencing are all listed in Table 2. PCR cycling conditions for *COI* and *16S* fragments are as follows: initial denaturing for 2 min at 94 °C, followed by 35 cycles of denaturing for 30 s at 94 °C, annealing for 30 s at 50 °C and extension for 45 s at 72°C and a final extension period of 10 min at 72 °C. The *COI* annealing temperature was relaxed to 48 °C for the NAF/NARCOI primers. PCR protocol for *28S* was initially denatured for 3 min at 94 °C, followed by 35 cycles of denaturing for 30 s at 94 °C, annealing for 30 s at 52.5 °C and extension for 2 min at 72 °C and a final extension period of 10 min at 72 °C. All PCR reactions were stained with ethidium bromide and run on 0.5% Tris/borate/EDTA agarose gel using electrophoresis. Successfully amplified fragments were purified using ExoSAP-IT enzymes and protocol (USB), and unsuccessful amplified reactions were excised using the Zymoclean Gel DNA Recovery Protocol.

Purified PCR product was cycle sequenced using fluorescently labelled dideoxynucleotides (ddNTPs) (Big Dye Terminator v3.1, Applied Biosystems). Cycle sequencing reactions were performed in 10 µL volumes. All regular cycle sequencing reactions had the same protocol for all primers; each reaction used 2 µL of PCR product and the following reaction components: 5.45 µL of millipore water, 1.5 µL of 5× Big Dye buffer, 0.3 µL of primer (10 µM), 0.75 µL of Big Dye 3.1. For those samples that required gel excision or had low PCR amplifications, we used modified cycle sequencing protocols that were performed in 20 µL volumes. Each reaction used 3 µL of PCR product and the following reaction components: 9.4 µL of millipore water, 3 µL of 5× Big Dye buffer, 0.6 µL of primer (10 µM), 4 µL of Big Dye 3.1 and followed the STeP protocol (Platt, Woodhall & George, 2007).

Fluorescently labelled sequences were precipitated using 2.5 µL of di-Na EDTA (125 mM) and cleaned with 30 µL of 100% EtOH then with 60 µL of 70% EtOH. The tubes were placed into a 65 °C incubator for 8 min to dry, then the DNA pellets were re-suspended in 10 µL deionized formamide and denatured at 94–96 °C for 2 min. Immediately afterwards, they were placed on an ABI 3130*xl* Genetic Analyser (Applied Biosystems), located in the Center for Comparative Genomics at the California Academy of Sciences.

Sequence alignment and phylogenetic analyses

Successfully sequenced markers were assembled and edited using Geneious 6.1 (Biomatters Ltd., 2005). The sequences were aligned using the Multiple Alignment using Fast Fourier Transform (MAFFT) algorithm (Katoh, Asimenos & Toh, 2009) with the settings set to default. Following MAFFT alignment, variable regions of rDNA fragments were manually optimized, and these alignments have been deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S19544). In sequences where confidence was low, ambiguities were deleted and not analysed. Finally, all sequences were trimmed to the length of the outgroup.

Evolutionary models for the targeted molecular markers were estimated using PartitionFinder v1.1.1 (Lanfear *et al.*, 2012) (Table 2). A concatenated alignment of all three

Table 2. Primers in PCR amplification and substitution models used for phylogenetic analyses

Primer	Source	Sequence (5′–3′)	Substitution model
16S			GTR+I+G
AR-L	Palumbi *et al.* (1991)	CGCCTGTTTATCAAAAACAT	
BR-H	Palumbi *et al.* (1991)	CCGGTCTGAACTCAGATCACGT	
28S			GTR+I+G
28SC1	Vonnemann *et al.* (2005)	ACCCGCTGAATTTAAGCAT	
28SC2F	Vonnemann *et al.* (2005)	GAAAAGAACTTTGAAGAGAGAGT	
28SC2R	Vonnemann *et al.* (2005)	ACTCTCTCTTCAAAGTTCTTTTC	
28SD3	Vonnemann *et al.* (2005)	GACGATCGATTTGCACGTCA	
COI			Codon positions (1,2,3): GTR+G
L1490	Folmer *et al.* (1994)	GGTCAACAAATCATAAAGATATTGG	
H2198	Folmer *et al.* (1994)	TAAACTTCAGGGAGACCAAAAAATCA	
NAFCOI	Anthes *et al.* (2008)	CCATCCTGGTAAAATTAAAATATA	
NARCOI	Anthes *et al.* (2008)	GCCTTTTCAACAAACCATAAAGA	

molecular markers was used to estimate Gastropteridae evolutionary relationships using both Bayesian inference (BI) and maximum likelihood (ML) approaches. BI searches were run using MrBayes v3.2.1 (Ronquist & Huelsenbeck, 2003) for a total of 2×10^7 generations with Markov chains sampled every 1000 generations with parameters unlinked. A conservative 25% burn-in was calculated, and the remaining trees were used to estimate the 50% majority rule consensus tree and corresponding posterior probabilities (PP). Convergence and stationarity of BI searches were checked using TRACER v1.5 (Drummond & Rambaut, 2007). ML search was run using RAxML v7.2.6 (Stamatakis, 2006) with the evolution model GTR-GAMMA. ML dataset was set for 50 000 fast bootstrapping runs. Support values for ML bootstrap (bs) ≥ 70 (Hillis & Bull, 1993) and Bayesian pp ≥ 0.95 were interpreted as significant.

Species delimitation analyses

Species were delimited through an integrative approach with the use of congruence of single-gene topologies, Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.*, 2012). ABGD uses genetic pairwise distances to identify breaks between intra- and interspecific variation, also referred to as the 'barcode gap'. *COI* genetic distance matrix was created using *MEGA* v6.06 (Tamura *et al.*, 2011) using the Tamura Nei model and uploaded to the ABGD web-based interface (available at http://wwwabi.snv.jussieu.fr/public/abgd/). Except for the relative gap width (X), which was set to 1, the remaining settings were left at their default configuration.

SYSTEMATICS

CEPHALASPIDEA P. FISCHER, 1883

FAMILY GASTROPTERIDAE SWAINSON, 1840

GASTROPTERON KOSSE, 1813

Type species

Gastropteron meckeli Blainville, 1825*, by monotypy*.

GASTROPTERON MINUTUM ONG & GOSLINER **SP. NOV.**

(FIGS 1A, B, 2, 3, 4A)

LSID urn:lsid:zoobank.org:act:73880269-2D0D-4091-B9FD-8EC86AE05CE2

Gastropteron sp. 4 Rudman, 2002.
Gastropteron sp. 5 Gosliner, Valdés & Behrens, 2015: 56, upper right fig.

Type material

Holotype: CASIZ 209032, originally CASIZ 182731, Honokowai Beach Park, Maui, Hawai'ian Islands, 1–6 m depth, 11 April 2010, Cory Pittman.

Paratypes: CASIZ 182731, two specimens, one dissected, Honokowai Beach Park, Maui, Hawai'ian Islands, 1–6 m depth, 11 April 2010, Cory Pittman. CASIZ 199181, Cemetery Beach (13.68428°N 120.83024°E), Maricaban Island, Tingloy, Luzon, Philippines, emerged from algae, 26 April 2014, Patrick Krug.

Type locality

Honokowai Beach Park, Maui, Hawai'ian Islands.

Geographical distribution

Known from Japan (Rudman, 2002), the Hawai'ian Islands, the Marshall Islands and the Philippines (Gosliner *et al.*, 2015).

Etymology

The name *minutum* is derived from the extremely small size of this species, reaching a maximum of 3 mm in length.

Description

External morphology: Living animal 2–3 mm in length (Fig. 1A, B). Preserved holotype <1 mm in length (Fig. 2A). Ground colour of head shield, parapodia, visceral hump and flagellum almost colourless with opaque white and orange mottling speckling body. Orange and off-white spots condensing around visceral hump to form low, rounded tubercles and covering parapodia. Head shield and flagellum having fewer spots, almost clear. Head shield narrow anteriorly, broadening out before again narrowing posteriorly. Posteriorly, head shield forming a simple rolled siphon without medial crest. Parapodia covering visceral hump when retracted. At posterior end of visceral hump, elongate, acutely pointed flagellum extending posteriorly. Foot extending posteriorly, almost entire length of animal from head to end of visceral hump. At posterior end, foot narrowing into elongate, acutely pointed posterior tip. Gill situated on right side of body and consisting of seven tiny lamellae.

Shell: Thinly calcified, planispiral, tightly coiled, *c.* 300 µm in diameter (Fig. 3A). Protoconch not clearly differentiated from remainder of shell.

Buccal mass: Buccal mass (Fig. 2B) moderately muscularized, with series of circular muscles anteriorly

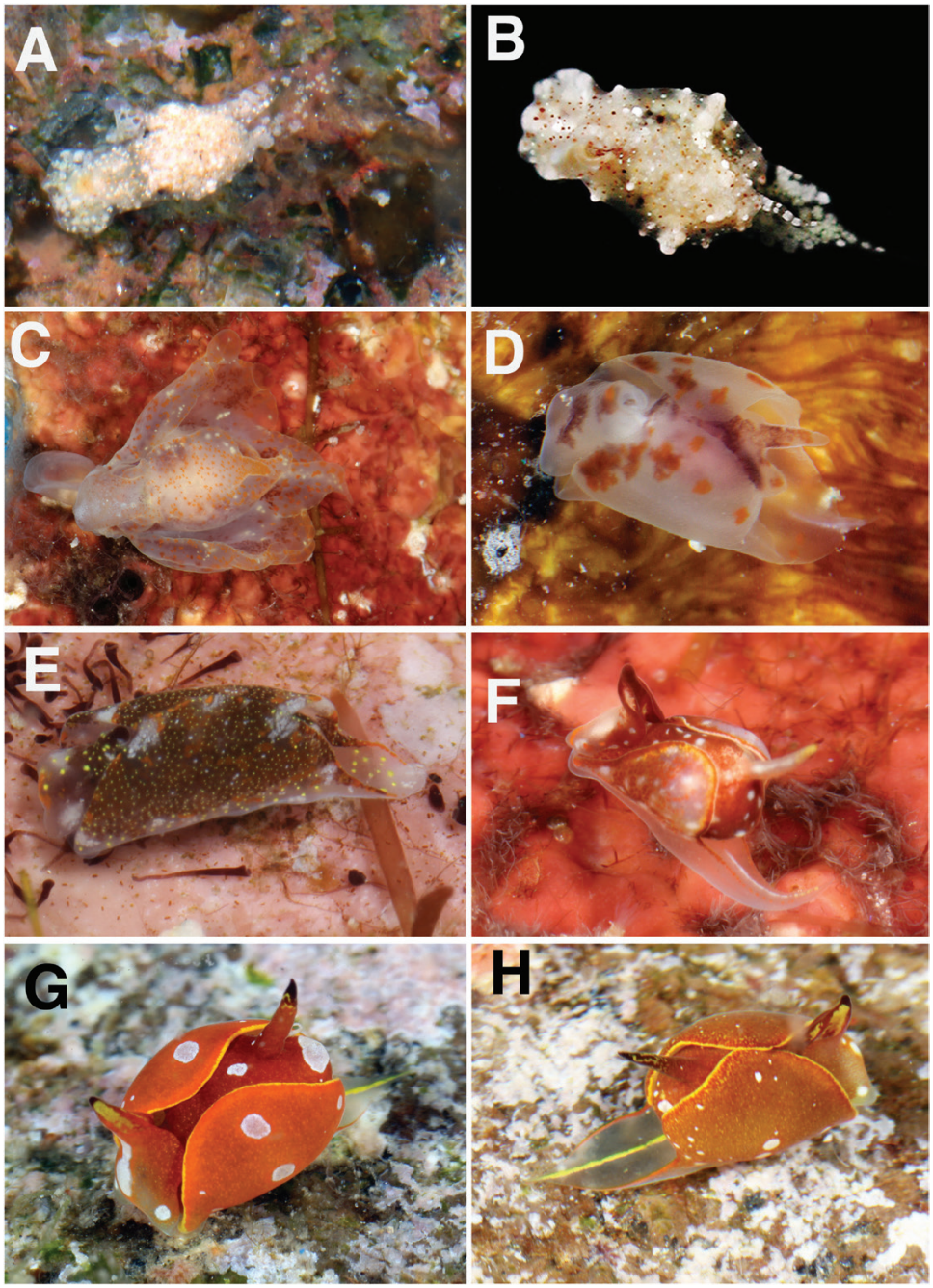

Figure 1. Living animals. (A) ***Gastropteron minutum* sp. nov.**, partaype, CASIZ 199181, Tingloy, Philippines. (B) ***Gastropteron minutum* sp. nov.**, holotype, CASIZ 209032, Maui, **Hawai'ian** Islands, photo by Cory Pittman. (C) ***Gastropteron multo* sp. nov.**, holotype NMP 041181, Mabini, Philippines. (D) ***Gastropteron multo* sp. nov.**, paratype, CASIZ 186048, Mabini, Philippines. (E) ***Sagaminopteron multimaculatum* sp. nov.**, holotype, NMP 041182, Tingloy, Philippines. (F) ***Siphopteron vermiculum* sp. nov.**, Paratype, CASIZ 199129, Tingloy, Philippines. (G) *Siphopteron flavolineatum*, holotype, NMP 041184, Tingloy, Philippines. (H) *Siphopteron flavolineatum*, paratype, CASIZ 199132, Tingloy, Philippines. (Photos by T. Gosliner unless otherwise indicated.)

and more complex musculature around radular sac. Buccal mass containing labial cuticle with pair of minute areas with small irregular rodlets (Fig. 3B). Radular formula 20 × 4.1.0.1.4 in one specimen (CASIZ 182731). Inner lateral teeth broad with single primary cusp. Masticatory margin of the inner laterals containing 13–14 acutely pointed denticles (Fig. 3C, D). Triangular thickening present on inner edge of

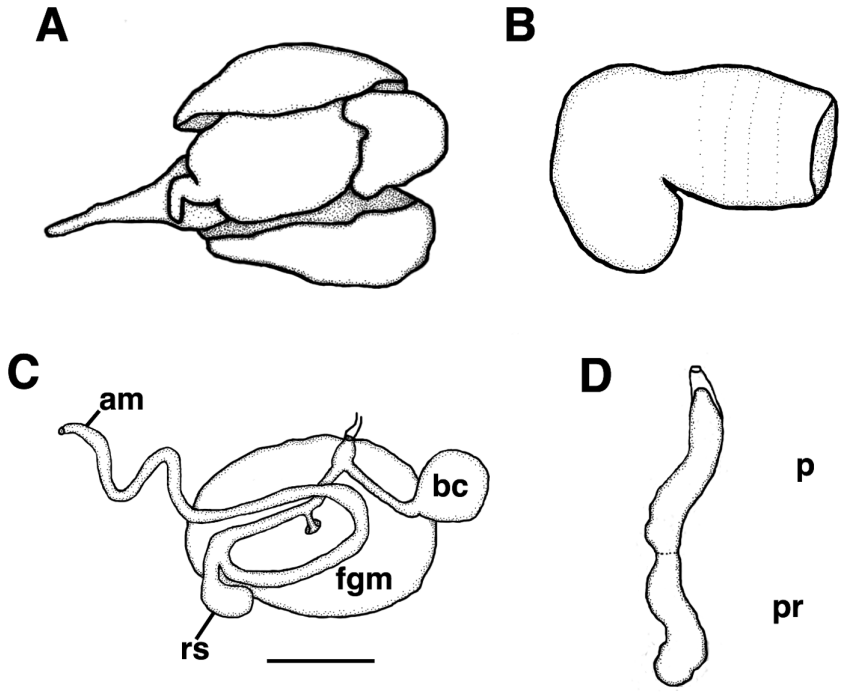

Figure 2. ***Gastropteron minutum*** **sp. nov.** paratype, CASIZ 182731, Maui, Hawai'ian Islands. (A) Dorsal view of preserved specimen, scale = 1.25 mm. (B) Buccal mass, scale = 0.75 mm. (C) Posterior reproductive organs. a = ampulla, bc = bursa copulatrix, fgm = female gland mass, rs = receptaculum seminis; scale = 0.5 mm. (D) Penis. p = penis, pr = prostate; scale = 0.75 mm.

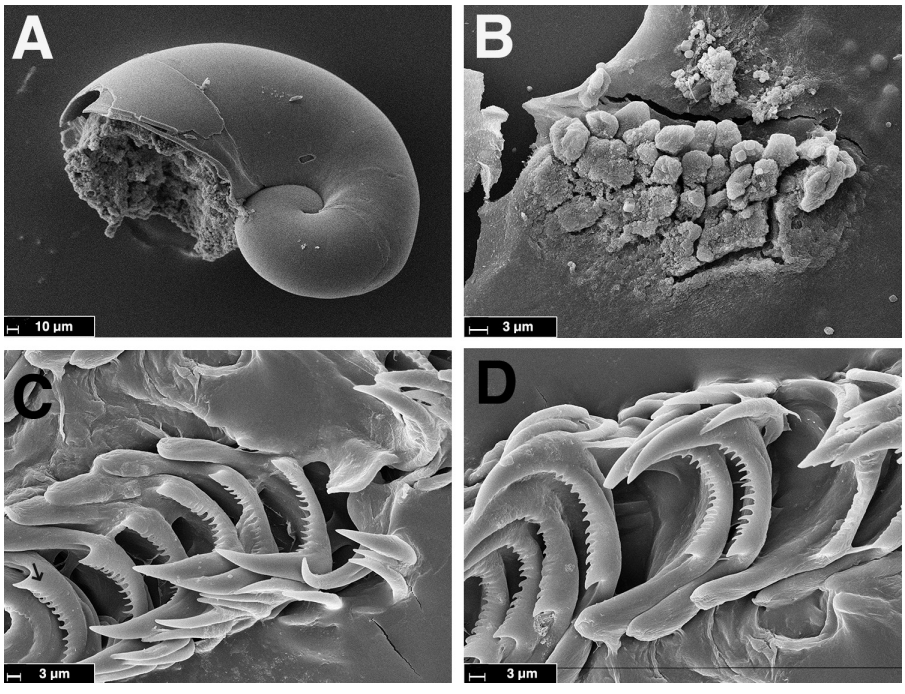

Figure 3. ***Gastropteron minutum*** **sp. nov.** paratype, CASIZ 182731, scanning electron micrographs. (A) Shell. (B) Jaw rodlets. (C) Half-row of radular teeth, triangular thickening indicated by arrow. (D) Half-row of radular teeth.

masticatory border of inner lateral teeth. Innermost outer lateral tooth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller, with narrower base; all lacking denticles (Fig. 3C).

Central nervous system: Arrangement of ganglia euthyneurous, with short visceral loop. Owing to small size of animal, details of arrangement of ganglia could not be determined in a single specimen dissected.

Reproductive system: Despite its small size, reproductive system is fully mature and well-developed; female glands clearly visible (Fig. 2C). Narrow ampulla extending into straighter hermaphroditic duct, curving around top of lobate mucous gland, and expanding into small receptaculum seminis before curving around female glands once more. Opening of hermaphroditic duct into female glands not visible, but hermaphroditic duct joining relatively short bursa copulatrix near gonopore, leading to external sperm groove. Sperm groove continuing on right side of the body to head, where penis is situated. Penis simple with slightly curved prostate. Penial papilla straight and devoid of penial armature (Figs 2D, 4A).

Remarks

The external anatomy of *G. minutum* clearly differentiates this species from all described species of *Gastropteron*. It is the only species with an off-white body colour with opaque white and orange spots. The presence of opaque white spots and rounded tubercles give the entire animal a granular rather than smooth appearance. Most species of *Gastropteron* have a smooth body without tubercles or granules. Of the seven species of *Gastropteron* known from the Pacific Ocean, none of them is known to have a single flagellum with an elongate extension of the foot. The only described species with an elongate foot is *G. bicornutum* Baba & Tokioka, 1965. It has two flagella, one more dorsally situated on the visceral hump and one more ventrally situated. It has a smooth rather than rugose body and has black and yellow spots over the dorsal surface. Internally, the inner lateral radular teeth have fewer denticles than *G. minutum*. Both species have a simple penis with an elongate prostate. In our molecular phylogeny, *G. minutum* is sister to *G. rubrum* (Rafinesque, 1814), known from the Mediterranean and West Africa, and is quite far removed from *G. bicornutum*.

Gastropteron minutum is morphologically very similar to specimens of *Gastropteron* sp. 2 from the Hawai'ian Islands (Pittman & Fiene, 2015) and are considered to represent the same species. The Hawai'ian specimens have fine black specks and appear to have larger tubercles on the body. The Philippine specimen and Hawai'ian specimens are very similar in their molecular phylogeny, and the ABGD analysis does not differentiate them as distinct groups. Their uncorrected p-distance for the *COI* gene is 3.2%, well within the expected variation of two widely separated populations of a single species.

GASTROPTERON MULTO ONG & GOSLINER SP. NOV.

(FIGS 1C, D, 4B, 5, 6)

LSID urn:lsid:zoobank.org:act:025F1253-A0D7-4D2A-B332-CE30DF011436

Gastropteron sp. 3 Gosliner *et al.*, 2015: 55, lower right fig.

Type material

Holotype, dissected, NMP 041181, originally CASIZ 199130, Mainit Bubbles (13.68688°N 120.89564°E), Mabini, Batangas, Luzon, Philippines, 5 m depth, 3 May 2014, Alexis Principe. Paratype, CASIZ 186048, one specimen, Anilao Pier (13.76001°N 120.92615°E), Mabini, Batangas, Luzon, Philippines, 5 m depth, 30 April 2011, T. Gosliner.

Type locality

Mainit Bubbles (13.68688°N 120.89564°E), Mabini, Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines (Gosliner *et al.* 2015).

Etymology

The species epithet, *multo*, is derived from Tagalog word for ghost, owing to the pale ghostly appearance of this species.

Description

External morphology: Living animals (Fig. 1C, D) 7–20 mm in length. Colour clear to translucent white with fine orange, brown and white dots speckling body or with series of brownish and orange patches. Opaque white digestive gland and ovotestis visible through visceral hump. Head shield, parapodia, flagella and foot translucent whitish. Small orange dots or brown patches covering body, concentrated on siphon and flagella. Dorsal flagellum centred on midline of visceral hump. Immediately ventral to this flagellum, second, slightly wider flagellar process, either longer or shorter than dorsal one (Fig. 5A). White spots outlining visceral hump and parapodia. Head shield shaped roughly like cauldron. Broadest anteriorly, narrowing and then

broadening again posteriorly. Head shield terminating in tubular, simple siphon, lacking mid-dorsal ridge. Broad parapodia covering body when the animal is actively crawling. Foot elongate with long, acutely pointed posterior extension. Gill with nine primary folds.

Shell: Thinly calcified slightly curved plate, 2 mm in length (Fig. 5B). Part of shell appearing decalcified.

Buccal mass: Entire buccal mass moderately muscularized with series of circular muscles anteriorly and more complex musculature present around radular sac. Buccal mass containing labial cuticle with pair of minute areas with small irregular rodlets (Fig. 6A). Radular formula 25 × 5.1.0.1.5 in one specimen (NMP 041181) (Fig. 6B). Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals containing 3–16 irregularly pointed denticles on inner edge of masticatory margin (Fig. 6C, D). Remainder of masticatory margin devoid of denticles. Triangular thickening present on inner edge of masticatory border of inner lateral teeth. Innermost outer lateral tooth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base and all lacking denticles (Fig. 6C).

Central nervous system: Arrangement of ganglia (Fig. 5C) euthyneurous, with short visceral loop. Cerebral ganglia large, separated by short commissure. Pedal ganglia as large as cerebral ganglia, separated by elongate commissure passing ventrally to buccal mass. Supraintestinal ganglion immediately posterior to right pleural ganglion. From there, visceral loop connecting to visceral and subintestinal ganglia and curving anteriorly to join left pleural ganglion.

Reproductive system: Fully mature and well-developed female glands clearly visible (Fig. 5D). Elongate, convoluted ampulla extending into straighter hermaphroditic duct that curves around top of lobate mucous gland, expanding into elongate lobe of receptaculum seminis before curving around female glands once more. Opening of hermaphroditic duct into female glands visible, with hermaphroditic duct joining relatively elongate duct of spherical bursa copulatrix near gonopore. Gonopore leading to external sperm groove. Sperm groove continuing on the right side of the body to head, where penis is situated. Penis simple with a short, sharply curved prostate. Penial retractor muscle elongate. Penial sac straight, with chitinous tubercle near base on left side. Extended penial papilla of holotype with wide, expansive flap. Papilla devoid of any penial armature (Figs 4B, 5E) with exception of basal triangular cuticular appendage situated at the base of penial sac.

Remarks

The external anatomy of *G. multo* clearly differentiates this species from all described species of *Gastropteron*. It is the only species with a translucent white body colour with orange spots and brown patches. Of the seven species of *Gastropteron* known from the Pacific Ocean, only *G. bicornutum* is known to have dorsal and ventral flagella with an elongate extension of the foot. In *G. bicornutum*, the posterior extension of the foot is thin and very elongate, while in *G. multo* it is short and triangular. *Gastropteron bicornutum* has black and yellow spots over the dorsal surface, which are absent in *G. multo*. Internally, the inner lateral radular teeth of *G. multo* have fewer denticles than *G. bicornutum* and are restricted to the outer edge of the masticatory border, whereas they are evenly distributed along the border of *G. bicornutum*. Both species have a simple penis, but the prostate is much shorter in *G. multo*. In our molecular phylogeny, *G. multo* is sister to *G. bicornutum*, and the two species differ by more than 22% in their *COI* gene and are also clearly separated in the ABGD analysis. The two specimens of *G. multo* that

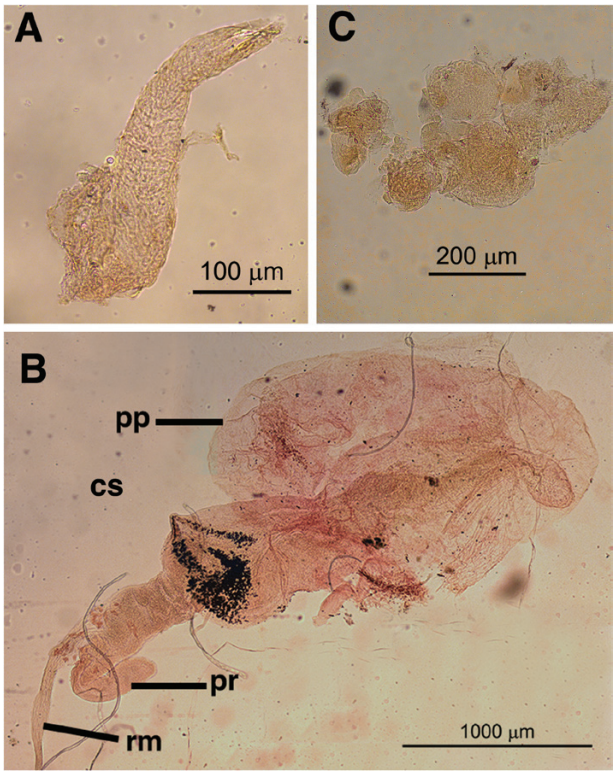

Figure 4. Penial anatomy. (A) ***Gastropteron minutum* sp. nov.** paratype, CASIZ 182731. (B) ***Gastropteron multo* sp. nov.** holotype, NMP 041181, Mabini, Philippines, cs = cuticular spine, pp = penial papilla, pr = prostate, rm = retractor muscle. (C) ***Sagaminopteron multimaculatum* sp. nov.** holotype, NMP 041182, Tingloy, Philippines.

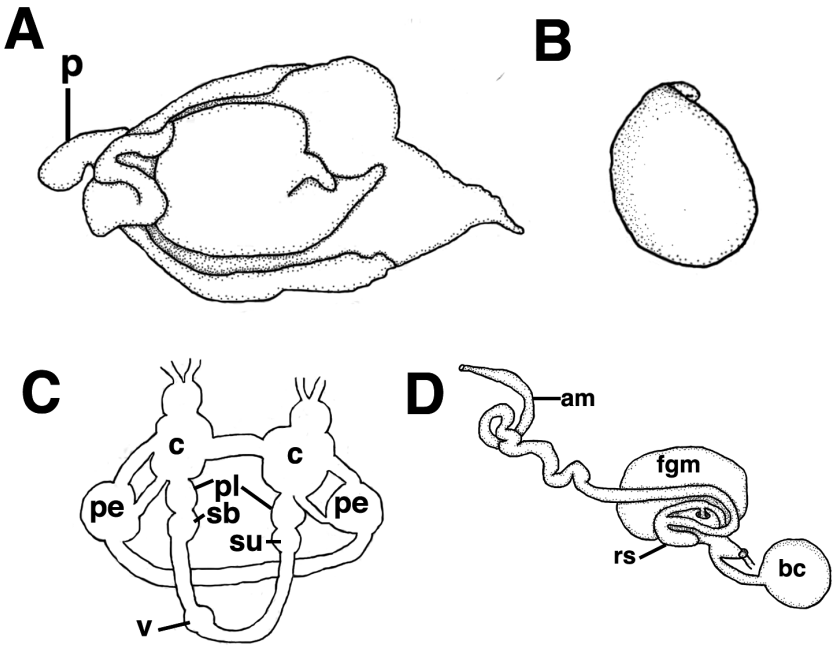

Figure 5. ***Gastropteron multo*** **sp. nov.** holotype, NMP 041181, Mabini, Philippines. (A) Dorsal view of preserved specimen, p = penis; scale = 4 mm. (B) Shell; scale = 0.75 mm. (C) Central nervous system, c = cerebral ganglion, pe = pedal ganglion. pl = pleural ganglion, sb = subintestinal ganglion, su = supraintestinal ganglion, v = visceral ganglion; scale = 1.5 mm. (D) Posterior reproductive organs, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, rs = receptaculum seminis; scale = 1.6 mm.

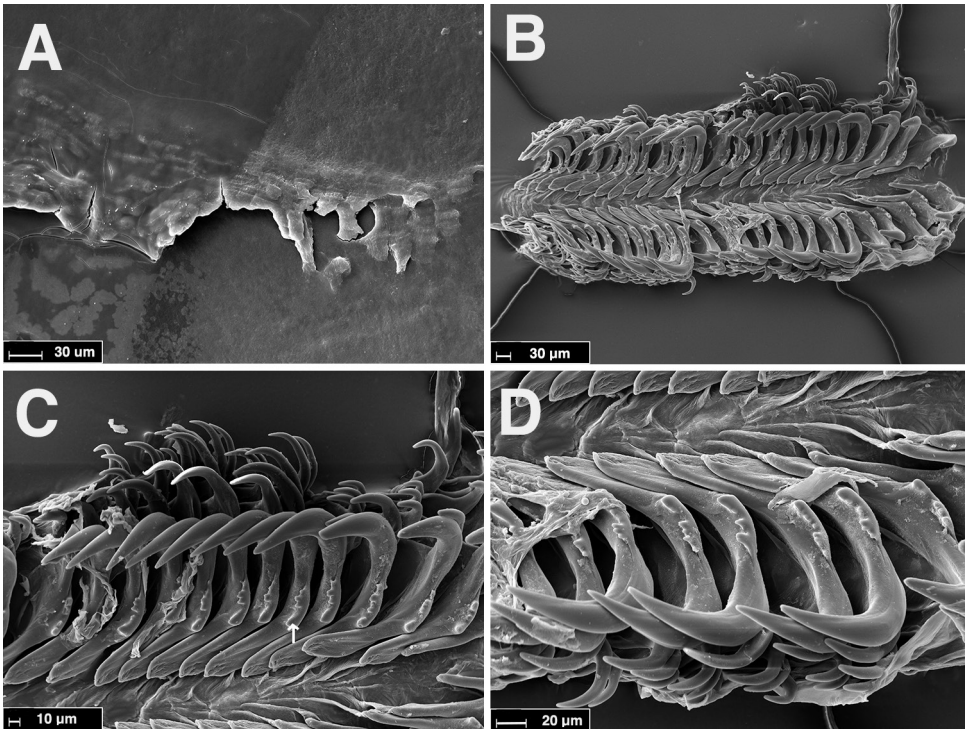

Figure 6. ***Gastropteron multo*** **sp. nov.** holotype, ex CASIZ 199130. NMP 041181, Mabini, Philippines. (A) Jaw rodlets. (B) Entire radula. (C) Half-row of radular teeth, triangular thickening indicated by arrow. (D) Half-row of radular teeth.

were sequenced do not exhibit any genetic variation between them.

GENUS *SAGAMINOPTERON* TOKIOKA & BABA, 1964

Type species

Sagaminopteron ornatum Tokioka & Baba, 1964, by original designation.

SAGAMINOPTERON MULTIMACULATUM ONG & GOSLINER **SP. NOV.**

(FIGS 1E, 4C, 7, 8)

LSID urn:lsid:zoobank.org:act:C54F7BAB-EB1F-478D-B828-7D2DF4A80BAB

Siphopteron pohnpei (Hoff & Carlson, 1983), Anthes *et al.*, 2008, misidentification.
Siphopteron sp. 8 Gosliner *et al.*, 2015: 60, middle left fig.

Type material

Holotype, dissected, NMP 041182, originally CASIZ 199127, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 2 May 2014, T. Gosliner.

Type locality

Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines (Gosliner *et al.*, 2015) and possibly Australia (Anthes *et al.*, 2008).

Etymology

The species epithet, *multimaculatum*, refers to the many coloured spots ornamenting the parapodia, head shield, visceral mass and foot of this species.

Description

External morphology: Living animal (Fig. 1E) 4 mm in length. Colour clear to translucent white around its foot. Majority of body green–brown with white, orange and canary yellow spots. Small yellow dots covering majority of elongate parapodia and extending well-beyond posterior end of visceral hump. Small orange dots lining the edges of parapodia. Small yellow dots centred linearly on head shield, base of foot and posterior end of foot. Larger orange splotch present on anterior side of head shield. White splotches present on either side of head shield. White splotches lining the edge of parapodia and anteriorly near foot. Foot translucent white and lined with orange spots. Small yellow dots also present on foot. Head shield roughly triangular, broadest anteriorly and narrowing posteriorly. Siphon with longitudinal ridge along its anterior margin. Parapodia covering body when retracted and overlapping above visceral hump. Distinct flagellum absent. Gill with four simple plicae.Shell: No trace of a shell found in specimen dissected.

Buccal mass: Moderately muscularized with series of circular muscles anteriorly and more complex musculature around radular sac (Fig. 7A). Buccal mass containing labial cuticle with a pair of minute areas with small irregular rodlets, not observed in the scanning electron micrographs. Radular formula 15 × 4.1.0.1.4. (Fig. 8A) in holotype specimen (NMP 041182). Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with eight to ten irregular, elongate, acutely pointed denticles along entire margin. Innermost outer lateral tooth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base, all lacking denticles (Fig. 8B).

Central nervous system: Arrangement of ganglia is euthyneurous, with a short visceral loop. Details of arrangement of ganglia cannot be determined in single specimen dissected.

Reproductive system: Reproductive system fully mature with well-developed female glands clearly visible (Fig. 7B). Elongate, convoluted ampulla extending into straighter hermaphroditic duct curving around top of lobate mucous gland and expanding into short lobe of receptaculum seminis before curving around female glands once more. Opening of hermaphroditic duct into female glands not visible, with hermaphroditic duct joining near gonopore, leading to external sperm groove. Bursa copulatrix not visible. Sperm groove continuing on the right side of the body to head where penis is situated. Penis simple with short, sharply curved prostate (Fig. 7C). Penial retractor muscle short. Penial sac straight and penial papilla lobed, but devoid of any penial armature (Fig. 4C).

Remarks

There have been some differences in the systematic placement of a few species of Gastropteridae, depending on whether morphological or molecular data have been used. Based on morphological characters, *Siphopteron pohnpei* was transferred to the genus

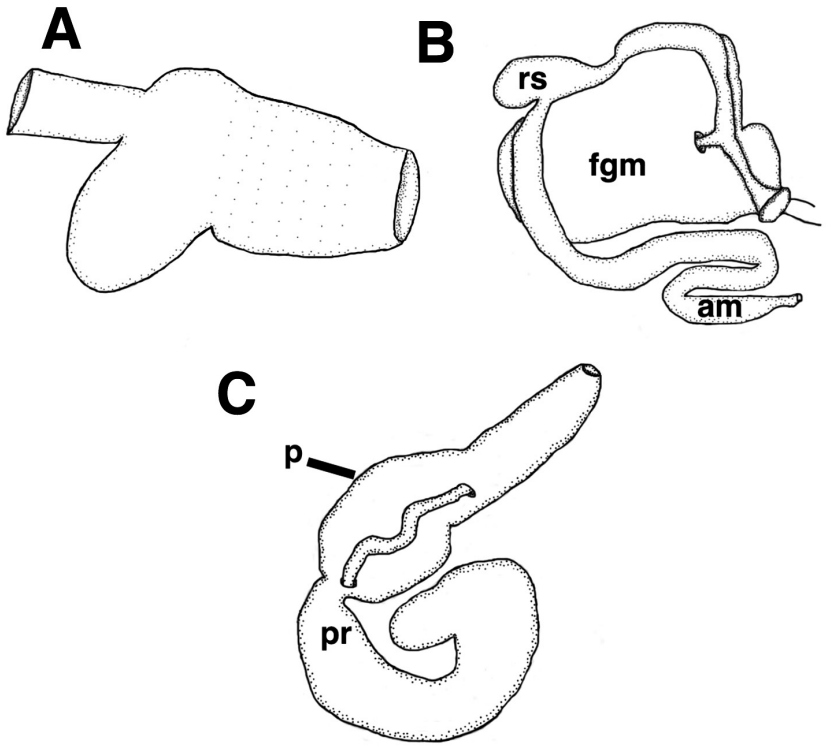

Figure 7. ***Sagaminopteron multimaculatum*** **sp. nov.** holotype, NMP 041182, Tingloy, Philippines. (A) Buccal mass, scale = 0.75 mm. (B) Posterior reproductive system, am = ampulla, fgm = female gland mas, rs = receptaculum seminis; scale = 0.67 mm. (C) Penis, p = penis, pr = prostate; scale = 0.85 mm.

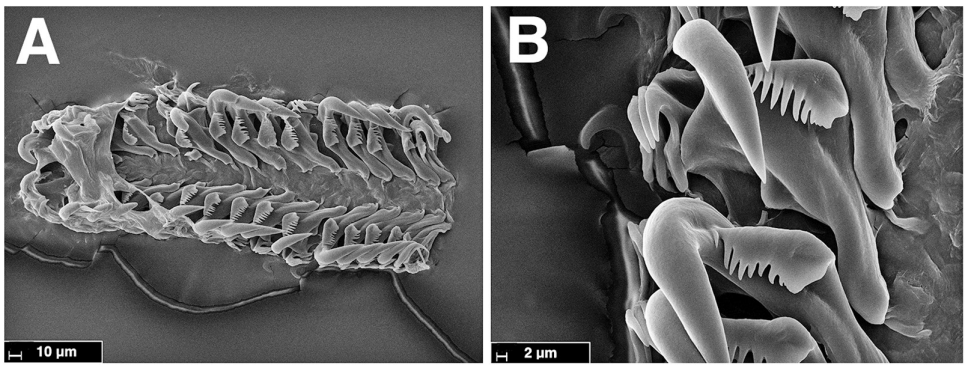

Figure 8. ***Sagaminopteron multimaculatum*** **sp. nov.** holotype, NMP 041182, Tingloy, Philippines, scanning electron micrographs. (A) Entire radula. (B) Half row of radular teeth.

Siphopteron (Gosliner, 1989). In the first molecular phylogeny of a large number of philinacean cephalaspideans (Anthes *et al.*, 2008), *S. pohnpei* clustered with two species of *Sagaminopteron*, *S. ornatum* and *Sagaminopteron psychedelicum* Carlson & Hoff, 1974. In this study, which includes many additional species, *S. pohnpei* and *S. multimaculatum* clearly cluster with other species of *Sagaminopteron* rather than with species of *Siphopteron*, and that relationship is strongly supported. On this basis, *S. pohnpei* and *S. multimaculatum* from the Philippines are placed in *Sagaminopteron*. *Sagaminopteron multimaculatum* is clearly similar in morphology to *S. pohnpei*, and both species have a simple penis as in other members of *Sagaminopteron*. The external anatomy of *S. multimaculatum* clearly differentiates it from all described species of *Sagaminopteron*. This species most closely resembles *S. pohnpei*. They are the only two species of *Sagaminopteron* that entirely lack a flagellum. In our molecular analysis, *S. multimaculatum* is sister to the

specimen Anthes *et al.* (2008) identified as *S. pohnpei*. These two specimens have an uncorrected *p*-distance value for the *COI* gene of 1.8%. This is consistent with the two specimens representing a single species with specimens being found in the Philippines and the Great Barrier Reef of Australia. In our ABGD analysis, the two are considered conspecific, and both represent *S. multimaculatum*. In contrast, the black specimen that we identified as *S. pohnpei* and the orange specimen we identified as *S. pohnpei* are only 0.3% different in their *COI* gene sequences and are sister to the two specimens of *S. multimaculatum*. The specimen of *S. multimaculatum* from the same locality in the Philippines is 7.4% different from the sympatric specimens of *S. pohnpei*, and the ABGD analysis clearly distinguishes them as distinct species. The specimen identified as *S. pohnpei* by Anthes *et al.* is 7.6% different from the Philippine specimen of *S. pohnpei* and probably represents another specimen of *S. multimaculatum*. Morphologically, *S. pohnpei* and *S. multimaculatum* are very similar. *Sagaminopteron pohnpei* ranges is colour from brown to orange, reddish or black with white or yellow spots, while *S. mutimaculatum* is greenish with orange, white and yellow spots. The radula is similar in the two species, with a broad flange on the inner margin of inner lateral teeth that bear elongate denticles. The primary morphological difference is in the anatomy of the penis. In *S. pohnpei* (Gosliner, 1989: fig. 14c; this study, Fig. 9A, B), the prostate is elongate with two distinct swollen bulbs, while in *S. mutimaculatum*, the prostate is simple, curved and relatively short with only one expanded area. The penial bulb is more highly muscularized in *S. pohnpei* than in *S. multimaculatum* (Figs 4C, 9A, B).

GENUS *SIPHOPTERON* GOSLINER, 1989

Type species

Siphopteron tigrinum Gosliner, 1989, by original designation

SIPHOPTERON VERMICULUM ONG & GOSLINER **SP. NOV.**

(FIGS 1F, 9C, D, 10, 11)

LSID urn:lsid:zoobank.org:act:87679EFCB0E8-427B-A63B-1B1521BD79D4

Siphopteron sp. 4, Gosliner *et al.*, 2015: 59, middle left fig.

Type material

Holotype, dissected, NMP 041183, originally CASIZ 199134, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 2 May 2014, T. Gosliner. Paratypes: CASIZ 199126, one specimen, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 2 May 2014, T. Gosliner. CASIZ 199129, three specimens, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 6 May 2014, T. Gosliner.

Type locality

Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines (Gosliner *et al.*, 2015).

Etymology

The species epithet, *vermiculum*, refers to the vermillion colour ornamenting the body of this species.

Description

External morphology: Living animals 4–5 mm in length (Fig. 1F). Parapodia and foot ground colour clear to translucent white to vermillion red. Parapodia lined with yellow and orange accents. White and orange spots dotting parapodia and head shield. Visceral hump more opaque than appendages, vermillion with white spots. Parapodial margin lined by translucent outer margin, followed by vermillion submarginal band and orange inner submarginal band. Elongate flagellum (Fig. 10A) opaque white with opaque white band, located centrally on visceral hump. White pigment transitioning into yellow band, followed by orange or brownish dot tip. Foot of animal translucent white, lined with vermillion lateral edges and central opaque white medial stripe, becoming interrupted and orange posteriorly. Flagellum centred on midline of visceral hump. Head shield quadrangular anteriorly with orange transverse band. Head shield broadest anteriorly and narrowing posteriorly. Two symmetrical orange dots present on either side of head shield, vermillion ground colour converging on siphon. Central white stripe present on the anterior side of siphon. Siphon lined with orange dots on either side. Posterior side of siphon with vermillion ridge, extending on to appendage extending slightly above lateral margins siphon. Gill small with only three small filaments.

Shell: No trace found in single specimen dissected.

Buccal mass: Moderately muscularized with series of circular muscles anteriorly and more complex

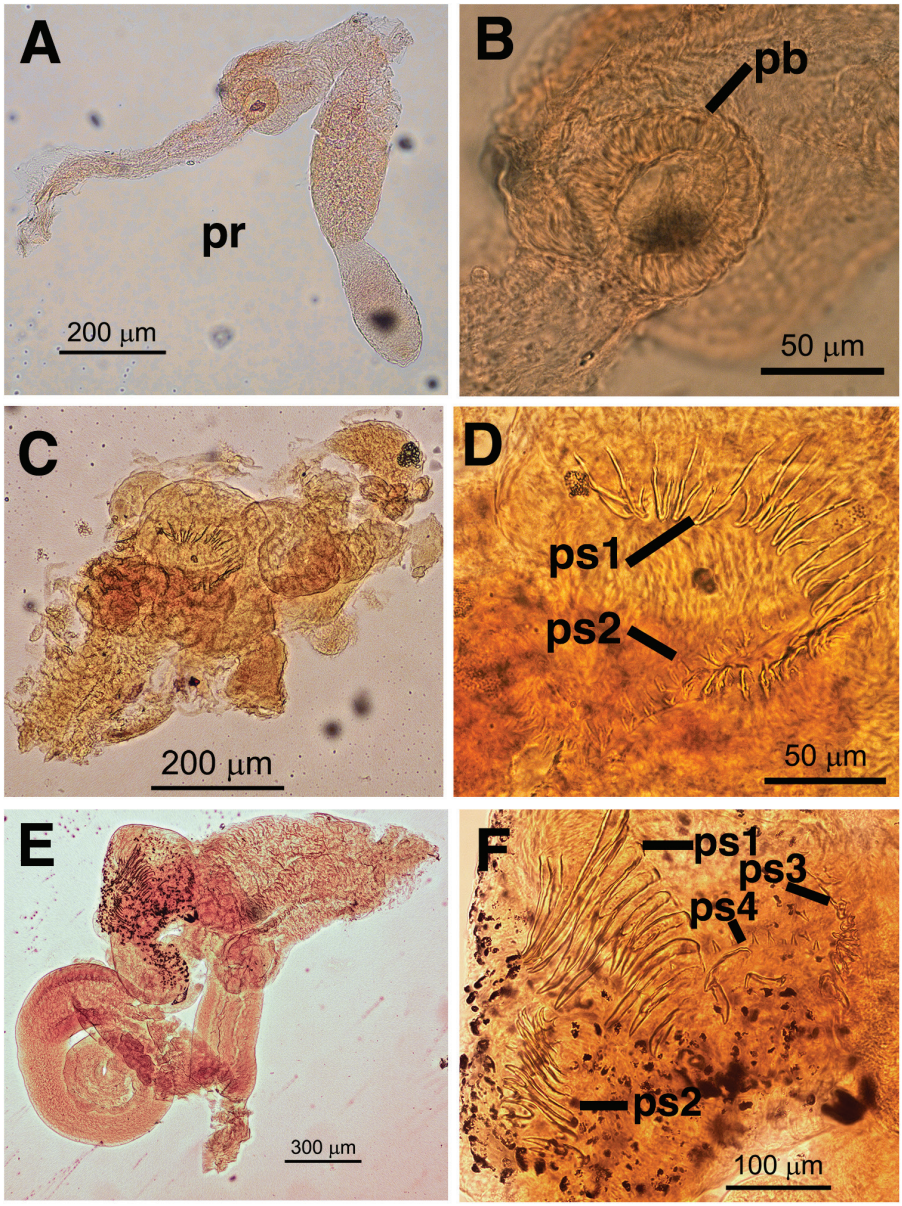

Figure 9. Penial anatomy. (A) *Sagaminopteron pohnpei* (Hoff & Carlson, 1983), CASIZ 180408, entire penis, pr = prostate. (B) *Sagaminopteron pohnpei* (Hoff & Carlson, 1983), CASIZ 180408, penial sac detail, pb = penial bulb. (C) ***Siphopteron vermiculum* sp. nov.**, holotype, NMP 041183. Tingloy, Philippines, Philippines, entire penis. (D) ***Siphopteron vermiculum* sp. nov.**, holotype, NMP 041183. Tingloy, Philippines, Philippines, penial bulb detail, ps = penial spines 1, ps 2 = penial spines (E) ***Siphopteron flavolineatum* sp. nov.**, paratype, CASIZ 199132. Tingloy, Philippines, Philippines, entire penis. (F) ***Siphopteron flavolineatum* sp. nov.**, CASIZ 199132. Tingloy, Philippines, Philippines, penial bulb detail, ps = penial spines 1, ps 2 = penial spines 2, ps3 = penial spines 3, ps4 = penial spines 4.

musculature around radular sac (Fig. 10B). Buccal mass containing labial cuticle with pair of minute areas of small irregular rodlets (Fig. 11A). Radular formula 18 × 2-3.1.0.1.2-3. (Fig. 11B) in one specimen (NMP 041183). Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with irregular series of 2–3 wide areas (Fig. 11C, D). Under higher magnification, these areas bear numerous striations (Fig. 11D), suggesting that they may represent fusion of denticles. Outer lateral teeth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base; all lacking denticles (Fig. 11D).

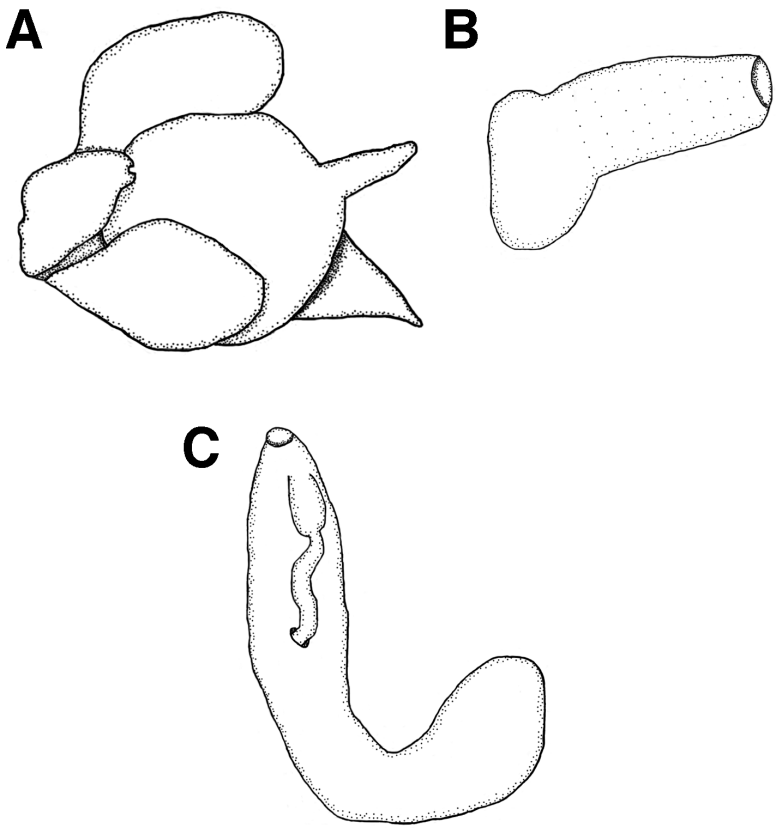

Figure 10. ***Siphopteron vermiculum*** **sp. nov.**, holotype, NMP 041183, Tingloy, Philippines. (A) Dorsal view of preserved specimen, scale = 1.7 mm. (B) Buccal mass, scale = 0.67 mm. (C) Penis, scale = 0.56 mm.

Central nervous system: Arrangement of ganglia euthyneurous, with short visceral loop. Details of arrangement of ganglia not determined in single specimen dissected.

Reproductive system: Fully mature but poorly preserved. Well-developed female glands clearly visible. Elongate, convoluted ampulla extending into straighter hermaphroditic duct curving around top of lobate mucous gland and expanding into short lobe of receptaculum seminis before curving around female glands once more. Opening of hermaphroditic duct into female glands not visible, and hermaphroditic duct joining near gonopore, leading to external sperm groove. Bursa copulatrix not visible. Sperm groove continuing on the right side of the body to head where penis is situated. Penis complex with elongate, sharply curved prostate (Fig. 10C). Secondary duct connecting anterior end of prostate with anterior part of penis. Penial sac straight, containing arch of *c*. 23 interiorly directed, acutely pointed cuticular spines (Fig. 9D, ps1). Second row of 20 much smaller spines found inside arch of the larger spines (Fig. 9D, ps2). Secondary papilla found at anterior end of penial sac, lacking any armature.

Remarks

Based on its coloration, *S. vermiculum* is distinct from other members of the genus. It is the only species with a bright vermillion red ground colour. Based on internal morphological characters, *S. vermiculum* appears to be most similar to *Siphopteron nigromarginatum* Gosliner, 1989 and *Siphopteron flavum* (Tokioka & Baba, 1964). All three species are the only members of the family known to have a complex penis with two papillae where the primary papilla has a series of cuticular spines and where the secondary papilla lacks armature (Gosliner, 1989). All three species also have an irregularly shaped masticatory margin of the inner lateral tooth, but the denticles in *S. vermiculum* are reduced to striations, whereas they are more prominent in *S. nigromarginatum* and *S. flavum*. In *S. vermiculum*, there are two rows of penial spines, whereas *S. flavum* possesses only a single band of penial spines, and *S. nigromarginatum* has four distinct bands of spines (Gosliner, 1989).

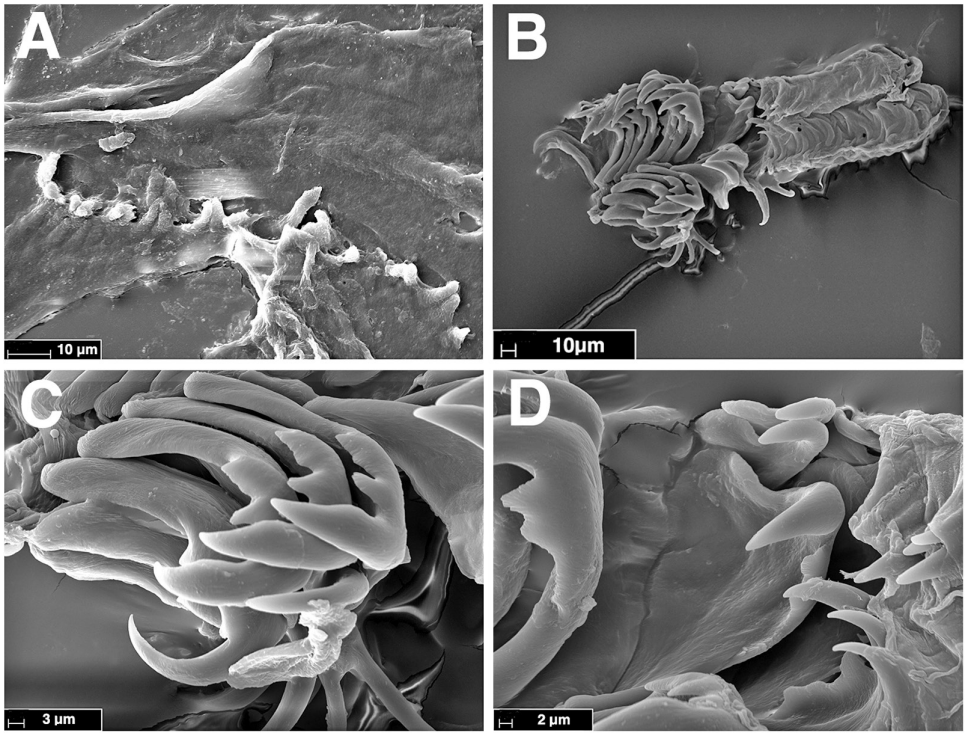

Figure 11. ***Siphopteron vermiculum*** **sp. nov.** holotype, NMP 041183, Tingloy, Philippines, scanning electron micrographs. (A) Jaw rodlets. (B) Entire radula. (C) Half-row of radular teeth. (D) Half-row of radular teeth showing detail of denticles and lateral teeth.

In our molecular analysis, *S. vermiculum* is sister to *Siphopteron* sp. 2 (AM421863) and both are sister to *S.* sp. 1 (AM421862). *Siphopteron vermiculum* and *Siphopteron* sp. 2 are only 4.4% different in their *COI* p-distance, suggesting that they may be the same species. No other information about the appearance of *S.* sp. 2 is available, based on the unpublished GenBank sequences.

SIPHOPTERON FLAVOLINEATUM ONG & GOSLINER SP. NOV.

(FIGS 1G, H, 9E, F, 12, 13)

LSID urn:lsid:zoobank.org:act:05A33467-CE3A-4E95-BA4A-57B2D47B4365

Siphopteron sp. 6 Gosliner *et al.*, 2015: 59, bottom two figs.

Type material

Holotype, NMP 041184, originally CASIZ 199132, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 6 May 2014, T. Gosliner. Paratypes: CASIZ 199132, two specimens, one dissected, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 6 May 2014, T. Gosliner. CASIZ, 199124, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 26 April 2014, T. Gosliner. CASIZ 204848, GAL 73, one specimen, Shipyard, Puerto Galera Harbor, Mindoro Oriental, Philippines, 18 m depth, T. Gosliner., CASIZ 204850, one specimen, GAL 98, Giant Clam, Puerto Galera Harbor, Mindoro Oriental, Philippines, 18 m depth, Gustav Paulay.

Type locality

Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines and Malaysia (Gosliner *et al.*, 2015).

Etymology

The species epithet, *flavolineatum*, refers to the yellow medial line on the posterior end of the foot, which distinguishes this species.

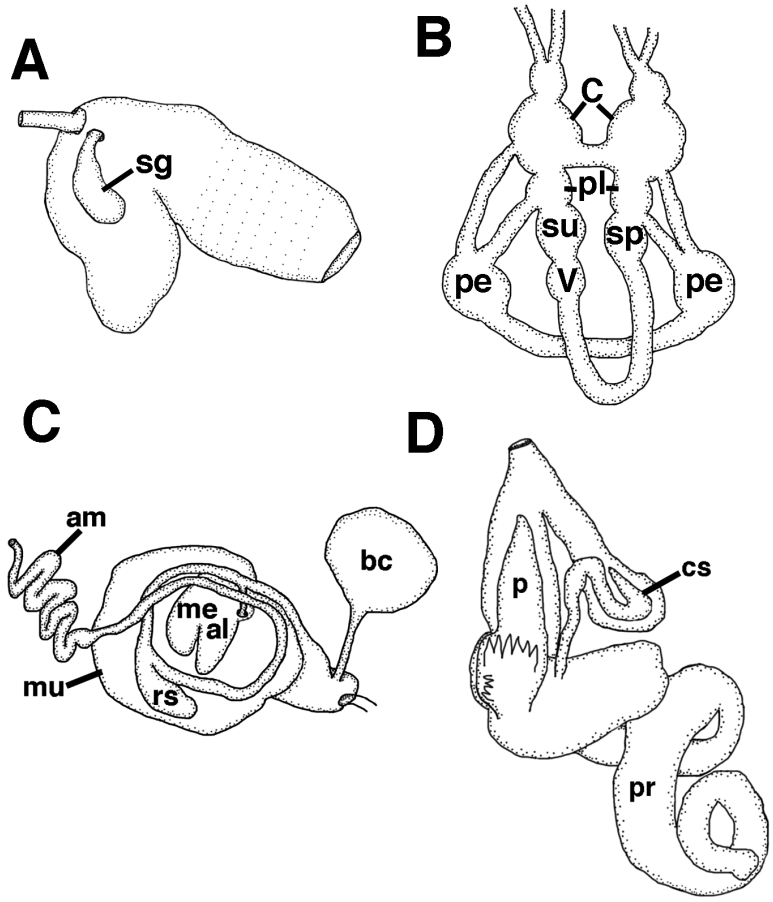

Figure 12. ***Siphopteron flavolineatum*** **sp. nov.** paratype, CASIZ 199132, Tingloy, Philippines. (A) Buccal mass, sg = salivary gland; scale = 0.8 mm. (B) Central nervous system, c = cerebral ganglion, pe = pedal ganglion. pl = pleural ganglion, su-subintestinal ganglion, sp = supraintestinal ganglion, v = visceral ganglion; scale = 0.56 mm. (C) Posterior reproductive system am = ampulla, al = albumen gland, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis; scale = 0.7 mm. (D) Penis, cs = copulatory spine, p = penis, pr = prostate; scale = 1.0 mm.

Description

External morphology: Living animal 5–7 mm in length (Fig. 1G, H). Parapodia and foot ground colour clear to translucent white to ochre. Parapodia lined with yellow and vermillion accents. White spots dotting parapodia, head shield and visceral hump. Visceral hump is more opaque than its appendages. Visceral hump ochre to vermillion towards flagellum with white spots. Flagellum opaque ochre with vermillion outlined by yellow stripes at the end with black tip. Foot translucent white, lined with orange edges and central yellow stripe down middle. Flagellum (Fig. 1G, H) centred on midline of visceral hump. Head shield roughly triangular in shape, broadest anteriorly and narrowing posteriorly into siphon. Siphon with central white stripe that bisects vertically on anterior side. Siphon with two symmetrical white dots on either side of head shield on a translucent ground colour transitioning posteriorly into ochre colour on siphon. Yellow stripe present on posterior side of siphon, lined with darker vermillion on either side. Siphon with prominent medial crest on posterior side, extending slightly above level of lateral margins. Gill small with three primary folds.

Shell: No trace of shell found in only specimen dissected.

Buccal mass: Highly muscularized with series of circular muscles anteriorly and more complex musculature around radular sac (Fig. 12A). Buccal mass containing labial cuticle with pair of minute areas with small irregular rodlets; not visible in scanning electron microscopy preparation. Radular formula 16 × 4.1.0.1.4. (Fig. 13A) in one specimen (CASIZ 199132) examined. Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with two large, well-separated triangular

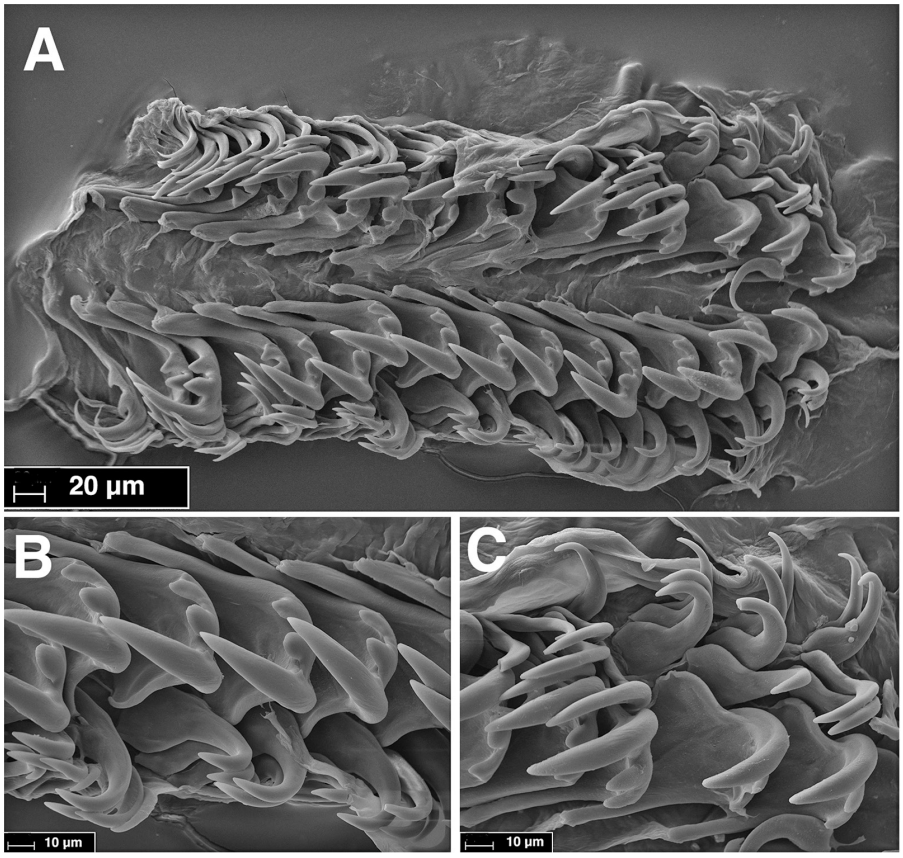

Figure 13. ***Siphopteron flavolineatum*** **sp. nov.** paratype, CASIZ 199132, Tingloy, Philippines, scanning electron micrographs. (A) Entire radula. (B) Half-row of radular teeth. (C) Half-row of radular teeth showing outer lateral teeth.

denticles (Fig. 13B, C). Outer lateral teeth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base. Outer laterals all lacking denticles (Fig. 13C).

Central nervous system: Arrangement of ganglia (Fig. 12B) euthyneurous, with short visceral loop. Cerebral ganglia large, separated by short commissure. Pedal ganglia as large as cerebral ganglia, separated by elongate commissure passing ventrally to buccal mass. Supraintestinal ganglion immediately posterior to right pleural ganglion. Visceral loop connecting to visceral and subintestinal ganglia and curving anteriorly to join left pleural ganglion.

Reproductive system: Reproductive system fully mature and well preserved (Fig. 12C). Well-developed female glands clearly visible. Elongate, convoluted ampulla extending into straighter hermaphroditic duct, curving around top of lobate mucous gland and expanding into elongate lobe of receptaculum seminis before curving around female glands once more. Branch of hermaphroditic duct entering base of albumen and membrane glands. From this junction, hermaphroditic duct joining genital atrium, near gonopore. Gonopore leading to external sperm groove. Bursa copulatrix spherical with relatively short narrow duct joining genital atrium near gonopore. Sperm groove continuing on right side of body to head, where penis situated. Penis complex with elongate, highly convoluted prostate (Fig. 12D). Secondary duct convoluted, connecting anterior end of prostate with side of penis. Penial sac straight, containing *c*. 14 large, interiorly directed, acutely pointed cuticular spines (Fig. 9F, ps1). More posteriorly, at base of penial sac, are about 13 bifid, slightly smaller spines (Fig. 9F, ps2). Another series of 13 small spines found on the right side of anterior portion of penial sac (Fig. 9F, ps3) along with another anteromedial row of 13 spines (Fig. 9F, ps4). Secondary papilla found at the anterior end of penial sac and appearing to have acutely pointed cuticular spine.

Remarks

The colour pattern of *S. flavolineatum* with an ochre colour with prominent white spots is unique to this

species. This pattern is consistent in all the specimens examined, but there is some variation in the size and the distribution of the white spots. In addition, the narrow yellow line on the posterior end of the foot also appears to be distinctive. Morphologically, this species is similar to *S. quadrispinosum* Gosliner, 1989, which has an inner lateral radular tooth with two large quadrangular cusps. *Siphopteron quadrispinosum* differs in its colour pattern with a yellow body with red pigment on the apex of the siphon and on the flagellum. This species also has a white margin along the edge of the parapodia. Internally, the penis is very different between the two species. The penis of *S. quadrispinosum* has four large basal cuticular spines with no smaller spines. There are small spines on the penial papilla. The secondary papilla has a massive cuticular spine that is used for hypodermic insemination (Gosliner, 1989; Anthes *et al.*, 2008). In contrast, *S. flavolineatum* has four distinct areas of spines, each with numerous spines. The secondary papilla has a relatively small spine compared to that found in *S. quadrispinosum*. The two specimens sequenced for genetic studies include one specimen from Tingloy, Batangas, and the other is from Puerto Galera, a distance of about 22 km. Despite this proximity, the two specimens differ in their *COI* gene by 1.7%. This suggests that there may be some genetic isolation between the north and south sides of the Verde Island Passage.

SIPHOPTERON NAKAKATUWA ONG & GOSLINER SP. NOV.

(FIGS 14A, B, 15, 16, 17A)

LSID urn:lsid:zoobank.org:act:0D0AFDD2-AA44-4C25-AA98-F59C138BA098

Siphopteron sp. 7 Gosliner *et al.*, 2015: 60, upper two figs.

Type material

Holotype, dissected, NMP 041185, ex CASIZ 199135, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 6 May 2014, T. Gosliner. Paratypes: CASIZ 199135, one specimen, Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines, 7 m depth, 6 May 2014, T. Gosliner. CASIZ 199125, one specimen, Mainit Bubbles (13.68688°N 120.89564°E), Mabini, Batangas, Luzon, Philippines, 7 m depth, 27 April 2014, Alexis Principe. CASIZ, 199114, one specimen, Bilbago Reef South, Calatagan (13.929165°N 120.612299°E), Batangas, Luzon, Philippines, 7 m depth, 17 May 2014, T. Gosliner.

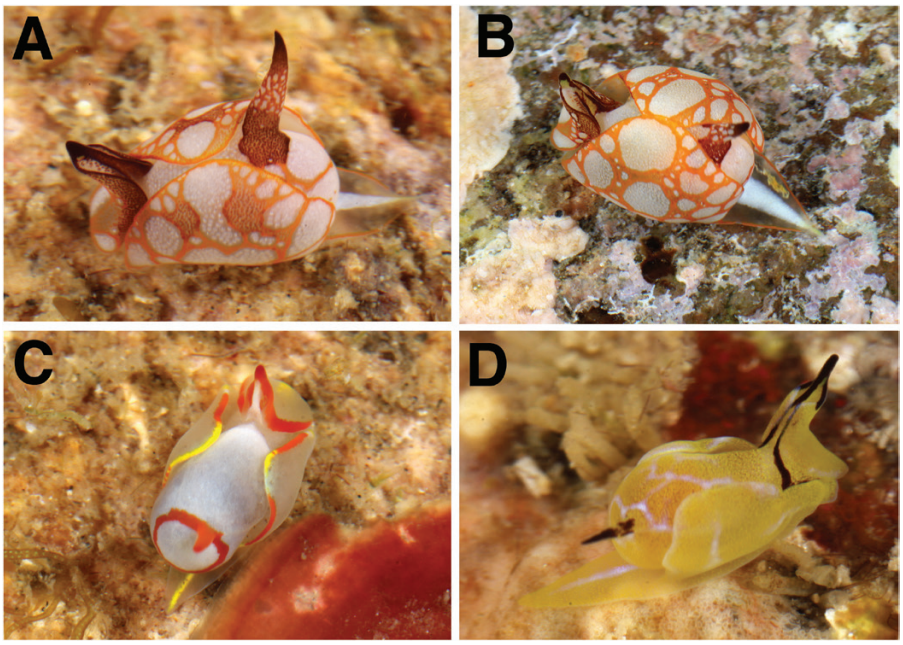

Figure 14. Living animals. (A) ***Siphopteron nakakatuwa* sp. nov.**, partaype, CASIZ 199114, Tingloy, Philippines. (B) ***Siphopteron nakakatuwa* sp. nov.**, holotype, NMP 041185, Tingloy, Philippines. (C) ***Siphopteron makisig* sp. nov.**, holotype NMP 041186, Calatagan, Philippines. (D) ***Siphopteron dumbo* sp. nov.**, NMP 041187, Puerto, Galera, Philippines. Photos by T. Gosliner.

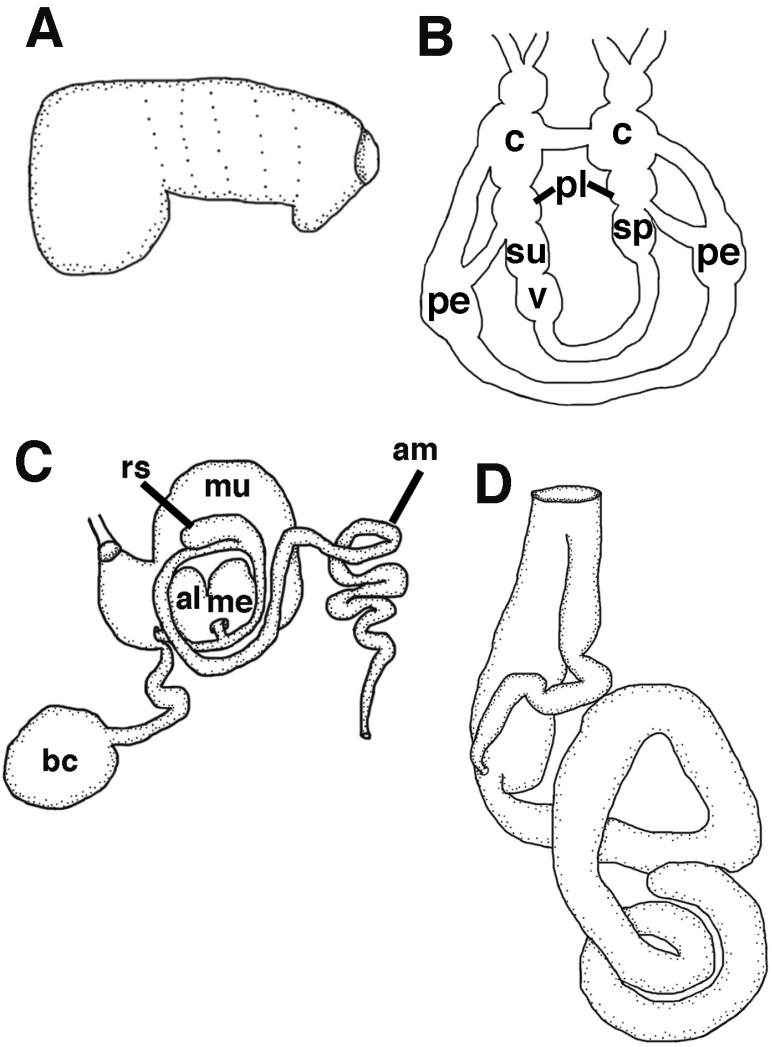

Figure 15. ***Siphopteron nakakatuwa*** **sp. nov.** holotype, NMP 041185, Tingloy, Philippines. (A) Buccal mass, scale = 0.5 mm. (B) Central nervous system, c = cerebral ganglion, pe = pedal ganglion. pl = pleural ganglion, su- subintestinal ganglion, sp = supraintestinal ganglion, v = visceral ganglion, Scale = 0.67 mm. (C) Posterior reproductive organs, a = ampulla, al = albumen gland, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis; scale = 0.58 mm. (D) Penis, scale = 0.5 mm.

Type locality

Cemetery Beach (13.68428°N 120.83024°E), Tingloy, Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines and Indonesia (Gosliner *et al.*, 2015).

Etymology

The species epithet, *nakakatuwa*, is a Tagalog word meaning 'amusing or cute'.

Description

External morphology: Living animals 4–7 mm in length (Fig. 14A, B). Parapodia and foot ground colour translucent white to orange. White spots covering parapodia; each spot lined by bright orange. Parapodia lined with accents converging on foot. White spots with opaque white punctations inside larger spot. These large spots dotting head shield, parapodia and visceral hump. Visceral hump rounded with long flagellum near midline of body. Elongate flagellum (Fig. 14A, B) opaque vermillion with white spots ending with black tip. Foot translucent white, lined with orange edges and central white triangular stripe down middle.

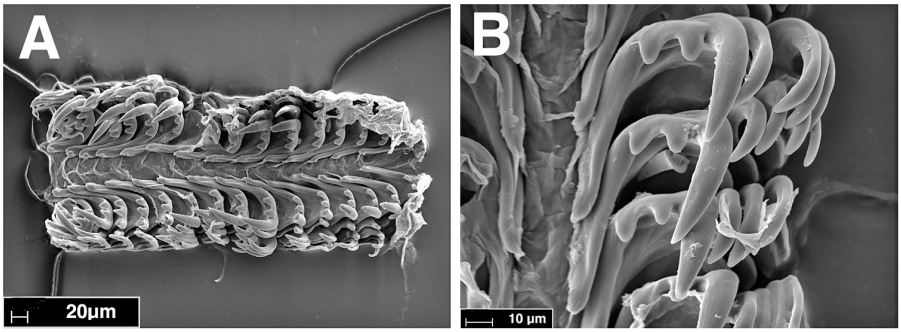

Figure 16. ***Siphopteron nakakatuwa*** **sp. nov.** holotype, NMP 041185, Tingloy, Philippines, scanning electron micrographs. (A) Entire radula. (B) Half row of radular teeth.

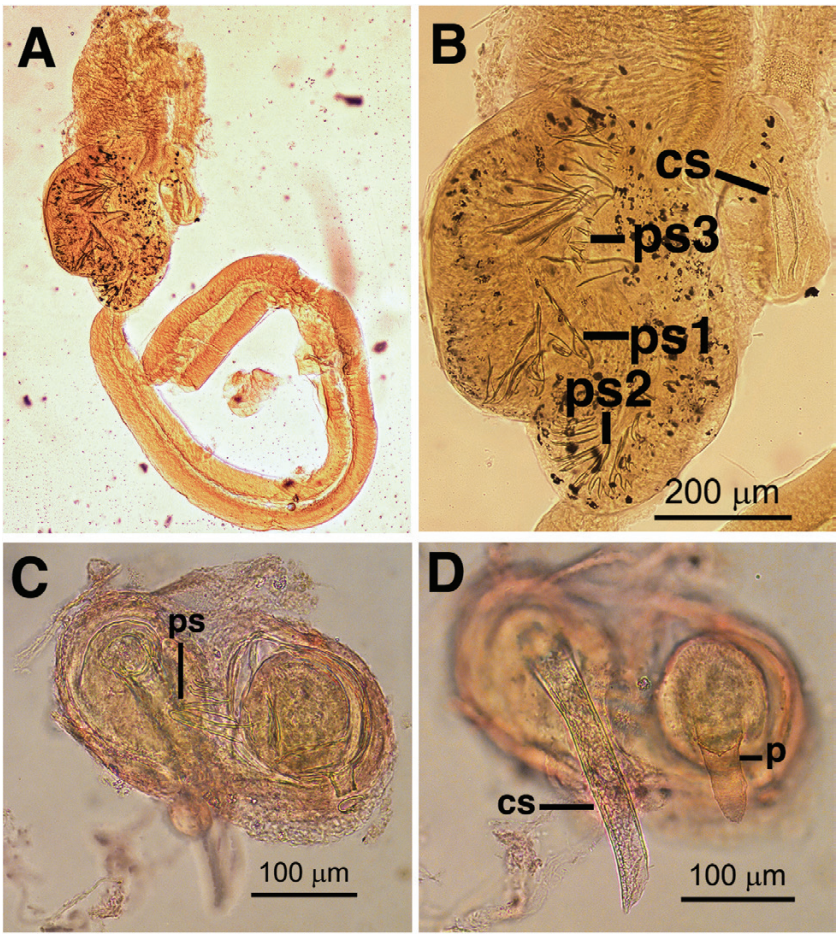

Figure 17. Penial anatomy. (A) ***Siphopteron nakakatuwa*** **sp. nov.**, holotype, NMP 041185, Tingloy, Philippines, entire penis. (B) ***Siphopteron nakakatuwa*** **sp. nov.**, holotype, NMP 041185, Tingloy, Philippines, penial sac detail, ps = penial spines 1, ps 2 = penial spines, ps3 = penial spines 3, cs = cuticular spine. (C) ***Siphopteron makisig*** **sp. nov.**, CASIZ 199134. Calatagan, Philippines, Philippines, detail of penial spines, ps = penial spines. (D) ***Siphopteron makisig*** **sp. nov.**, CASIZ 199134. Calatagan, Philippines, Philippines, detail of cuticular spine and penial papilla, cs = cuticular spine, p = penial papilla.

Stripe merging into yellow tip. Head shield roughly triangular, broadest anteriorly, and narrowing posteriorly into siphon. Siphon with central white stripe on anterior face, bisecting vertically. Posterior side of siphon with prominent ridge extending above lateral margins. Siphon with vermillion ground colour and

yellow tip with vermillion edges and white spots. Gill with four simple folds.

Shell: No trace of a shell found in specimen dissected.

Buccal mass: Highly muscularized with series of circular muscles anteriorly and more complex musculature around radular sac (Fig. 15A). Buccal mass containing labial cuticle with a pair of minute areas with small irregular rodlets, Rodlets not visible in scanning electron microscopy preparation. Radular formula 16 × 4.1.0.1.4. (Fig. 16A) in one specimen (NMP 041185) examined. Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with two large, well-separated, triangular denticles (Fig. 16B). Outer lateral teeth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base; all lacking denticles (Fig. 16B).

Central nervous system: Arrangement of ganglia (Fig. 15B) euthyneurous with short visceral loop. Cerebral ganglia large; separated by a short commissure. Pedal ganglia as large as cerebral ganglia, separated by elongate commissure passing ventrally to buccal mass. Supraintestinal ganglion immediately posterior to right pleural ganglion. Visceral loop connecting to visceral and subintestinal ganglia and curving anteriorly to join left pleural ganglion.

Reproductive system: Fully mature and well preserved (Fig. 15C). Well-developed female glands clearly visible. Elongate, convoluted ampulla extending into straighter hermaphroditic duct curving around top of lobate mucous gland and expanding into elongate lobe of receptaculum seminis before curving around female glands once more. Branch of hermaphroditic duct entering base of albumen and membrane glands. Hermaphroditic duct joining genital atrium near gonopore from this junction. Gonopore leading to external sperm groove. Bursa copulatrix spherical with curved, narrow duct joining genital atrium near gonopore. Sperm groove continuing on the right side of the body to head where penis is situated. Penis complex with elongate, highly convoluted prostate (Figs 15D, 17A). Secondary duct convoluted and connecting anterior end of prostate with side of penis. Penial sac (Fig. 17B) straight and containing approximately 13 large, posteriorly directed, acutely pointed cuticular spines (Fig. 17B, ps1). More posteriorly, at tbase of penial sac, about 14 slightly smaller, bifid, or trifid spines (Fig. 17B, ps2) present. Another series of 19 small spines found on the right side of the anterior portion of penial sac (Fig. 17B, ps3). Secondary papilla found at the anterior end of penial sac appearing to have acutely pointed cuticular spine (Fig. 17B, cs).

Remarks

The colour pattern of *S. nakakatuwa*, with an orange body colour with prominent white spots, is unique to this species. This pattern is consistent in all the specimens examined, but there is some variation in the size and the distribution of the white spots. In addition, the narrow opaque white triangular line on the posterior end of the foot also appears to be distinctive. Morphologically, this species is similar to *S. flavolineatum* and *S. quadrispinosum*, both of which have an inner radular tooth with two large quadrangular cusps. *Siphopteron quadrispinosum* differs in its colour pattern with a yellow body with red pigment on the apex of the siphon and on the flagellum. This species also has a white margin along the edge of the parapodia. *Siphopteron flavolineatum* differs from *S. nakakatuwa* in having an ochre rather than orange pigment on the body, dark pigment only on the tip of the siphon and flagellum, and in having a narrow yellow medial line on the foot as compared to a triangular white one *in S. nakakatuwa*. Internally, the radula of all three species is very similar. The penial morphology of *S. nakakatuwa* is very similar to that of *S. flavolineatum*, with the exception that the largest spines of *S. nakakatuwa* are much larger than those of *S. flavolineatum*. The penis of *S. quadrispinosum* has four large basal cuticular spines with no smaller spines. In *S. quadrispinosum*, there are also small spines on the penial papilla. The secondary papilla has a massive cuticular spine that is used for hypodermic insemination (Gosliner, 1989; Anthes *et al.*, 2008). In contrast, *S. nakakatuwa* has four distinct areas of spines, each with numerous spines. The secondary papilla has a relatively small spine compared to that found in *S. quadrispinosum*.

In the molecular phylogenetic analysis, *S. nakakatuwa* and *S. flavolineatum* are sister species and are found sympatrically in the Philippines. The two differ in their *COI* gene sequences by 8.8% and are considered as distinct species in our ABGD analysis.

SIPHOPTERON MAKISIG ONG & GOSLINER SP. NOV.

(FIGS 14C, 17C, D, 18, 19)

LSID urn:lsid:zoobank.org:act:9E247ACD-9C5B-49A4-BE53-B8A62C7C6961

Siphopteron sp. 1 Lange *et al.*, 2013: fig. 1b.
Siphopteron sp. 5 Gosliner *et al.*, 2015: 59, middle right fig.

Type material

Holotype, dissected, NMP 041186, ex CASIZ 199113, one specimen, Bilbago Reef South, Calatagan (13.929165°N 120.612299°E), Batangas, Luzon, Philippines, 7 m depth, 17 May 2014, T. Gosliner.

Type locality

Bilbago Reef South, Calatagan (13.929165°N 120.612299°E), Batangas, Luzon, Philippines.

Geographical distribution

Thus far, known only from the Philippines, Indonesia and Australia (Gosliner *et al.*, 2015).

Etymology

The species epithet, *makisig*, is a Tagalog word meaning 'elegant or refined'.

Description

External morphology: Living animal 4 mm in length (Fig. 14C). Parapodia, head shield and foot translucent white to faint vermillion red. Head shield roughly triangular, tapering posteriorly to siphon. Medial yellow line present on the anterior part of head shield. Additional red orange line found along lateral margins of head shield and extending to tip of siphon with medial white ridge along its posterior edge, extending to red orange apex. Apex higher than lateral margins (Fig. 18A). Parapodia lined with yellow and orange marginal accents. Visceral hump more opaque white than head shield or parapodia with bright red orange ring around posterior end of visceral hump. Flagellum translucent white with bright orange-red tip. Foot translucent white with central yellow stripe down in the middle. Flagellum found on the right side of visceral hump. Gill with four simple folds.

Shell: No trace of shell found in dissected specimen.

Buccal mass: Highly muscularized with series of circular muscles anteriorly and more complex musculature around radular sac (Fig. 18B). Buccal mass containing labial cuticle with a pair of minute areas with small irregular rodlets (Fig. 19A). Radular formula 18 × 4.1.0.1.4. (Fig. 19B) in one specimen (NMP 041186) examined. Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with two large, triangular, well-separated denticles (Fig. 19C, D). Outer lateral teeth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base and all lacking denticles (Fig. 19D).

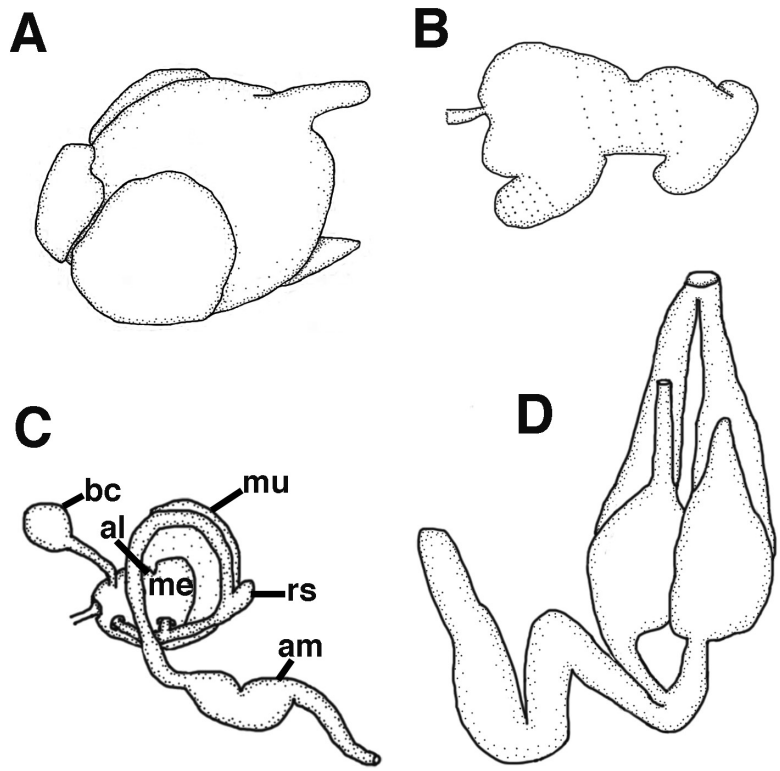

Figure 18. ***Siphopteron makisig*** **sp. nov.** holotype, NMP 041186, Puerto Galera, Philippines. (A) Preserved animal, scale = 1.4 mm. (B) Buccal mass, Scale = 0.71 mm. (C) Posterior reproductive organs, am = ampulla, al = albumen gland, bc = bursa copulatrix, me = membrane gland, mu = mucus gland, rs = receptaculum seminis; scale = 1.0 mm. (D) Penis, p = penis, pr = prostate; scale = 0.9 mm.

Central nervous system: Arrangement of ganglia euthyneurous, with short visceral loop. Details of arrangement of ganglia not determined in single specimen dissected.

Reproductive system: Fully mature and well preserved (Fig. 18C). Well-developed female glands clearly visible. Elongate, convoluted ampulla extending into straighter hermaphroditic duct that curves around the top of lobate mucous gland and expands into elongate lobe of receptaculum seminis before curving around female glands once more. Branch of hermaphroditic duct entering the base of albumen and membrane glands. From this junction, hermaphroditic duct joining genital atrium, near gonopore. Gonopore leading to external sperm groove. Bursa copulatrix spherical with short, narrow duct joining genital atrium near gonopore. Sperm groove continuing on the right side of body to head, where penis is situated. Penis complex with elongate, highly convoluted prostate (Fig. 18D). Secondary duct convoluted, connecting anterior end of prostate with side of penis. Penial sac straight, containing five spines that gradually diminish in size (Fig. 17C). From basal spines, conical penial papilla extending anteriorly. Papilla bearing a few minute tubercles or spines (Fig. 17D). Secondary papilla found at anterior end of penial sac, terminating in large, acutely pointed cuticular spine (Fig. 17D).

Remarks

The external morphology and penial morphology of *S. makisig* were described by Lange *et al.* (2013, as *Siphopteron* sp. 1). The colour pattern of *S. makisig*, with a white body colour with prominent red-orange pigment on the siphon, flagellum and visceral hump spots, is unique to this species. Lange *et al.* also described the details of the hypodermic mating interactions in this species. Morphologically, this species is similar to *S. quadrispinosum* Gosliner, 1989, where both species have an inner radular tooth with two large quadrangular cusps. *Siphopteron quadrispinosum* differs in its colour pattern with a yellow body with red pigment on the apex of the siphon and on the flagellum. This species also has a white margin along the edge of the parapodia. In *S. quadrispinosum*, the base of the penis has four large spines surrounding the base of the penial papilla (Gosliner, 1989), while in *S. makisig* there is a row of five penial spines that are graduated in size. *Siphopteron flavolineatum* and *S. nakakatuwa* also have inner radular teeth but differ in their colour pattern and in the morphology of the penis.

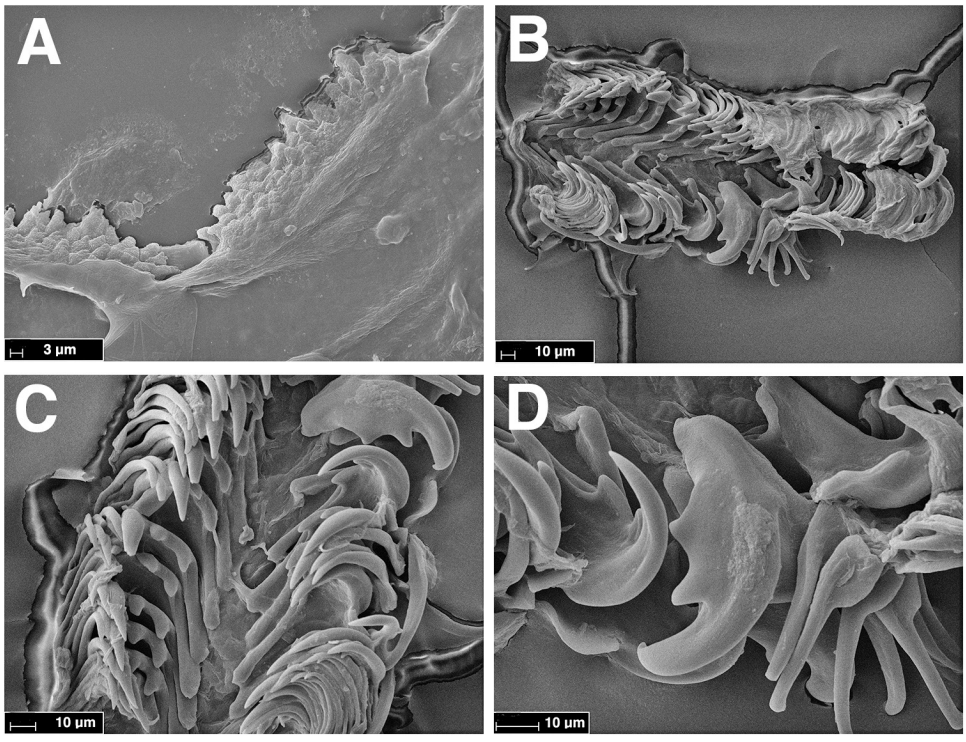

Figure 19. ***Siphopteron makisig*** **sp. nov.** holotype, NMP 041186, Puerto Galera, Philippines, scanning electron micrographs. (A) Jaw rodlets, (B) Entire radula. (C) Entire radular width. (D) Detail of inner and outer lateral teeth.

In our molecular phylogeny, *S. makisig* is sister to a clade containing four individuals of *S. quadrispinosum*. For the *COI* gene, the uncorrected p-distance between *S. makisig* and *S. quadrispinosum* ranges between 9.0 and 9.9%. Our ABGD analysis also clearly demonstrates that *S. makisig* and *S. quadrispinosum* represent distinct species.

When Gosliner (1989) described *S. quadrispinosum*, he noted differences in the coloration of specimens (specimens from type locality of Hawai'i had a white marginal band on the parapodia, whereas additional Papua New Guinea specimens lacked the band and have an orange margin on the head shield that is absent in the Hawai'ian specimens) and in penial morphology between Hawai'ian specimens. Gosliner did not consider these differences significant enough to warrant specific separation. The holotype of *S. quadrispinosum* was a Hawai'ian specimen. Subsequently, Klussmann-Kolb & Klussmann (2003) described *S. leah* from specimens from Australia that had the same morphological features as the specimens Gosliner reported from Papua New Guinea. Rudman (2004) considered *S. leah* as a synonym of *S. quadrispinosum*. In this study, we were able to sequence a Hawai'ian specimen of *S. quadrispinosum* to compare with the Australian specimens that were sequenced by Anthes *et al.* (2008). The *COI* gene shows 9.3–9.8% difference between the Hawai'ian and Australian specimens. The ABGD analysis also shows that the Hawai'ian specimens should be regarded as distinct species from the Australian ones. On this basis, we consider *S. leah* from the western Pacific Ocean to be distinct from the Hawai'ian species, *S. quadrispinosum*. With this new perspective, *S. leah* is sister to *S. quadrispinosum*, and *S. makisig* is sister to both of these other species. Our ABGD analysis confirms the distinctness of the three species.

SIPHOPTERON DUMBO ONG & GOSLINER SP. NOV.

(FIGS 14D, 20, 21, 22)

LSID urn:lsid:zoobank.org:act:C4E5B8E4-5C13-4D08-9E7C-CCC19FCDC1F0

Type material

Holotype, dissected, NMP 041187, ex CASIZ 204849, one specimen, La Laguna, Puerto Galera (13.525953°N 120.970160°E), Mindoro Oriental, Philippines, 20 m depth, 26 April 2015, T. Gosliner.

Type locality

La Laguna, Puerto Galera (13.525953°N 120.970160°E), Mindoro Oriental, Philippines.

Geographical distribution

Thus far, known only from the Philippines and probably Japan (Ono, 1999).

Etymology

The species epithet, *dumbo*, refers to the similarity of this species to the Disney character, Dumbo the elephant, as it swims through the water.

Description

External morphology: Living animal 3 mm in length (Fig. 14D). Parapodia, head shield and foot pale yellowish over entire surface. Head shield and parapodia with pale blue marginal line. Additional irregularly shaped pale blue network of interconnected squiggles present on parapodia and head shield. Pale blue pigment also found on sides and centre of head shield. Pale blue also present as medial line on posterodorsal portion of foot. Head shield roughly triangular, tapering posteriorly to siphon. Siphon with medial white ridge along posterior edge, extending to well-elevated apex that is much higher than lateral margins. Two black lines found on posterior end of head and lateral margins of siphon. Dorsally black lines merging on to siphonal ridge and continuing to apex. Additional black lines also found on dorsal margins of siphon. Flagellum situated to right of midline on visceral hump (Fig. 20A). Flagellum elongate and acutely pointed. Scattered black pigment found at the base of flagellum. Outer two-thirds of flagellum with solid black pigment. Gill very small with two simple folds.

Shell: No trace of a shell found in specimen dissected.

Buccal mass: Highly muscularized with series of circular muscles anteriorly and more complex musculature around radular sac (20 B). Buccal mass containing labial cuticle with pair of minute areas with small irregular rodlets. Rodlets not visible in scanning electron microscope preparation. Radular formula 15 × 4.1.0.1.4 (Fig. 21A) in one specimen (NMP 041187) examined. Inner lateral teeth broad with single primary cusp. Masticatory margin of inner laterals broad with large triangular denticle flanked on either side by series of crowded smaller denticles (Fig. 21B, C). Outer lateral teeth with moderately broad base and primary cusp without secondary denticles. Successive outer laterals becoming progressively smaller with narrower base and lacking denticles (Fig. 21B).

Central nervous system: Arrangement of ganglia euthyneurous, with short visceral loop. Details of arrangement of ganglia not determined in single specimen dissected.

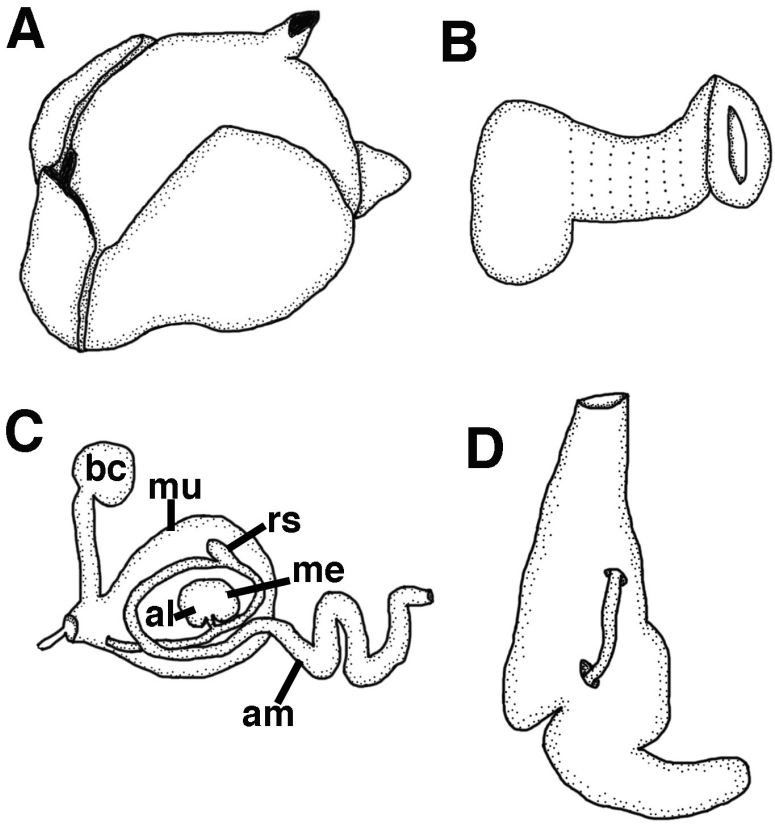

Figure 20. ***Siphopteron dumbo*** **sp. nov.** NMP 041187, Puerto Galera, Philippines. (A) Preserved animal, Scale = 0.8 mm. (B) Buccal mass, Scale = 0.3 mm. (C) Posterior reproductive organs, am = ampulla, al = albumen gland, bc = bursa copulatrix, me = membrane gland, mu = mucous gland, rs = receptaculum seminis; scale = 0.27 mm. (D) Penis, scale = 0.33 mm.

Reproductive system: Fully mature and well-preserved (Fig. 20C). Well-developed female glands clearly visible. Elongate, convoluted ampulla extending into straighter hermaphroditic duct curving around top of lobate mucous gland and expanding into short lobe of receptaculum seminis before curving around female glands once more. Branch of hermaphroditic duct entering base of albumen and membrane glands. From this junction, hermaphroditic duct joining genital atrium, near gonopore. Gonopore leading to external sperm groove. Bursa copulatrix spherical with moderately elongate, narrow duct joining genital atrium near gonopore. Sperm groove continuing on the right side of the body to the head where penis situated. Penis complex with short, curved prostate (Figs 20D, 22A). Secondary duct curved and connecting anterior end of prostate with side of penis. Penial sac straight (Fig. 22A) containing arc of 34 small spines (Fig. 22B). Secondary papilla found at the anterior end of penial sac with fleshy blunt apex devoid of armature.

Remarks

What appears to be *Siphopteron dumbo* has been confused previously with *S. flavum* (Rudman, 1999: lower photo). *Siphopteron dumbo* has a colour pattern similar to several other species that have a yellowish ground colour: *S. flavum*, *Siphopteron citrinum* (Carlson & Hoff, 1974), *Siphopteron brunneomarginatum* (Carlson & Hoff, 1974) and *S. nigromarginatum*. *Siphopteron flavum*, originally described from Japan, has a bright yellow body with black pigment on the siphon and flagellum. The black pigment on the siphon is found along the posterior margins and on the entire apex and anterior face of the siphon in *S. dumbo*. The pigment is a much finer line only on the posterior side of the siphon. In addition, *S. flavum* has a short apex to the siphonal crest, whereas it is elongate in *S. dumbo*. The flagellum is short and blunt and situated medially in *S. flavum*, whereas it is elongate and located well to the right of the midline in *S. dumbo*. Internally, there are differences between the two species. The radula of *S. flavum* has an even row of small denticles on the inner lateral tooth

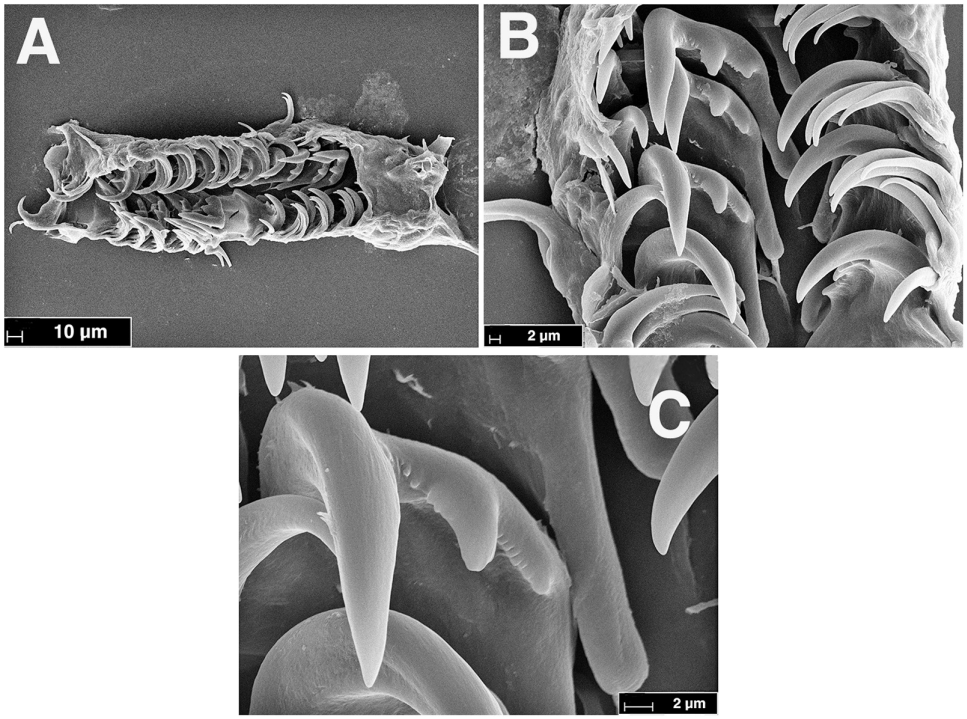

Figure 21. ***Siphopteron dumbo*** **sp. nov.** NMP 041187, Puerto Galera, Philippines, scanning electron micrographs. (A) Entire radula. (B) Half row of radular teeth. (C) Detail of inner lateral teeth showing minute denticles.

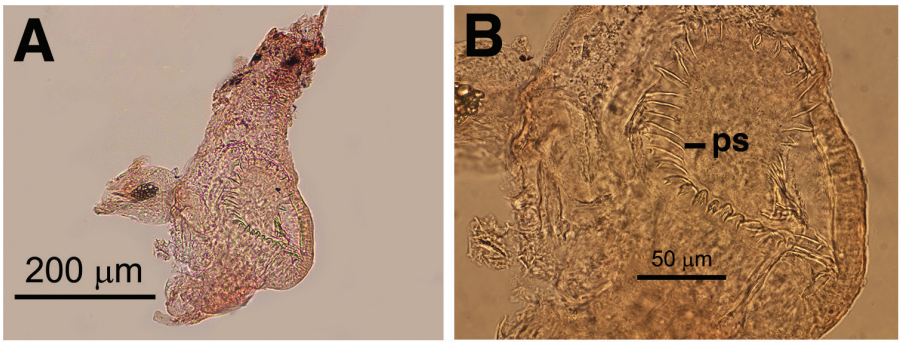

Figure 22. ***Siphopteron dumbo*** **sp. nov.** NMP 041187, Puerto Galera, Philippines, penial anatomy. (A) Entire penial sac. (B) Detail of penial spines, ps = penial spines.

and only three rows of outer lateral teeth (Gosliner, 1989). In *S. dumbo*, the inner lateral tooth has a prominent large triangular denticle with smaller denticles flanking either side and has four rows of outer lateral teeth. Both species have a similar penial morphology with an arch of small penial spines, but with several key differences. In *S. flavum*, the secondary penial papilla is large and pointed (Gosliner, 1989), whereas in *S. dumbo* it is short and blunt. The prostate is more elongate and curved in *S. flavum* than in *S. dumbo*.

Siphopteron citrinum has a pink body colour with yellow spots and patches on the head shield, the posterior shield and parapodia. It has black pigment on the very tip of the siphon and on the entire flagellum. Internally, there are many differences between the two species (Gosliner, 1989). The inner radular teeth of *S. citrinum* have a single triangular cusp along the masticatory border vs. the triangular cusp of *S. dumbo* that is flanked on either side by smaller crowded denticles. *Siphopteron citrinum* has three rather than four outer lateral teeth. The penis of *S. citrinum* has two elongate prostate lobes in contrast to the short single lobe of *S. dumbo*. The penial papilla of *S. citrinum* has three chitinous lobes but lacks the numerous chitinous

Figure 23. Bayesian and ML phylogram of relationships of Gastropteridae. Bootstrap values and posterior probabilities are shown at each node when they are <0.95 or 70, respectively. All other values indicated with an asterisk (*) are highly supported.

hooks found in *S. dumbo*. The secondary penial papilla of *S. citrinum* is elongate and pointed in contrast to the short flat papilla of *S. dumbo*.

Siphopteron brunneomarginatum has a pale yellow body with a dark brown to black parapodial margin and brown or black extending on to the anterior surface of the siphon (Gosliner, 1989). It also has a transverse brown or black line on the visceral hump that continues on the entire length of the flagellum. None of these features are present in *S. dumbo*. Internally, the inner radular teeth of *S. brunneomarginatum* have a few well-separated, acutely pointed denticles along the masticatory border vs. the triangular cusp of *S. dumbo* that is flanked on either side by smaller crowded denticles. *Siphopteron brunneomarginatum* has three rather than four outer lateral teeth. The penial papilla of *S. brunneomarginatum* has two chitinous lobes but lacks the numerous chitinous hooks found in *S. dumbo*. The secondary penial papilla of *S. brunneomarginatum* has a short, flat papilla similar to that of *S. dumbo*.

Siphopteron nigromarginatum has a yellow body colour with black margins along the parapodia that extend almost to the posterior end of the foot (Gosliner, 1989) and lacks the black line on the posterior side of the head shield that are found in *S. dumbo*. In *S. nigromarginatum*, the light blue squiggles and medial line on the foot, which

characterize *S. dumbo*, are absent. Internally, the inner lateral radular teeth of *S. nigromarginatum* have a continuous line of numerous short rounded denticles that extend on to what appears to be a triangular extension of the masticatory border. In a second specimen, there is a simple the triangular cusp with a few vestigial denticles similar to that of *S. dumbo*. *Siphopteron nigromarginatum* has three rather than four outer lateral teeth. The penis of *S. nigromarginatum* has two distinct, elongate prostate lobes vs. the short single prostate of *S. dumbo*. The primary penial papilla of *S. nigromarginatum* has four distinct arches of chitinous spines in contrast to the single arch of spines present in *S. dumbo*. The secondary penial papilla of *S. nigromarginatum* is elongate and pointed in contrast to the short flat papilla of *S. dumbo*.

In our molecular phylogeny, *S. dumbo* is sister to *S. nigromarginatum*. For the *COI* gene, the uncorrected *p*-distance between *S. dumbo* and *S. nigromarginatum* is 8.5%. Our ABGD analysis also clearly demonstrates that *S. dumbo* and *S. nigromarginatum* represent distinct species. *Siphopteron dumbo* clearly belongs in a different clade that *S. brunneomarginatum*. No suitably preserved specimens of *S. citrinum* or *S. flavum* are available for comparative molecular studies.

Molecular phylogeny

The topologies of individual gene trees for *COI*, *16S* and *28S* consistently show the monophyly of Gastropteridae and the major clades within the family. The aligned concatenated dataset was 1839 base pairs in length. This included 750 bp for *28S*, 657 bp for *COI* and 432 bp for *16S* (including gaps and variable regions). RAxML and Bayesian analyses have nearly identical topologies. Tracer files showed that BI searchers all converged on the same likelihood score. For comparison purposes, the combined gene Bayesian tree is shown with their respective non-parametric bootstrap (bs) and posterior probability (pp) values from ML and BI (Fig. 23). The only difference between the two trees is that there are three lineages of *S. psychedelicum* in the Bayesian tree and two in the RAxML tree.

In all three individual gene trees and both concatenated analyses, Gastropteridae is monophyletic. *Gastropteron* and *Siphopteron* are not supported in either analysis, while *Sagaminopteron* is strongly supported (bs = 88, pp = 1.00). The two clades of *Gastropteron* are strongly supported (*rubrum* clade: bs = 78, pp = 1.00; *bicornutum* clade: bs = 97, pp = 1.00) as are the three clades of *S. tigrinum* clade (clade 1): bs = 97, pp = 1.00; *quadrispinosum* clade (clade 3): bs = 89, pp = 1.00; and the sp. CAS 181575 clade (clade 2).

In calculating the species boundaries, we utilized both the corrected p-distance data (Table 3) for the *COI* gene and conducted an ABGD analysis. The analysis revealed 25 distinct groups of taxa with a *COI* barcode gap between ~5 and 7%.

DISCUSSION

Contribution of Gastropteridae to understanding of global biodiversity

This study adds to the known diversity of Gastropteridae. All eight potentially undescribed species recognized from living animals have been demonstrated to represent new taxa and are described here. This brings the total number of described species of Gastropteridae from 33 to 41 species. Of the total known diversity of the family worldwide, 17 species (or 41% of the known global taxa) have been documented from just the Verde Island Passage of the Philippines. This again reinforces the nature of the species richness of the region (Carpenter & Springer, 2005; Gosliner *et al.*, 2015) as the Center of the Center of Marine Biodiversity. In addition to a high species richness, the phyletic diversity represented in this region spans most of the lineages represented in the phylogeny of Gastropteridae, with only the absence of *Enotepteron*. However, *E. rosewateri* Gosliner, 1988 has been found farther south in the Philippines (Gosliner *et al.*, 2015) and likely also occurs within the Verde Island Passage. The extreme species richness and phylogenetic diversity together strengthen the importance of this region for preserving marine biodiversity and for the prioritization of developing sound conservation practices to insure that Verde Island Passage's diversity is protected for future generations.

Genetic variation and allopatry

This study also sheds light on the nature of genetic variation in widely separated populations of Gastropteridae. In comparing, populations that are geographically separated, there are wide differences in the amount of genetic divergence based on differences in the *COI* (Table 3).

This gene was used as a standard given that barcoding genes are prevalent on GenBank, and a broader sample of diversity was present. Morphologically, clearly distinct sister species shed light on the genetic distance between closely related species. Sympatric specimens of the sister taxa, *S. flavolineatum* and *S. nakakatuwa*, have about 8.8% difference in nucleotides for the *COI* gene, whereas the sympatric sister taxa, *S. dumbo* and *S. nigromarginatum*, are 8.5% divergent. The sympatric sister taxa, *Sagaminopteron pohnpei* and *S. multimaculatum*, are 7.2–7.5% divergent and

Table 3. Uncorrected p-distances for *COI*

Uncorrected *p*-distances for *COI* gene within *Gastropteron* clade				
	rubrum	*minutum*	*bicornutum*	*multo*
rubrum	–			
minutum	0.186	0.032		
bicornutum	0.205	0.195–0.202	–	
multo	0.212	0.228–0.231	0.220 0	
Uncorrected *p*-distances for *COI* gene within *Sagaminopteron* clade				
	nigropunctatum	*ornatum*	*psychedelicum*	*pohnpei*
nigropunctatum	0.088			
ornatum	0.104–0.123	0.044		
psychedelicum	0.184–0.193	0.163–0.193	0.010–0.123	
pohnpei	0.152–0.155	0.117–0.123	0.172–0.186	0.003
multimaculatum	0.164–0.167	0.123–0.128	0.181–0.191	0.072–0.75
Uncorrected *p*-distances for *COI* gene within *Sagaminopteron psychedelicum*				
	GenBank Australia	177772 Philippines	191213 PNG	
177772 Philippines	0.011	–	–	
191213 PNG	0.012	0.014	–	
GenBank Madagascar	0.111	0.117	0.123	
Uncorrected *p*-distances for *COI* gene within *Siphopteron tigrinum* clade				
	brunneomarginatum 177515	*brunneomarginatum* isolate E4	*michaeli*	*tigrinum* 199128
brunneomarginatum isolate E4	0.148	–		
michaeli	0.152	0.110	–	
tigrinum 199128	0.149	0.105	0.102	–
tigrinum isolate 45	0.158	0.122	0.081	0.123
Uncorrected *p*-distances for *COI* gene within *Siphopteron quadrispinosum* clade				
	makisig	*leah*		
leah	0.089–0.094	0.005–0.009		
quadrispinosum	0.098	0.093–0.099		
Uncorrected *p*-distances for COI gene within *Siphopteron nigromarginatum* clade				
	dumbo	*flavolineatum*	*nakakatuwa*	*nigromarginatum*
flavolineatum	0.134–0.137	0.017	–	–
nakakatuwa	0.144	0.088	–	–
nigromarginatum	0.085	0.145	0.132	–
vermiculum	0.150	0.161–0.163	0.157	0.142

sympatric *Sagaminopteron nigropunctatum* and *S. ornatum* are 11.0% divergent. Geographically isolated sister species such as *S. leah* and *S. quadrispinosum* are 9.3–9.9% divergent, whereas *S. michaeli* and *S. tigrinum* are 10.2% divergent. In contrast, allopatric conspecific Hawai'ian and Philippine specimens of *Gastropteron minutum* are 3.2% divergent. Widely separated specimens of some apparent conspecifics exhibit some intriguing patterns of divergence. A Red Sea specimen of *Sagaminopteron nigropunctatum* is 8.8% different to a specimen of what has been considered the same species from the Philippines. Three western Pacific specimens of *S. psychedelicum* from Australia, Papua New Guinea and the Philippines are 1.1–1.4% divergent to each other, whereas the specimen from Madagascar is 11.1–12.3% divergent to the western Pacific specimens. The data for both *S. nigropunctatum* and *S. psychedelicum* strongly suggest that the Red Sea and western Indian Ocean specimens of these species represent distinct cryptic species and are in need of more detailed study. The western Pacific and western Indian Ocean specimens of *S. tigrinum* are strongly divergent (12.3%). In fact, *S. michaeli* is more similar to the western Indian Ocean specimen of *S. tigrinum* (8.1%) than the two *S. tigrinum* specimens are related to each other. It appears that the species listed as *S. brunneomarginatum* by Anthes *et al.* (2008) represents a distinct taxon from the specimen

identified as *S. brunneomarginatum* and sequenced in this study as these two taxa are 14.8% divergent in their *COI* sequences and 10.5% divergent from its closest relative, *S. tigrinum*. The identity of this taxon remains questionable and no voucher specimens exist.

Relationships between morphology and molecular phylogeny

Much of the comparative anatomy and phylogenetic relationships based on morphological characters were presented by Gosliner (1989). In that study, four genera were distinguished: *Gastropteron*, *Enotepteron*, *Sagaminopteron* and *Siphopteron* with *Gastropteron and Enotepteron* as sister taxa and with *Sagaminopteron* and *Siphopteron* as sister taxa. Anthes *et al.* (2008) found a similar arrangement of taxa but did not include any species of *Enotepteron* in their molecular analysis. In their study, *S. pohnpei* nested with species of *Sagaminopteron* rather than with species of *Siphopteron*. In this study, we find a similar result with both *S. pohnpei* and *S. multimaculatum* nesting within *Sagaminopteron* and have placed these taxa within this genus. No suitably preserved specimens of *Enotepteron* were available to include in the molecular analysis and the specimen initially identified as *Enotepteron* sp. is nested within *Siphopteron*, as clade 2, and was likely misidentified. This species is the sister to the remainder of *Siphopteron*, but was not observed alive.

Three of the four genera of Gastropteridae recognized by Gosliner (1989) were studied here. Of those, only *Sagaminopteron* is strongly supported as monophyletic, while *Gastropteron* and *Siphopteron* are not. Nevertheless, they have morphological synapomorphies that support their continued use until more robust phylogenies are developed. Gosliner (1989) noted that species of *Gastropteron* had a synapomorphy of possessing a triangular thickening on the inner lateral tooth that is also present in *G. multo* and *G. minutum*, described here (Figs 3C, 6C, indicated by arrow). The same is true for *Siphopteron*. While we transferred *Sagaminopteron pohnpei* together with its sister taxon, *S. multimaculatum* to *Sagaminopteron*, the remaining species of *Siphopteron* all have a complex penis and narrow, triangular inner lateral teeth with a reduced number of denticles, attributes that are considered to be synapomorphies in the morphological phylogeny of Gosliner (1989).

While the monophyly of *Gastropteron* and *Siphopteron* was not supported, the various well-supported clades recovered in our molecular phylogeny have strong morphological correlates. In *Gastropteron*, the strongly supported subclade that includes *G. multo* and *G. bicornutum*, both sister taxa have a pair of posterior flagella, whereas in the strongly supported subclade of *G. minutum* and *G. rubrum* have only a single flagellum. Unfortunately, molecular data are not available for other species of *Gastropteron* to ascertain, for example, whether the Indo-Pacific *G. minutum* is indeed most closely related to the Atlantic *G. rubrum* or whether other taxa from different geographical regions are more closely related to these two taxa. Inclusion of these taxa in the future is necessary for further testing the monophyly of *Gastropteron*, which was not supported in this study.

In *Sagaminopteron*, the clade that includes *S. ornatum*, *S. nigropunctatum* and *S. psychedelicum* all have a simple penis and inner lateral teeth with two large cusps (Tokioka & Baba, 1964; Gosliner, 1989), while *S. pohnpei* and *S. multimaculatum* have a more complex penis with a secondary duct and have an inner lateral tooth with many elongate denticles (Gosliner, 1989; this study). Only when *S. pohnpei* and *S. multimaculatum* are added to *Sagaminopteron*, is the monophyly of this genus strongly supported.

The three clades of *Siphopteron* recovered here also have some unifying morphological features. In the first well-supported clade of *Siphopteron* (Fig. 23, clade 1) that includes, *S. tigrinum*, *S. michaeli* and *S. brunneomarginatum*, the inner radular teeth have a weakly developed masticatory margin with a series of small denticles. The penial papilla of *S. tigrinum* and *S. michaeli* have cuticular spines, whereas the penis of their sister species, *S. brunneomarginatum*, lacks spines. The strongly supported large clade 3 that includes *S. nakakatuwa*, *S. flavolineatum*, *S. vermiculum*, *S.* sp. 1, *S.* sp. 2, *S. nigromarginatum*, *S. dumbo*, *S. quadrispinosum*, *S. leah* and *S. makisig*, the radula has an inner tooth with two large, triangular denticles. These are the only species of *Siphopteron* with this form of dentition. In the well-supported subclade of clade 3 that includes *S. quadrispinosum*, *S. leah* and *S. makisig*, the penis is complex with a few large basal cuticular spines on the penial papilla that has spirally arranged spines or tubercles and a cuticular stylet present on a secondary papilla. In the remaining species in the second subclade of clade 3, there are multiple rows of cuticular spines associated with the penis and the penial papilla is not elongate with a series of spirally arranged spines. The anatomy of *S.* sp. CASIZ 181575 (clade 2) that is the sister taxon to the remainder of *Siphopteron* remains unstudied.

CONCLUSIONS

Based on our morphological studies and molecular phylogeny, we confirmed that the eight new species hypothesized from our field observations of living animals all represent new species that are described here. Our molecular phylogeny also indicates the likely existence

of geographically isolated cryptic species within previously classified specimens. *Sagaminopteron psychedelicum* from Madagascar appears to represent a cryptic species distinct from western Pacific populations, as is *Sagaminopteron nigropunctatum* from Saudi Arabia. Also, the western Indian Ocean specimen of *S. tigrinum* represents a cryptic species distinct from the western Pacific *S. tigrinum*. The lack of strong support for the monophyly of *Gastropteron* and *Siphopteron* requires additional study of taxa to determine whether greater support of these lineages is found when taxon sampling is increased. Also the phylogenetic and systematic relationship of *Enotepteron* needs to be examined when members of this taxon become available for molecular studies.

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REFERENCES

Anthes N, Schulenburg H, Michiels NK. 2008. Evolutionary links between reproductive morphology, ecology and mating behavior in opisthobranch gastropods. *Evolution* **62:** 900–916.

Baba K, Tokioka T. 1965. Two more new species of *Gastropteron* from Japan, with further notes on *G. flavum* T. & B. (Gastropoda: Opisthobranchia). *Publications of the Seto Marine Biological Laboratory* **12:** 363–378.

Blainville HM. (D. de). 1825–1827. *Manuel de Malacologie et de Conchyliologie*. Paris: Levrault.

Brodie GA, Klussmann-Kolb A, Gosliner T. 2001. Anatomy and histology of a new species of *Enotepteron* (Cephalaspidea: Gastropteridae) from tropical northeastern Australia. *The Veliger* **44:** 362–369.

Cairns S. 2007. Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science* **81:** 311–322.

Camacho-García YE, Ornelas-Gatdula E, Gosliner TM, Valdés Á. 2014. Phylogeny of the family Aglajidae (Pilsbry, 1895) (Heterobranchia: Cephalaspidea) inferred from mtDNA and nDNA. *Molecular Phylogenetics and Evolution* **71:** 113–126.

Carlson CH, Hoff PJ. 1973. Two new species of Gastropteridae from Guam, Marianas Islands (Opisthobranchia: Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* **21:** 141–151.

Carlson CH, Hoff PJ. 1974. The Gastropteridae of Guam, with descriptions of four new species (Opisthobranchia: Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* **21:** 345–363.

Carpenter K, Springer VG. 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environmental Biology of Fishes* **72:** 467–480.

Dinapoli, A, Klussmann-Kolb,A. 2010. The long way to diversity – phylogeny and evolution of the Heterobranchia (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution* **55**: 60–76.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3:** 294–299.

Gosliner T. 1984. Two new species of Gastropteron (Gastropoda: Opisthobranchia) from southern Africa. *Publications of the Seto Marine Biological Laboratory* **29:** 231–247.

Gosliner T. 1988. The Philinacea (Mollusca: Gastropoda: Opisthobranchia) of Aldabra Atoll, with descriptions of five new species and a new genus. *Biological Society of Washington Bulletin* **8:** 79–100.

Gosliner T. 1989. Revision of the Gastropteridae (Opisthobranchia: Cephalaspidea) with descriptions of a new genus and six new species. *The Veliger* **32:** 333–381.

Gosliner T, Armes P. 1984. A new species of Gastropteron from Florida (Gastropoda: Opisthobranchia). *The Veliger* **27:** 54–64.

Gosliner TM, Behrens DW Valdés Á. 2008. *Indo-Pacific nudibranchs and sea slugs: a field guide to the World's most diverse fauna*. Gig Harbor/San Francisco: Sea Challengers/California Academy of Sciences.

Gosliner T, Valdés A, Behrens DW. 2015. *Nudibranch and sea slug identification: Indo-Pacific*. Jacksonville: New World Press.

Gosliner T, Williams G. 1988. A new species of *Gastropteron* (Gastropoda: Opisthobranchia) from Reunion Island, Indian Ocean. *The Veliger* **30:** 315–318.

Hallas JM, Gosliner TM. 2015. Family matters: the first molecular phylogeny of the Onchidoriddidae Gray, 1827 (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution* **88:** 16–27.

Hallas JM, Simison WB, Gosliner TM. 2016. Dating and biogeographical patterns in the sea slug genus *Acanthodoris* Gray, 1850 (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution* **97:** 19–31.

Hamatani I. 2009. A new species of *Enotepteron* (Gastropoda: Opisthobranchia: Gastropteridae) from off Niigata (Japan) prefecture, in the Sea of Japan. *Venus* **68:** 9–14.

Hamatani I. 2013. A new species, *Enotepteron rubropunctatum* (Gastropoda: Opisthobranchia: Gastropteridae), from Niigata Prefecture, the Sea of Japan. *Venus* **71:** 209–211.

Hillis DM, Bull JJ. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42:** 182–192.

Hoff PJ, Carlson CH. 1983. *Gastropteron pohnpei*, a new Gastropteridae from Micronesia (Opisthobranchia: Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* **27:** 261–264.

Katoh K, Asimenos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. In Posada D, ed. Bioinformatics for DNA sequence analysis. *Methods in Molecular Biology* **537:** 39–64.

Klussmann-Kolb A, Klussmann A. 2003. A new species of Gastropteridae (Gastropoda, Opisthobranchia, Cephalaspidea) from tropical Northeast Australia. *Zootaxa* **156:** 1–12.

Kosse JFJ. 1813. De Pteropodum ordine et novo ipsius Genere. *Halle, typis Hendelianis*: 1–16.

Lanfear R, Calcott B, Ho SY, Guindon S. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29:** 1695–1701.

Lange R, Wermkinghausen J, Anthes N. 2013. Cephalotraumatic secretion transfer in a hermaphrodite sea slug. *Proceedings of the Royal Society of London B: Biological Sciences* **281:** 20132424.

Minichev Y. 1967. Studies on the morphology of the lower Opisthobranchia. On the evolutionary significance of the detorsion process. Trudy Zoologicheskogo Instituta. *Akademiia nauk SSSR* **44:** 109–182.

Ono A. 1999. *Siphopteron flavum* from Kerama Island. [In] *Sea slug forum*. Sydney: Australian Museum. Available at: http://www.seaslugforum.net/find/1135. Assessed on 22 December 2016.

Oskars TR, Bouchet P, Malaquias MA. 2015. A new phylogeny of the Cephalaspidea (Gastropoda: Heterobranchia) based on expanded taxon sampling and gene markers. *Molecular Phylogenetics and Evolution* **89:** 130–150.

Palumbi SR, Martin AP, Romano S, McMillan WO, Stice L, Grabowski G. 1991. *The simple fool's guide to PCR*. Honolulu: Department of Zoology, University of Hawaii.

Pittman C, Fiene P. 2015. *Sea slugs of Hawai'i*. Available at: http://seaslugsofhawaii.com/species/Gastropteron-sp2-a.html. Assessed on 22 December 2016.

Platt AR, Woodhall RW, George AL Jr. 2007. Improved DNA sequencing quality and efficiency using an optimized fast cycle sequencing protocol. *BioTechniques* **43:** 58, 60, 62.

Pola, M, Gosliner, T. 2010. The first molecular phylogeny of the cladobranchian Opisthobranchs (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution* **56**:931-941.

Puillandre N, Lambert A, Brouillet S, Achaz G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* **21:** 1864–1877.

Rafinesque CS. 1814. *Précis des découvertes et travaux somiologiques de Mr. C.S. Rafinesque-Schmaltz entre 1800 et 1814; ou choix raisonné de ses principales découvertes en zoologie et en botanique, pour servir d'introduction à ses ouvrages futurs.* Palerme: 1–55.

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen G, McAllister RDE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB. 2002. *Marine biodiversity hotspots and conservation priorities for tropical reefs. Science* **295:** 1280.

Ronquist F, Huelsenbeck JP. 2003. Mr. Bayes 3: Bayesian phylogenetics inference under mixed models. *Bioinformatics* **19:**1572–1574.

Rudman WB. 1999. *Siphopteron flavum* (Tokioka & Baba, 1964). [In] *Sea slug forum*. Sydney: Australian Museum. Available at: http://www.seaslugforum.net/find/siphflav. Assessed on 22 December 2016.

Rudman WB. 2002. *Gastropteron* sp. 4. *[In] Sea slug forum*. Sydney: Australian Museum. Available at: http://www.seaslugforum.net/factsheet/gastsp4. Assessed on 22 December 2016.

Rudman WB. 2004. *Siphopteron quadrispinosum* & *S. leah*. [In] *Sea slug forum*. Sydney: Australian Museum. Available at: http://www.seaslugforum.net/find/11935. Assessed on 22 December 2016.

Stamatakis S. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22:** 2688–2690.

Swainson W. 1840. *A treatise on malacology: or the natural classification of shells and shellfish*. London: Lardner's Cabinet Cyclopedia.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28:** 2731–2739.

Tokioka T, Baba K. 1964. Four new species and a new genus of the family Gastropteridae from Japan (Gastropoda: Opisthobranchia). *Publications of the Seto Marine Biological Laboratory* **12:** 201–229.

Vonnemann V, Schröl M, Klussmann-Kolb A, Wägele H. 2005. Reconstruction of the phylogeny of the Opisthobranchia (Mollusca: Gastropoda) by means of 18S and 28S rRNA gene sequences. *Journal of Molluscan Studies* **71:** 113–125

World Register of Marine Species. 2015. http://www.marinespecies.org/aphia.php?p=taxdetails&id=23045. Assessed on 22 December 2016.