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A new genus and three new species of mangrove slugs from the Indo-West Pacific (Mollusca: Gastropoda: Euthyneura: Onchidiidae)

Benoît DAYRAT [1,*], Tricia C. GOULDING [2], Munawar KHALIL [3], Deepak APTE [4], Adam J. BOURKE [5], Joseph COMENDADOR [6] & Shau Hwai TAN [7]

[1,2] Department of Biology, Pennsylvania State University, University Park, PA 16802, USA.
[2] Current address: Malacology, Bernice Pauahi Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA.
[3] Department of Marine Science, Universitas Malikussaleh, Reuleut Main Campus, Kecamatan Muara Batu, North Aceh, Aceh, 24355, Indonesia.
[4] Bombay Natural History Society, Mumbai, Hornbill House, Opp. Lion Gate, Shaheed Bhagat Singh Road, Mumbai 400 001, Maharashtra, India.
[5] EcoScience NT, 29 Ostermann St., Coconut Grove, NT 0810, Australia.
[6] National Museum of the Philippines, Taft Ave., Ermita, Manila, 1000 Metro Manila, Philippines.
[7] School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia.
[7] Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia.

[*] Corresponding author: bad25@psu.edu, bdayrat@gmail.com
[2] Email: tc.goulding@gmail.com
[3] Email: khalil@unimal.ac.id
[4] Email: spiderconch@gmail.com
[5] Email: ecoscience2@bigpond.com
[6] Email: joseph.comendador@gmail.com
[7] Email: aileen@usm.my

[1] urn:lsid:zoobank.org:author:192B0AF4-A4B0-4129-8422-DEF8D0FB4A45
[2] urn:lsid:zoobank.org:author:6009A165-E73E-4124-96C6-C143FC51B18F
[3] urn:lsid:zoobank.org:author:6D38234D-0DE1-4CDE-9F7E-603070C9B27D
[4] urn:lsid:zoobank.org:author:5335B286-7B3A-440A-B16B-FBABCD90274B
[5] urn:lsid:zoobank.org:author:AAF38199-57BF-4E7E-A888-468A9B01720C
[6] urn:lsid:zoobank.org:author:0EAAEF74-7E54-47BA-9A3A-D3A4ED40AD85
[7] urn:lsid:zoobank.org:author:6E9B8F28-EFCC-42F1-A7C4-3957C92995AA

Abstract. Mangroves of the Indo-West Pacific have remained poorly explored, so even the diversity of the onchidiid slugs, which are some of the most abundant animals in mangroves of the Indo-West Pacific, is not well known. Thanks to several years spent exploring mangroves in the Indo-West Pacific (more than 260 stations), especially in South-East Asia, the diversity of mangrove gastropods can now be addressed through revisions following an integrative taxonomy approach (nomenclature, field observations, comparative anatomy and DNA sequences). A new genus of onchidiid slugs is described, *Paromoionchis* Dayrat & Goulding gen. nov., which includes five species, three of which are new: *Paromoionchis boholensis* Dayrat & Goulding gen. et sp. nov., *P. daemelii* (Semper, 1880) com. nov.,

P. goslineri Dayrat & Goulding gen. et sp. nov., *P. penangensis* Dayrat & Goulding gen. et sp. nov. and *P. tumidus* (Semper, 1880) comb. nov. *Paromoionchis* gen. nov. is distributed from western India to the subtropical waters of Japan (33° N) and southeastern Australia (33° S). The creation of new taxon names is supported by rigorous nomenclature: the types of all existing species names in the family were examined, the original descriptions carefully studied and nomenclatural issues addressed. The diversity and biogeography of this new genus is discussed in a broader context.

Keywords. Biodiversity, Coral Triangle, integrative taxonomy, revisionary systematics, South-East Asia.

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Introduction

Onchidiid slugs are closely related to land snails and slugs, but they are truly marine because their larvae develop in seawater and because their adult life takes place in the intertidal (Dayrat *et al.* 2011a). Exceptionally, a few species are terrestrial and live in high-elevation rainforests (Dayrat 2010). Onchidiids are distributed worldwide, except at the poles. One subclade – traditionally referred to as *Onchidium* Buchannan, 1800 – has diversified in the Indo-West Pacific, especially South-East Asia. Another subclade – traditionally referred to as *Onchidella* J.E. Gray, 1850 – has diversified outside the Indo-West Pacific, especially in temperate waters. These subclades overlap geographically at the borders between the subtropical Indo-West Pacific and temperate waters (i.e., southeastern Australia, South Africa and Japan).

Even though onchidiids are widespread and common, their biodiversity has remained very poorly understood (Dayrat 2009). Some of the obvious reasons explaining this situation are that 1) onchidiid taxonomy has not been revised for more than 80 years, 2) new species names were often being created with little to no consideration for existing names, 3) internal characters (which are key at both specific and generic levels) were often ignored and 4) species were described based on preserved specimens without any field observations on live animals. As a result, 150 species names exist in the literature, but, until now, no onchidiid species could be properly identified, which is especially true in the Indo-West Pacific, where onchidiids are common and diverse (with dozens of species). Species relationships at the generic level also need to be completely re-evaluated. For instance, it was recently demonstrated that the genus name *Onchidium* actually applies to a small clade including only three species (Dayrat *et al.* 2016).

The Dayrat lab is in the process of revising the taxonomy of the entire family, using an integrative approach (Dayrat 2005). Our efforts have focused on collecting fresh material, getting new morphological and molecular data, addressing the nomenclatural status of every single existing species- and genus-group name by re-examining the totality of the types available (many museum collections were visited specifically for that purpose) and critically going through the entire primary and secondary literature. Over the past few years, we have spent considerable time collecting fresh material, most especially in the mangroves of South-East Asia and Australia, where onchidiids are often the most abundant animals. We have collected thousands of specimens from more than 300 stations worldwide (as of August 2018), including many original type localities. This exploration has allowed us to gather invaluable information on the natural history and color variation of live onchidiids. Those new collections were used to build a large integrative data set which now includes approximately 80 species and 10 clades of generic level. Each taxon is strongly supported by both morphological and molecular data.

In order to finally establish some order in the taxonomy of the Onchidiidae, we are comprehensively revising every genus, focusing on one genus at a time. Several genera and many species in our data set are new to science. Also, species with existing names are often known only from the original description and need to be fully re-described. Six revisions have already been published on *Onchidium* (Dayrat *et al.* 2016), *Onchidina* Semper, 1882 (Dayrat & Goulding 2017), *Melayonchis* Dayrat & Goulding, 2017 (Dayrat *et al.* 2017), *Alionchis* Goulding & Dayrat, 2018 (Goulding *et al.* 2018a), *Peronina* Plate, 1893 (Goulding *et al.* 2018b) and *Wallaconchis* Goulding & Dayrat, 2018 (Goulding *et al.* 2018c).

The purpose of the present contribution is to describe a new genus, *Paromoionchis* Dayrat & Goulding gen. nov., which includes five species. Two of those species were known only from the original description and are re-described here for the first time with many new geographical records. The three other species are new to science. The nomenclatural status of several other existing species names is addressed. Three species names are shown to be junior synonyms of a *Paromoionchis* gen. nov. species name. Five species names are regarded as names of doubtful application (nomina dubia) for a variety of reasons.

Material and methods

Field collecting and sampling

Only five specimens (out of 156) used in this study were not collected by us: two Queensland specimens of *P. daemelii* (Semper, 1880) and one Queensland specimen of *P. tumidus* (Semper, 1880) were found in the collections of the Australian Museum, Sydney; two specimens of *P. tumidus* collected during an expedition led by Philippe Bouchet to Madang, Papua New Guinea, were obtained from the Muséum national d'Histoire naturelle. All other 151 specimens examined here were collected by us in the context of an exploration of mangrove snails and slugs across the Indo-West Pacific, which provided fresh material for DNA sequencing and invaluable natural history observations. Collecting parties were led by Benoît Dayrat in the Andaman Islands (India), Brunei Darussalam, Malaysia, New South Wales and Northern Territory (Australia) and the Philippines, by Tricia Goulding in eastern and western India, Queensland (Australia) and Vietnam, by Rebecca Cumming in Japan and by Munawar Khalil in Indonesia. We were often accompanied by local guides (villagers or fishermen). Sites were accessed by car or by boat. Each site was explored for an average of two hours, but the exact time spent at each site also depended on the time of the low tide, the weather, etc. At each site, photographs were taken to document the kind of mangrove being visited as well as the diverse microhabitats where specimens were collected.

In the field, specimens were individually numbered and photographed in their habitat (it is very important to take photographs before animals are touched because they retract when disturbed and do not relax again for a long time). Importantly, a piece of tissue was cut from all specimens individually numbered (for DNA extraction) and the rest of each specimen was relaxed and fixed for comparative anatomy.

In the field, detailed notes were written, commenting on whether specimens could be part of the same species or not. We tried our best to sample as much diversity as possible at each site. In addition to numbering the specimens that looked different individually, we also numbered many specimens that looked similar individually, so that we could test for the presence of cryptic diversity. This practice ended up being absolutely key to discovering all the species described here and documenting their natural history, because they are externally cryptic, which is something we did not know when we first started. Per species, the numbers of specimens included in the present study are: 33 (*P. boholensis* gen. et sp. nov.), 11 (*P. daemelii*), 22 (*P. penangensis* gen. et sp. nov.), 21 (*P. goslineri* gen. et sp. nov.) and 69 (*P. tumidus*). Finally, only three COI sequences from mainland China were found in GenBank for *P. tumidus* (misidentified as *Paraoncidium reevesii* (J.E. Gray, 1850)) and were added to our molecular data set.

Type material, museum vouchers and collections

Sound taxonomy is impossible without re-examining all types available. So, the types of existing onchidiid species names were all borrowed for re-examination. Many museum collections were visited in person (by the first author) in order to track types, because types are actually often mixed in with the general collections. Original descriptions surely are important (especially when the type material is lost), but re-examining all types is absolutely indispensable in order to address the status of all existing names and determine whether species are new or not. Most species described in the past were based on syntypes. We designate a few lectotypes here in order to clarify some nomenclatural situations.

All specimens were deposited as vouchers in institutions of the country where they were collected. Acronyms of collections are:

AM = Australian Museum, Sydney, New South Wales, Australia
BNHS = Bombay Natural History Society, Mumbai, India
BDMNH = Brunei Museum, Natural History, Brunei Darussalam
ITBZC = Institute of Tropical Biology, Zoology Collection, Vietnam Academy of Science and Technology, Ho Chi Minh City, Vietnam
MNHN = Muséum national d'Histoire naturelle, Paris, France
MTQ = Museum of Tropical Queensland, Townsville, Queensland, Australia
NHM = Natural History Museum, London, United Kingdom
NHMD = Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Denmark (formerly ZMUC)
NSMT = National Museum of Nature and Science, Tokyo, Japan
NTM = Museum and Art Gallery Northern Territory, Darwin, Northern Territory, Australia
PNM = National Museum of the Philippines, Manila, Philippines
RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SMF = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany
UMIZ = Universitas Malikussaleh, North Aceh, Sumatra, Indonesia
USMMC = Universiti Sains Malaysia, Mollusk Collection, Penang, Malaysia
ZMB = Museum für Naturkunde, Berlin, Germany
ZMH = Zoologisches Museum, Hamburg, Germany

Animal preparation and anatomical description

All anatomical observations were made under a dissecting microscope and drawn with a camera lucida. In addition, organs were prepared for scanning electron microscopy (SEM). Radulae were cleaned in 10% NaOH for a week, rinsed in distilled water for at least a week, briefly cleaned in an ultrasonic water bath (less than a minute), sputter-coated with gold-palladium and examined by SEM. Soft parts (penis and penial hooks) were dehydrated in ethanol and critical point dried before coating. When a lot included several specimens, all pieces of the dissected specimens were carefully numbered, both inside the jar and on the SEM stubs. Individualized numbers (in square brackets) and measurements (length/width) are provided for each specimen in the 'Material examined' sections (all specimens included in the material examined sections are included in the molecular data set).

The anatomy of *P. tumidus*, the type species, is fully detailed. The written description of the many anatomical features that are virtually identical between species (nervous system, heart, etc.) is given only for the type species to avoid repetition. Thus, any feature that is only mentioned for *P. tumidus* is identical in the four other species. The color of live animals is described in detail for all species in order to demonstrate the overlapping individual variation between species. As expected, differences between species are mostly found in the male copulatory apparatus, which is described and illustrated in detail

for each species. Special attention has been paid to illustrating the holotype of each of the three new species. For instance, the line drawings (digestive system, female reproductive system, male copulatory apparatus) systematically feature the holotype, the color plate with live animals always includes a photograph of the holotype and the plate illustrating the species' habitat also includes a photograph from the type locality.

DNA extraction and PCR amplification

DNA was extracted using the phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB). Portions of three mitochondrial genes (COI, 16S, 12S) were amplified using the following universal primers (all 5′–3′): COIF GGT CAA CAA ATC ATA AAG ATA TTG G and COIR TAA ACT TCA GGG TGA CCA AAR AAY CA (Folmer *et al.* 1994) for COI; 16Sar CGC CTG TTT ATC AAA AAC AT (Palumbi 1996) and 16S 972R CCG GTC TGA ACT CAG ATC ATG T (Dayrat *et al.* 2011a) for 16S; 12Sa-H GAG GGT GAC GGG CGG TGT GT and 12Sai AAA CTA GGA TTA GAT ACC CTA TTA T (Palumbi 1996) for 12S. Portions of two nuclear genes (ITS2, 28S) were amplified with the following primers (all 5′–3′): LSU-1 CTA GCT GCG AGA ATT AAT GTG A and LSU-3 ACT TTC CCT CAC GGT ACT TG (Wade & Mordan 2000) for ITS2; 28SC1 ACC CGC TGA ATT TAA GCA T (Hassouna *et al*. 1984) and 28SD3 GAC GAT CGA TTT GCA CGT CA (Vonnemann *et al*. 2005) for 28S. The 25 µl PCRs (COI and 16S) contained 15.8 µl of water, 2.5 µl of 10× PCR buffer, 1.5 µl of 25 mM $MgCl_2$, 0.5 µl of each 10 µM primer, 2 µl of dNTP mixture, 0.2 µl (1 unit) of TaKaRa Taq (code no. R001A), 1 µl of 20 ng/µl template DNA and 1 µl of 100× BSA (Bovine Serum Albumin). The 24.5 µl PCR (12S) was identical except that the salt and the 100× BSA were replaced by 4 µl Q-solution (with $MgCl_2$). The PCR for ITS2 used the reagents in the same amounts as COI, 16S and 12S, except that water was reduced to 14.8 µl and the amount of 100× BSA was increased to 2 µl. The PCRs for 28S included 14.8 µl of water, 2.5 µl of 10× PCR buffer, 0.5 µl of each 10 µM primer, 1 µl of dNTP mixture, 5 µl of Q solution (which includes $MgCl_2$) and 0.5 µl of 20 ng/µl template DNA. The thermoprofile used for COI and 16S was: 5 minutes at 94°C; 30 cycles of 40 seconds at 94°C, 1 minute at 46°C and 1 minute at 72°C; and 10 minutes at 72°C. The thermoprofile used for 12S was identical except that it ran for 40 cycles. The thermoprofile used for ITS2 was: 1 minute at 96°C; 35 cycles of 30 seconds at 94°C, 30 seconds at 50°C and 1 minute at 72°C; and a final extension of 10 minutes at 72°C. The thermoprofile used for 28S was: 4 minutes at 94°C; 38 cycles of 50 seconds at 94°C, 1 minute at 52°C and 2 minutes 30 seconds at 72°C; and a final extension of 10 minutes at 72°C. The PCR products were cleaned with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) prior to sequencing. Untrimmed sequence fragments represented approximately 680 bp for COI, 530 bp for 16S, 360 bp for 12S, 740 bp for ITS2 and 1000 bp for 28S.

Phylogenetic analyses

Chromatograms were consulted to resolve rare ambiguous base calls. Sequences were aligned using Clustal W in MEGA 6 (Tamura *et al.* 2013). Eight onchidiid species were selected as outgroups: *Onchidella floridana* (Dall, 1885), *Peronina tenera* (Stoliczka, 1869), *Peronia* sp. (Okinawa), *Peronia* sp. (Hawaii), *Onchidina australis* (Semper, 1880), *Onchidium stuxbergi* (Westerlund, 1883), *O. typhae* Buchannan, 1800 and *Platevindex luteus* (Semper, 1880). Outgroup sequences are from previous studies from our lab (Dayrat *et al.* 2011a, 2016, 2017; Dayrat & Goulding 2017) or new. Analyses were not run enforcing the *a priori* monophyly of *Paromoionchis* sequences. Other (unpublished) analyses were performed using different combinations of outgroups, which all yielded identical results.

DNA sequences were all deposited in GenBank and vouchers deposited in museum collections (Table 1). The ends of each alignment were trimmed and sequences were concatenated. The COI alignment included 582 nucleotide positions. The concatenated COI, 16S and 12S alignment included a total of 1321 nucleotide positions: 582 (COI), 398 (16S) and 341 (12S). The ITS2 alignment included 850

Table 1. (continued on next three pages) GenBank accession numbers for COI, 16S, 12S, ITS2 and 28S DNA sequences. All sequences are new, except the COI and 16S sequences of six of the seven outgroups (Dayrat *et al.* 2011a, 2016; Dayrat & Goulding 2017) and three COI sequences of *P. tumidus* (unit #1) from mainland China found in GenBank (misidentified as *Paraoncidium reevesii* (J.E. Gray, 1850) in Sun *et al.* 2014).

Species (mitochondrial unit)	Individual (DNA #)	Locality	COI	16S	12S	ITS2	28S
Onchidella floridana	713	Tobago	HQ660035	HQ659903	MG971017	–	–
Peronina tenera	960	Peninsular Malaysia	–	–	–	MG958840	MG958874
Peronia sp.	696	Okinawa, Japan	HQ660043	HQ659911	MG971015	MG958871	MG958883
Peronia sp.	706	Hawaii, USA	HQ660038	HQ659906	MG971016	MG958722	MG971212
Platevindex luteus	1001	Singapore	MG958714	MG958716	MG971010	MG958718	MG958888
Onchidina australis	1523	NSW, Australia	KX179548	KX179561	MG971012	MG958719	MG971209
Onchidium typhae	965	Peninsular Malaysia	KX179509	KX179525	MG971013	MG958720	MG971210
Onchidium stuxbergi	5605	Vietnam	KX179520	KX179537	MG971014	MG958721	MG971211
***P. tumidus* unit #1**	928	Peninsular Malaysia	MH054945	–	–	MH055193	–
–	963	Peninsular Malaysia	MH054946	MH055101	MH055147	MH055194	MH055266
–	1035	Brunei Darussalam	MH054947	–	–	–	–
–	1036	Brunei Darussalam	MH054948	MH055102	MH055148	MH055195	MH055267
–	1062	Brunei Darussalam	MH054949	–	–	–	–
–	1119	Andaman, India	MH054950	MH055103	MH055149	–	–
–	1732	Sumatra, Indonesia	MH054951	MH055104	MH055150	MH055196	MH055268
–	1754	Sumatra, Indonesia	MH054952	–	–	–	–
–	1755	Sumatra, Indonesia	MH054953	–	–	–	–
–	1798	Sumatra, Indonesia	MH054954	–	–	–	–
–	2200	Sulawesi, Indonesia	MH054955	–	–	–	–
–	2201	Sulawesi, Indonesia	MH054956	–	–	–	–
–	2240	Sulawesi, Indonesia	MH054957	–	–	MH055197	–
–	2345	Sulawesi, Indonesia	MH054958	–	–	–	–
–	2355	Sulawesi, Indonesia	MH054959	–	–	–	–
–	2839	Ambon, Indonesia	MH054960	–	–	–	–
–	2840	Ambon, Indonesia	MH054961	MH055105	MH055151	MH055198	MH055269
–	3541	Ambon, Indonesia	MH054962	–	–	–	–
–	2832	Ambon, Indonesia	MH054963	–	–	–	–
–	2874	Seram, Indonesia	MH054964	–	–	MH055199	–
–	2875	Seram, Indonesia	MH054965	–	–	MH055200	–
–	2950	Lombok, Indonesia	MH054966	–	–	MH055201	–
–	2952	Lombok, Indonesia	MH054967	–	–	–	–
–	2961	Lombok, Indonesia	MH054968	–	–	–	–
–	3051	Bali, Indonesia	MH054969	–	–	–	–
–	3070	Bali, Indonesia	MH054970	–	–	–	–
–	5042	Halmahera, Indonesia	MH054971	–	–	–	–
–	5082	Halmahera, Indonesia	MH054972	–	–	–	–
–	5102	Halmahera, Indonesia	MH054973	–	–	MH055202	–
–	5103	Halmahera, Indonesia	MH054974	–	–	–	–
–	3171	Luzon, Philippines	MH054975	–	–	–	–
–	3192	Luzon, Philippines	MH054976	–	–	–	–

Table 1. (continued) GenBank accession numbers for COI, 16S, 12S, ITS2 and 28S DNA sequences.

Species (mitochondrial unit)	Individual (DNA #)	Locality	COI	16S	12S	ITS2	28S
***P. tumidus* unit #1**	3200	Luzon, Philippines	MH054977	MH055106	MH055152	–	MH055270
–	3205	Luzon, Philippines	MH054978	–	–	MH055203	–
–	3222	Luzon, Philippines	MH054979	–	–	MH055204	–
–	3344	Bohol, Philippines	MH054980	–	–	MH055205	–
–	3371	Bohol, Philippines	MH054981	–	–	MH055206	–
–	3416	Bohol, Philippines	MH054982	–	–	–	–
–	3761	Japan	MH054983	MH055107	MH055153	MH055207	MH055271
–	5619	Vietnam	MH054984	–	–	–	–
–	5642	Vietnam	MH054985	–	–	–	–
–	5682	Vietnam	MH054986	–	–	–	–
–	1522	NSW, Australia	MH054987	–	–	–	–
–	1528	NSW, Australia	MH054988	MH055108	MH055154	MH055208	MH055272
–	1529	NSW, Australia	MH054989	–	–	–	–
–	1530	NSW, Australia	MH054990	–	–	–	–
–	1634	NT, Australia	MH054991	–	–	MH055209	–
–	1645	NT, Australia	MH054992	MH055109	MH055155	–	–
–	1686	NT, Australia	MH054993	–	–	–	–
–	1705	NT, Australia	MH054994	–	–	MH055210	–
–	1531	Queensland, Australia	MH054995	MH055110	MH055156	–	–
–	2562	Queensland, Australia	MH054996	–	–	–	–
–	2602	Queensland, Australia	MH054997	–	–	–	–
–	2627	Queensland, Australia	MH054998	–	–	–	–
–	2637	Queensland, Australia	MH054999	–	–	–	–
–	2652	Queensland, Australia	MH055000	–	–	–	–
–	2657	Queensland, Australia	MH055001	–	–	–	–
–	2701	Queensland, Australia	MH055002	–	–	–	–
–	–	China	JN543146	–	–	–	–
–	–	China	JN543150	–	–	–	–
–	–	China	JN543151	–	–	–	–
***P. tumidus* unit #2**	1638	NT, Australia	MH055003	–	–	–	–
–	1651	NT, Australia	MH055004	MH055111	MH055157	–	–
–	1794	Sumatra, Indonesia	MH055005	MH055112	MH055158	–	MH055273
–	2960	Lombok, Indonesia	MH055006	MH055113	MH055159	MH055211	MH055274
–	3172	Luzon, Philippines	MH055007	MH055114	MH055160	MH055212	MH055275
–	3202	Luzon, Philippines	MH055008	–	–	MH055213	–
–	3229	Luzon, Philippines	MH055009	MH055115	MH055161	MH055214	MH055276
–	3237	Luzon, Philippines	MH055010	–	–	MH055215	–
–	3610	Luzon, Philippines	MH055011	–	–	MH055216	–
***P. tumidus* unit #3**	5432	Papua New Guinea	MH055012	MH055116	MH055162	MH055217	MH055277
–	5433	Papua New Guinea	MH055013	MH055117	MH055163	MH055218	MH055278
***P. boholensis* unit #1**	3283	Bohol, Philippines	MH055014	MH055118	MH055164	MH055219	MH055279
–	3288 H	Bohol, Philippines	MH055015	–	–	MH055220	MH055280
–	3369	Bohol, Philippines	MH055016	–	–	MH055221	–

Table 1. (continued) GenBank accession numbers for COI, 16S, 12S, ITS2 and 28S DNA sequences.

Species (mitochondrial unit)	Individual (DNA #)	Locality	COI	16S	12S	ITS2	28S
***P. boholensis* unit #1**	3372	Bohol, Philippines	MH055017	MH055119	MH055165	MH055222	MH055281
–	3411	Bohol, Philippines	MH055018	–	–	MH055223	–
–	3412	Bohol, Philippines	MH055019	MH055120	MH055166	MH055224	MH055282
–	3413	Bohol, Philippines	MH055020	–	–	MH055225	–
–	3417	Bohol, Philippines	MH055021	–	–	MH055226	–
–	3422	Bohol, Philippines	MH055022	MH055121	MH055167	MH055227	MH055283
–	3423	Bohol, Philippines	MH055023	–	–	MH055228	–
–	3619	Bohol, Philippines	MH055024	–	–	MH055229	–
–	3609	Luzon, Philippines	MH055025	MH055122	MH055168	MH055230	MH055284
***P. boholensis* unit #2**	2128	NE Sulawesi, Indonesia	MH055026	–	–	–	–
–	2129	NE Sulawesi, Indonesia	MH055027	MH055123	MH055169	MH055231	MH055285
–	2175	NE Sulawesi, Indonesia	MH055028	–	–	MH055232	–
–	2199	NE Sulawesi, Indonesia	MH055029	–	–	–	–
–	2316	NE Sulawesi, Indonesia	MH055030	MH055124	MH055170	–	–
–	2360	SE Sulawesi, Indonesia	MH055031	–	–	–	–
–	2849	Ambon, Indonesia	MH055032	–	–	–	–
–	2850	Ambon, Indonesia	MH055033	–	–	–	–
–	2851	Ambon, Indonesia	MH055034	MH055125	MH055171	MH055233	MH055286
–	2884	Seram, Indonesia	MH055035	–	–	MH055234	–
–	2896	Kei, Indonesia	MH055036	MH055126	MH055172	–	–
–	2901	Kei, Indonesia	MH055037	–	–	–	–
–	2903	Kei, Indonesia	MH055038	–	–	MH055235	–
–	2911	Kei, Indonesia	MH055039	–	–	–	–
–	2935	Kei, Indonesia	MH055040	–	–	MH055236	–
–	2937	Kei, Indonesia	MH055041	–	–	–	–
–	3565	Kei, Indonesia	MH055042	–	–	MH055237	–
–	3117	Bali, Indonesia	MH055043	MH055127	MH055173	MH055238	MH055287
–	5019	Halmahera, Indonesia	MH055044	MH055128	MH055174	MH055239	MH055288
–	5140	Halmahera, Indonesia	MH055045	–	–	–	–
–	5146	Halmahera, Indonesia	MH055046	–	–	–	–
P. daemelii	1510	NSW, Australia	MH055047	–	–	MH055240	–
–	1511	NSW, Australia	MH055048	MH055129	MH055175	MH055241	MH055289
–	1512	NSW, Australia	MH055049	–	–	MH055242	–
–	1514	NSW, Australia	MH055050	–	–	MH055243	–
–	1515	NSW, Australia	MH055051	–	–	MH055244	–
–	1518	NSW, Australia	MH055052	MH055130	MH055176	–	–
–	1519	NSW, Australia	MH055053	–	–	MH055245	–
–	1521	NSW, Australia	MH055054	MH055131	MH055177	MH055246	MH055290
–	1532	Queensland, Australia	MH055055	MH055132	MH055178	–	–
–	1533	Queensland, Australia	MH055056	–	–	MH055247	–
–	2668	Queensland, Australia	MH055057	MH055133	MH055179	MH055248	MH055291

Table 1. (continued) GenBank accession numbers for COI, 16S, 12S, ITS2 and 28S DNA sequences.

Species (mitochondrial unit)	Individual (DNA #)	Locality	COI	16S	12S	ITS2	28S
P. penangensis	1086	Andaman Islands, India	MH055058	MH055134	MH055180	–	–
–	1100	Andaman Islands, India	MH055059	–	–	–	–
–	1101	Andaman Islands, India	MH055060	–	–	–	–
–	1117	Andaman Islands, India	MH055061	MH055135	MH055181	–	–
–	1118	Andaman Islands, India	MH055062	–	–	–	–
–	1129	Andaman Islands, India	MH055063	–	–	–	–
–	1130	Andaman Islands, India	MH055064	–	–	–	–
–	1167	Western India	MH055065	–	–	–	–
–	1173	Western India	MH055066	MH055136	MH055182	–	–
–	1175	Western India	MH055067	–	–	–	–
–	1176	Western India	MH055068	–	–	–	–
–	1177	Western India	MH055069	–	–	–	–
–	1182	Western India	MH055070	–	–	–	–
–	5990	Peninsular Malaysia	MH055071	–	–	–	–
–	5991	Peninsular Malaysia	MH055072	–	–	MH055249	–
–	6020	Peninsular Malaysia	MH055073	–	–	MH055250	–
–	6031	Peninsular Malaysia	MH055074	–	–	MH055251	–
–	6033	Peninsular Malaysia	MH055075	–	–	MH055252	–
–	6037 H	Peninsular Malaysia	MH055076	–	–	MH055253	MH055292
–	6039	Peninsular Malaysia	MH055077	–	–	MH055254	–
–	957	Peninsular Malaysia	MH055078	MH055137	MH055183	MH055255	MH055293
–	958	Peninsular Malaysia	MH055079	MH055138	MH055184	MH055256	MH055294
***P. goslineri* unit #1**	3221	Luzon, Philippines	MH055080	MH055139	MH055185	MH055257	MH055295
–	3232	Luzon, Philippines	MH055081	MH055140	MH055186	MH055258	MH055296
–	3233 H	Luzon, Philippines	MH055082	MH055141	MH055187	MH055259	MH055297
–	6049	Luzon, Philippines	MH055083	–	–	MH055260	–
***P. goslineri* unit #2**	2210	Sulawesi, Indonesia	MH055084	MH055142	MH055188	MH055261	MH055298
–	2241	Sulawesi, Indonesia	MH055085	MH055143	MH055189	–	–
–	3060	Bali, Indonesia	MH055086	–	–	–	–
–	3066	Bali, Indonesia	MH055087	MH055144	MH055190	–	–
–	3068	Bali, Indonesia	MH055088	–	–	MH055262	–
–	3072	Bali, Indonesia	MH055089	–	–	–	–
–	3074	Bali, Indonesia	MH055090	–	–	–	–
–	3078	Bali, Indonesia	MH055091	–	–	–	–
–	3079	Bali, Indonesia	MH055092	–	–	MH055263	–
–	3118	Bali, Indonesia	MH055093	–	–	–	–
–	3120	Bali, Indonesia	MH055094	–	–	–	–
–	3555	Ambon, Indonesia	MH055095	MH055145	MH055191	–	–
–	5072	Halmahera, Indonesia	MH055096	–	–	–	–
–	5073	Halmahera, Indonesia	MH055097	MH055146	MH055192	MH055264	MH055299
–	5145	Halmahera, Indonesia	MH055098	–	–	MH055265	–
–	5890	Timor, Indonesia	MH055099	–	–	–	–
–	5891	Timor, Indonesia	MH055100	–	–	–	–

nucleotide positions (including gaps). The concatenated ITS2 and 28S alignment included 1600 nucleotide positions. Four independent sets of analyses were performed: 1) Maximum Likelihood and Bayesian phylogenetic analyses with just COI sequences, performed with 159 individuals (not counting outgroups), i.e., all the 156 specimens examined here and 3 additional sequences obtained from GenBank; 2) Maximum Likelihood and Bayesian phylogenetic analyses with concatenated mitochondrial COI, 16S and 12S sequences for a subset of 46 individuals (not counting outgroups); 3) Maximum Parsimony analyses with concatenated nuclear ITS2 and 28S sequences for a subset of 34 individuals (not counting outgroups); 4) Maximum Parsimony analyses with only ITS2 sequences, performed with 73 individuals (not counting outgroups).

Prior to Maximum Likelihood and Bayesian analyses, the best-fitting evolutionary model was selected independently for each marker using the Model Selection option of Topali ver. 2.5 (Milne *et al.* 2004). A GTR + G model was independently selected for each mitochondrial marker and a HKY + G model was independently selected for each nuclear marker. Other (unpublished) analyses were performed using different models, which all yielded identical results. Maximum Likelihood analyses were performed using PhyML (Guindon & Gascuel 2003) as implemented in Topali. Node support was evaluated using bootstrapping with 100 replicates. Bayesian analyses were performed using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003) as implemented in Topali, with five simultaneous runs of 1.5×10^6 generations each, sample frequency of 100 and burn-in of 25% (posterior probabilities were also calculated). Topali did not detect any issue with respect to convergence. Maximum Parsimony analyses were conducted in PAUP ver. 4.0 (Swofford 2002), with gaps coded as a 5th character state and 100 bootstrap replicates conducted using a full heuristic search. All analyses were run several times and yielded the same result. In addition, pairwise genetic distances between COI sequences were calculated in MEGA 6. COI sequences were also translated into amino acid sequences in MEGA using the invertebrate mitochondrial genetic code to check for the presence of stop codons (no stop codon was found).

Results

Molecular phylogenetic analyses

DNA sequences were used to test species limits within *Paromoionchis* gen. nov. The monophyly of this genus is strongly supported in all analyses (Figs 1–4). In analyses based on mitochondrial COI, 16S and 12S concatenated sequences, three clades (clades A, B and C in Fig. 1) are strongly supported, with bootstrap support and posterior probabilities of 88 and 1, 100 and 1, and 100 and 1, respectively. The relationships between clades A, B and C are not well supported. Each of these three clades includes three strongly-supported, least-inclusive units that are reciprocally monophyletic (Fig. 1). The monophyly of each unit is strongly supported by a bootstrap support of 100 and a posterior probability of 1; the bootstrap support for *P. goslineri* gen. et sp. nov. unit #1 is 98 (Fig. 1).

The phylogenetic analyses with just COI yielded similar results, even though, as expected, the deeper nodes are not as strongly supported (Fig. 2). The monophyly of *Paromoionchis* gen. nov. is recovered but not well supported. The monophyly of clades A, B and C is strongly supported with the following values (bootstrap/posterior probabilities): 91/0.99, 94/1 and 92/1. The monophyly of each of the nine units is also strongly supported: 100/1 (*P. goslineri* gen. et sp. nov. unit #2, *P. penangensis* gen. et sp. nov., *P. daemelii*, *P. boholensis* gen. et sp. nov. unit #1, *P. tumidus* unit #2 and *P. tumidus* unit #1), 99/1 (*P. boholensis* gen. et sp. nov. unit #2), 96/1 (*P. tumidus* unit #3) and 85/0.95 (*P. goslineri* gen. et sp. nov. unit #1). There is some phylogenetic structure within *P. tumidus* unit #1 (which cannot be divided into strongly supported and reciprocally monophyletic subunits) but little to no structure within the eight other units (Fig. 2).

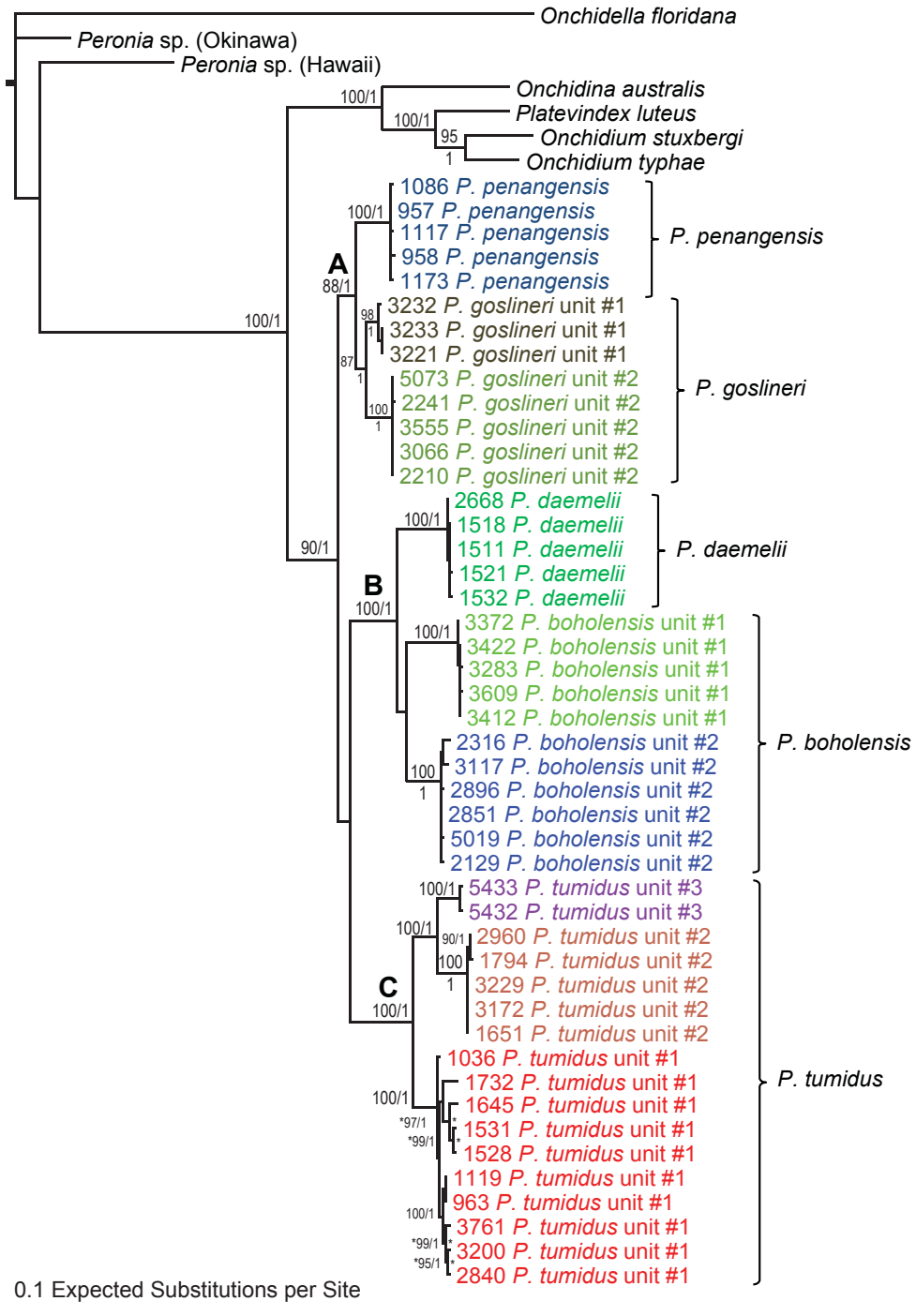

Fig. 1. Phylogenetic relationships within *Paromoionchis* gen. nov. based on concatenated COI, 16S and 12S sequences for 53 individuals (including 7 outgroups). Numbers by the branches are the bootstrap values (maximum likelihood analysis, ML) and the posterior probabilities (Bayesian analysis). Only numbers >70% (ML) and >0.9 (Bayesian) are indicated. Numbers for each individual correspond to unique identifiers for DNA extraction. All sequences for specimens of *Paromoionchis* gen. nov. are new. Some outgroup sequences are from previous studies (Dayrat *et al.* 2011a, 2016; Dayrat & Goulding 2017). Information on specimens can be found in the lists of material examined and in Table 1. The letters A, B and C correspond to three clades which are referred to in the text. The color used for each (mitochondrial) unit is the same as that used in Figs 2–6.

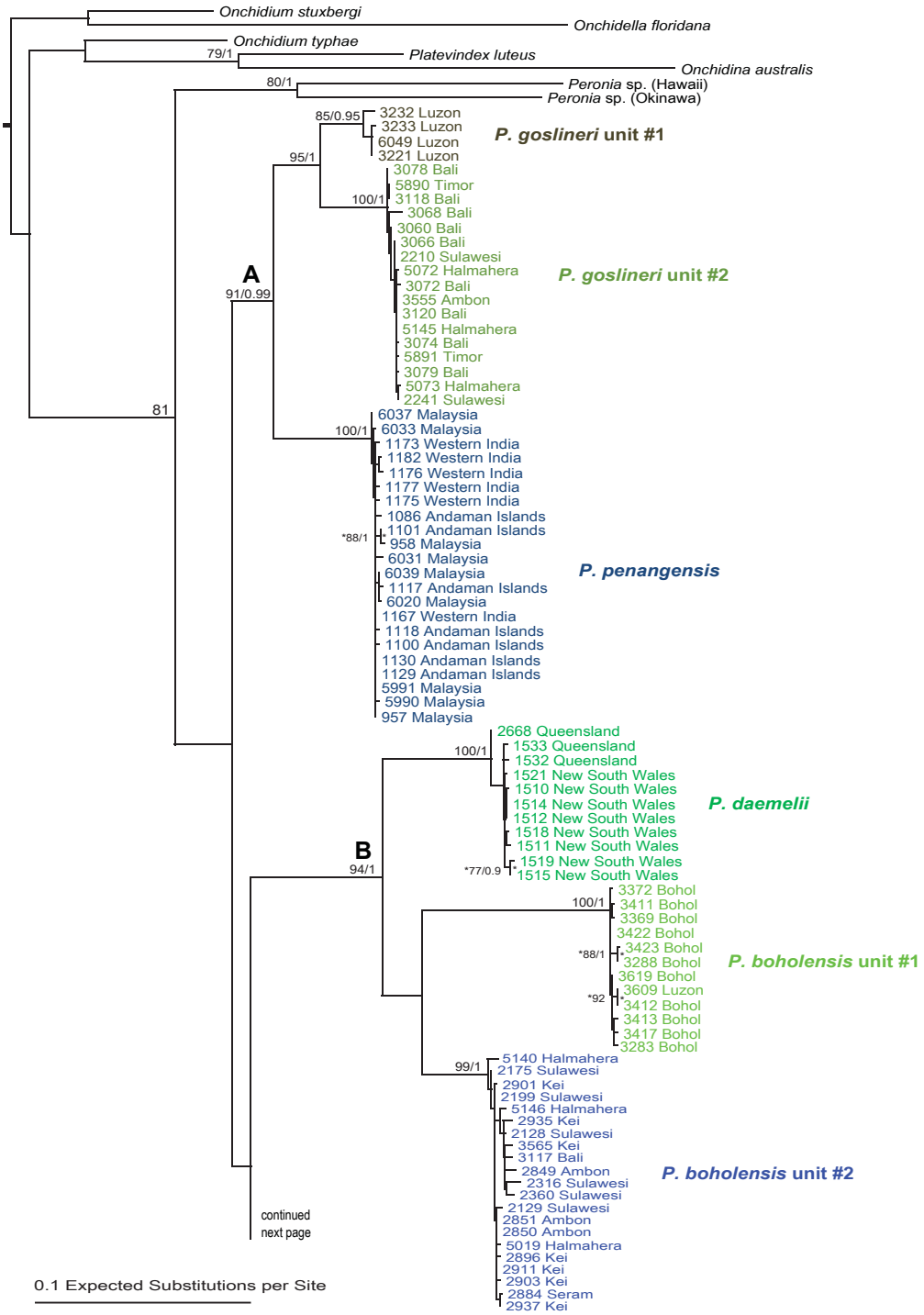

Fig. 2. (continued on next page) Phylogenetic relationships within *Paromoionchis* gen. nov. based on COI sequences of 166 individuals. Numbers by the branches are the bootstrap values (maximum likelihood analysis, ML) and the posterior probabilities (Bayesian analysis). Only numbers > 70% (ML) and > 0.9 (Bayesian) are indicated. Numbers for each individual correspond to unique identifiers for DNA extraction. All sequences for specimens of *Paromoionchis* gen. nov. are new, except for the three sequences of *P. tumidus* (Semper, 1880) comb. nov. from China found in GenBank (in which they were misidentified as *Paraoncidium reevesii* (J.E. Gray, 1850)). Information on specimens can be found in the lists of material examined and in Table 1. The letters A, B and C correspond to three clades referred to in the text. The color used for each (mitochondrial) unit is the same as that used in Figs 1 and 3–6.

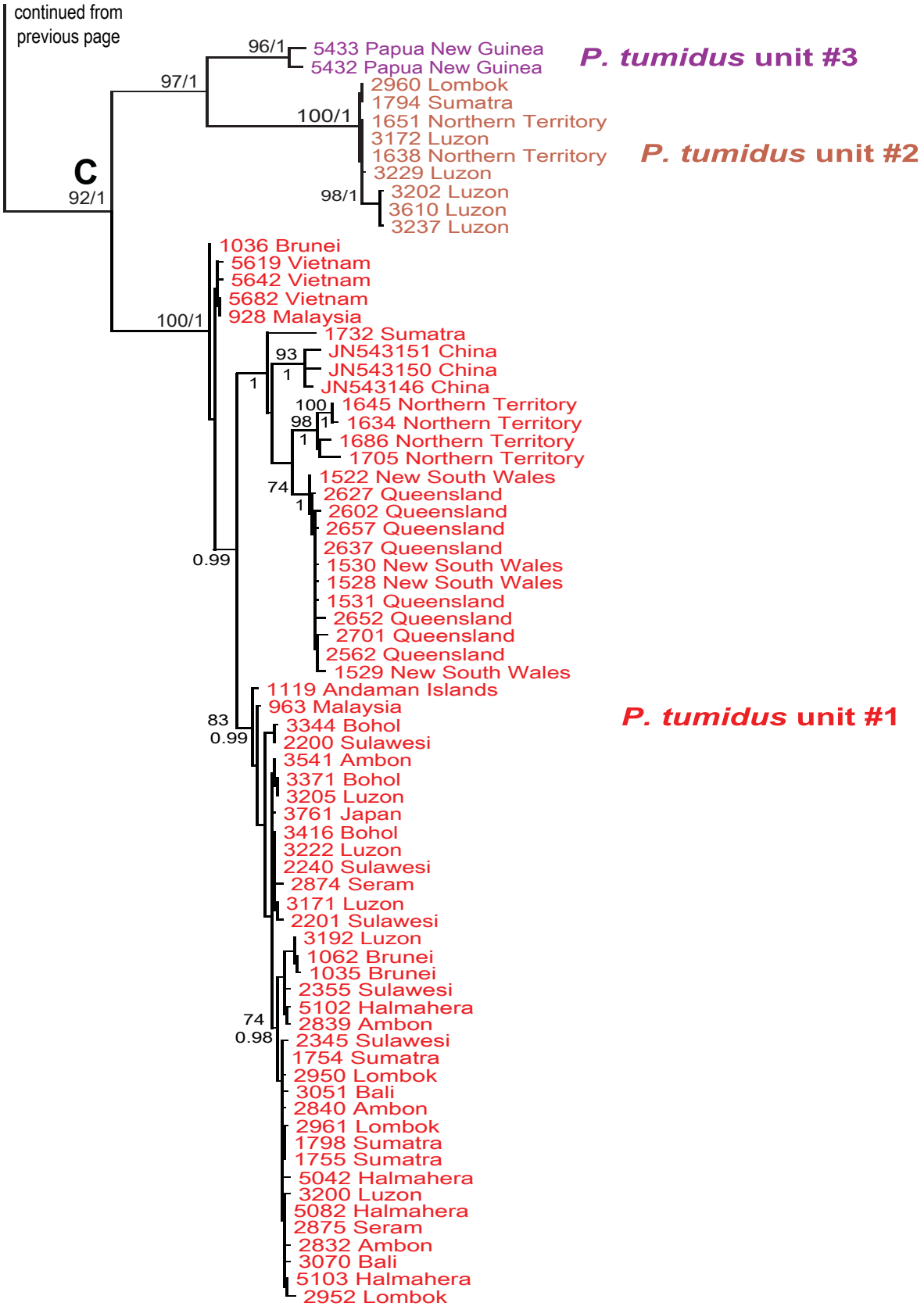

Fig. 2. (continued) Phylogenetic relationships within *Paromoionchis* gen. nov. based on COI sequences of 166 individuals.

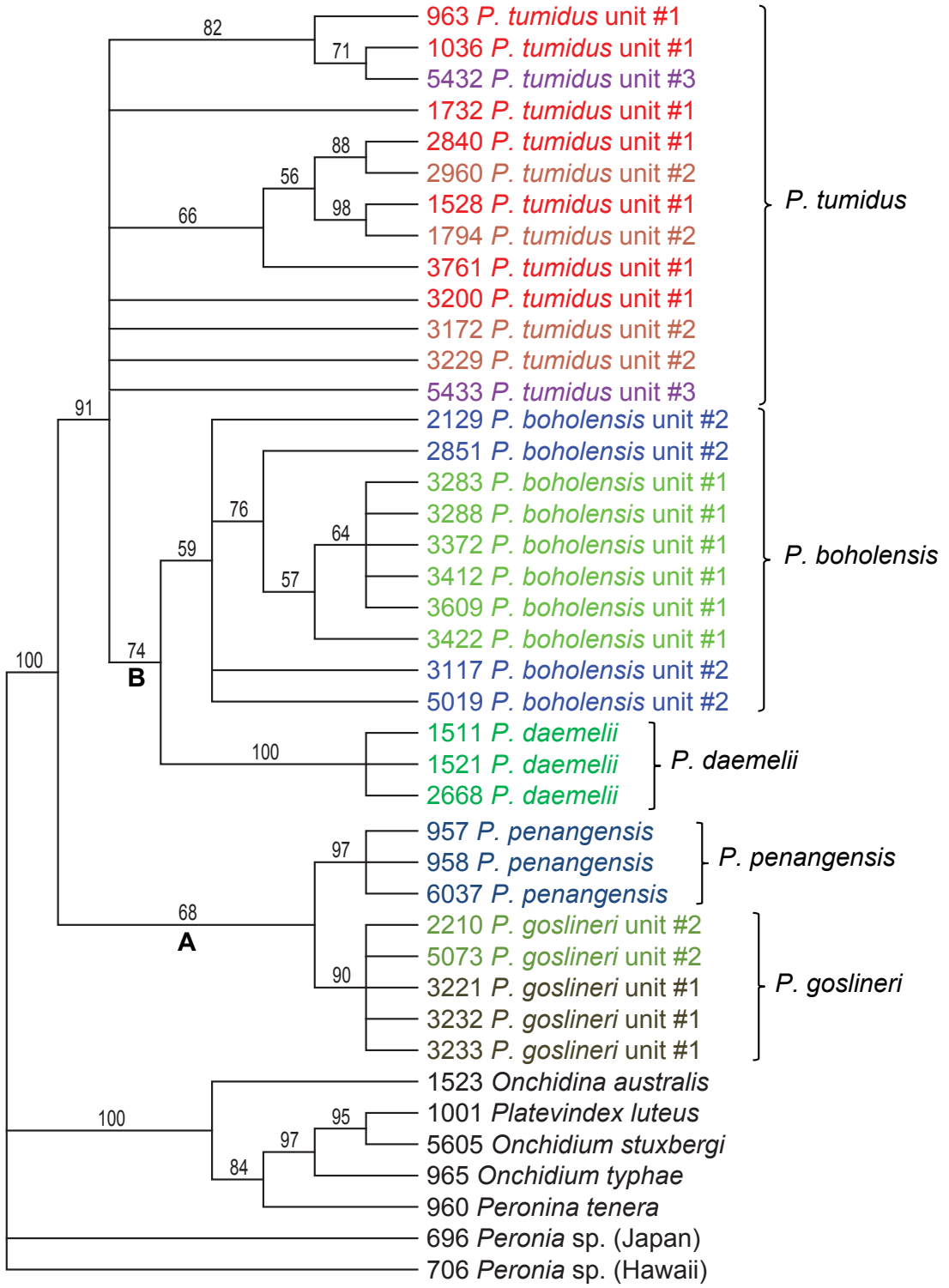

Fig. 3. Maximum parsimony consensus tree within *Paromoionchis* gen. nov., performed with concatenated ITS2 and 28S DNA sequences from 41 individuals (including 7 outgroups). Numbers by the branches are the bootstrap values (only numbers > 50% are indicated). Numbers for each individual correspond to unique identifiers for DNA extraction. All sequences for specimens of *Paromoionchis* gen. nov. are new. Information on specimens can be found in the lists of material examined and in Table 1. Letters A and B correspond to clades referred to in the text. The color used for each (mitochondrial) unit is the same as that used in Figs 1–2 and 4–6.

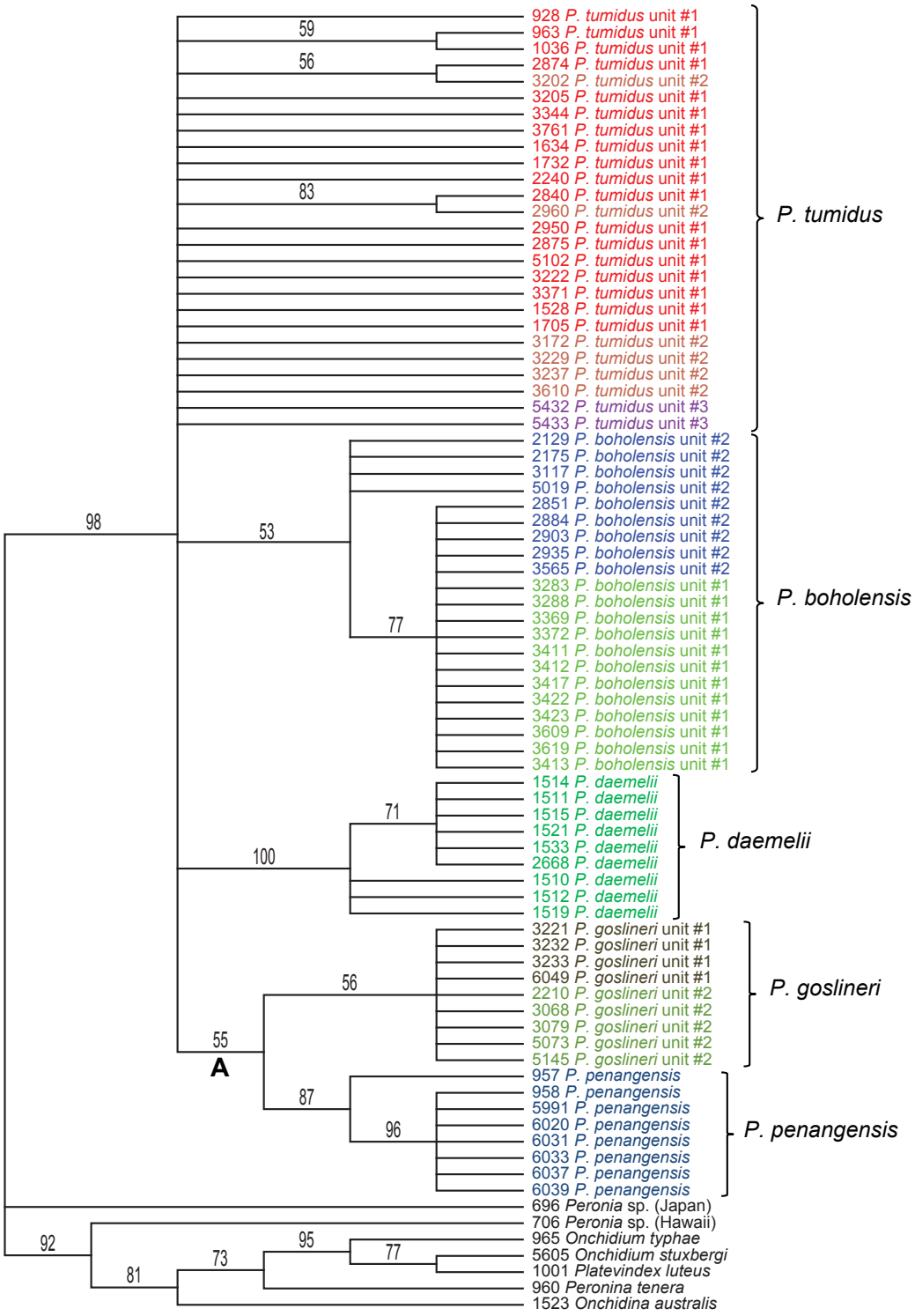

Fig. 4. Maximum parsimony consensus tree within *Paromoionchis* gen. nov., performed with ITS2 DNA sequences from 80 individuals (including 7 outgroups). Numbers by the branches are the bootstrap values (only numbers > 50% are indicated). Numbers for each individual correspond to unique identifiers for DNA extraction. All sequences for specimens of *Paromoionchis* gen. nov. are new. Information on specimens can be found in the lists of material examined and in Table 1. The letter A corresponds to a clade referred to in the text. The color used for each (mitochondrial) unit is the same as that used in Figs 1–3 and 5–6.

Table 2. Pairwise genetic distances between individual sequences within and between mitochondrial units, based on our data set of 159 COI sequences (Table 1). Ranges of minimum to maximum distances are indicated (as percentages). For instance, within *P. tumidus* (Semper, 1880) unit #1, individual sequences are between 0 and 3.2% divergent; individual sequences between *P. tumidus* unit #1 and *P. boholensis* gen. et sp. nov. unit #2 are minimally 6.4% and maximally 7.9% divergent; also, overall, the distance gap between *P. tumidus* unit #1 and the eight other mitochondrial units is between 3.2% (the maximum intra-unit distance within *P. tumidus* unit #1) and 5% (the minimum distance between *P. tumidus* unit #1 and *P. tumidus* unit #3). The data from this table are illustrated in Figure 5 to help visualize the large gap between intra-specific and inter-specific distances.

Species (mitochondrial unit)	*tumid.* 1	*boh.* 2	*boh.* 1	*daeme.*	*tumid.* 2	*tumid.* 3	*penan.*	*gosli.* 2	*gosli.* 1
P. tumidus unit #1	0–3.2								
P. boholensis unit #2	6.4–7.9	0–1.3							
P. boholensis unit #1	6.8–8.1	5.6–6.4	0–0.5						
P. daemelii	7.0–8.4	5.0–5.8	6.2–6.9	0–0.8					
P. tumidus unit #2	5.7–7.2	7.8–9.0	7.9–8.9	8.8–9.8	0–0.6				
P. tumidus unit #3	5.0–6.0	7.1–7.8	7.5–8.0	8.3–8.8	4.2–4.8	0.6			
P. penangensis	5.5–6.8	6.6–7.6	7.0–7.8	7.1–7.8	7.1–8.0	6.3–6.8	0–0.5		
P. goslineri unit #2	5.9–7.4	6.7–7.6	7.3–8.3	6.9–7.6	7.4–8.2	6.6–7.2	4.7–5.4	0–0.7	
P. goslineri unit #1	5.9–7.2	6.2–7.3	7.7–8.0	6.9–7.6	7.9–8.9	6.5–6.7	4.3–5.0	3.4–3.8	0–0.8

Nuclear sequences (ITS2 alone and ITS2 and 28S concatenated) yielded fewer monophyletic units than the mitochondrial sequences (Figs 3–4). Three units are highly supported (with bootstrap values > 90 %): *P. daemelii*, *P. goslineri* gen. et sp. nov. and *P. penangensis* gen. et sp. nov. One unit, *P. boholensis* gen. et sp. nov., is less strongly supported (with bootstrap values > 50%) but is consistently recovered in all analyses with nuclear sequences. Finally, there is not enough phylogenetic signal to support the monophyly of *P. tumidus*, which, in the analyses based on nuclear sequences, includes a series of unresolved basal branches (Figs 3–4). Most importantly, individuals of the *P. goslineri* gen. et sp. nov. mitochondrial units #1 and #2 (Figs 1–2) are mixed together. Nuclear data do not support the existence of two distinct, reciprocally-monophyletic units within *P. goslineri* gen. et sp. nov. (Figs 3–4). The exact same remark applies to *P. boholensis* gen. et sp. nov. As for *P. tumidus*, individuals from the three mitochondrial units #1, #2 and #3 are all mixed together as well, even though they represent unresolved branches at the base of the nuclear trees (Figs 3–4). Finally, support is generally low for deeper nodes with nuclear sequences (Figs 3–4): clade A (*P. penangensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov.) is recovered in both the analysis with ITS2 and 28S concatenated and in the analysis with just ITS2; clade B (*P. daemelii* and *P. boholensis* gen. et sp. nov.) is only recovered in the ITS2 and 28S concatenated analysis; clade C (*P. tumidus* units) is not recovered (as unresolved branches at the base of the tree).

Pairwise genetic divergences

Pairwise genetic distances (between COI sequences) also support the existence of nine least-inclusive molecular units of *Paromoionchis* gen. nov. and there is a wide and unambiguous gap between intra-unit and inter-unit distances (Table 2, Fig. 5). In seven of the units (i.e., all nine units but *P. tumidus* unit #1 and *P. boholensis* gen. et sp. nov. unit #2), the intra-unit distances are below 0.8 % and the inter-unit distances vary from 3.4% (between *P. goslineri* gen. et sp. nov. unit #1 and *P. goslineri* gen. et sp. nov. unit #2) to 9.8% (between *P. daemelii* and *P. tumidus* unit #2). Data are similar for *P. boholensis* gen. et sp. nov. unit #2, with intra-unit distances below 1.3% and inter-unit distances varying from 5.6 to 9.0%.

There also is a strong gap between intra- and inter-unit distances for *P. tumidus* unit #1, but it is slightly shifted: intra-unit distances are below 3.4% and inter-unit distances vary from 5.0 to 8.4%. Genetic distances do not mean anything in absolute terms and one should not expect the gap between intra- and inter-unit distances to always be the same between genera and even within genera. It all depends on the context. In clade A, the gap is between 0.8% and 3.4% and inter-unit divergences do not exceed 8.9%. In clade B, data display a similar pattern but numbers are slightly shifted, with a gap between 1.3% and 5% and inter-unit divergences going up to 9.8%. Finally, in clade C, the gap between intra- and inter-unit distances seems smaller if all three units are considered together (between 3.2% and 4.2%). However, in clade C, distances need to be analyzed with *P. tumidus* unit #1 being taken separately because of its higher intra-unit distances (up to 3.2%). There is still an obvious gap in genetic distances between *P. tumidus* unit #1 and unit #3 (inter-unit distances above 5.0%) and between *P. tumidus* unit #1 and unit #2 (inter-unit distances above 5.7%). Finally, the gap is obvious between *P. tumidus* unit #2 and unit #3 (intra-unit distances below 0.6% and inter-unit distances above 4.2%).

So, overall, there is always a gap between intra-unit and inter-unit distances, but the actual values vary depending on the phylogenetic context and the units being considered (Fig. 5). In other words, one should not focus on where the gap is situated (between 2% and 5%, between 3% and 6%, etc.) but on whether there is an actual gap separating units, especially those that are most closely related.

Comparative anatomy

In the field, specimens of *Paromoionchis* gen. nov. were often correctly identified at the generic level, i.e., we most often recognized that they were in the same genus. Because these slugs bear a large dorsal,

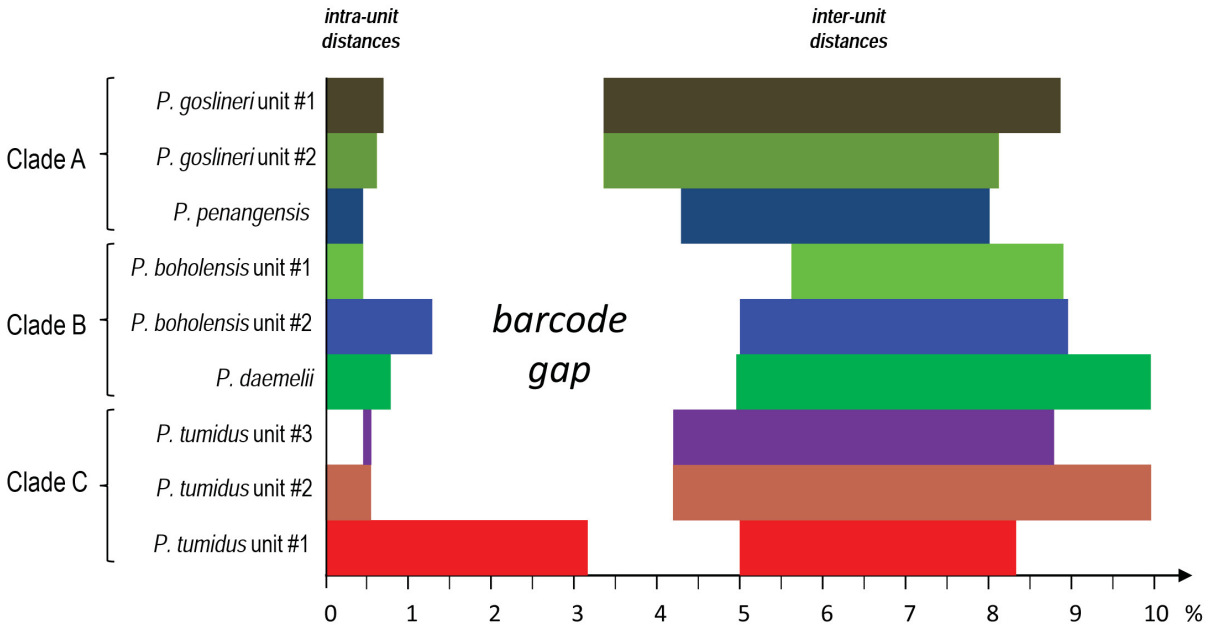

Fig. 5. Diagram that helps to visualize the data on pairwise genetic distances between COI sequences within and between mitochondrial units in *Paromoionchis* gen. nov. (see Table 3). Ranges of minimum to maximum distances are indicated (in percentages). For instance, within *P. tumidus* (Semper, 1880) unit #1, individual sequences are between 0 and 3.2% divergent; individual sequences between *P. tumidus* unit #1 and the other units are minimally 5% and maximally 8.4% divergent; overall, the distance gap between *P. tumidus* unit #1 and the eight other units is between 3.2 and 5%. The colors used for each unit are the same as those used in Figs 1–4 and 6.

Table 3. Summary of internal traits that can help distinguish species of *Paromoionchis* gen. nov. All traits may be subject to individual variation. Traits are described in detail in the corresponding species descriptions and discussed in the species remarks. Traits are indicated for the mitochondrial units (when applicable) to show that those units are cryptic anatomically.

Species	Mitoch. unit	Clade (Figs 1–4)	Retractor muscle (penis) attachment site	Accessory penial gland & spine (size)	Penis shape	Penis hooks	Distribution
P. tumidus	#1	C	~ heart	yes (1 to 2 mm)	thin	yes (< 20 µm)	from Andaman Islands to Japan and New South Wales
	#2	C	~ heart	yes (1.2 to 1.8 mm)	thin	yes (< 22 µm)	Northern Territory, Sumatra, Lombok, Luzon and Bohol
	#3	C	~ heart	yes (0.8 to 1 mm)	thin	yes (< 28 µm)	Papua New Guinea
P. daemelii	–	B	very short or vestigial	yes (2.5 to 2.7 mm)	thin	no	New South Wales and Queensland
P. boholensis	#1	B	vestigial	yes (1 to 1.2 mm)	thin	no	Bohol and Luzon
	#2	B	none or vestigial	yes (1.1 to 1.8 mm)	thin	no	Ambon, Bali, Halmahera, Kei, Seram and Sulawesi
P. penangensis	–	A	strong and ~heart	no	large	no	from Western India to Malaysia
P. goslineri	#1	A	thin (~ central nervous system) or vestigial	no	thin	no	Luzon
	#2	A	long and ~ heart	no	thin	no	Ambon, Bali, Halmahera, Sulawesi and Timor

central, retractable papilla that looks like a peduncle, we called them the 'peduncle' slugs in the field. This peduncle, however, is not fully reliable, because a similar structure is found in other genera; for instance, a similar peduncle is found in *Wallaconchis buetschlii* (Stantschinsky, 1907) (see Goulding *et al.* 2018c), and it often cannot be seen because it is fully retractable inside the notum. In the field, 'peduncle' slugs were numbered individually without any *a priori* species designation, because they all live in a similar habitat and are not distinct externally (their color patterns are similar and individual variation is high). Even though slugs in *Paromoionchis* gen. nov. are not distinct externally, they differ internally for characters from the male copulatory apparatus (Table 3).

Within clade A, *P. penangensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov. are distinct anatomically from each other and from all the slugs in clades B and C (Figs 1–4, Table 3): *P. penangensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov. lack an accessory penial gland, which is present in clades B (*P. daemelii* and *P. boholensis* gen. et sp. nov.) and C (*P. tumidus* mitochondrial units); also, *P. penangensis* gen. et sp. nov. is characterized by a large penis while *P. goslineri* gen. et sp. nov. is characterized by a thin penis. There is no anatomical difference between *P. goslineri* gen. et sp. nov. mitochondrial unit #1 and unit #2.

Within clade B, *P. daemelii* and *P. boholensis* gen. et sp. nov. are distinct anatomically from all the slugs in clades A and C (Figs 1–4, Table 3): *P. daemelii* and *P. boholensis* gen. et sp. nov. are characterized by an accessory penial gland, which is lacking in clade A (*P. penangensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov.) and the penis of *P. daemelii* and *P. boholensis* gen. et sp. nov. bears no hooks, which are present in clade C (*P. tumidus* mitochondrial units). Also, *P. daemelii* and *P. boholensis* gen. et sp. nov. are anatomically distinct from each other: the spine of the accessory penial gland is longer in *P. daemelii* than in *P. boholensis* gen. et sp. nov. However, there is no anatomical difference between *P. boholensis* gen. et sp. nov. mitochondrial unit #1 and unit #2.

Within clade C, the three mitochondrial units of *P. tumidus* are not anatomically distinct from each other, but they differ from all the slugs in clades B and C (Figs 1–4, Table 3): *P. tumidus* is characterized by an accessory penial gland, which is lacking in clade A (*P. penangensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov.); also, the penis of *P. tumidus* bears hooks which are lacking in clade B (*P. daemelii* and *P. boholensis* gen. et sp. nov.).

Species delineation

According to mitochondrial DNA sequences, there are nine least-inclusive, reciprocally monophyletic units (Figs 1–2, Table 3). Several of those units, however, cannot be distinguished anatomically: the three mitochondrial units of *P. tumidus* (units #1, #2 and #3) are completely cryptic (externally and internally), as well as the two mitochondrial units of *P. boholensis* gen. et sp. nov. (units #1 and #2) and the two mitochondrial units of *P. goslineri* gen. et sp. nov. (units #1 and #2). Furthermore, nuclear DNA sequences show that there likely is gene flow between some of the mitochondrial units because they are not recovered as reciprocally monophyletic (Figs 3–4): in analyses based on nuclear sequences, individuals of *P. tumidus* units #1, #2 and #3 are all mixed together, as well as those of *P. boholensis* gen. et sp. nov. units #1 and #2 and those of *P. goslineri* gen. et sp. nov. units #1 and #2.

Therefore, only five species of *Paromoionchis* are recognized here: *P. boholensis* gen. et sp. nov., *P. daemelii*, *P. goslineri* gen. et sp. nov., *P. penangensis* gen. et sp. nov. and *P. tumidus*. These five species are cryptic externally but are distinct anatomically: their male parts differ greatly (Table 3). Their monophyly is supported by both nuclear and mitochondrial sequences, with the exception of *P. tumidus*, recovered as unresolved branches in nuclear trees (Figs 1–4). The existence of least-inclusive mitochondrial units which are anatomically cryptic within *P. tumidus* (units #1, #2 and #3), *P. boholensis* gen. et sp. nov. (units #1 and #2) and *P. goslineri* gen. et sp. nov. (units #1 and #2) can be explained with reference to the mode of inheritance of the mitochondrial genome and the complex geological history of the region, especially the many changes in sea levels (see Discussion).

Systematics and anatomical descriptions

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia Burmeister, 1837
Order Systellomatophora Pilsbry, 1948
Superfamily Onchidioidea Rafinesque, 1815
Family Onchidiidae Rafinesque, 1815

Paromoionchis Dayrat & Goulding gen. nov.
urn:lsid:zoobank.org:act:4506A7F2-CC0B-4F23-8F5E-4DE2AA42B61F

Type species

Onchidium tumidum Semper, 1880, designated here.

Diagnosis

Body not flattened. No dorsal gills. Dorsal eyes present on notum. Retractable, central papilla (usually with four dorsal eyes) present, often raised above dorsal surface. Eyes at tip of short ocular tentacles. Male opening below right ocular tentacle and to its left. Foot wide. Pneumostome median, on ventral hyponotum. Intestinal loops of type II. Rectal gland absent. Accessory penial gland present or absent. When present, accessory penial gland with muscular sac. Penis with or without hooks.

Differential diagnosis

No external diagnostic feature unambiguously distinguishes *Paromoionchis* gen. nov. from all other genera (which is not surprising because many onchidiid species from different genera are very similar externally). However, *Paromoionchis* gen. nov. is characterized by a unique combination of internal and external characters: no dorsal gills, male opening below and to the left of the right eye tentacle, no rectal gland and intestinal loops of type II (see Labbé 1934a: 177, fig. 3, for a comparison of digestive types). According to our data, any onchidiid slug with this combination of characters must belong to a species of *Paromoionchis* gen. nov.

Etymology

The name *Paromoionchis* is a combination of *parómoios* (παρόμοιος), which means 'similar' in Greek (because members look very similar externally) and *onchis*, a word derived from the Greek *onchos* (ὁ ὄγκος) and one of the early names used to refer to onchidiid slugs.

Gender

Masculine, the gender of *onchis* (ICZN Art. 30.1.1), a word derived from the masculine Greek word ὁ ὄγκος (*onchos*), which means 'mass' or 'tumor.' As a result (ICZN Art. 31.2), the ending of the specific name *tumidum* (a Latin adjective) must be changed from neuter (because *Onchidium* is a name of neuter gender) to masculine (*tumidus*).

Distribution

The new genus described here is distributed from the western coast of India in the west, all the way to the subtropical waters of Japan (~33° N), Papua New Guinea and the subtropical waters of southeastern Australia (~32° S) in the east (Fig. 6). We did not find *Paromoionchis* gen. nov. in South Africa, Madagascar or Mauritius, but it is possible that it is present in areas east of Papua New Guinea, such as Fiji and New Caledonia, where we did not collect.

Habitat

The five known species of *Paromoionchis* gen. nov. primarily live on mud, in or next to mangroves, which explains why three species have just been discovered now, because the mangroves of South-East Asia have been very poorly explored. Occasionally, these slugs can also be found in or on muddy logs, coral rubble, sandy mud or even sand with very little mud in it. *Paromoionchis tumidus*, which is widespread and very common, can be found in nearly all these habitats, even though the mud surface remains where it is most commonly found, like all other species of the genus. Because members of *Paromoionchis* gen. nov. prefer the mud surface, live animals are often covered with mud.

Remarks

A new generic name is needed because no existing name applies to the clade described here. Our remarks are based on the examination of all the type specimens available, especially those of the type species of all genera, the careful analyses of all the original descriptions (especially when no type specimens were available), and our ongoing taxonomic revision of each genus of the family. Three existing generic names are junior synonyms of *Onchidella* J.E. Gray, 1850, which is not found in the tropical Indo-West Pacific and is characterized by a completely different anatomy (Dayrat 2009; Dayrat *et al.* 2011b). Seven generic names apply to the clade including all the onchidiid slugs with dorsal gills, i.e., *Peronia* Fleming, 1822 (Dayrat 2009). *Labella* Starobogatov, 1976 is a junior synonym of *Onchidium* Buchannan, 1800, which applies to a distinct clade including three species (Dayrat *et al.* 2016). *Paraoncidium* Labbé, 1934 is a junior synonym of *Onchidina* Semper, 1882, which applies to a

distinct monotypic genus from southeastern Australia (Dayrat & Goulding 2017). *Peronina* Plate, 1893 applies to a clade including slugs characterized by a pneumostome located at the margin between the dorsal notum and the ventral hyponotum. *Platevindex* Baker, 1938 applies to a clade including species with a distinctly flattened body and a narrow foot. *Semperoncis* Starobogatov, 1976 applies to species characterized by a very different anatomy and which are adapted to terrestrial life in the Philippines (Dayrat 2010). And, finally, *Melayonchis* Dayrat & Goulding, 2017 applies to a distinct clade including slugs with a different anatomy (Dayrat *et al.* 2017).

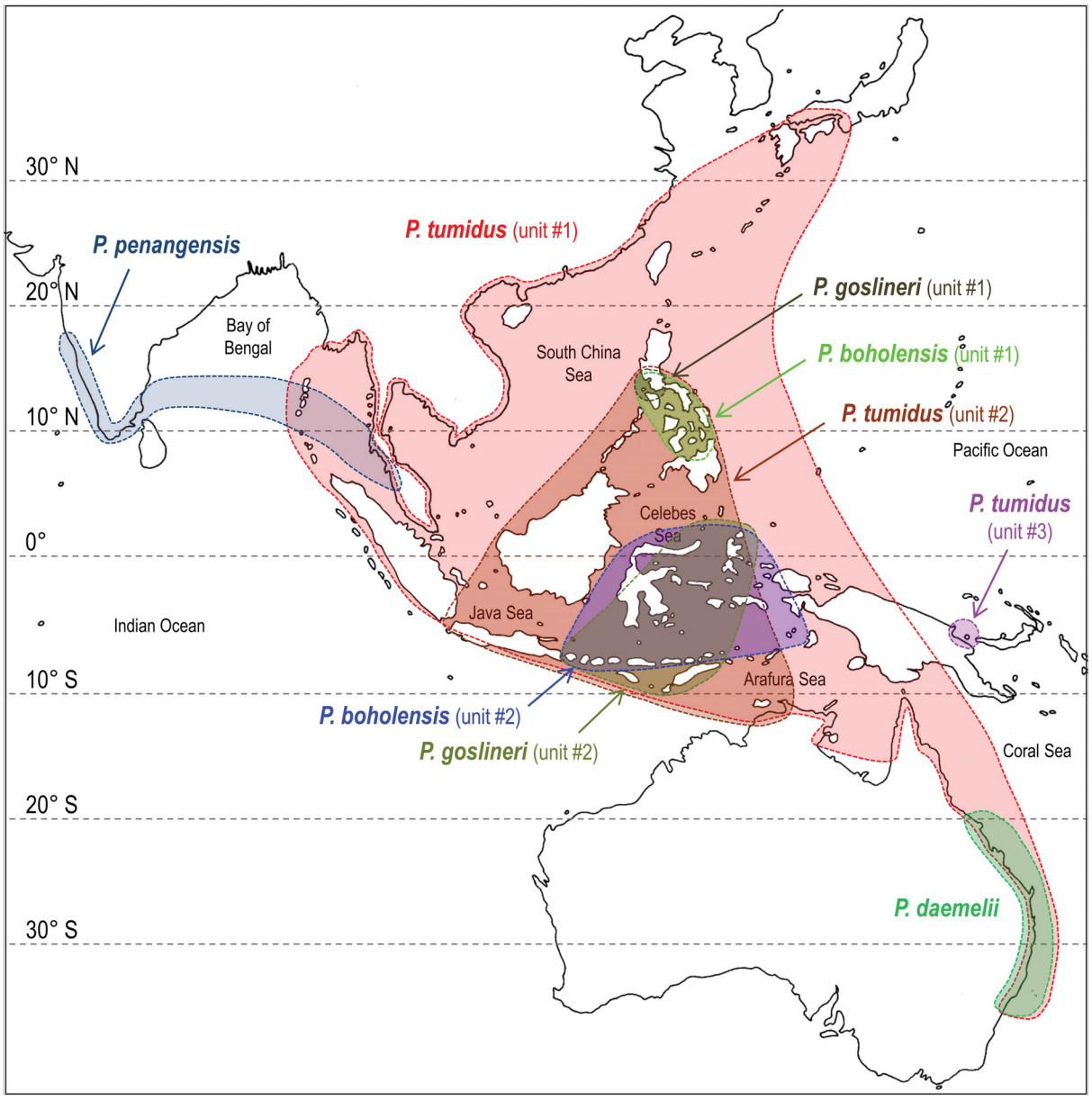

Fig. 6. Geographic distribution of the five species of *Paromoionchis* gen. nov. Distinct colors are used for each mitochondrial unit found in *P. tumidus* (Semper, 1880) comb. nov., *P. boholensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov., and the colors used for each unit are the same as those used in Figs 1–5. Colored areas correspond to hypothetical ranges proposed based on known records (all of which are new here except for the type localities of *P. tumidus* and *P. daemelii* (Semper, 1880) comb. nov.).

Paromoionchis tumidus (Semper, 1880) comb. nov.
Figs 7–25

Onchidium tumidum Semper, 1880: 262–263, pl. 20, figs 3–4, pl. 23, fig. 4.
Onchidium samarense Semper, 1880: 268–269, pl. 20, figs 9, 13, pl. 23, fig. 7. **Syn. nov.**
Onchidium mertoni Simroth, 1918: 294–296, pl. XX, figs 43–47. **Syn. nov.**
Onchidium hongkongense Britton, 1984: 188–190, figs 6–7. **Syn. nov.**

Onchidium samarense – Semper 1882: 268–269, pl. 21, fig. 5.

Material examined

Type material

SINGAPORE • lectotype (here designated; 28/22 mm); ZMB 39019a • 15 paralectotypes; ZMB 39019b • 2 paralectotypes; NHMD 300305 • 1 paralectotype; SMF 333603/1.

AUSTRALIA • 2 paralectotypes; Queensland, Mackay; ZMB 39020.

Other type material

PHILIPPINES • lectotype of *Onchidium samarense* (here designated; 22/17 mm); Samar Island, Palapa harbor; ZMB 39025a • 2 paralectotypes of *O. samarense* (24/20 and 20/15 mm); same locality as lectotype; ZMB 39025b.

INDONESIA • lectotype of *Onchidium mertoni* (here designated; 15/9 mm); Aru Islands, Kobroor, Sungai; 5 Jan. 1908; ZMB 121591a • 4 paralectotypes of *O. mertoni* (14/8, 14/10, 15/14 and 14/10 mm); same data as for lectotype; ZMB 121591b.

CHINA • holotype of *Onchidium hongkongense* (17/13 mm); Hong Kong; NHM 1982290 • 15 paratypes; same locality as holotype; NHM 1982291 to 1982292.

Notes on type material

Onchidium tumidum. Lectotype, 28/22 mm, designated here (ZMB 39019a). All other syntypes become paralectotypes (the 15 paralectotypes from the same lot are now ZMB 39019b). According to the original description, the type material included 42 specimens from Singapore and an unknown number of specimens from Port Mackay, Queensland, Australia. A total of 21 syntypes were located in museum collections: 19 specimens from Singapore (16 specimens, ZMB 39019; 2 specimens, NHMD 300305; 1 specimen, SMF 333603/1) and 2 specimens from Mackay (ZMB 39020). There also are two possible syntypes from Australia (ZMH 27480/2). Two similar species of *Paromoionchis* gen. nov. are found at Port Mackay, *P. tumidus* and *P. daemelii*, which anatomically can only be distinguished based on the insertion of the retractor muscle of the penis. In the lectotype designated here from Singapore, the retractor muscle inserts near the heart, exactly as in the species described here. However, in one of the two paralectotypes of *P. tumidus* from Mackay (ZMB 39020), the retractor muscle is vestigial, as in *P. daemelii* (in the other paralectotype from Mackay, the male apparatus was destroyed prior to the present investigation and could not be examined). Hence, it was necessary to designate a lectotype from Singapore in order to clarify the application of *P. tumidus*. Note that the type material was fixed in formalin more than 130 years ago and no DNA sequencing could be attempted.

Onchidium samarense. Lectotype, 22/17 mm, designated here (ZMB 39025a). The two other syntypes become paralectotypes (ZMB 39025b). According to the original description, the type material included only two specimens from the same locality in Samar, Philippines. However, the jar with the type material currently contains three similar-looking specimens (syntypes), all of which were dissected prior to the present study. It is not excluded that the original description was based on only two of those three

specimens but it is also possible that Semper himself identified all three specimens as *O. samerense* [sic] (with a minor typo in the original description). The lectotype still contains all its internal organs, including the male copulatory parts. One paralectotype (24/20 mm) is mostly destroyed, with no internal organs left except the digestive gland (a few destroyed pieces of organs are in a vial). The other paralectotype (20/15 mm) still contains internal organs, but the male parts are missing. Our observations and comments are mostly based on the only specimen with male parts; hence its designation as a lectotype. Note that the type material was fixed in formalin more than 130 years ago and no DNA sequencing could be attempted. Note also that if, in the future, *Onchidium samarense* were to be regarded as a valid species name in *Paromoionchis* gen. nov., the specific name *samarense* (neuter) would need to become *samarensis* (masculine).

Onchidium mertoni. Lectotype, 15/9 mm, designated here (ZMB 121591a). The four other syntypes become paralectotypes (ZMB 121591b). Simroth mentioned in the original description that all five specimens were very hard. Indeed, it seems that they dried out at some point and they are very poorly preserved. The lectotype designated here is the only specimen that is complete. It was partially dissected for the present study (the penial hooks, identical to those of *O. tumidum*, are illustrated here). Two paralectotypes (14/8 and 14/10 mm) were dissected prior to the present study and are completely empty. Two other paralectotypes (15/14 and 14/10 mm) are in very poor condition (the body is extremely hard and the digestive system is partly outside the body through the foot). A lectotype is designated here to clarify the application of the name *O. mertoni* because several species of *Paromoionchis* gen. nov. are potentially sympatric in the Aru Islands and so it cannot be excluded that the five original syntypes belong to different species. Note that the type material was fixed in formalin more than 100 years ago and no DNA sequencing could be attempted.

Onchidium hongkongense. Holotype, 17/13 mm, by original designation (NHM 1982290) and 15 paratypes (NHM 1982291, NHM 1982292). The holotype is largely destroyed due to prior dissection, likely by Britton. Large parts of the notum and of the reproductive organs are missing. Even though it is mostly destroyed, the digestive system is confirmed to be of type II. A few paratypes were checked for the present study and their anatomy matches that of the holotype. Note that the type material was fixed in formalin more than 40 years ago and no DNA sequencing could be attempted. Note also that the specific name *hongkongensis* (masculine or feminine gender) originally used by Britton is corrected to *hongkongense* (neuter) for gender agreement with *Onchidium*. Should *Onchidium hongkongense* ever become a valid species name in *Paromoionchis* gen. nov., *hongkongense* would then need to be changed back to *hongkongensis*.

Other material

AUSTRALIA – **New South Wales** • 1 spec. (20/15 [1522] mm); Sydney, Pittwater, Careel Bay; 33°37.323′ S, 151°19.878′ E; 24 Nov. 2011; station 40; supratidal zone on margin of salt marsh, mangrove patch on side of creek; AM C.468918.005 • 1 spec. (35/20 [1529] mm); Sydney, Hawkesbury River, Cheero Point; 33°30.687′ S, 151°11.669′ E; 25 Nov. 2011; station 42; open mangrove with old logs; AM C.468924.001 • 1 spec. (33/20 [1528] mm); same data as for preceding; AM C.468923.002 • 1 spec. (32/20 [1530] mm); same data as for preceding; AM C.468925.001. – **Northern Territory** • 1 spec. (45/32 [1634] mm); Darwin, near Channel Island Road; 12°34.979′ S, 130°55.992′ E; 16 Aug. 2012; station 65; sequence of *Sonneratia*, *Rhizophora* and *Ceriops*; NTM P.57620 • 1 spec. (40/25 [1686] mm); Darwin, end of Channel Island Road; 12°33.557′ S, 130°52.894′ E; 17 Aug. 2012; station 66; sequence of *Sonneratia*, *Rhizophora* and *Ceriops*; NTM P.57621 • 1 spec. (42/38 [1638] mm); same data as for preceding; NTM P.57623 • 2 spec. (30/17 [1705] and 17/12 [1645] mm); Darwin, close to Tiger Brenan Road (small service road); 12°28.782′ S, 130°54.750′ E; 19 Aug. 2012; station 69; high tidal *Ceriops*; NTM P.57622 • 1 spec. (36/22 [1651] mm); Darwin, Elizabeth Road; 12°32.893′ S, 130°57.642′ E; 20 Aug. 2012; station 70; *Ceriops* and old logs in *Rhizophora* forest; NTM P.57624.

– **Queensland** • 1 spec. (45/30 [2562] mm); Cairns, Yorkey's Knob; 16°48.558′ S, 145°42.768′ E; 17 Jun. 2013; station 101; hard, red mud with grasses; MTQ • 1 spec. (45/30 [2602] mm); Townsville, Magnetic Island; 19°09.938′ S, 146°49.029′ E; 24 Jun. 2013; station 109; water on the mud; MTQ • 1 spec. (15/10 [2627] mm); Bowen; 20°00.658′ S, 148°15.878′ E; 1 Jul. 2013; station 115; back of mangrove across from beach, dense *Rhizophora*, *Avicennia* trees with soft mud around; MTQ • 1 spec. (55/30 [2637] mm); Bowen; 20°00.913′ S, 148°15.745′ E; 1 Jul. 2013; station 116; mangrove away from ocean, small area of open *Avicennia* mangrove, surrounded by *Rhizophora*; MTQ • 1 spec. (20/10 [2652] mm); Bowen, Doughty Creek; 20°01.264′ S, 148°14.345′ E; 2 Jul. 2013; station 117; narrow *Avicennia* and *Rhizophora* mangrove, by creek, some muddy areas and some very sandy; MTQ • 1 spec. (35/20 [2657] mm); Bowen; 20°01.478′ S, 148°14.224′ E; 3 Jul. 2013; station 119; *Rhizophora* and *Avicennia* mangrove; MTQ • 1 spec. (30/20 [2701] mm); Mackay; 20°08.511′ S, 149°12.076′ E; 8 Jul. 2013; station 125; large, dense and sandy mangrove and, by side of river, small strip of mud with *Avicennia* and *Rhizophora*; MTQ • 1 spec. (30/25 [1531] mm); Thirsty Sound, Plum Tree, beach in front of Endeavour Park; 22°08.144′ S, 150°01.856′ E; 14 Sep. 2002; I. Loch, D.L. Beechey and A.C. Miller leg.; sheltered, muddy cobble shore; AM C.575588.

BRUNEI DARUSSALAM • 3 spec. (55/30 [1036], 35/20 [1035] and 20/15 [1062] mm); Pulau Pyatan, Teluk Brunei; 04°55.246′ N, 115°02.764′ E; 27 Jul. 2011; station 32; open *Avicennia* and *Rhizophora* mangrove, with hard mud; BDMNH.

INDIA • 1 spec. (26/17 [1119] mm); Andaman Islands, Middle Andaman, Shantipur, Kadamtala; 12°19.843′ N, 092°46.377′ E; 12 Jan. 2011; station 58; open area with hard mud and many old logs, next to a mangrove with medium trees; BNHS 88.

INDONESIA – **Sumatra** • 1 spec. (24/15 [1732] mm); Kualapenet; 05°16.275′ S, 105°51.287′ E; 17 Oct. 2012; station 77; narrow band of mangrove between ocean and fish ponds; UMIZ 00121 • 2 spec. (35/20 [1754] and 26/16 [1755] mm); Bakauheni; 05°50.560′ S, 105°46.200′ E; 21 Oct. 2012; station 81; small mangrove, not far from road and next to large harbor, very impacted mangrove; UMIZ 00122 • 1 spec. (38/30 [1794] mm); same data as for preceding; UMIZ 00138 • 1 spec. (20/12 [1798] mm); S of Bandar Lampung; 05°32.66′ S, 105°15.113′ E; 28 Oct. 2012; station 83; high intertidal, fairly dense roots with some *Avicennia* and *Nypa*, edge of mangrove by road; UMIZ 00123. – **Sulawesi** • 2 spec. (25/15 [2200] and 20/12 [2201] mm); Tamperong; 01°41.513′ N, 125°00.797′ E; 12 Mar. 2013; station 87; muddy mangrove with small *Rhizophora* in dense patches; UMIZ 00124 • 1 spec. (27/15 [2240] mm); Sondaken; 01°21.777′ N, 124°32.594′ E; 13 Mar. 2013; station 89; sand, small rocks, pieces of wood outside narrow coastal mangrove of mostly *Rhizophora*; UMIZ 00125 • 1 spec. (30/20 [2345] mm); Makassar, Tallo mangrove; 05°06.117′ S, 119°26.777′ E; 21 Mar. 2013; station 92; small mangrove used as outhouse by village, very impacted with trash; UMIZ 00126 • 1 spec. (20/13 [2355] mm); Barru; 04°25.437′ S, 119°35.953′ E; 22 Mar. 2013; station 93; forest of mostly *Avicennia* and *Rhizophora*, with hard and sandy mud; UMIZ 00127. – **Ambon** • 1 spec. (25/15 [3541] mm); Lateri; 03°38.261′ S, 128°14.716′ E; 12 Feb. 2014; station 128; mudflat next to small creek in low intertidal of mangrove preserve; UMIZ 00128 • 3 spec. (45/30 [2832], 22/12 [2839] and 35/22 [2840] mm); Lateri; 03°38.237′ S, 128°14.783′ E; 14 Feb. 2014; station 131; muddy mangrove with *Rhizophora*; UMIZ 00129. – **Seram** • 2 spec. (20/15 [2874] and 30/15 [2875] mm); Kawa; 02°58.240′ S, 128°07.066′ E; 18 Feb. 2014; station 135; mud next to a seawall adjacent to a mangrove; UMIZ 00130. – **Lombok** • 2 spec. (30/20 [2950] and 20/12 [2952] mm); Tanjung Batu village; 08°45.748′ S, 116°02.892′ E; 24 Mar. 2014; station 145; *Avicennia* forest; UMIZ 00131 • 1 spec. (20/14 [2961] mm); Seriwe Bay; 08°51.960′ S, 116°32.838′ E; 25 Mar. 2014; station 146; *Avicennia* mangrove with hard mud and rocks; UMIZ 00132 • 1 spec. (18/10 [2960] mm); same data as for preceding; UMIZ 00139. – **Bali** • 1 spec. (25/14 [3051] mm); Denpasar; 08°47.435′ S, 115°13.197′ E; 1 Apr. 2014; station 153; large mangrove by road, very soft mud; UMIZ 00133 • 1 spec. (30/20 [3070] mm); Denpasar; 08°46.126′ S, 115°10.803′ E;

2 Apr. 2014; station 154; large mangrove by road, with shallow mud; UMIZ 00134. – **Halmahera** • 1 spec. (25/15 [5082] mm); Akelamo; 01°01.329′ N, 127°39.091′ E; 10 Mar. 2015; station 207; sandy-muddy beach at margin of mangrove near village; UMIZ 00135 • 2 spec. (50/35 [5102] and 55/35 [5103] mm); Buli; 00°55.446′ N, 128°20.612′ E; 16 Mar. 2015; station 212; logged area in front of old *Rhizophora* forest, by the road; UMIZ 00136 • 1 spec. (55/30 [5042] mm); Buli; 00°55.367′ N, 128°20.647′ E; 17 Mar. 2015; station 213; tall and old *Rhizophora* forests, high intertidal; UMIZ 00137.

JAPAN • 1 spec. (22/10 [3761] mm); Ehime Prefecture, Misho Bay; 32°57.634′ N, 132°33.205′ E; 4 Aug. 2014; station o28; mudflats; NSMT Mo 78984.

MALAYSIA • 1 spec. (40/25 [963] mm); Peninsular Malaysia, Nibong Tebal, Pulau Burung; 05°12.488′ N, 100°25.564′ E; 11 Jul. 2011; station 17; soft mud, open mangrove of *Rhizophora*, with a few *Sonneratia*; USMMC 00057 • 1 spec. (18/12 [928] mm); E Peninsular Malaysia, Balok; 03°53.219′ N, 103°21.978′ E; 14 Jul. 2011; station 19; mostly *Rhizophora*, with some *Avicennia*, hard mud with shallow pools, patches of soft mud; USMMC 00058.

PAPUA NEW GUINEA • 1 spec. (18/14 [5432] mm); Madang, Meiro River, near airport; 05°12.2′ S, 145°47.4′ E; 5 Nov. 2012; MNHN expedition Papua Niugini leg.; station PM01; *Nypa* palm swamp; MNHN IM-2013-10478 • 1 spec. (17/12 [5433] mm); same data as for preceding; MNHN IM-2013-10479.

PHILIPPINES – **Luzon** • 1 spec. (26/18 [3610] mm); Lian, Batangas; 13°58.130′ N, 120°37.471′ E; 5 Jul. 2014; station 179; narrow and impacted mangrove of *Avicennia* near village, very sandy, little to no mud; PNM 041261 • 2 spec. (30/20 [3171] and 25/15 [3192] mm); Nasugbu, Batangas; 14°10.714′ N, 120°36.817′ E; 6 Jul. 2014; station 182; near village, well-preserved and dense forest of *Avicennia* and *Rhizophora*; PNM 041255 • 1 spec. (22/14 [3172] mm); same data as for preceding; PNM 041262 • 2 spec. (30/20 [3200] and 35/22 [3205] mm); Calantagan, Batangas; 13°55.319′ N, 120°37.260′ E; 7 Jul. 2014; station 183; rocks next to *Avicennia* and *Rhizophora* forest; PNM 041256 • 1 spec. (30/18 [3202] mm); same data as for preceding; PNM 041263 • 1 spec. (35/22 [3222] mm); Calantagan, Batangas; 13°53.278′ N, 120°37.124′ E; 8 Jul. 2014; station 184; narrow forest on the shore, *Avicennia* and young *Rhizophora*; PNM 041257 • 1 spec. (33/15 [3229] mm); same data as for preceding; PNM 041264 • 1 spec. (27/18 [3237] mm); Calantagan, Batangas; 13°51.264′ N, 120°37.383′ E; 8 Jul. 2014; station 185; next to village, impacted, narrow *Avicennia* mangrove by the shore; PNM 041265. – **Bohol** • 1 spec. (40/25 [3344] mm); Mabini; 09°51.532′ N, 124°31.685′ E; 17 Jul. 2014; station 194; narrow mangrove on edge of fish ponds, tall *Rhizophora* and *Avicennia* trees, many old logs; PNM 041258 • 1 spec. (26/15 [3371] mm); Mabini; 09°51.586′ N, 124°34.155′ E; 18 Jul. 2014; station 196; *Avicennia* and *Sonneratia* open forest with sand, algae and coral rubble; PNM 041259 • 1 spec. (30/18 [3416] mm); Maribojoc; 09°44.280′ N, 123°49.389′ E; 20 Jul. 2014; station 202; uplifted coral rubble with sand and algae, near *Sonneratia* trees; PNM 041260.

VIETNAM • 2 spec. (45/30 [5619] and 40/30 [5682] mm); Nha Trang; 12°12.778′ N, 109°09.572′ E; 27 Jul. 2015; station 237; small strip of mud with a few *Rhizophora* trees next to a small river, by fish ponds and houses; ITBZC IM 00019 • 1 spec. (25/15 [5642] mm); Nha Trang; 12°24.168′ N, 109°10.058′ E; 29 Jul. 2015; station 239; mostly *Avicennia* and some small *Rhizophora*, with shallow mud; ITBZC IM 00020.

Color and morphology of live animals (Figs 7–10)

Live animals of units #1 and #2 are often abundantly covered with mud, in which case their dorsal color can hardly be seen. The background of the dorsal notum is brown, light to dark. That background can be homogenous or clearly mottled with darker or lighter areas and, occasionally, also with red areas.

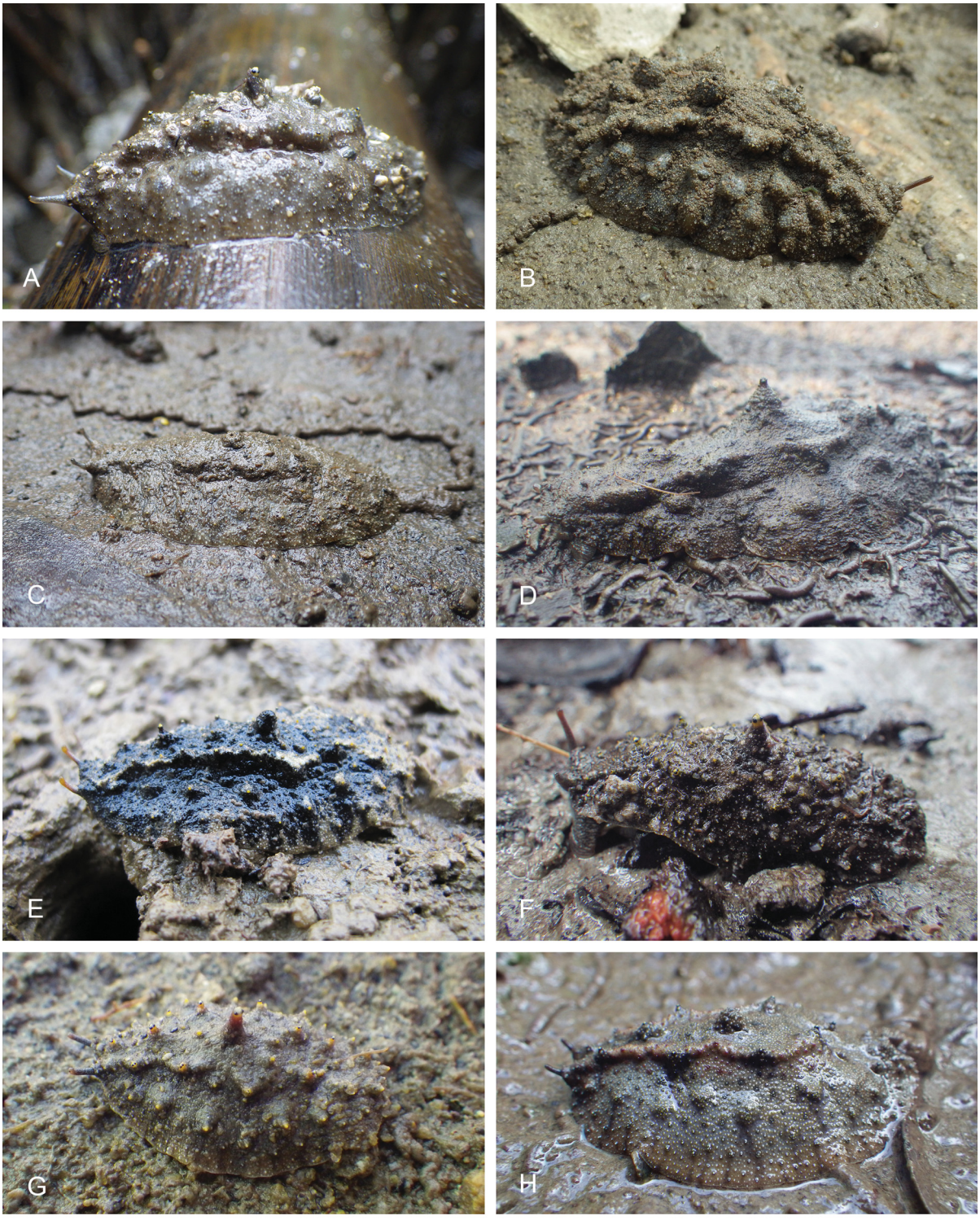

Fig. 7. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, live animals. **A**. Dorsal view, 35 mm long [3205], Philippines, Luzon (PNM 041256). **B**. Dorsal view, 40 mm long [5682], Vietnam (ITBZC IM 00019). **C**. Dorsal view, 33 mm long [3222], Philippines, Luzon (PNM 041257). **D**. Dorsal view, 54 mm long [5042], Indonesia, Halmahera (UMIZ 00137). **E**. Dorsal view, 30 mm long [1705], Australia, Northern Territory (NTM P.57622). **F**. Dorsal view, 26 mm long [2875], Indonesia, Seram (UMIZ 00130). **G**. Dorsal view, 17 mm long [2627], Australia, Queensland (MTQ). **H**. Dorsal view, 27 mm long [1755], Indonesia, Sumatra (UMIZ 00122).

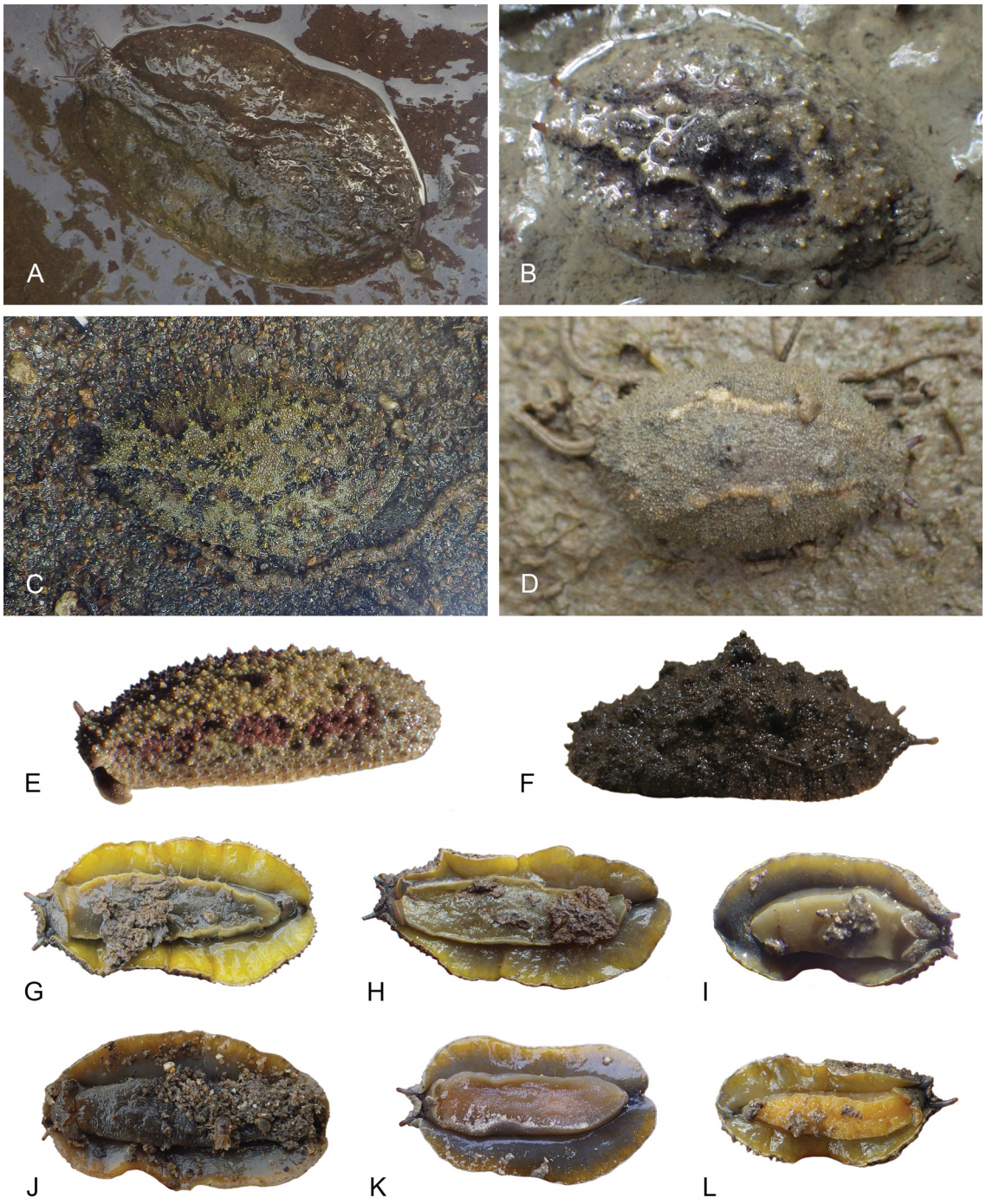

Fig. 8. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, live animals. **A**. Dorsal view, 55 mm long [5103], Indonesia, Halmahera (UMIZ 00136). **B**. Dorsal view, 22 mm long [1732], Indonesia, Sumatra (UMIZ 00121). **C**. Dorsal view, 22 mm long [5082], Indonesia, Halmahera (UMIZ 00135). **D**. Dorsal view, 22 mm long [5642], Vietnam (ITBZC IM 00020). **E**. Dorsal view, 45 mm long [2657], Australia, Queensland (MTQ). **F**. Dorsal view, 31 mm long [1522], Australia, New South Wales (AM C.468918.005). **G**. Ventral view, 42 mm long [1686], Australia, Northern Territory (NTM P.57621). **H**. Ventral view, 47 mm long [2562], Australia, Queensland (MTQ). **I**. Ventral view, 19 mm long [2961], Indonesia, Lombok (UMIZ 00132). **J**. Ventral view, 44 mm long [5619], Vietnam (ITBZC IM 00019). **K**. Ventral view, 33 mm long [3416], Philippines, Bohol (PNM 041260). **L**. Ventral view, 24 mm long [3371], Philippines, Bohol (PNM 041259).

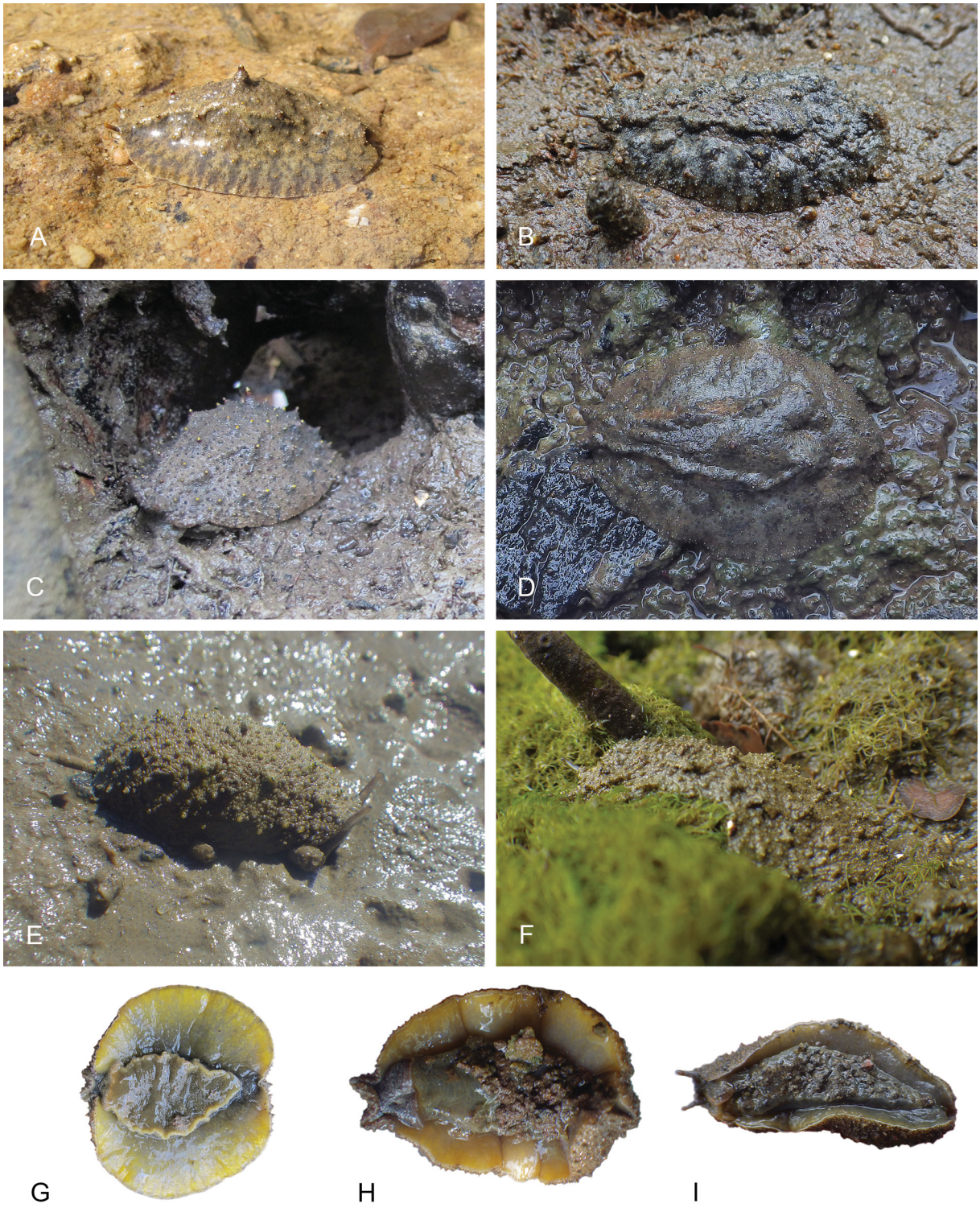

Fig. 9. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #2, live animals. **A**. Dorsal view, 38 mm long [1651], Australia, Northern Territory (NTM P.57624). **B**. Dorsal view, 32 mm long [3237], Philippines, Luzon (PNM 041265). **C**. Dorsal view, 45 mm long [1638], Australia, Northern Territory (NTM P.57623). **D**. Dorsal view, 43 mm long [1794], Indonesia, Sumatra (UMIZ 00138). **E**. Dorsal view, 17 mm long [2960], Indonesia, Lombok (UMIZ 00139). **F**. Dorsal view, 27 mm long [3610], Philippines, Luzon (PNM 041261). **G**. Ventral view, same as C. **H**. Ventral view, same as D. **I**. Ventral view, 32 mm long [3229], Philippines, Luzon (PNM 041264).

In addition, in some animals the tip of the dorsal papillae (with and without dorsal eyes) can be bright yellow. The foot varies from gray (light or dark) to yellow or orange. The hyponotum is almost always yellow, from pale yellow to bright yellow and even orange. This variable yellow component can cover the entire hyponotum or just an outer ring (the inner ring being light to dark gray). The color of the foot and of the hyponotum of an individual can change rapidly, especially when disturbed. The ocular tentacles are brown (variable from light to dark) and may or may not be speckled with tiny white dots, exactly like the head. The ocular tentacles are short (just a few millimeters long).

No live pictures were available for unit #3, so the following description is based on preserved specimens (Fig. 10). It is possible that bright colors (yellow, orange) were lost during preservation on both the ventral and dorsal sides. The background of the dorsal notum is brown, mottled with darker or lighter areas. The foot is light gray. The hyponotum is gray-brown, with a reddish hue on the margin (which could possibly be orange in live animals). The color of the ocular tentacles (retracted, likely short) cannot be determined.

Generally speaking, the dorsal notum of any given live animal can rapidly change from almost perfectly smooth to covered by many papillae. However, when animals are not disturbed, the dorsum is usually covered by papillae of various sizes. In some animals, larger papillae may be arranged in two longitudinal and lateral ridges (on either side of the median line), but those ridges can appear and disappear rapidly. Some papillae bear from two to four black dorsal eyes at their tip (most papillae bear three eyes). The number of papillae with dorsal eyes is variable (between 10 and 15, on average) and they mostly are on the central part of the notum. Their tip is usually yellow, but not always. A central, much larger papilla, which bears four dorsal eyes (sometimes three), is entirely retractable within the notum. In addition to all these large papillae, the notum is covered by smaller, rounded papillae, which can make it look granular.

External morphology (Fig. 11A–B)

Preserved specimens no longer display the color of live animals. The body is not flattened (although, exceptionally, animals on mud with a thin layer of water can look flattened). The notum is oval. Dorsal gills are absent. The large, central, retractable papilla at the center of the notum can only be seen in live animals. In preserved specimens, it is retracted inside the notum. The hyponotum is horizontal. The width of the hyponotum relative to the total width of the ventral surface (pedal sole and hyponotum) varies among individuals, from approximately one third to half. In the anterior region, the left and right ocular tentacles are superior to the mouth. Eyes are located at the tip of the two ocular tentacles. Inferior to the ocular tentacles, superior to the mouth, the head bears a pair of oral lobes. The latter are smooth, with no transversal protuberance. The male opening (of the copulatory complex) is below and to the left of the right ocular tentacle (i.e., between the two ocular tentacles). The anus is posterior, median, close to the edge of the pedal sole. On the right side (to the left in ventral view), a peripodial groove

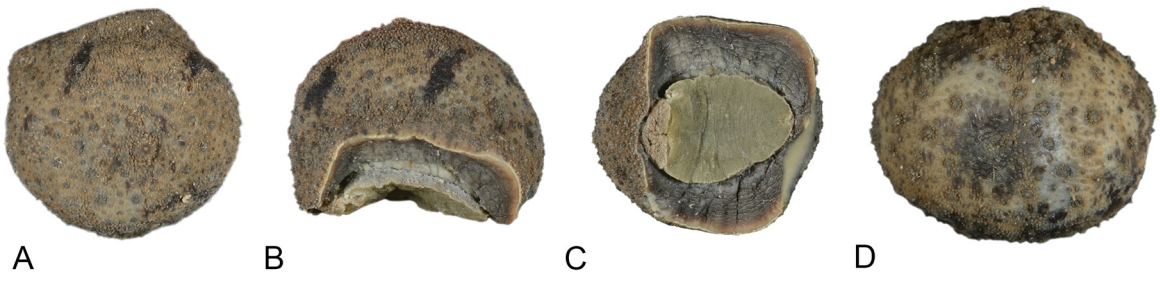

Fig. 10. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #3, preserved specimens, Papua New Guinea, Madang. **A**. Dorsal view, 13 mm long [5432] (MNHN IM-2013-10478). **B**. Lateral view, same as A. **C**. Ventral view, same as A. **D**. Dorsal view, 14 mm long [5433] (MNHN IM-2013-10479).

is present at the junction between the foot and the hyponotum, running longitudinally from the buccal area to the posterior end, a few millimeters from the anus and the pneumostome. The pneumostome is median. Its position on the hyponotum relative to the notum margin and the edge of the pedal sole varies among individuals but averages in the middle. The position of the female pore (at the posterior end of the peripodial groove) does not vary much among individuals.

Visceral cavity and pallial complex

The anterior pedal gland is oval and flattened, lying free on the floor of the visceral cavity below the buccal mass. The heart, enclosed in the pericardium, is on the right side of the visceral cavity, slightly posterior to the middle. From the anterior ventricle an anterior vessel exits that supports several anterior organs such as the buccal mass, the nervous system and the copulatory complex. The auricle is posterior. The kidney is more or less symmetrical, the right and left parts being equally developed. The kidney is intricately attached to the respiratory complex. The lung is in two more or less symmetrical parts, left and right.

Digestive system (Figs 12–15)

There are no jaws. The left and right salivary glands, heavily branched, join the buccal mass dorsally, on either side of the esophagus. The radula is in between two large postero-lateral muscular masses. Radulae measure up to 5.2 mm in length (unit #1), 4.1 mm (unit #2) and 2.8 mm (unit #3). Each radular row contains a rachidian tooth and two half rows of lateral teeth of similar size and shape. Examples of radular formulae are presented in Table 4. The rachidian teeth are unicuspid: the median cusp is always present; there are no conspicuous cusps on the lateral sides of the base of the rachidian tooth. The length of the rachidian teeth (approximately 25 µm) tend to be approximately half the size of the lateral teeth (approximately 50 µm). The lateral aspect of the base of the rachidian teeth is straight, occasionally slightly convex. The half rows of lateral teeth form an angle of 45° with the rachidian axis. With the

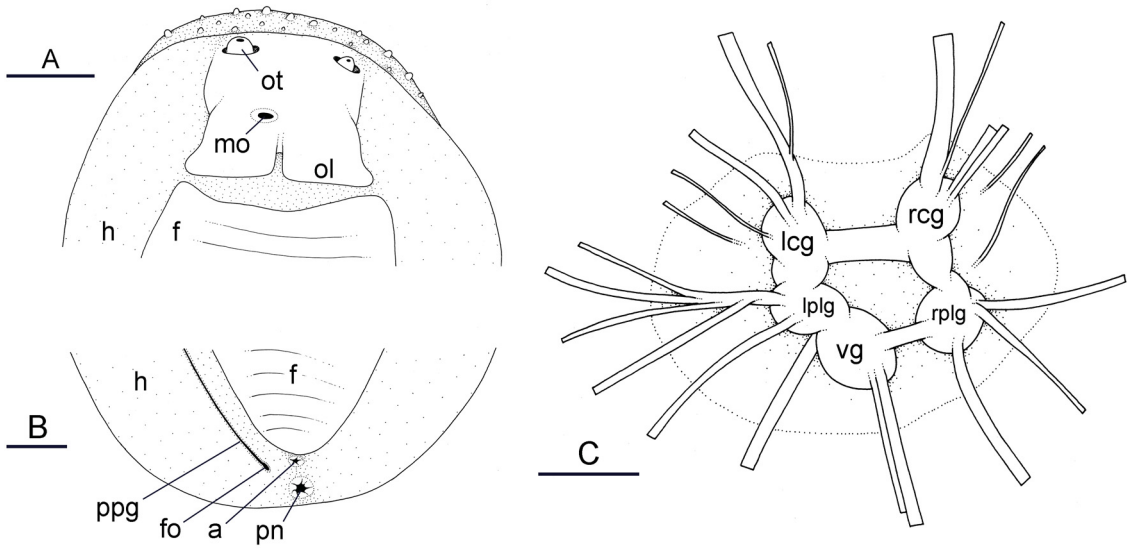

Fig. 11. *Paromoionchis tumidus* (Semper, 1880) comb. nov., external morphology and nervous system. **A**. Anterior, ventral view, lectotype of *Onchidium mertoni* Simroth, 1918 (ZMB 121591a). **B**. Unit #1, posterior, ventral view, Indonesia, Sulawesi [2240] (UMIZ 00125). **C**. Nervous system, dorsal view, same as B. Abbreviations: a = anus; f = foot; fo = female opening; h = hyponotum; lcg = left cerebral ganglion; lplg = left pleural ganglion; mo = male opening; ol = oral lobe; ot = ocular tentacle; pn = pneumostome; ppg = peripodial groove; rcg = right cerebral ganglion; rplg = right pleural ganglion; vg = visceral ganglion. Scales: A–B = 2 mm; C = 0.5 mm.

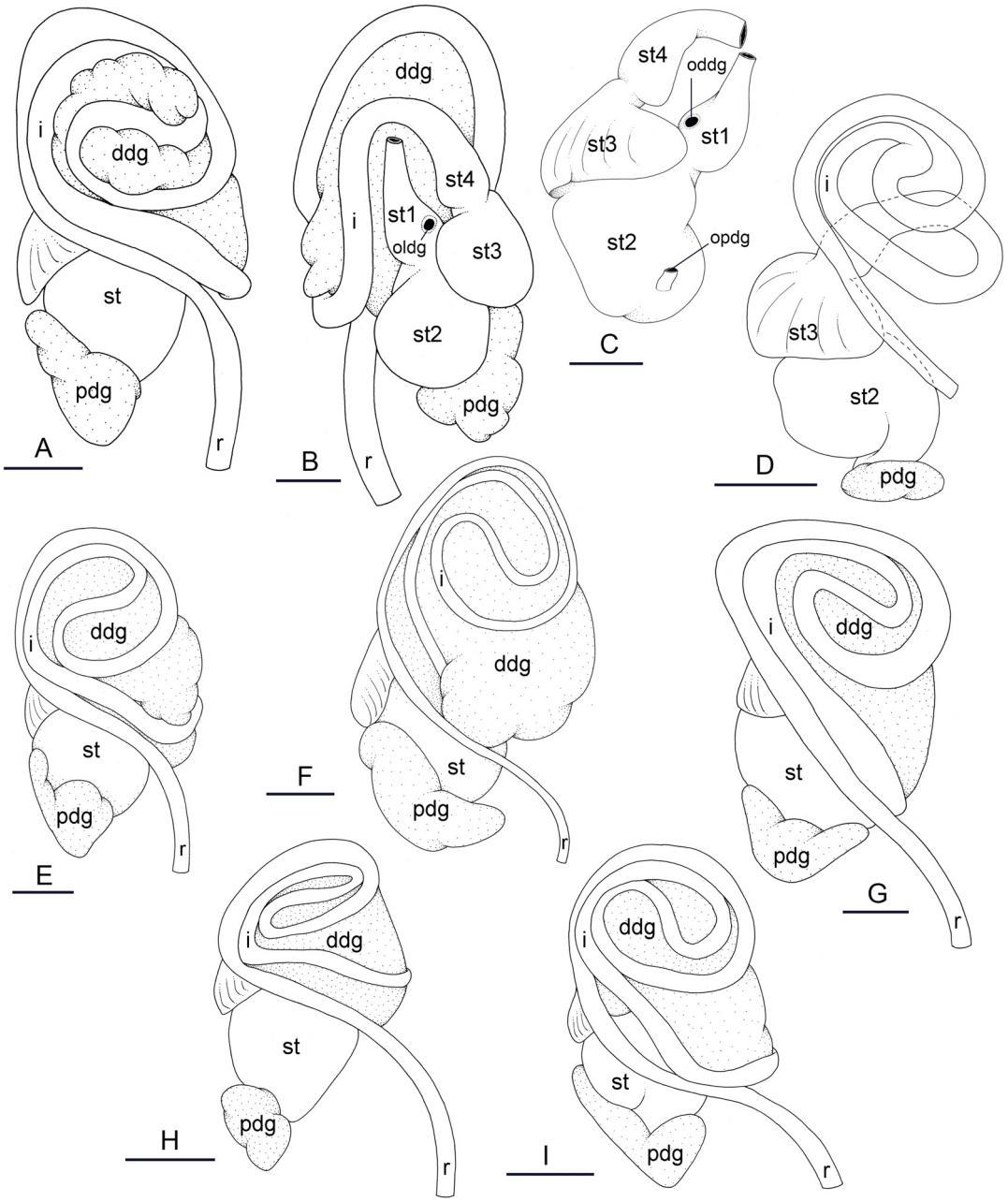

Fig. 12. *Paromoionchis tumidus* (Semper, 1880) comb. nov., digestive system. **A**. Unit #1, dorsal view, Indonesia, Sulawesi [2240] (UMIZ 00125). **B**. Ventral view (lateral digestive gland removed), same as A. **C**. Stomach, dorsal view, same as A. **D**. Dorsal view (digestive gland removed prior to present study, intestinal loops loose), holotype of *Onchidium honkongense* Britton, 1984 (NHM 1982290). **E**. Unit #2, dorsal view, Australia, Northern Territory [1638] (NTM P.57623). **F**. Unit #3, dorsal view, Papua New Guinea, Madang [5433] (MNHN IM-2013-10479). **G**. Dorsal view, lectotype of *Onchidium mertoni* Simroth, 1918 (ZMB 121591a). **H**. Dorsal view, lectotype of *Onchidium tumidum* (ZMB 39019a). **I**. Dorsal view, lectotype of *Onchidium samarense* Semper, 1880 (ZMB 39025a). Abbreviations: ddg = dorsal lobe of digestive gland; i = intestine; oddg = opening of dorsal lobe of digestive gland; oldg = opening of lateral lobe of digestive gland; opdg = opening of posterior lobe of digestive gland; pdg = posterior lobe of digestive gland; r = rectum; st = stomach; st1 = stomach chamber 1; st2 = stomach chamber 2; st3 = stomach chamber 3; st4 = stomach chamber 4. Scales: A–C, F = 2 mm; D, I = 3 mm; E = 5 mm; G = 1 mm; H = 4 mm.

Table 4. Radular formulae for the five species of *Paromoionchis* gen. nov. following the same format: number of rows × (number of lateral teeth per left half row - 1 rachidian tooth - number of lateral teeth per right half row). Each DNA extraction number corresponds to one particular individual. DNA extraction numbers are used on Figs 1–4 (the phylogenetic trees), Table 1 and in the material examined section for each species.

Species	Radular formula	Spm length (mm)	Voucher	DNA extraction number
P. tumidus unit #1	70 × 80-1-80	55	MTQ	2637
–	65 × 60-1-60	50	UMIZ 00136	5102
–	60 × 75-1-75	40	PNM 041258	3344
–	55 × 80-1-80	45	NTM P.57620	1634
–	55 × 80-1-80	20	UMIZ 00123	1798
–	55 × 65-1-65	45	UMIZ 00129	2832
–	55 × 65-1-65	35	PNM 041256	3205
–	50 × 60-1-60	30	UMIZ 00131	2950
–	50 × 60-1-60	25	UMIZ 00133	3051
P. tumidus unit #2	65 × 105-1-105	42	NTM P.57623	1638
–	60 × 85-1-85	27	PNM 041265	3237
–	45 × 65-1-65	22	PNM 041262	3172
P. tumidus unit #3	60 × 65-1-65	18	MNHN IM-2013-10478	5432
–	50 × 60-1-60	17	MNHN IM-2013-10479	5433
P. daemelii	75 × 105-1-105	60	AM C.468917.001	1519
–	70 × 90-1-90	50	AM C.468919.001	1521
–	55 × 60-1-60	17	AM C.468911.001	1510
P. boholensis unit #1	70 × 80-1-80	28	PNM 041266	3288 Holotype
–	65 × 85-1-85	35	PNM 041269	3372
–	60 × 70-1-70	16	PNM 041268	3283
P. boholensis unit #2	65 × 90-1-90	35	UMIZ 00140	3117
–	60 × 85-1-85	18	UMIZ 00149	2911
–	60 × 80-1-80	45	UMIZ 00146	2851
P. penangensis	60 × 70-1-70	48	USMMC 00062	6020
–	55 × 60-1-60	30	USMMC 00060	5991
–	50 × 60-1-60	26	USMMC 00059	6037 Holotype
P. goslineri unit #1	65 × 65-1-65	22	PNM 041272	3221
–	60 × 70-1-70	25	PNM 041271	3233 Holotype
–	55 × 75-1-75	28	PNM 041273	3232
–	60 × 70-1-70	20	PNM 041272	6049
P. goslineri unit #2	55 70-1-70	22	UMIZ 00155	3078
–	55 × 60-1-60	35	UMIZ 00159	5145
–	50 × 65-1-65	18	UMIZ 00153	2241

exception of the few innermost and few outermost lateral teeth, the size and shape of the lateral teeth do not vary along the half row, nor do they vary among half rows. The lateral teeth seem to be unicuspid with a flattened and curved hook (approximately 50 μm long) with a rounded tip, but there is also a pointed spine on the outer lateral expansion of the base (basal lateral spine). In most cases, the basal lateral spine cannot be observed because it is hidden below the hook of the next, outer lateral tooth. It can only be observed when the teeth are not too close (such as in the innermost and outermost regions)

or when teeth are placed in an unusual position. The inner and outer lateral aspects of the hook of the lateral teeth are straight (i.e., not wavy and not with any protuberance).

The esophagus is narrow and straight, with thin internal folds. The esophagus enters the stomach anteriorly. Only a portion of the posterior aspect of the stomach can be seen in dorsal view because it is partly covered by the lobes of the digestive gland. The dorsal lobe is mainly on the right. The left, lateral lobe is mainly ventral. The posterior lobe covers the posterior aspect of the stomach. The stomach is a U-shaped sac divided into four chambers. The first chamber, which receives the esophagus, is delimited by thin tissue and receives the ducts of the dorsal and lateral lobes of the digestive gland. The second, posterior chamber, delimited by thick muscular tissue, receives the duct of the posterior lobe of the digestive gland. The third, funnel-shaped chamber is delimited by thin tissue with high ridges internally. The fourth chamber is continuous and externally similar to the third, but it bears only low, thin ridges internally. The intestine is long and narrow and the intestinal loops are of type II. There is no rectal gland.

Nervous system (Fig. 11C)

The circum-esophageal nerve ring is post-pharyngeal and pre-esophageal. The paired cerebral ganglia are close and the cerebral commissure is short (but its length does vary among individuals). Paired pleural and pedal ganglia are also all distinct. The visceral commissure is short but distinctly present and

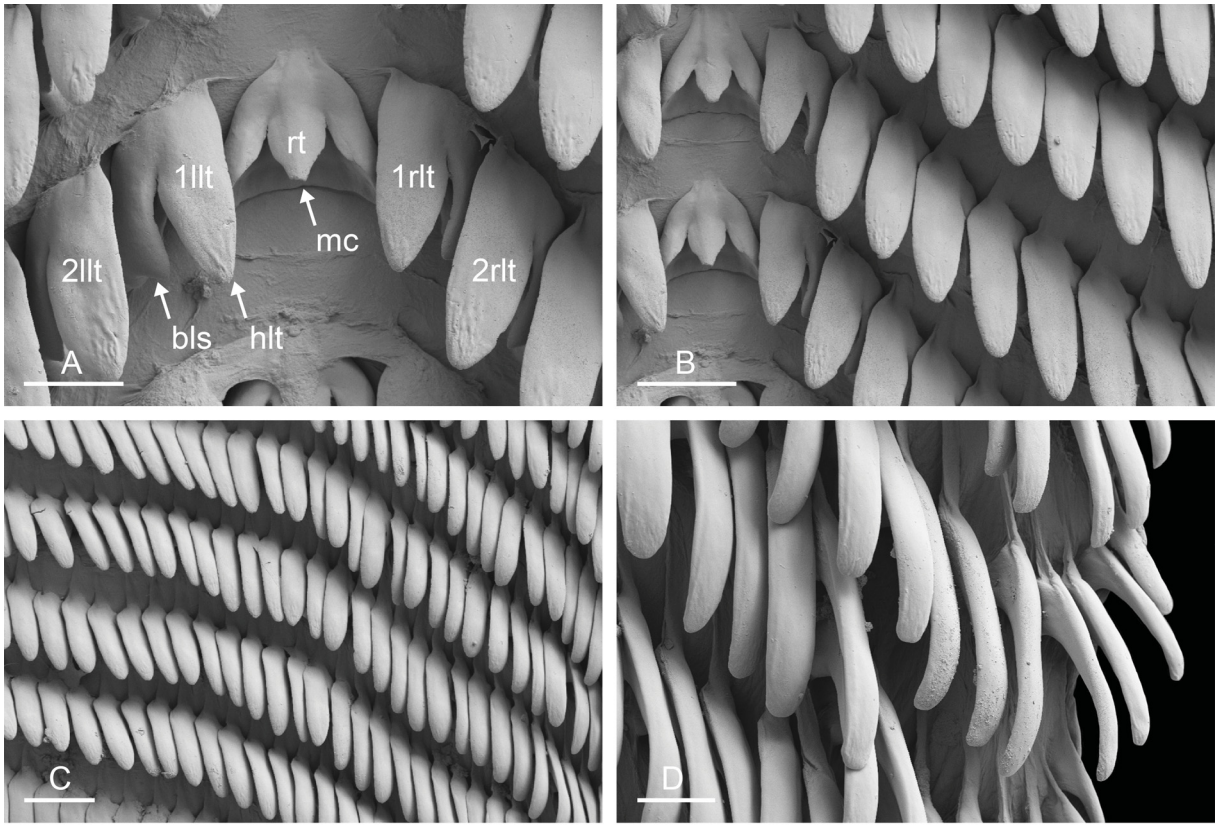

Fig. 13. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, radula, Indonesia, Bali [3051] (UMIZ 00133). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Abbreviations: 1llt = first left lateral tooth; 1rlt = first right lateral tooth; 2llt = second left lateral tooth; 2rlt = second right lateral tooth; bls = basal lateral spine; hlt = hook of lateral tooth; mc = median cusp; rt = rachidian tooth. Scales: A = 20 µm; B = 30 µm; C = 50 µm; D = 10 µm.

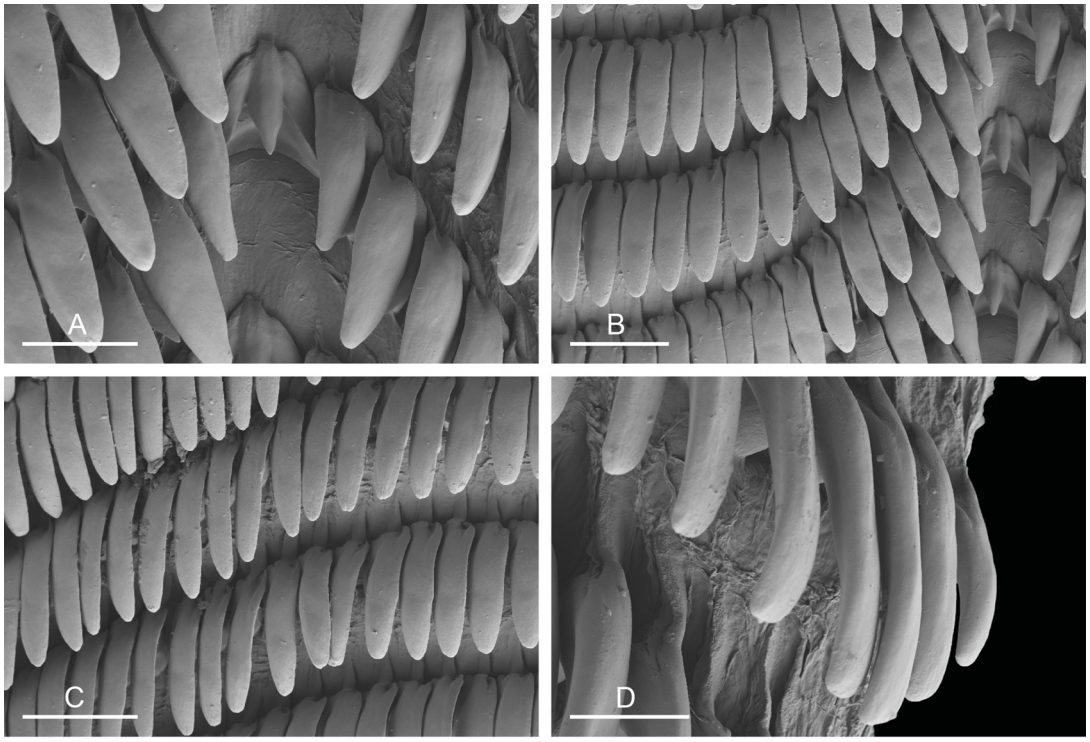

Fig. 14. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #2*,* radula, Australia, Northern Territory [1638] (NTM P.57623). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A = 30 μm; B–C = 50 μm; D = 20 μm.

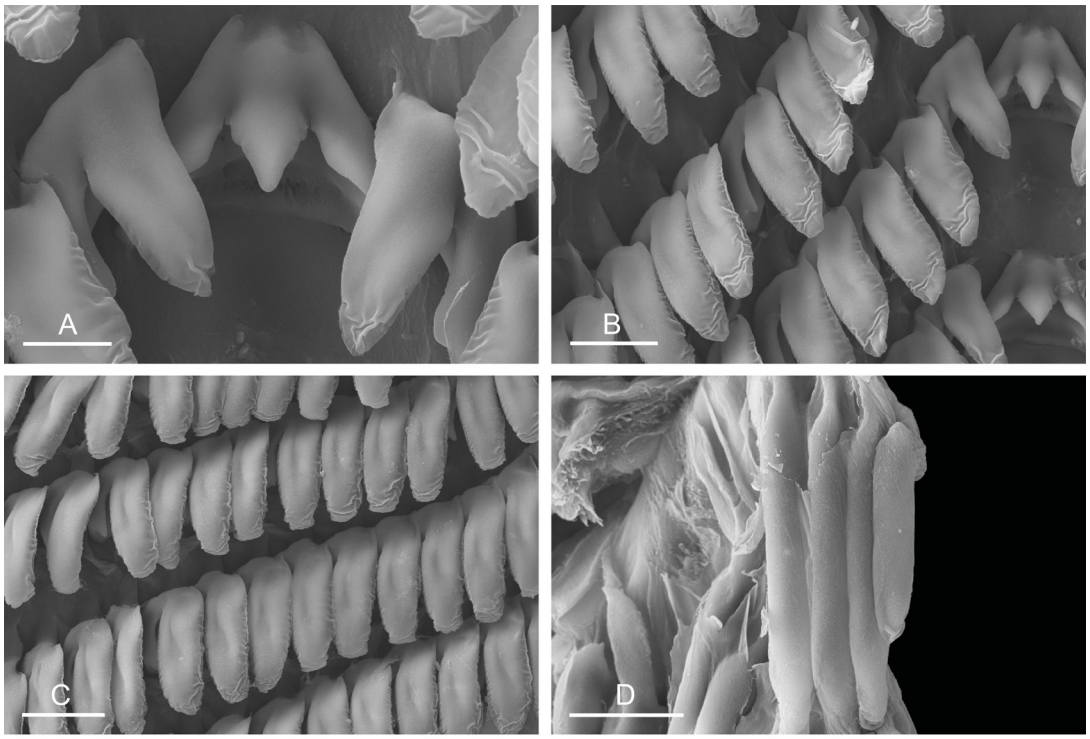

Fig. 15. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #3*,* radula, Papua New Guinea, Madang. **A**. Rachidian and innermost lateral teeth, [5432] (MNHN IM-2013-10478). **B**. Lateral teeth with rachidian teeth, same as A. **C**. Lateral teeth, same as A. **D**. Outermost lateral teeth, [5433] (MNHN IM-2013-10479). Scales: A = 10 μm; B, D = 20 μm; C = 25 μm.

the visceral ganglion is more or less median. Cerebro-pleural and pleuro-pedal connectives are short and pleural and cerebral ganglia touch each other on either side. Nerves from the cerebral ganglia innervate the buccal area and the ocular tentacles and, on the right side, the penial complex. Nerves from the pedal ganglia innervate the foot. Nerves from the pleural ganglia innervate the lateral and dorsal regions of the mantle. Nerves from the visceral ganglia innervate the visceral organs.

Reproductive system (Figs 16–23)

Sexual maturity is correlated with animal length. Mature individuals have large female organs (with a large female gland mass) and fully-developed male copulatory parts. Immature individuals (< 15 mm long) may have inconspicuous (or no) female organs and rudimentary anterior male parts.

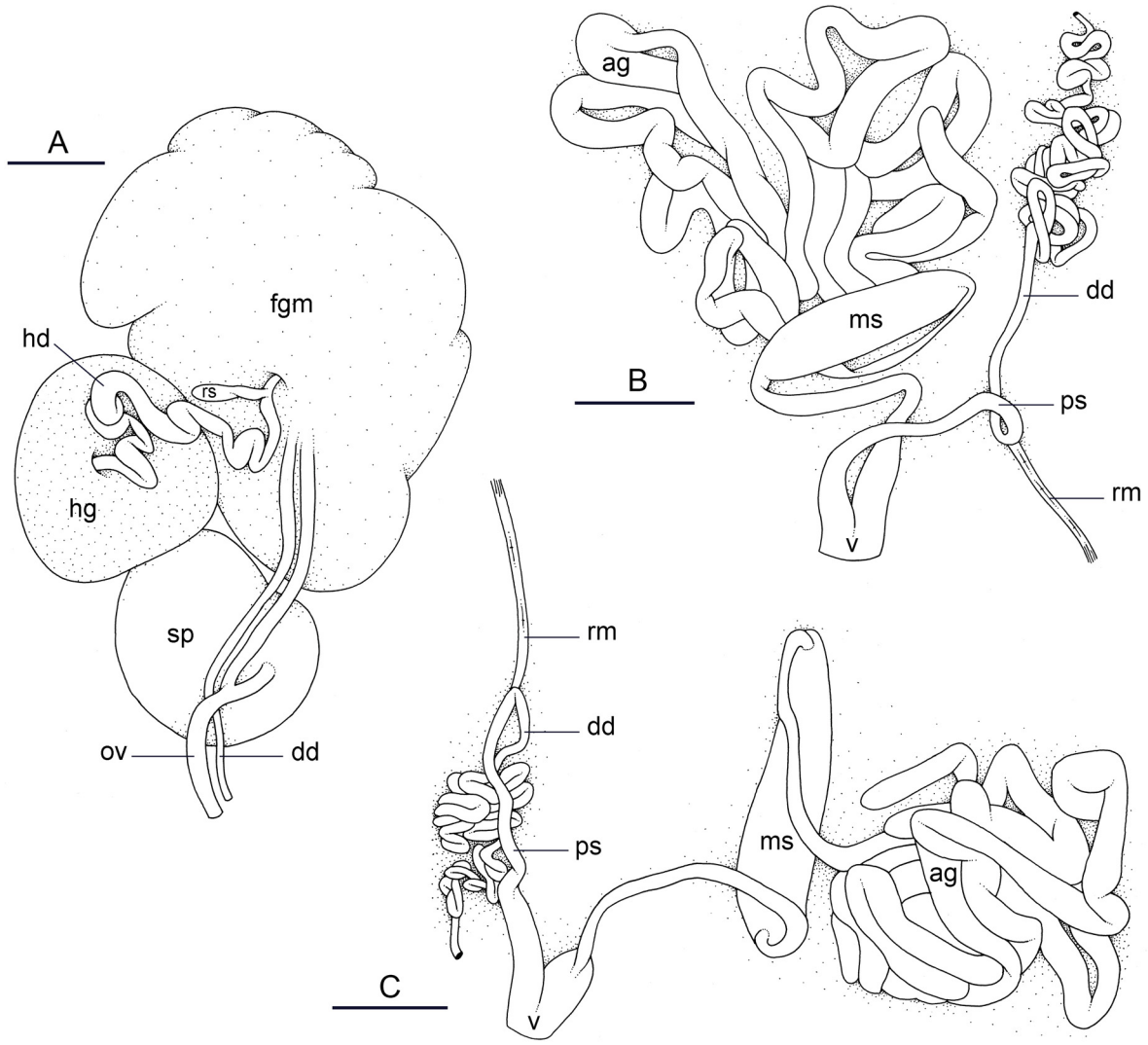

Fig. 16. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, reproductive system. **A**. Posterior hermaphroditic (female) reproductive system, Australia, Northern Territory [1634] (NTM P.57620). **B**. Male copulatory organs, Philippines, Bohol [3344] (PNM 041258). **C**. Male copulatory organs, lectotype of *Onchidium tumidum* (ZMB 39019a). Abbreviations: ag = accessory penial gland; dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ms = muscular sac (of accessory penial gland); ov = oviduct; ps = penial sheath; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; v = vestibule. Scales = 3 mm.

The female organs are located at the posterior end of the visceral cavity, mixed with some male parts (Figs 16A, 17A–B). The hermaphroditic gland is a single mass, joining the spermoviduct through the hermaphroditic duct (which conveys the eggs and the autosperm). There is a narrow and bent

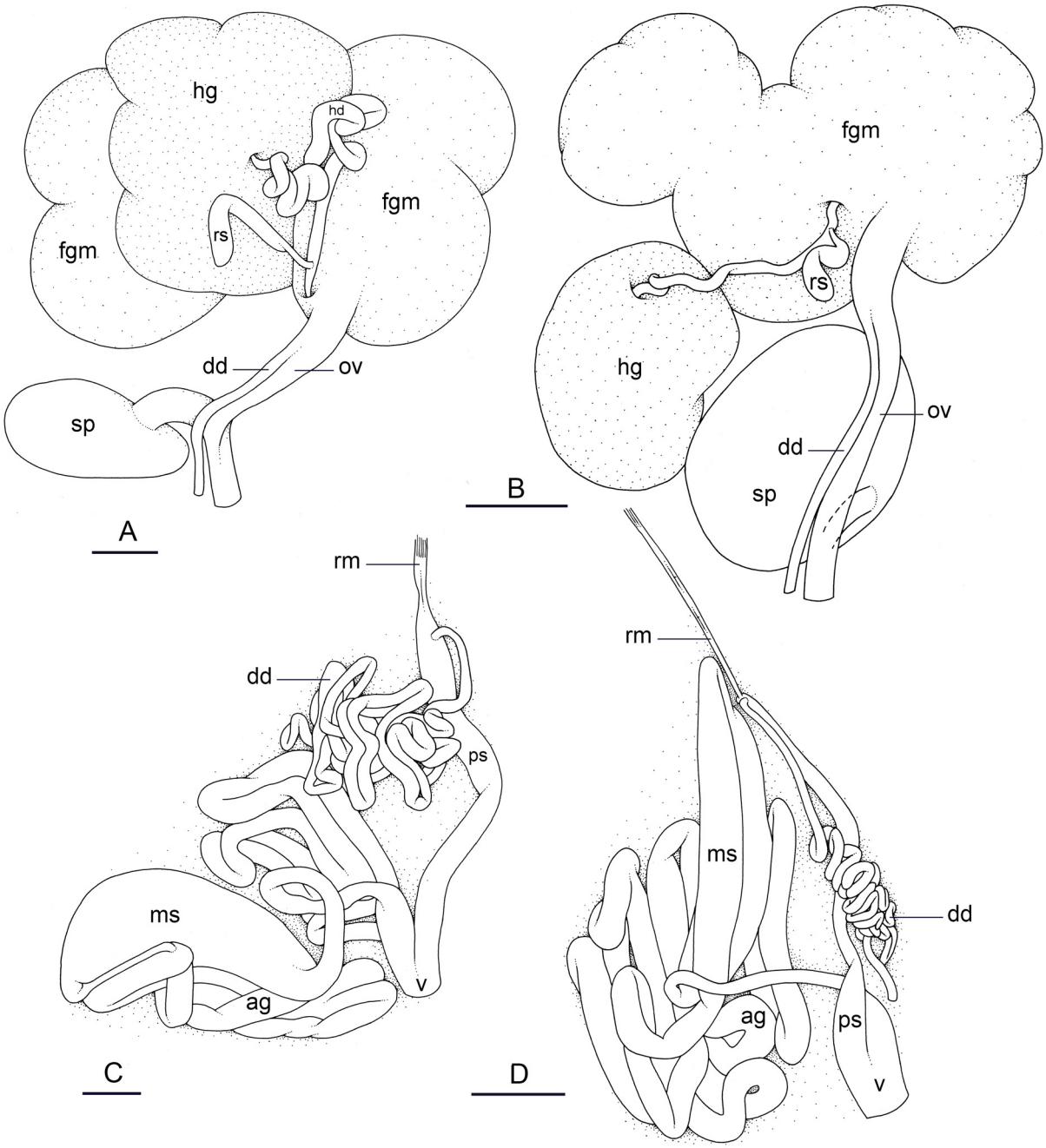

Fig. 17. *Paromoionchis tumidus* (Semper, 1880) comb. nov., reproductive system. **A**. Unit #3, posterior hermaphroditic (female) reproductive system, Papua New Guinea, Madang [5433] (MNHN IM-2013-10479). **B**. Unit #2, posterior hermaphroditic (female) reproductive system, Australia, Northern Territory [1638] (NTM P.57623). **C**. Male copulatory organs, same as A. **D**. Male copulatory organs, same as B. Abbreviations: ag = accessory penial gland; dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ms = muscular sac (of accessory penial gland); ov = oviduct; ps = penial sheath; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; v = vestibule. Scales: A, C = 1 mm; B, D = 3 mm.

receptaculum seminalis (caecum) along the hermaphroditic duct. The female gland mass contains various glands (mucus and albumen) which can hardly be separated by dissection and of which the exact connections remain uncertain. The hermaphroditic duct becomes the spermoviduct (which conveys eggs, exosperm and autosperm). Proximally, the spermoviduct is not divided (at least externally) and is embedded within the female gland mass. Distally, the spermoviduct branches into the deferent duct (which conveys the autosperm up to the anterior region, running through the body wall) and the oviduct.

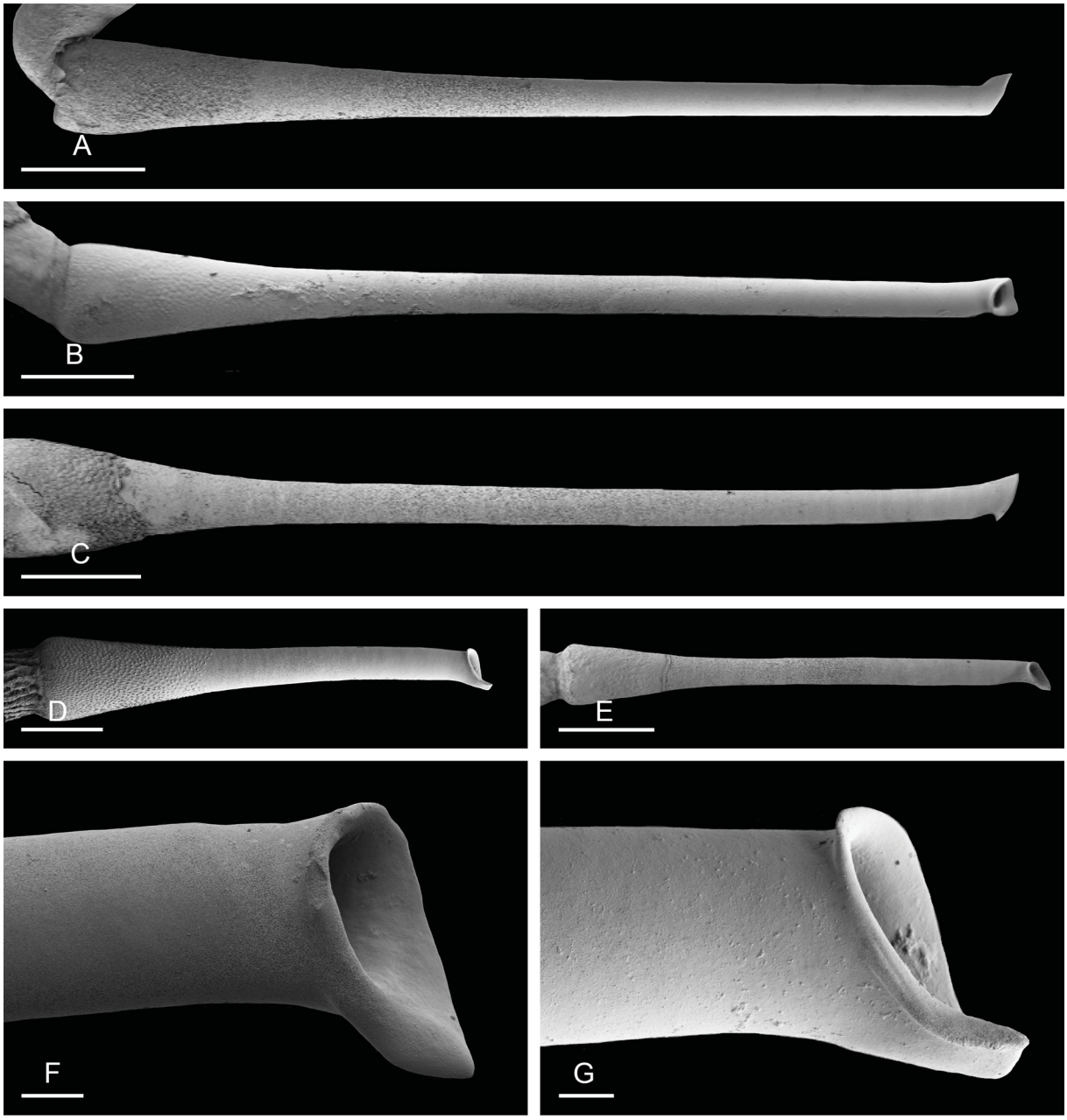

Fig. 18. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, spine of accessory penial gland. **A**. Indonesia, Lombok [2950] (UMIZ 00131). **B**. Philippines, Bohol [3344] (PNM 041258). **C**. Indonesia, Ambon [2832] (UMIZ 00129). **D**. Australia, Northern Territory [1634] (NTM P.57620). **E**. Australia, Queensland [2637] (MTQ). **F**. Distal tip of spine, Indonesia, Halmahera [5102] (UMIZ 00136). **G**. Distal tip of spine, same as D. Scales: A–D = 200 μm; E = 400 μm; F–G = 20 μm.

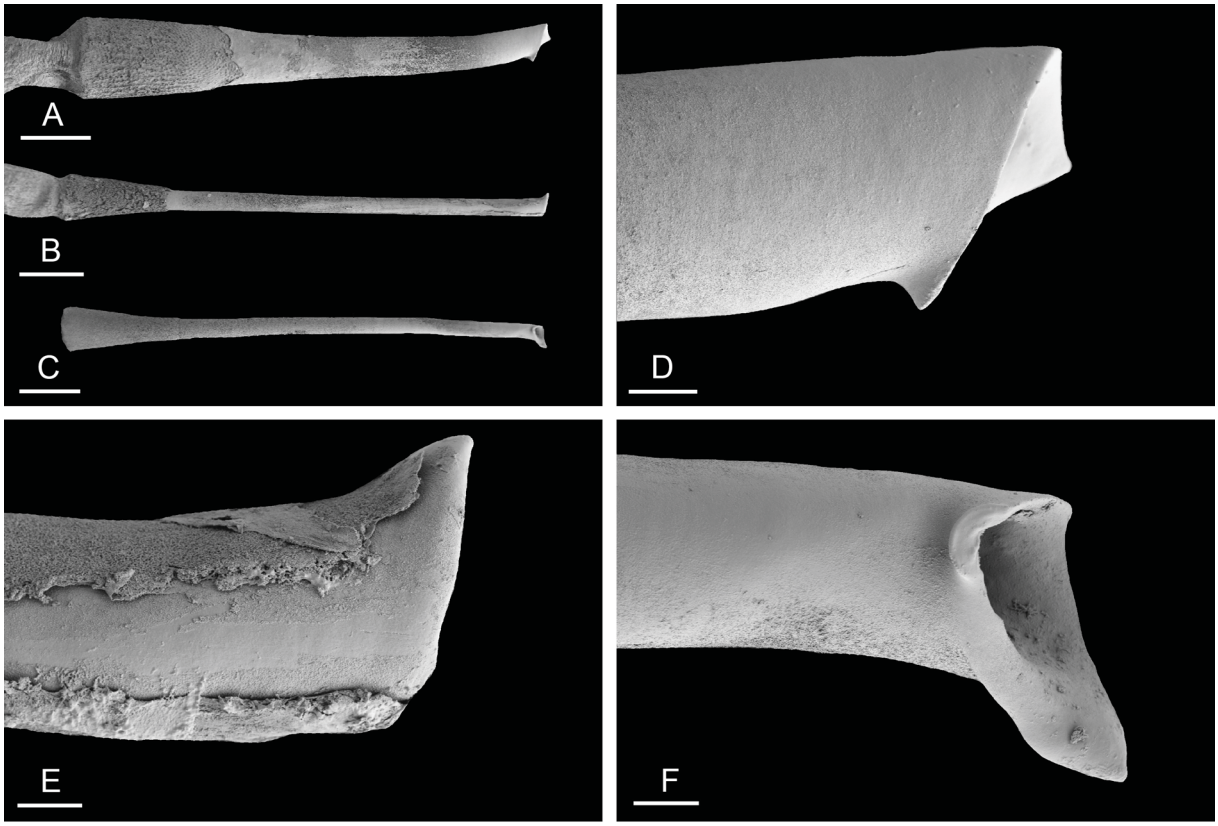

Fig. 19. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #2, spine of accessory penial gland. **A**. Australia, Northern Territory [1638] (NTM P.57623). **B**. Philippines, Luzon [3237] (PNM 041265). **C**. Philippines, Luzon [3172] (PNM 041262). **D**. Distal tip of spine, same as A. **E**. Distal tip of spine, same as B. **F**. Distal tip of spine, same as C. Scales: A = 150 μm; B–C = 200 μm; D–F = 20 μm.

The free oviduct conveys the eggs up to the female opening and the exosperm from the female opening up to the fertilization chamber. The large, ovate-spherical spermatheca connects to the oviduct through a narrow and short duct. The oviduct is narrow and straight. There is no vaginal gland.

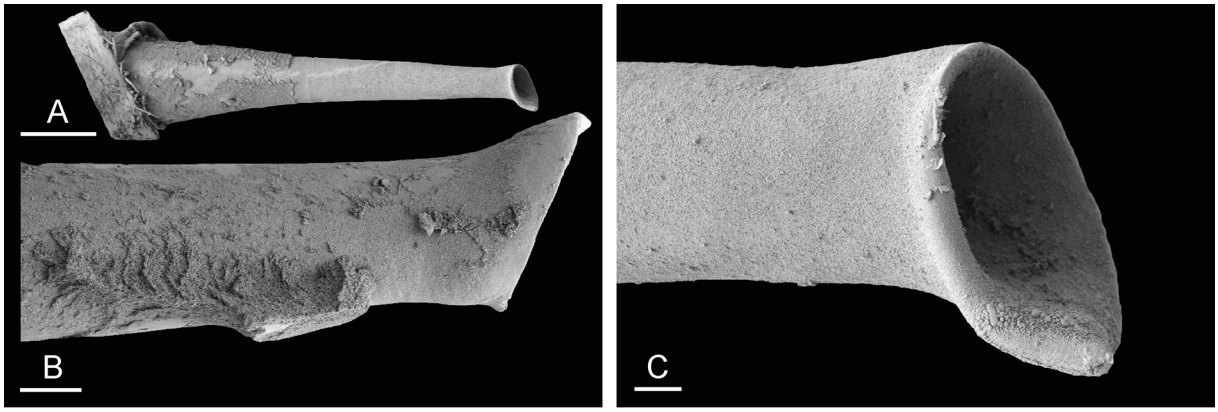

Fig. 20. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #3, spine of accessory penial gland, Papua New Guinea, Madang. **A**. [5432] (MNHN IM-2013-10478). **B**. [5433] (MNHN IM-2013-10479). **C**. Distal tip of spine, same as A. Scales: A = 100 μm; B = 20 μm; C = 10 μm.

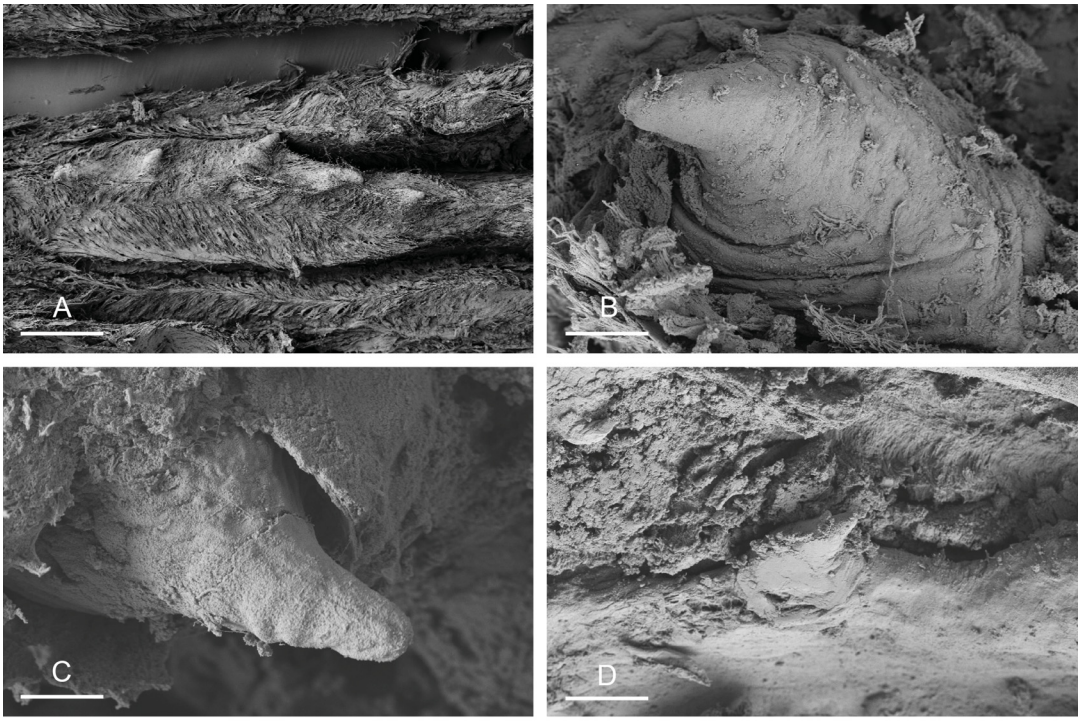

Fig. 21. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, penial hooks. **A**. Indonesia, Sulawesi [2240] (UMIZ 00125). **B**. Indonesia, Ambon [2832] (UMIZ 00129). **C**. Lectotype of *Onchidium mertoni* Simroth, 1918 (ZMB 121591a). **D**. Lectotype of *Onchidium tumidum* (ZMB 39019a). Scales: A = 60 μm; B = 10 μm; C = 4 μm; D = 25 μm.

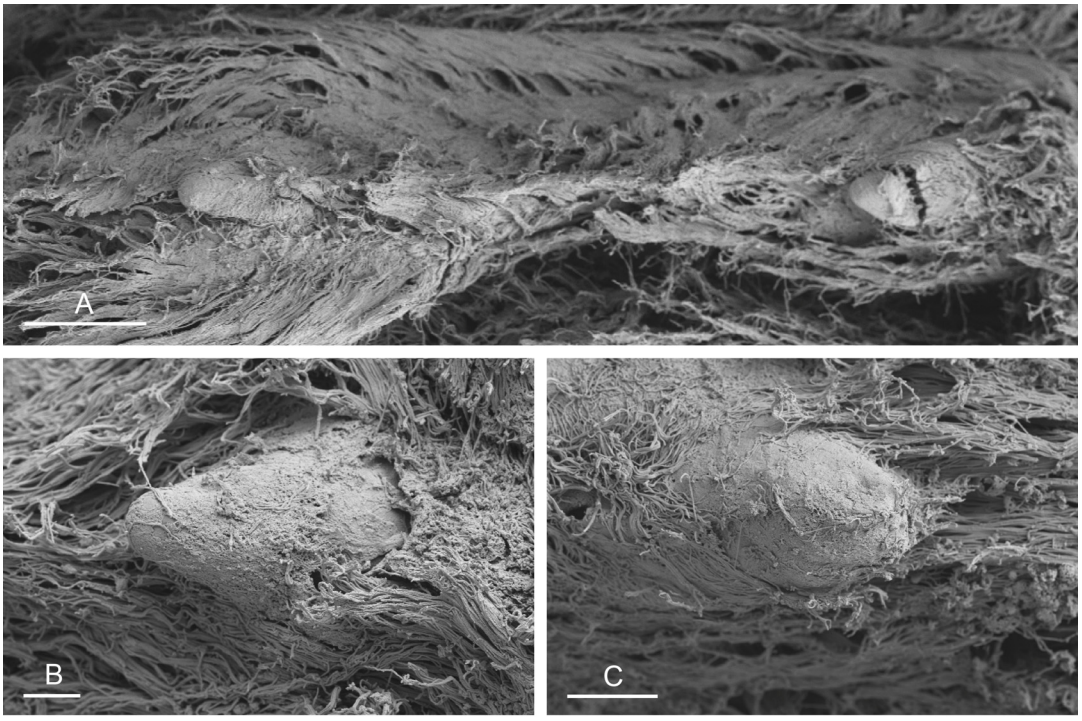

Fig. 22. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #2, penial hooks. **A**. Indonesia, Sumatra [1794] (UMIZ 00138). **B**. Philippines, Luzon [3237] (PNM 041265). **C**. Same as B. Scales: A = 20 μm; B = 4 μm; C = 6 μm.

The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle) and the accessory penial gland (Figs 16B–C, 17C–D). The penial complex and the accessory penial gland share the same vestibule and the same anterior male opening. The penial gland is a long, tube-like flagellum with a proximal dead end. The length of the flagellum of the penial gland varies among individuals but it is always heavily coiled. Near its distal end (just before the hollow spine), the flagellum is enlarged into a thick muscular sac. Distally, the flagellum ends in a hard, hollow spine protected by a sheath which opens into the vestibule. The hollow spine is narrow, elongated and slightly curved (Figs 18–20). Its base is conical. Its diameter is between 60 and 100 μm. The diameter of the opening at its tip measures between 30 and 60 μm. Its length ranges from 1 mm ([1634] NTM P.57620) to 2 mm ([5619] ITBZC IM 00019, [5102] UMIZ 00136) for unit #1, from 1.2 mm ([1638] NTM P.57623) to 1.8 mm ([3237] PNM 041265, [3172] PNM 041262) for unit #2 and from 0.8 mm ([5433] MNHN IM-2013-10479) to 1 mm ([5432] MNHN IM-2013-10478) for unit #3, and its shape does vary between individuals (Figs 18–20). There is no disc separating the spine of the penial gland and the vestibule.

The penial sheath is narrow and elongated (Figs 16B–C, 17C–D). The penial sheath protects the penis for its entire length. The beginning of the retractor muscle marks the separation between the penial sheath (and the penis inside) and the deferent duct. The retractor muscle is shorter than the penial sheath and inserts on the wall of the body cavity, near the heart. The deferent duct is also highly convoluted, with many loops. Inside the penial sheath, the penis is a narrow, elongated, soft, hollow tube of approximately 200 μm in diameter. Inside the tube-like penis, six longitudinal ridges bear sparse, tiny, conical (but not pointed) hooks which are less than 20 μm long in unit #1, less than 22 μm long in unit #2 and less than 28 μm in unit #3 (Figs 21–23). When the penis is retracted inside the penial sheath, the hooks are inside the tube-like penis; during copulation, the penis is evaginated like a glove and the hooks are outside.

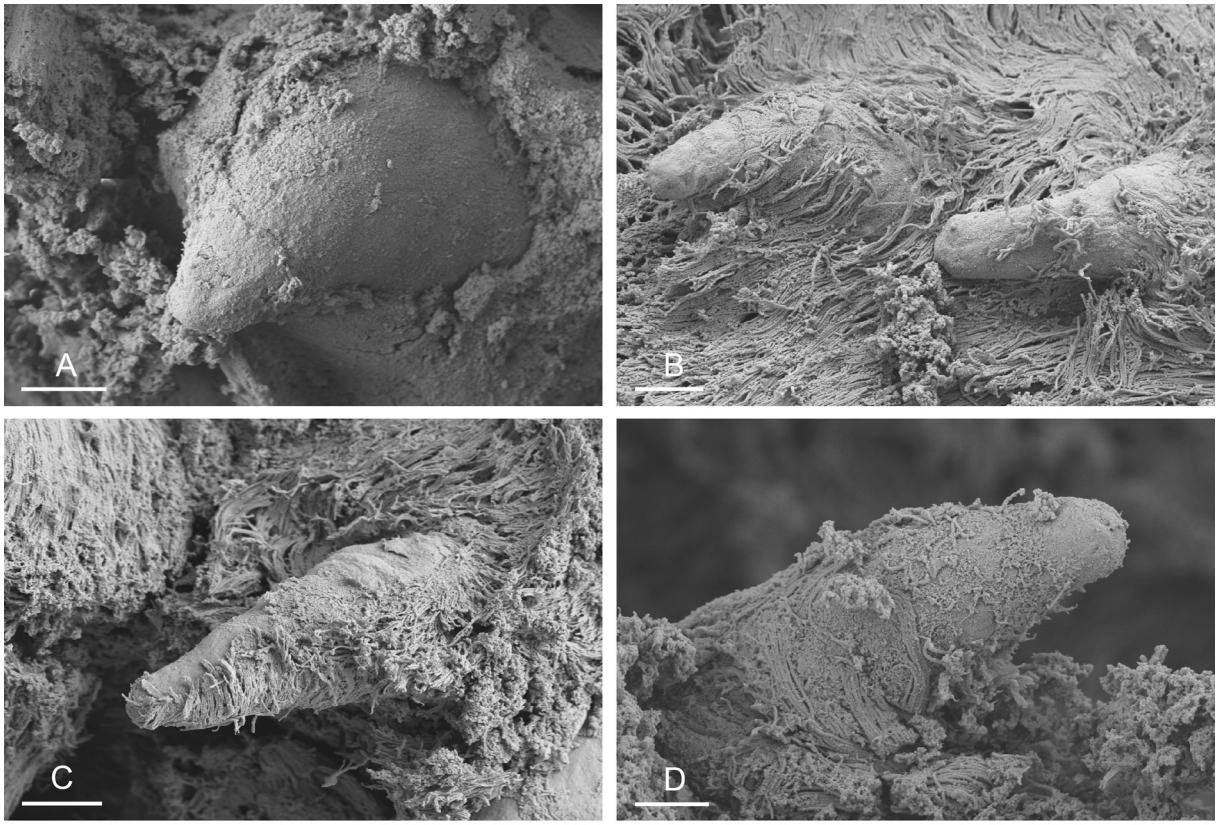

Fig. 23. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #3, penial hooks, Papua New Guinea, Madang. **A**. [5433] (MNHN IM-2013-10479). **B**. Same as A. **C**. [5432] (MNHN IM-2013-10478). **D**. Same as C. Scales: A, D = 3 μm; B–C = 6 μm.

Distinctive diagnostic features

Externally, *Paromoionchis tumidus* (Semper, 1880) cannot be distinguished from other species of *Paromoionchis* gen. nov. Internally, the presence of penial hooks distinguishes it from other species of the genus (Table 3).

Distribution (Fig. 6)

All records here are new, except for the type localities.

Unit #1. Australia: New South Wales, Northern Territory, Queensland. Brunei Darussalam. Hong Kong (type locality of *Onchidium hongkongense*). India: Andaman Islands. Indonesia: Ambon, Aru Islands, Bali, Halmahera, Lombok, Seram, Sulawesi, Sumatra. Japan. Malaysia: Peninsular Malaysia. Singapore (type locality of *Onchidium tumidum*). Philippines: Bohol, Luzon, Samar (type locality of *Onchidium samarense*). Vietnam. The southernmost locality is in Sydney, New South Wales, Australia (33°37.323′ S) and the northernmost locality is in Misho Bay, Ehime Prefecture, Japan (32°57.634′ N).

Unit #2. Australia: Northern Territory. Indonesia: Sumatra, Lombok. Philippines: Luzon.

Unit #3. Papua New Guinea: Madang.

Habitat (Figs 24–25)

Paromoionchis tumidus unit #1 is predominantly found on mud, hard or soft, inside or near mangroves, or on mudflats (Fig. 24). It is also found on old, muddy logs, inside or near mangroves. It occasionally is found on muddy sand, or even rocks and coral rubble, usually in the proximity of some mangrove trees. It is not found on rocky shores. *Paromoionchis tumidus* unit #2 is found in mangroves, mostly on mud and occasionally on sand (Fig. 25). *Paromoionchis tumidus* unit #3 is found in *Nypa* palm swamps and seems rare (only two specimens are known).

Paromoionchis tumidus is very common across its entire distribution range. It is by far the most abundant species of *Paromoionchis* gen. nov. and arguably the most abundant onchidiid species in the Indo-West Pacific. Most individuals of *P. tumidus* are part of unit #1, because *P. tumidus* unit #2 is rare across its entire distribution (it is only known from a total of nine specimens collected at nine stations) and *P. tumidus* unit #3 is restricted to two individuals from Papua New Guinea.

Remarks

The publication dates of the various sections of the volume on *Landmollusken* by Carl Semper in the *Reisen im Archipel der Philippinen* series were clarified by Johnson (1969). The species name *Onchidium tumidum* was published by Semper with a complete description (text and figures) in 1880.

The anatomy of the species described here is fully compatible with Semper's original description of *Onchidium tumidum* as well as our own observation of the lectotype (and paralectotypes) from Singapore (Table 3). The most important characters are the lack of a rectal gland, a digestive system of type II, an accessory penial gland, a retractor muscle of the penis inserting near the heart, a male opening between the two eye tentacles (not just below the right eye tentacle), and a penis with hooks (Figs 12H, 21D). According to Semper (1880: 263, our translation), the male opening is "almost exactly midway between the two [eye tentacles]," but it actually is closer to the right tentacle. Also, Semper (1880: 263, our translation) described a penis with an "anterior tooth-bearing portion [which] is reduced, namely at most 2 mm long." It is confirmed here with SEM (Fig. 21D) that the penis of the lectotype bears tiny hooks (< 20 μm) and is fully compatible with the species described here.

The lectotype of *O. mertoni* is anatomically identical to the species described here, *P. tumidus*. Simroth did not describe the internal anatomy of *O. mertoni*, but a description of its lectotype is provided here.

Simroth mentioned a male aperture below the right ocular tentacle, but it clearly is to the left of the right tentacle (Fig. 11A); the intestinal loops are of type II; the male apparatus includes an accessory penial

Fig. 24. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #1, habitats. **A**. Australia, Queensland, mangrove by creek with *Rhizophora* and *Avicennia* (station 119). **B**. Indonesia, Ambon, mangrove with large *Rhizophora* and some open spaces between trees (station 131). **C**. Indonesia, Lombok, mudflat at the margin of mangrove (station 145). **D**. Philippines, Bohol, narrow forest on the edge of fish ponds, with tall *Rhizophora* and *Avicennia* trees, and different types of mud (station 194). **E**. Indonesia, Halmahera, logged area by an old *Rhizophora* forest (station 212). **F**. Vietnam, Nha Trang, mostly *Avicennia* trees, mud not deep (station 239).

gland; the penial retractor muscle inserts to the body wall near the heart; the penis bears tiny hooks which are identical to the hooks of the species described here (Fig. 21C).

The type material of *O. hongkongense* is anatomically identical to the species described here and it is characterized by the exact same combination of characters: no rectal gland, intestinal loops of type II (Fig. 12D), an accessory penial gland, a retractor muscle inserting near the heart, a male opening between the two eye tentacles and a penis with tiny hooks (which Britton illustrated and measured as <20 µm).

Strictly speaking, *Onchidium samarense* probably should be regarded as a nomen dubium because 1) the jar with the type material includes three specimens while Semper only mentioned two specimens in the original description, 2) the male organs of two of the syntypes are gone (possibly dissected by Semper) and cannot be checked, and 3) important features (e.g., the insertion of the retractor muscle) are not mentioned in the original description. However, our observations are compatible with the original description and it is possible that all three specimens were actually identified as *O. samarense* by Semper himself. According to Semper (1882: 269, our translation), the penis of *O. samarense* is "very similar to that of *O. tumidum*." Indeed, the male apparatus of the lectotype is very similar to that of the species described here. In particular, the retractor muscle of the penis (not described by Semper) is thin but reaches the heart, following some nerves, as in the species described here. Semper described no

Fig. 25. *Paromoionchis tumidus* (Semper, 1880) comb. nov. unit #2, habitats. **A**. Australia, Northern Territory, large mangrove of *Sonneratia, Rhizophora and Ceriops* (st. 66). **B**. Indonesia, Sumatra, small patch of mangrove, very impacted (st. 81). **C**. Indonesia, Lombok, open *Avicennia* mangrove (station 146). **D**. Philippines, Luzon, narrow and very sandy *Avicennia* mangrove, with no mud (st. 179).

'cartilaginous teeth.' However, that can be easily explained by the fact that the hooks inside the penis of *O. tumidum* are soft and tiny (< 20 μm) and, unlike the large and solid hooks found in some other onchidiids, can hardly be seen under a light microscope (in fact, because there are not many hooks, they are hard to find even with SEM). Our collections currently do not include any specimen from Samar, the type locality of *O. samarense*, but we did collect many species of onchidiids in Luzon, just next to Samar, as well as in Bohol, a bit further south in the Philippines. Given the anatomy of *O. samarense* (no rectal gland, digestive system of type II, male opening clearly on the left of the right eye tentacle, accessory penial gland and retractor muscle inserting near the heart), it is most likely that *O. samarense* applies to the same species as *O. tumidum*. Because its nomenclatural status still remains problematic (it could be regarded as a nomen dubium) and because its written description was published in 1882 and not in 1880, *O. samarense* is regarded as a junior synonym of *O. tumidum*.

Plate (1893) identified five specimens from Ponape (now Pohnpei, Micronesia) and one specimen from Singapore as *Onchidium tumidum*. Given that their intestinal loops were of type I, the specimens from Ponape were misidentified. It is impossible to determine whether the specimen from Singapore (with intestinal loops of type II) actually belongs to *P. tumidus*. Bretnall (1919) listed previous records but did not examine any new material. Bretnall also suggested that *Onchidium punctatum* Quoy & Gaimard, 1832 could possibly refer to the same species as *O. tumidum*. However, *O. punctatum* clearly belongs to the genus *Peronia*. In fact, it was transferred to *Scaphis* Labbé, 1934 by Labbé (1934a: 203) as *Scaphis punctata* and *Scaphis* is a junior synonym of *Peronia*. Hoffmann (1928) mentioned *O. tumidum*, *O. samarense* and *O. mertoni* but did not examine any new material. Hoffmann also suggested that the record of *Onchidium tabularis* (Tapparone-Canefri, 1883), listed by Boettger (1923) from the Aru and Kei Islands, was a misidentification for *O. mertoni* (Boettger provided a record but did not describe any specimens). However, Hoffmann's claim cannot be checked because the application of *Onchidella tabularis* Tapparone-Canefri, 1883 (as *Oncidiella*) is very unclear (the type material could not be located and the original description is not informative).

Three onchidiid sequences from mainland China were obtained from GenBank, the only ones that are not new in our data set (Table 1). These sequences were misidentified as *Paraoncidium reevesii* (J.E. Gray, 1850). *Paraoncidium* Labbé, 1934 is not a valid name: it is a junior synonym of *Onchidina* Semper, 1882. Also, *Onchidium reevesi* (J.E. Gray, 1850) is actually one of the three valid species of *Onchidium* (Dayrat *et al.* 2016).

Paromoionchis daemelii (Semper, 1880) comb. nov.
Figs 26–30

Onchidium dämelii Semper, 1880: pl. 20, fig. 2.

Onchidium dämelii – Semper 1882: 270–271, pl. 21, fig. 9.

Material examined

Type material

AUSTRALIA • lectotype (here designated; 17/14 mm); New South Wales, Sydney; ZMB 31640a • 1 paralectotype (17/17 mm); same locality as lectotype; ZMB 31640b • 1 paralectotype (destroyed, dried); same locality as lectotype; ZMB 39035 • 2 paralectotypes (?); same locality as lectotype; ZMH 27476/2.

Notes on type material

The lectotype, 17/14 mm, is designated here (ZMB 31640a). All other syntypes become paralectotypes. According to the original description, the type material included only three specimens. However, five possible syntypes could be located in museum collections, all from Sydney, Australia: 2 specimens,

one of which, dissected with male parts remaining inside (17/14 mm), is designated as lectotype (ZMB 31640a) and the other one, still entire (17/17 mm), is a paralectotype (ZMB 31640b); 1 specimen destroyed, in pieces and completely dried (ZMB 39035); and 2 specimens (ZMH 27476/2), both entire. It is unclear exactly which specimens Semper used for the description, but it is safe to assume that the anatomical details he provided are based on the only two dissected specimens. Two species of *Paromoionchis* gen. nov. are present in Sydney, *P. tumidus* and the species described here, which are cryptic externally but distinct internally. Thus, the specimens that were not dissected by Semper could belong either to *P. tumidus* or to the species treated here. Hence the necessity of designating a lectotype in order to clarify the application of the name *Onchidium daemelii*.

Other material

AUSTRALIA – **New South Wales** • 1 spec. (37/25 [1511] mm); Sydney, Middle Harbour, N of Roseville Bridge, W bank; 33°46.332′ S, 151°12.106′ E; 23 Nov. 2011; station 38; open mangrove, in old logs on the mud; AM C.468910.001 • 1 spec. (17/10 [1510] mm); same data as for preceding;

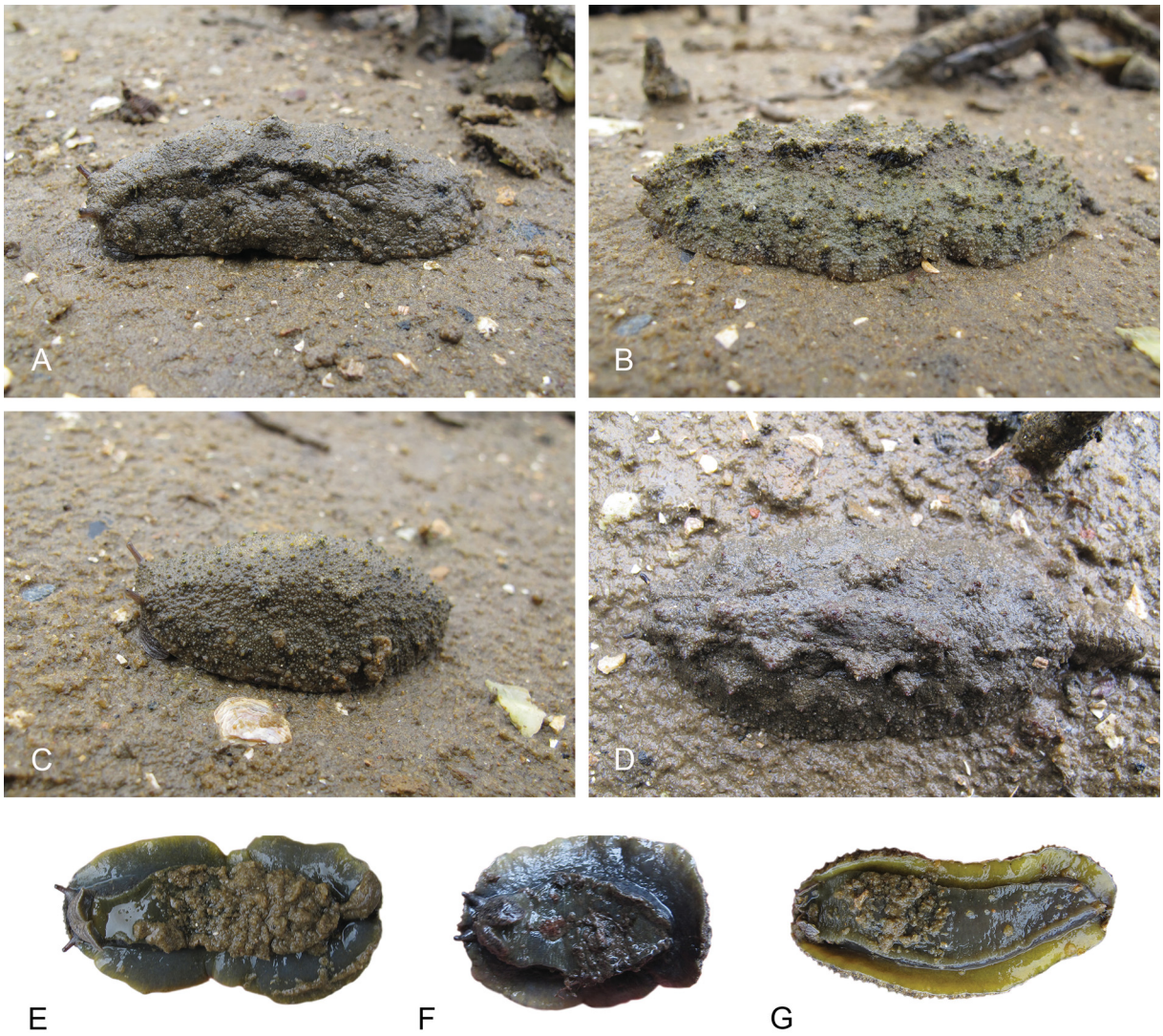

Fig. 26. *Paromoionchis daemelii* (Semper, 1880) comb. nov., live animals, Australia, New South Wales. **A**. Dorsal view, 51 mm long [1514] (AM C.468912.002). **B**. Dorsal view, 56 mm long [1519] (AM C.468917.001). **C**. Dorsal view, 31 mm long [1515] (AM C.468914.001). **D**. Dorsal view, 62 mm long [1518] (AM C.468913.001). **E**. Ventral view, 42 mm long [1512] (AM C.468912.003). **F**. Ventral view, 36 mm long [1511] (AM C.468910.001). **G**. Ventral view, same as C.

AM C.468911.001 • 1 spec. (65/35 [1518] mm); Sydney, Pittwater, Church Point, next to yacht club; 33°39.107′ S, 151°17.363′ E; 24 Nov. 2011; station 39; muddy sand next to small patch of mangrove and rocks on sandy beach; AM C.468913.001 • 1 spec. (60/35 [1519] mm); same data as for preceding; AM C.468917.001 • 1 spec. (28/18 [1515] mm); same data as for preceding; AM C.468914.001 •

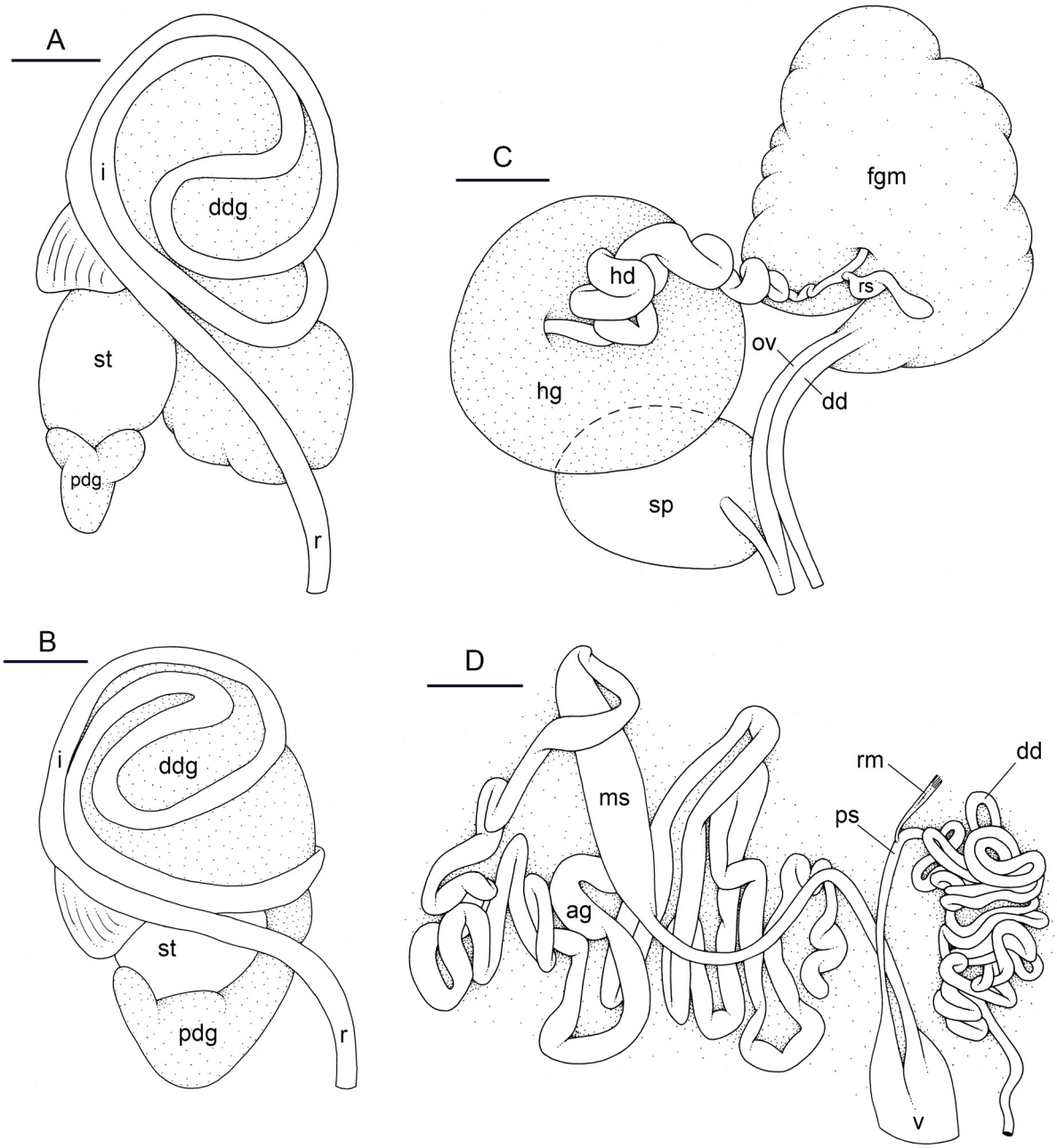

Fig. 27. *Paromoionchis daemelii* (Semper, 1880) comb. nov. **A**. Digestive system, Australia, New South Wales [1519] (AM C.468917.001). **B**. Digestive system, lectotype of *Onchidium daemelii* (ZMB 31640a). **C**. Posterior hermaphroditic (female) reproductive system, same as A. **D**. Male copulatory organs, same as A. Abbreviations: ag = accessory penial gland; dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ms = muscular sac (of accessory penial gland); ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath; r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scales: A = 4 mm; B–D = 3 mm.

1 spec. (52/28 [1514] mm); same data as for preceding; AM C.468912.002 • 1 spec. (40/20 [1512] mm); same data as for preceding; AM C.468912.003 • 1 spec. (50/25 [1521] mm); Sydney, Pittwater, Careel Bay; 33°37.323′ S, 151°19.878′ E; 24 Nov. 2011; station 40; supratidal zone on the margin of salt marsh, mangrove patch on side of creek; AM C.468919.001. – **Queensland** • 2 spec. (15/12 [1532] and 8/6 [1533] mm); Thirsty Sound, Plum Tree, beach in front of Endeavour Park; 22°08.144′ S, 150°01.856′ E; 14 Sep. 2002; I. Loch, D.L. Beechey and A.C. Miller leg.; sheltered, muddy cobble shore; AM C.415270 • 1 spec. (8/6 [2668] mm); Bowen, Doughty Creek; 20°01.478′ S, 148°14.224′ E; 3 Jul. 2013; station 119; mangrove of *Rhizophora* and *Avicennia* on one side of creek; MTQ.

Color and morphology of live animals (Fig. 26)

Live animals are often covered with mud, in which case their dorsal color can hardly be seen. The background of the dorsal notum is brown, occasionally mottled with darker or lighter areas. In addition, in some animals, the tip of dorsal papillae (with and without dorsal eyes) can be bright yellow. The foot is gray. The hyponotum is gray (same color as the foot), yellow, or both (yellow outer ring and gray inner ring). The color of the foot and of the hyponotum of an individual can change rapidly, especially when disturbed. The ocular tentacles are gray or brown, and may or may not be speckled with white dots, like the head. The ocular tentacles are short (just a few millimeters long).

Digestive system (Figs 27A–B, 28)

Radulae measure up to 5.4 mm in length. Examples of radular formulae are presented in Table 4.

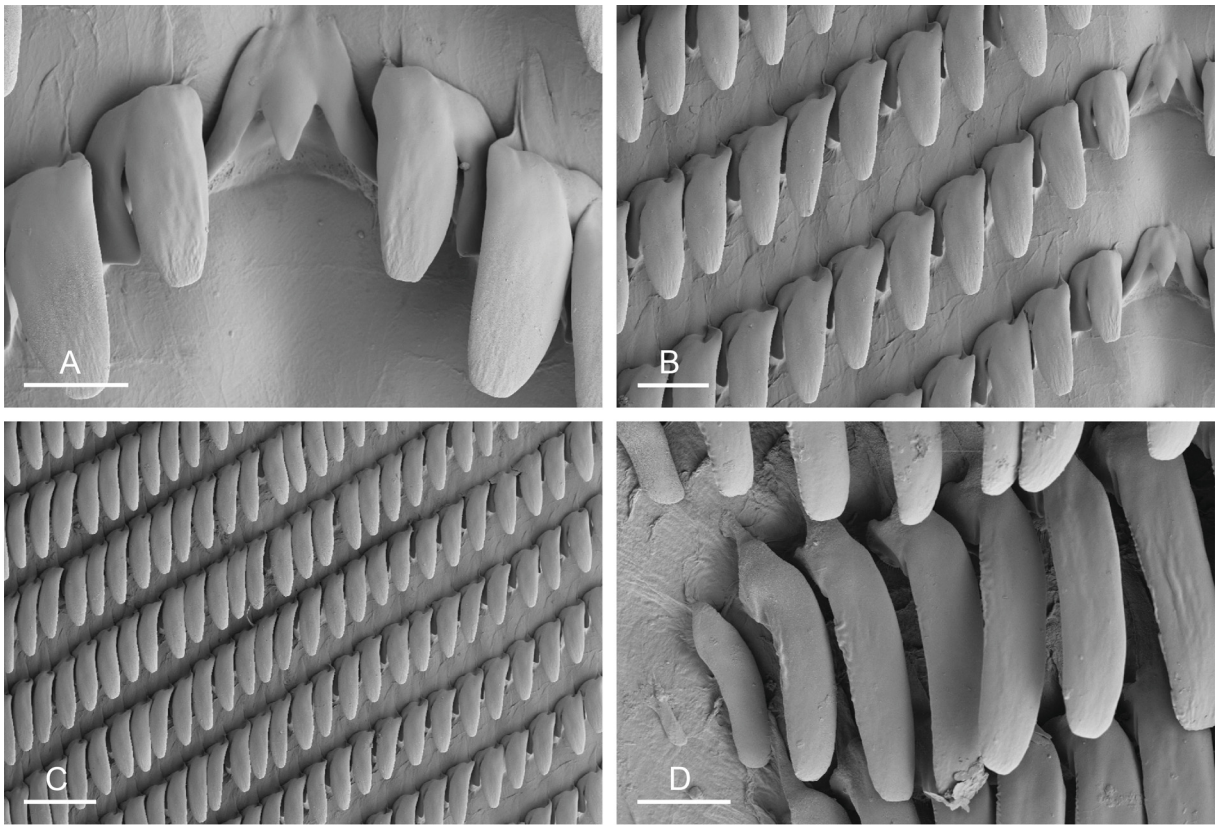

Fig. 28. *Paromoionchis daemelii* (Semper, 1880) comb. nov., radula, Australia, New South Wales [1519] (AM C.468917.001). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A, D = 20 μm; B–C = 30 μm.

Reproductive system (Figs 27C–D, 29)

The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle) and the accessory penial gland (flagellum and hollow spine). The hollow spine of the accessory penial gland is narrow, elongated, slightly curved. Its base is conical. Its diameter is approximately 80 μm for most of its length, except at its base (200 μm) and tip (60 μm). Its length ranges from 2.5 mm ([1519] AM C.468917.001) to 2.7 mm ([1521] AM C.468919.001), and its shape does vary between individuals (Fig. 29). The penial sheath is narrow and elongated. The retractor muscle is short (shorter than the penial sheath) or even vestigial (its distal end being free in the visceral cavity, with no clear insertion). The deferent duct is highly convoluted, with many loops. Inside the penial sheath, the penis is a narrow, elongated, soft, hollow tube of approximately 100 μm in diameter; internally, the penis bears a few smooth (no hooks) longitudinal ridges.

Distinctive diagnostic features

Externally, *Paromoionchis daemelii* cannot be distinguished from other species of *Paromoionchis* gen. nov. (Table 3). Also, its internal anatomy (accessory penial gland, vestigial penial retractor muscle, smooth penis) is very similar to that of *P. boholensis* gen. et sp. nov. The distribution range of *P. daemelii* overlaps with that of only one species of *Paromoionchis* gen. nov., *P. tumidus* (Fig. 6). Both species live in similar habitats and can even be found at the same station. They can only be distinguished internally thanks to a few anatomical details: in *P. daemelii*, the penis is smooth and the penial retractor muscle is very short or even vestigial, while in *P. tumidus* the penis bears some tiny hooks and the penial retractor muscle inserts near the heart (Table 3).

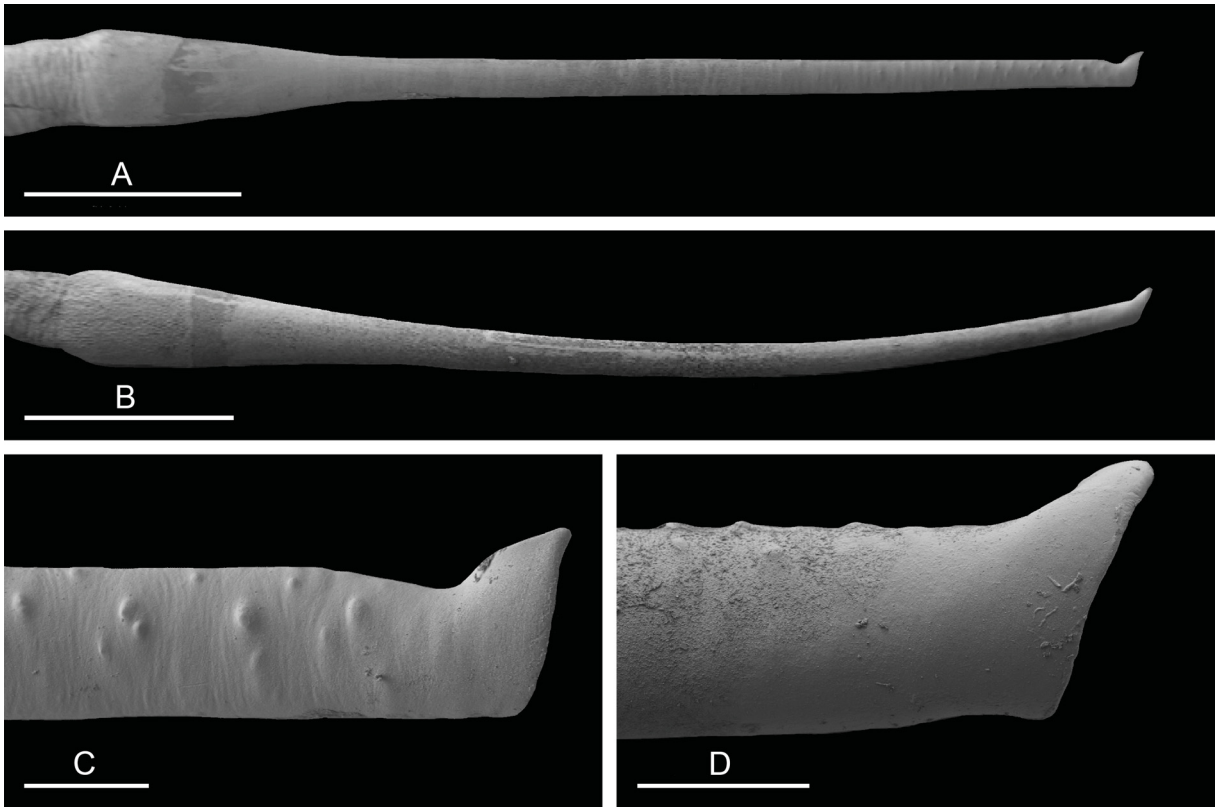

Fig. 29. *Paromoionchis daemelii* (Semper, 1880) comb. nov., spine of accessory penial gland. **A**. Australia, New South Wales [1519] (AM C.468917.001). **B**. Australia, New South Wales [1521] (AM C.468919.001). **C**. Distal tip of spine, same as A. **D**. Distal tip of spine, same as B. Scales: A–B = 500 μm; C–D = 50 μm.

Distribution (Fig. 6)

Australia: New South Wales (type locality, present study), Queensland (present study).

Habitat (Fig. 30)

Paromoionchis daemelii is found on mud or muddy logs, inside or near mangroves, or on muddy sand. It is not common in central Queensland or New South Wales, but its abundance in southern Queensland is unknown.

Remarks

The publication dates of the various sections of the volume on *Landmollusken* by Carl Semper in the *Reisen im Archipel der Philippinen* series were clarified by Johnson (1969). The species name *Onchidium daemelii* was first published by Semper in 1880 with one figure (pl. 20, fig. 2) but no written description. Because *Onchidium daemelii* was published before 1931, ICZN Article 12.2.7 applies and the name is available (Semper's figures are regarded as an indication accompanying the name *Onchidium daemelii*). Also, the specific name was originally spelled *dämelii*. However, according to ICZN Article 32.5.2.1., the correct spelling is *daemelii*. Both *dæmelii* (e.g., Labbé 1934a) and *damelii* (e.g., Kenny & Smith 1987, 1988) are spelling mistakes.

According to our current data, there are only two species of *Paromoionchis* gen. nov. in New South Wales (Fig. 6): *P. tumidus* and *P. daemelii*. They cannot be distinguished externally but they differ anatomically (Table 3). Both species are characterized by the lack of a rectal gland, a digestive system of type II, a male opening clearly to the left of the right eye tentacle (Semper described a male opening under the right eye tentacle, but it is distinctly below and left of it) and an accessory penial gland. The retractor muscle of the penis of *O. daemelii*, described as "very thin" by Semper, is vestigial in the lectotype, whereas the retractor muscle of *P. tumidus* is not vestigial and inserts near the heart. No "teeth" (the term he used to refer to penial hooks) are mentioned by Semper in the original description of *O. daemelii*, while the penis of *P. tumidus* bears some hooks. Therefore, the combination of characters found in the lectotype of *O. daemelii* and in Semper's original description (retractor muscle vestigial and soft penis with no hooks) is only compatible with the species described here, not with *P. tumidus*, which justifies the present application of *P. daemelii*.

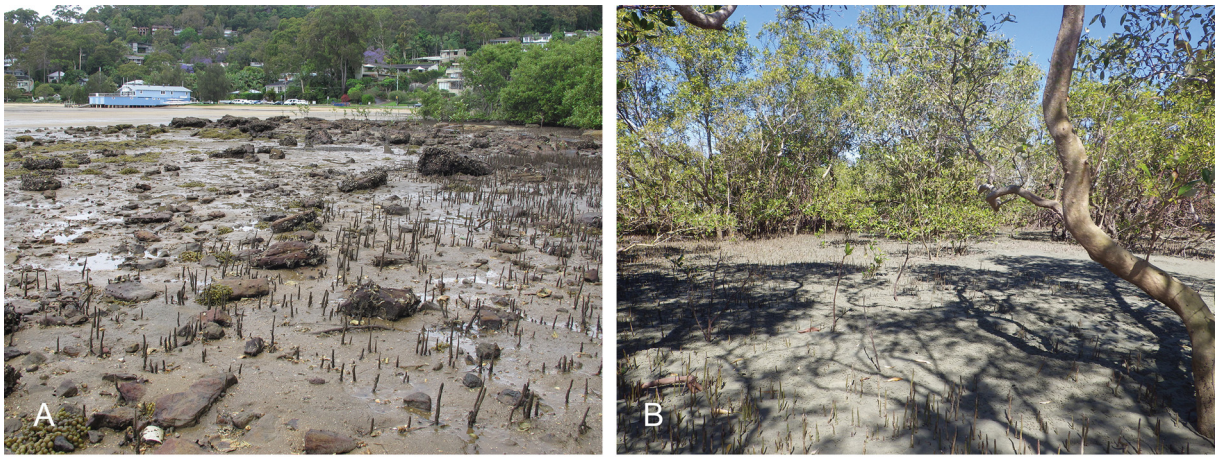

Fig. 30. *Paromoionchis daemelii* (Semper, 1880) comb. nov., habitats. **A**. Australia, New South Wales, muddy sand next to small patch of mangrove and rocks on sandy beach (station 39). **B**. Australia, Queensland, *Rhizophora* and *Avicennia* mangrove (station 119).

Onchidium daemelii was recorded from New South Wales (Lendenfeld 1886; Tenison-Woods 1888) and even New Guinea (Tapparone-Canefri 1883) but it is not possible to determine whether it was identified properly without re-examining the material which these authors examined (which may or may not have been deposited). Bretnall (1919), Hoffmann (1928) and Labbé (1934a) mentioned *Onchidium daemelii* without adding any new material. Finally, Kenny & Smith (1987) published an ecological study on a species they identified as *Onchidium damelii* in a mangrove on Magnetic Island, Queensland. However, given that *P. daemelii* is rare in northern and central Queensland and that its identification requires detailed study of the internal anatomy, Kenny & Smith likely studied *P. tumidus* rather than *P. daemelii* (or a mix of both species).

Paromoionchis boholensis Dayrat & Goulding gen. et sp. nov.
urn:lsid:zoobank.org:act:104C35EF-FBF9-4EC2-A5A8-89AC30009270
Figs 31–40

Etymology

Paromoionchis boholensis gen. et sp. nov. is named after Bohol Island, where the type locality is.

Material examined

Holotype

PHILIPPINES • holotype (28/18 [3288] mm); Bohol, Maribojoc; 09°43.645′ N, 123°50.988′ E; 15 Jul. 2014; station 193; small island at end of boardwalk, sandy mud and rocks in back of mangrove; PNM 041266.

Other material

INDONESIA – **Sulawesi** • 2 spec. (35/22 [2128] and 37/20 [2129] mm); Wori; 01°36.055′ N, 124°51.730′ E; 9 Mar. 2013; station 84; tall mangrove forest of *Sonneratia* and *Avicennia*, with old logs; UMIZ 00141 • 1 spec. (9/6 [2175] mm); Bahoi; 01°43.355′ N, 125°01.232′ E; 10 Mar. 2013; station 85; sand, small rocks and pieces of wood, near narrow coastal mangrove; UMIZ 00142 • 1 spec. (20/13 [2199] mm); Tamperong; 01°41.513′ N, 125°00.797′ E; 12 Mar. 2013; station 87; muddy mangrove with small and dense *Rhizophora*; UMIZ 00143 • 1 spec. (12/8 [2316] mm); Mantehang; 01°41.880′ N, 124°46.741′ E; 15 Mar. 2013; station 91; *Sonneratia* at low intertidal and *Rhizophora* at high intertidal; UMIZ 00144 • 1 spec. (20/13 [2360] mm); Panikkiang Island; 04°21.730′ S, 119°35.630′ E; 25 Mar. 2013; station 94; *Rhizophora*, *Avicennia*, *Sonneratia* and old logs; UMIZ 00145. – **Ambon** • 3 spec. (40/25 [2849], 45/30 [2850] and 45/25 [2851] mm); Wai; 03°34.652′ S, 128°19.526′ E; 15 Feb. 2014; station 132; narrow band of old *Avicennia* trees on sandy mud, old logs on ground; UMIZ 00146. – **Seram** • 1 spec. (45/28 [2884] mm); Piru; 03°04.072′ S, 128°11.362′ E; 19 Feb. 2014; station 136; *Sonneratia* mangrove next to fish market, next to beach of palms and ferns, with cattle roaming around; UMIZ 00147. – **Kei Islands** • 2 spec. (10/8 [2896] and 17/8 [2901] mm); Un; 05°38.273′ S, 132°45.738′ E; 23 Feb. 2014; station 137; *Bruguiera* and *Rhizophora*, some muddy areas and some with coral rubble; UMIZ 00148 • 2 spec. (15/10 [2903] and 18/8 [2911] mm); Un; 05°38.273′ S, 132°45.738′ E; 25 Feb. 2014; station 140; back of mangrove, on rocks, on mud, inside logs and under leaf litter; UMIZ 00149 • 3 spec. (40/22 [3565], 30/20 [2935] and 40/22 [2937] mm); Fiditan; 05°35.957′ S, 132°45.112′ E; 28 Feb. 2014; station 144; rocks behind muddy *Rhizophora* mangrove; UMIZ 00150. – **Bali** • 1 spec. (35/17 [3117] mm); Gilimanuk; 08°10.156′ S, 114°26.652′ E; 4 Apr. 2014; station 156; muddy mangrove with *Rhizophora* and *Avicennia* trees; UMIZ 00140. – **Halmahera** • 1 spec. (25/16 [5019] mm); Sofifi; 00°45.473′ N, 127°35.897′ E; 8 Mar. 2015; station 205; *Sonneratia* mangrove, with dense roots and hard mud; UMIZ 00151 • 2 spec. (47/30 [5140] and 35/22 [5146] mm); Gamkonora; 01°26.911′ N, 127°31.625′ E; 21 Mar. 2015; station 219; mostly *Rhizophora* mangrove with some sandy areas and some open muddy spaces; UMIZ 00152.

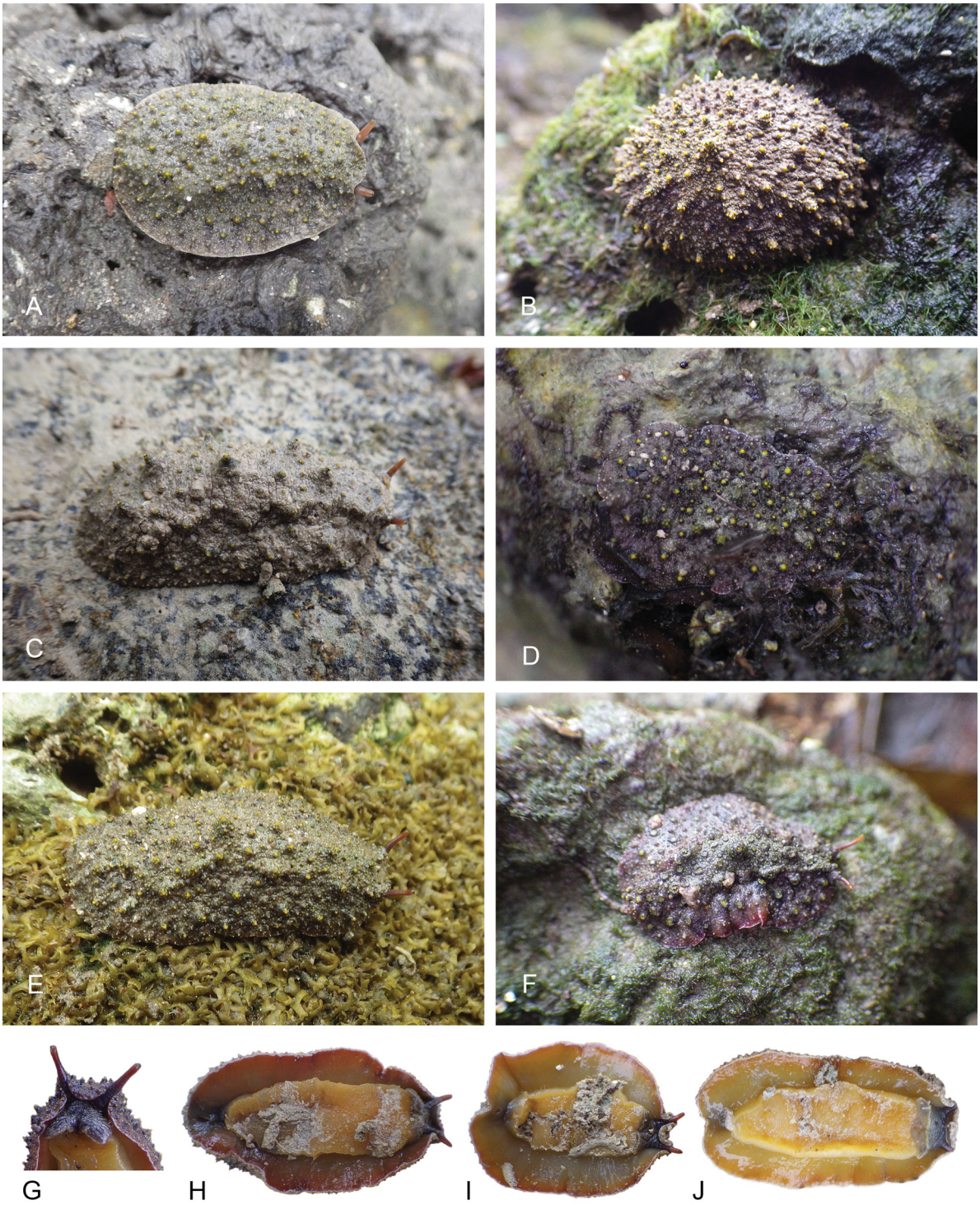

Fig. 31. *Paromoionchis boholensis* gen. et sp. nov., unit #1, live animals. **A**. Holotype, dorsal view, 28 mm long [3288], Philippines, Bohol (PNM 041266). **B**. Dorsal view, 26 mm long [3609], Philippines, Luzon (PNM 041267). **C**. Dorsal view, 38 mm long [3417], Philippines, Bohol (PNM 041270). **D**. Dorsal view, 17 mm long [3283], Philippines, Bohol (PNM 041268). **E**. Dorsal view, 30 mm long [3372], Philippines, Bohol (PNM 041269). **F**. Dorsal view, 17 mm long [3619], Philippines, Bohol (PNM 041268). **G**. Ventral view, same as E. **H**. Ventral view, 38 mm long [3422], Philippines, Bohol (PNM 041270). **I**. Ventral view, 32 mm long [3413], Philippines, Bohol (PNM 041270). **J**. Ventral view, same as C.

Fig. 32. *Paromoionchis boholensis* gen. et sp. nov., unit #2, live animals. **A**. Dorsal view, 37 mm long [2129], Indonesia, Sulawesi (UMIZ 00141). **B**. Dorsal view, 45 mm long [2851], Indonesia, Ambon (UMIZ 00146). **C**. Dorsal view, 35 mm long [3117], Indonesia, Bali (UMIZ 00140). **D**. Dorsal view, 18 mm long [2911], Indonesia, Kei (UMIZ 00149). **E**. Dorsal view, 40 mm long [2937], Indonesia, Kei (UMIZ 00150). **F**. Dorsal view, 15 mm long [2903], Indonesia, Kei (UMIZ 00149). **G**. Ventral view, 45 mm long [2884], Indonesia, Seram (UMIZ 00147). **H**. Ventral view, same as B. **I**. Ventral view, 45 mm long [2850], Indonesia, Ambon (UMIZ 00146). **J**. Frontal view, 17 mm long [2901], Indonesia, Kei (UMIZ 00148).

PHILIPPINES – **Luzon** • 1 spec. (25/18 [3609] mm); Lian, Batangas; 13°58.130′ N, 120°37.471′ E; 5 Jul. 2014; station 179; narrow and impacted mangrove of *Avicennia* near village, very sandy, little to no mud; PNM 041267. – **Bohol** • 2 spec. (16/9 [3283] and 17/10 [3619] mm); same data as for holotype; PNM 041268 • 3 spec. (20/15 [3369], 35/18 [3372] and 27/20 [3411] mm); Mabini; 09°51.586′ N, 124°34.155′ E; 18 Jul. 2014; station 196; open *Avicennia* and *Sonneratia* forest with sand, algae and coral rubble; PNM 041269 • 5 spec. (30/22 [3412], 30/23 [3413], 40/17 [3417], 40/20 [3422] and 42/25 [3423] mm); Maribojoc; 09°44.280′ N, 123°49.389′ E; 20 Jul. 2014; station 202; uplifted coral rubble with sand and algae, near *Sonneratia* trees; PNM 041270.

Color and morphology of live animals (Figs 31–32)

Live animals are often covered with mud, in which case their dorsal color can hardly be seen. In unit #1, the background of the dorsal notum is brown, occasionally mottled with darker or lighter areas, while in unit #2 it ranges from very light brown (almost white) to dark brown, mottled or not. In some animals,

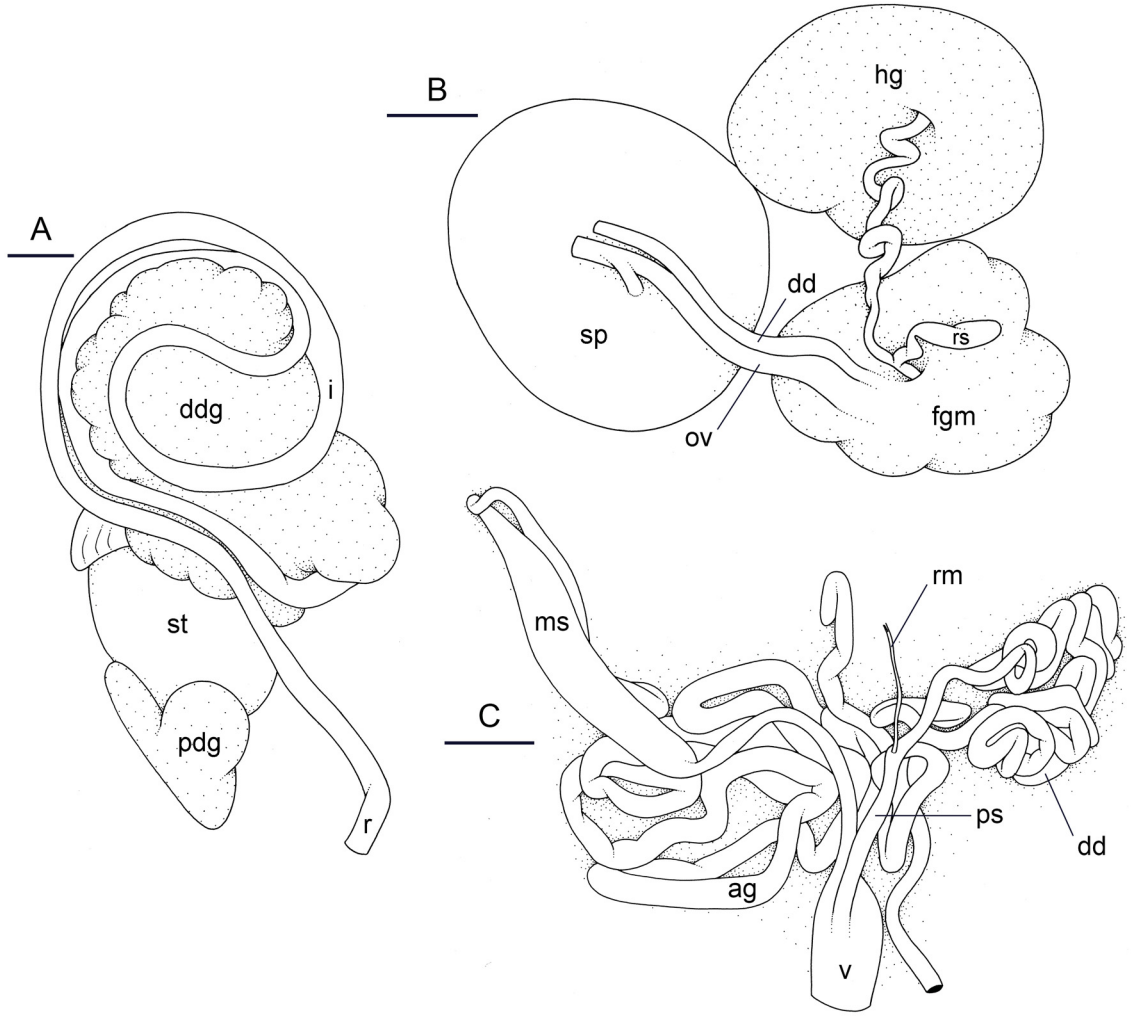

Fig. 33. *Paromoionchis boholensis* gen. et sp. nov., unit #1, holotype, Philippines, Bohol [3288] (PNM 041266). **A**. Digestive system. **B**. Posterior hermaphroditic (female) reproductive system. **C**. Male copulatory organs. Abbreviations: ag = accessory penial gland; dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ms = muscular sac (of accessory penial gland); ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath; r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scales = 2 mm.

there is a reddish hue on the margin of the dorsal notum (unit #1). In addition, in most animals the tip of the dorsal papillae (with and without dorsal eyes) can be bright yellow. The foot is orange (unit #1) or varies from gray to yellow and orange (unit #2). The hyponotum is also orange, often with a darker ring on the margin which may be bright red (unit #1) or homogenously gray, yellow, or orange, but can also display a mix of two or three of those colors (unit #2). The color of both the foot and the hyponotum of an individual can change very rapidly, especially when disturbed. The ocular tentacles are reddish brown and may or may not be speckled with white dots, like the head. The ocular tentacles are short (just a few millimeters long).

Digestive system (Figs 33A, 34A, 35–36)

Radulae measure up to 4.5 mm (unit #1) and 4 mm (unit #2) in length. Examples of radular formulae are presented in Table 4.

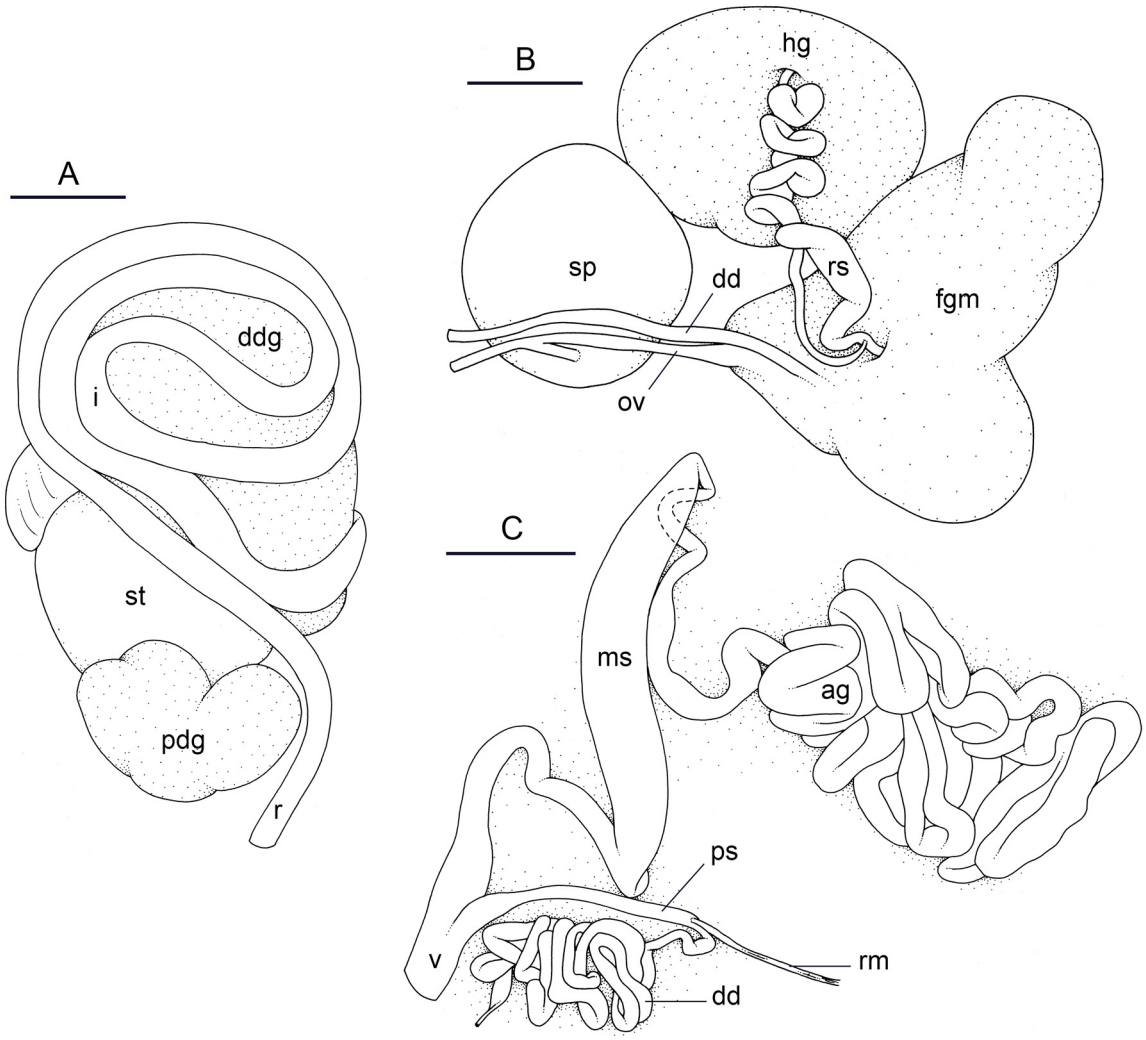

Fig. 34. *Paromoionchis boholensis* gen. et sp. nov., unit #2, Indonesia, Bali [3117] (UMIZ 00140). **A**. Digestive system. **B**. Posterior hermaphroditic (female) reproductive system. **C**. Male copulatory organs. Abbreviations: ag = accessory penial gland; dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ms = muscular sac (of accessory penial gland); ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath; r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scales: A–B = 2 mm; C = 3 mm.

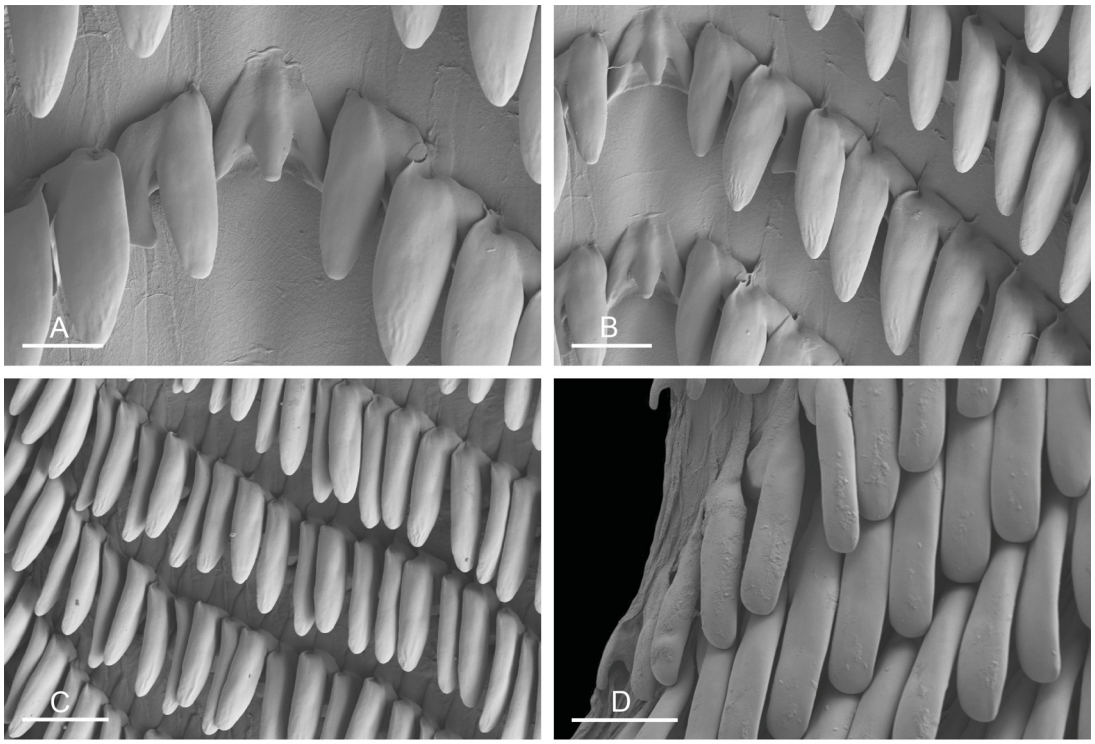

Fig. 35. *Paromoionchis boholensis* gen. et sp. nov., unit #1, radula, Philippines, Bohol [3372] (PNM 041269). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A = 20 μm; B, D = 30 μm; C = 50 μm.

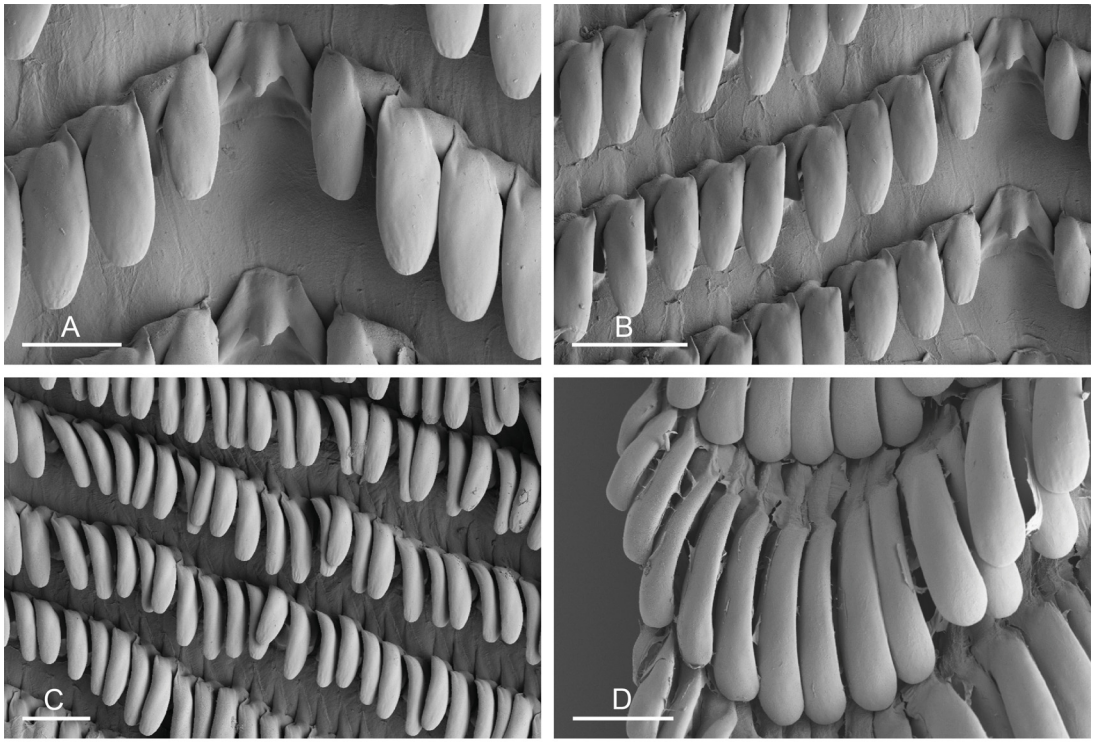

Fig. 36. *Paromoionchis boholensis* gen. et sp. nov., unit #2, radula, Indonesia, Ambon [2851] (UMIZ 00146). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A, D = 30 μm; B–C = 50 μm.

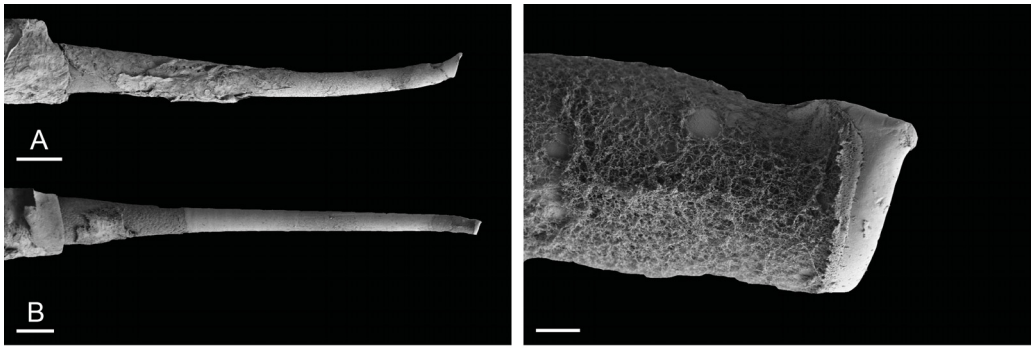

Fig. 37. *Paromoionchis boholensis* gen. et sp. nov., unit #1, spine of accessory penial gland. **A**. Holotype, Philippines, Bohol [3288] (PNM 041266). **B**. Philippines, Bohol [3372] (PNM 041269). **C**. Distal tip of spine, same as B. Scales: A–B = 100 μm; C = 10 μm.

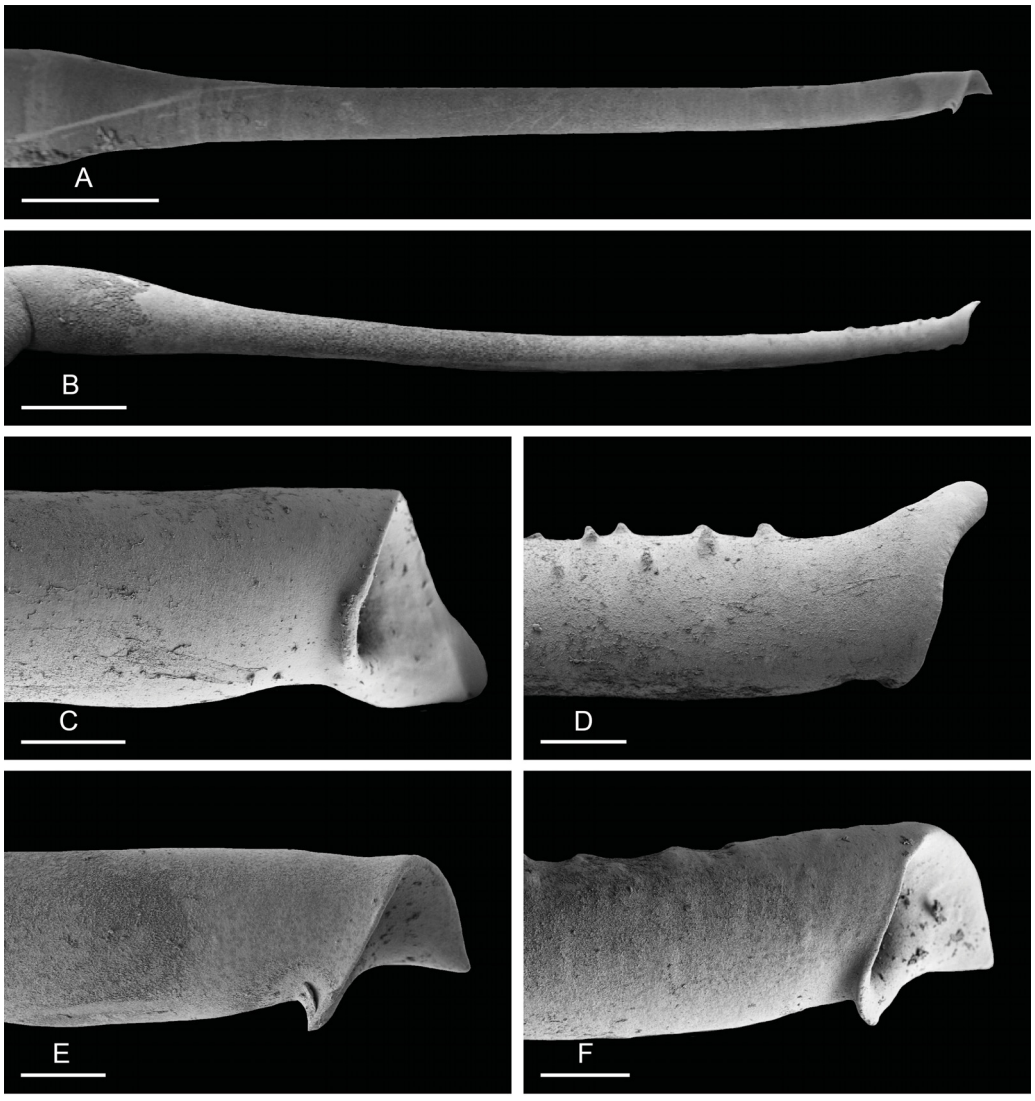

Fig. 38. *Paromoionchis boholensis* gen. et sp. nov., unit #2, spine of accessory penial gland. **A**. Indonesia, Bali [3117] (UMIZ 00140). **B**. Indonesia, Kei [2911] (UMIZ 00149). **C**. Tip of spine, Indonesia, Ambon [2851] (UMIZ 00146). **D**. Distal tip of spine, same as B. **E**. Tip of spine, same as A. **F**. Tip of spine, Indonesia, Halmahera [5140] (UMIZ 00152). Scales: A–B = 200 μm; C–F = 30 μm.

Reproductive system (Figs 33B–C, 34B–C, 37–38)

The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle) and the accessory penial gland (flagellum and hollow spine). The hollow spine of the accessory penial gland is narrow, elongated, slightly curved. Its base is conical. Its diameter is approximately 50 to 70 µm for most of its length and 100–130 µm at its base (unit #1) and approximately 70 to 80 µm for most of its length and 150–200 µm at its base (unit #2). Its length ranges from 1 mm ([3288] PNM 041266, holotype) to 1.2 mm ([3372] PNM 041269) in unit #1 and from 1.1 mm ([5019] UMIZ 00151) and 1.3 mm ([3117] UMIZ 00140) to 1.8 mm ([2911] UMIZ 00149, [5140] UMIZ 00152) in unit #2, and its shape does vary between individuals (Fig. 38). The penial sheath is narrow and elongated. The retractor muscle is vestigial, i.e., with its distal end being free in the visceral cavity, with no clear insertion (unit #1), or absent or vestigial (unit #2). The deferent duct is highly convoluted, with many loops. Inside the penial sheath, the penis is a narrow, elongated, soft, smooth (no hooks) and hollow tube of approximately 200 µm in diameter.

Distinctive diagnostic features

Externally, the color of the foot and hyponotum can help one to identify *Paromoionchis boholensis* gen. et sp. nov., but unfortunately it is not fully reliable. Specimens with a bright orange foot and hyponotum are only found in *P. boholensis* gen. et sp. nov., especially in unit #1 but also in unit #2; the

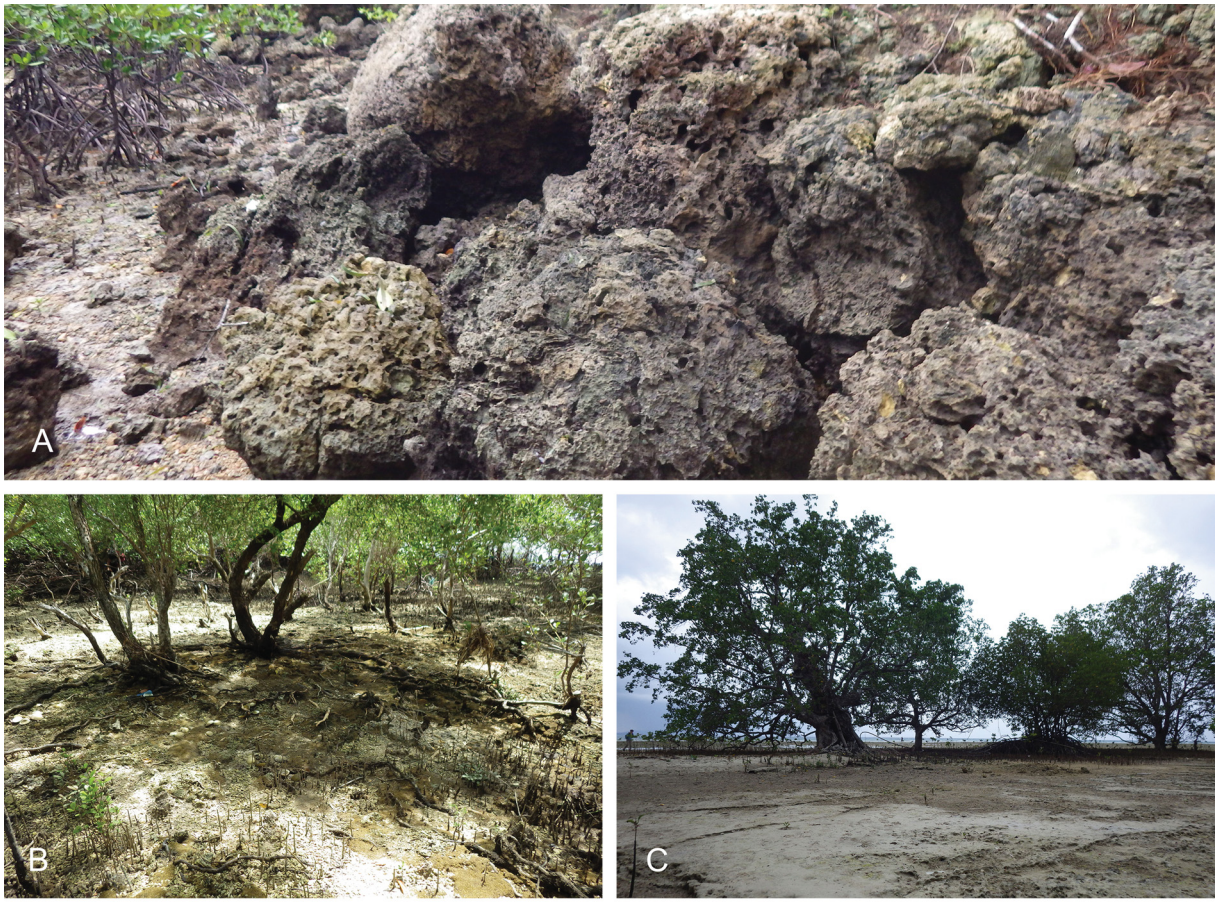

Fig. 39. *Paromoionchis boholensis* gen. et sp. nov., unit #1, habitats. **A**. Philippines, Bohol, Maribojoc, large porous rocks behind mangrove (station 193, type locality). **B**. Philippines, Bohol, Mabini, open *Avicennia* and *Sonneratia* forest with large gravel of coral pieces, sand and algae on surface (station 196). **C**. Philippines, Bohol, Maribojoc, uplifted, dead coral flat covered with sand and algae adjacent to a few mangrove trees (station 202).

Fig. 40. *Paromoionchis boholensis* gen. et sp. nov., unit #2, habitats. **A**. Indonesia, Bali, muddy mangrove with *Rhizophora* and *Avicennia* trees (station 156). **B**. Indonesia, Sulawesi, sand, small rocks and pieces of wood outside a narrow coastal mangrove (station 88). **C**. Indonesia, Ambon, narrow band of old *Avicennia* trees on sandy mud, with old logs on ground (station 132). **D**. Indonesia, Kei, back of mangrove with rocks, mud, logs and leaf litter (station 140). **E**. Indonesia, Halmahera, mostly *Rhizophora*, with some sandy areas and some open muddy areas (station 219).

ventral side of *P. tumidus*, which is sympatric with *P. boholensis* (Fig. 6), can be orange but not bright orange. However, specimens with a more yellowish or greyish foot and hyponotum cannot be identified externally. The internal anatomy of *P. boholensis* gen. et sp. nov. (accessory penial gland, vestigial penial retractor muscle, penis with no hooks) is similar to that of *P. daemelii*. However, *P. boholensis* gen. et sp. nov. and *P. daemelii* do not overlap geographically, at least based on the present data. Thus, within its distribution range *P. boholensis* gen. et sp. nov. is the only species with this combination of internal characters. Indeed, the internal characters of the two species of *Paromoionchis* gen. nov. with which *P. boholensis* gen. et sp. nov. is sympatric (*P. goslineri* gen. et sp. nov. and *P. tumidus*) are different (Table 3). It must be noted that the known distribution of species of *Paromoionchis* gen. nov. may change as new records are found in the future and so the use of geographic data should only be used with caution for identification.

Distribution (Fig. 6)

Philippines (unit #1): Bohol (type locality), Luzon. Indonesia (unit #2): Ambon, Bali, Halmahera, Kei Islands, Seram, Sulawesi.

Habitat (Figs 39–40)

Unit #1 of *Paromoionchis boholensis* gen. et sp. nov. is found on sandy mud or sand with very little mud, in mangroves or near mangrove trees and is rare (it was found at only four stations). Unit #2 is found in open or dense mangroves, on soft or hard mud, as well as on muddy sand and is common (but not as common as *P. tumidus* unit #1).

Paromoionchis penangensis Dayrat & Goulding gen. et sp. nov.
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Figs 41–44

Etymology

Paromoionchis penangensis gen. et sp. nov. is named after Penang Island, Malaysia, in the Strait of Malacca, which is the type locality.

Material examined

Holotype

MALAYSIA • holotype (26/14 [6037] mm); Peninsular Malaysia, Penang, Pantai Acheh; 05°24.922′ N, 100°11.571′ E; 1 Aug. 2016; station 261; *Avicennia* mangrove, with both very soft mud and hard mud; USMMC 00059.

Other material

INDIA –**Andaman Islands** • 1 spec. (18/10 [1086] mm); Middle Andaman, Rangat, Yerrata, Saban; 12°27.451′ N, 092°53.792′ E; 10 Jan. 2011; station 56; open, impacted mangrove patch by a creek, near village, with medium trees and old logs; BNHS 92 • 2 spec. (18/8 [1100] and 9/6 [1101] mm); Middle Andaman, Rangat, Shyamkund; 12°28.953′ N, 092°50.638′ E; 11 Jan. 2011; station 57; by a large river, deep mangrove with tall trees, small creeks and plenty of old logs, next to a road and a small cemented bridge over a creek; BNHS 53 • 2 spec. (20/10 [1117] and 22/12 [1118] mm); Middle Andaman, Shantipur, Kadamtala; 12°19.843′ N, 092°46.377′ E; 12 Jan. 2011; station 58; open area with hard mud and many old logs, next to a mangrove with medium trees; BNHS 11 • 2 spec. (30/15 [1129] and 12/7 [1130] mm); South Andaman, Bamboo Flat, Shoal Bay; 11°47.531′ N, 092°42.577′ E; 13 Jan. 2011; station 59; open mangrove with medium trees, hard mud, dead logs, next to a road and a small cemented bridge for creek; BNHS 4. – **Maharashtra** • 1 spec. (35/20 [1167] mm); Watad; 17°15.791′ N, 73°17.623′ E; 23 Dec. 2011; station 46; *Avicennia* mangrove, by field, with deep and very watery mud; BNHS 46 • 3 spec. (30/18 [1177], 20/14 [1175] and 15/10 [1173] mm); same data as for preceding;

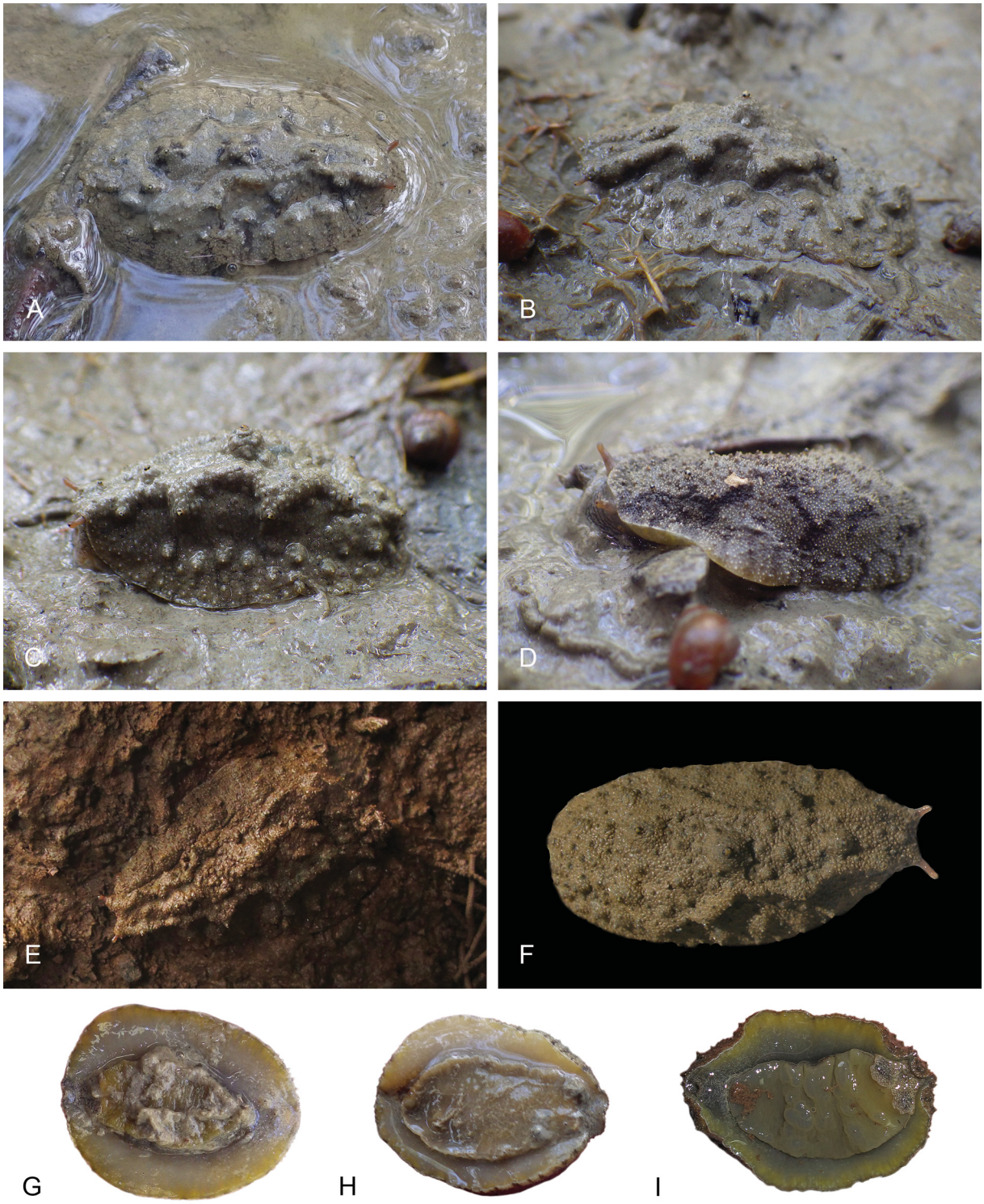

Fig. 41. *Paromoionchis penangensis* gen. et sp. nov., live animals. **A**. Dorsal view, 29 mm long [5990], Malaysia, Matang (USMMC 00060). **B**. Dorsal view, 26 mm long [6039], Malaysia, Penang (USMMC 00063). **C**. Holotype, dorsal view, 25 mm long [6037], Malaysia, Penang (USMMC 00059). **D**. Dorsal view, 22 mm long [6031], Malaysia, Penang (USMMC 00063). **E**. Dorsal view, 37 mm long [1167], India, Maharashtra (BNHS 46). **F**. Dorsal view, 30 mm long [1129], India, Andaman Islands (BNHS 4). **G**. Ventral view, same as D. **H**. Ventral view, same as A. **I**. Ventral view, 27 mm long [1182], India, Maharashtra (BNHS 42).

BNHS 98 • 2 spec. (16/11 [1176] and 27/21 [1182] mm); Aare Ware; 17°04.404′ N, 73°17.747′ E; 24 Dec. 2011; station 47; mangrove with soft mud and some areas with pools, mostly *Avicennia* with a few small *Rhizophora*; BNHS 42.

MALAYSIA – **Peninsular Malaysia** • 2 spec. (30/20 [5990] and 30/20 [5991] mm); Kuala Gula; 04°55.991′ N, 100°26.917′ E; 29 Jul. 2016; station 259; mostly *Avicennia*, a few *Bruguiera* and *Rhizophora*, along a creek, both soft and hard mud; USMMC 00060 • 2 spec. (20/14 [957] and 15/10 [958] mm); Nibong Tebal, Pulau Burung; 05°12.488′ N, 100°25.564′ E; 11 Jul. 2011; station 17; soft mud, open mangrove of *Rhizophora*, with a few *Sonneratia*; USMMC 00061 • 1 spec. (48/35 [6020] mm); Nibong Tebal, Pulau Burung; 05°12.488′ N, 100°25.564′ E; 30 Jul. 2016; station 260; soft mud, open mangrove of *Rhizophora*, with a few *Sonneratia*; USMMC 00062 • 3 spec. (25/12 [6031], 25/18 [6033] and 25/16 [6039] mm); same data as for holotype; USMMC 00063.

Color and morphology of live animals (Fig. 41)

Live animals are most often covered with mud, in which case their dorsal color can hardly be seen. The background of the dorsal notum is brown, occasionally mottled with darker or lighter areas. In addition,

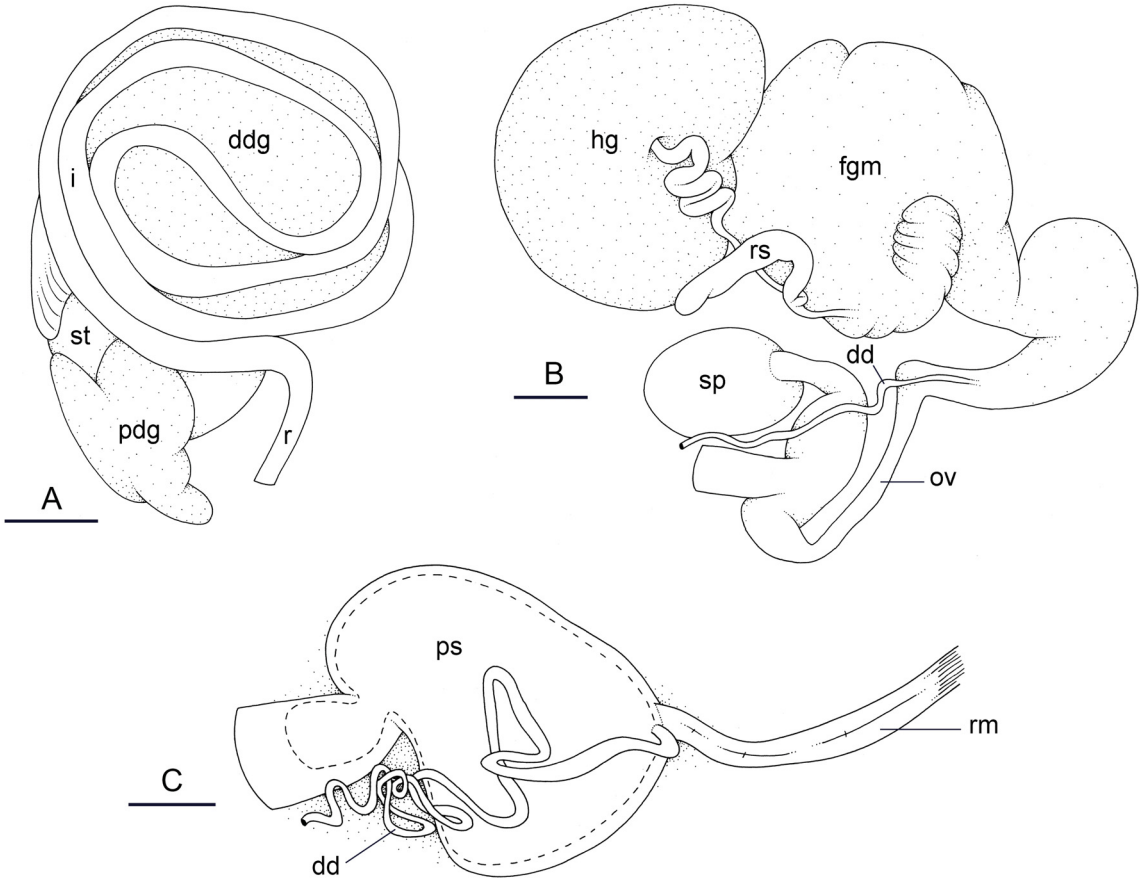

Fig. 42. *Paromoionchis penangensis* gen. et sp. nov., holotype, Malaysia, Penang [6037] (USMMC 00059). **A**. Digestive system. **B**. Posterior hermaphroditic (female) reproductive system. **C**. Male copulatory organs. Abbreviations: dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath (penis inside indicated by dotted line); r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach. Scales: A = 2 mm; B–C = 1 mm.

in some animals, the tip of dorsal papillae (with and without dorsal eyes) can be yellow. The foot is gray, occasionally with a light yellow hue. The hyponotum is uniform gray or gray (inner ring) and yellow (outer ring). The color of both the foot and the hyponotum of an individual can change rapidly, especially when disturbed. The ocular tentacles are brown and may or may not be speckled with white dots, like the head. The ocular tentacles are short (just a few mm long).

Digestive system (Figs 42A, 43)

Radulae measure up to 3.2 mm in length. Examples of radular formulae are presented in Table 4.

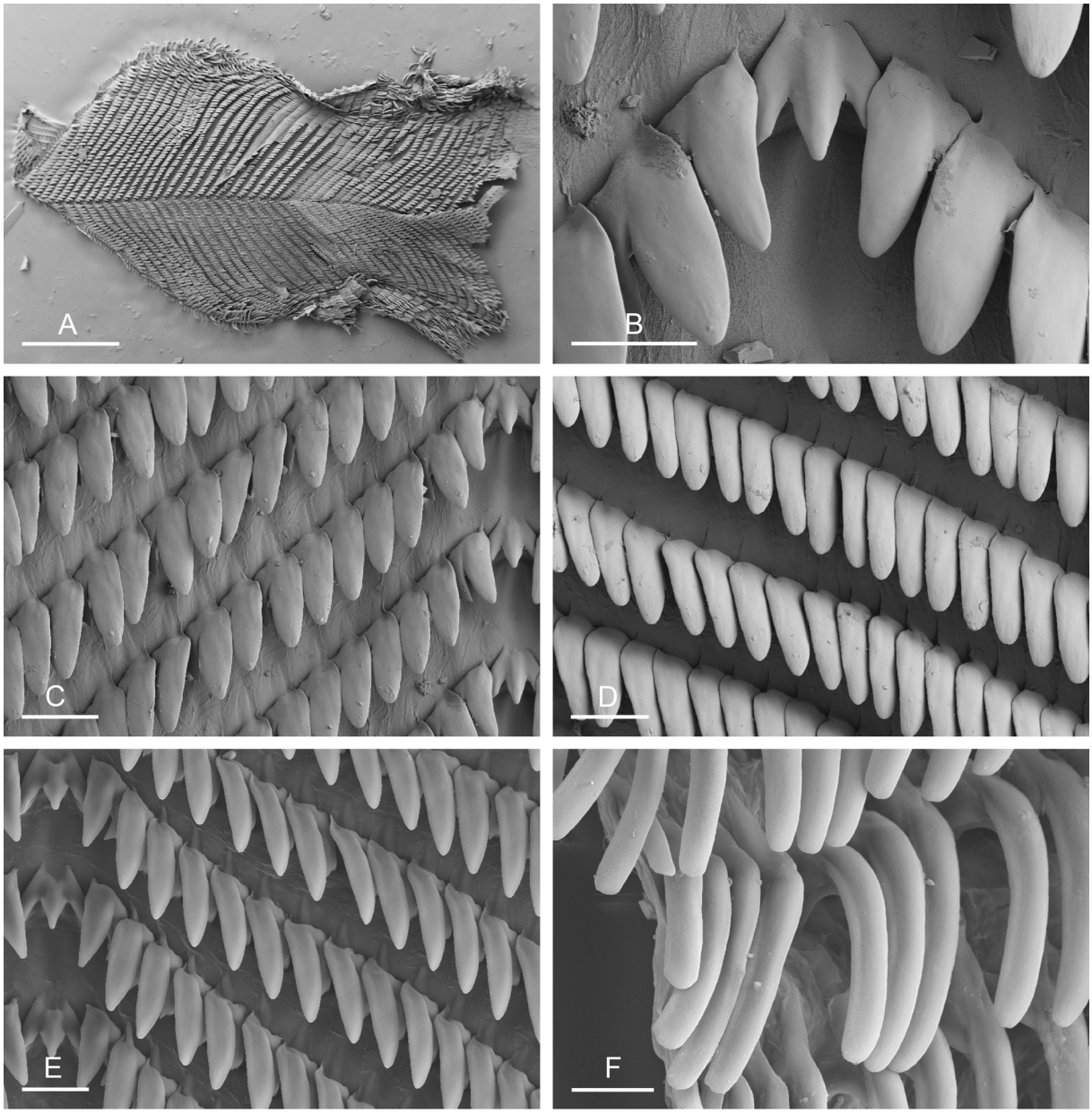

Fig. 43. *Paromoionchis penangensis* gen. et sp. nov., radula. **A**–**D**. Holotype, Malaysia, Penang [6037] (USMMC 00059). A. Entire radula. B. Rachidian and innermost lateral teeth. C. Lateral teeth with rachidian teeth. D. Lateral teeth. **E**–**F**. Western Peninsular Malaysia [6020] (USMMC 00062). E. Lateral teeth with rachidian teeth. F. Outermost lateral teeth. Scales: A = 0.5 mm; B, F = 20 μm; C–E = 30 μm.

Reproductive system (Fig. 42B–C)

In the posterior (female) organs, the distal portion of the oviduct and of the duct to the spermatheca is wider than in other species, which makes sense given the wide penis. The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle). An accessory penial gland is absent. The penial sheath is large (at least ten times as large as the deferent duct). The retractor muscle is strong, long and inserts near the heart. The deferent duct is convoluted, with many loops. Inside the penial sheath, the penis is a large (wider than long), smooth (no hooks), muscular mass.

Distinctive diagnostic features

Externally, *Paromoionchis penangensis* gen. et sp. nov. cannot be reliably distinguished from other species of *Paromoionchis* gen. nov. Its distribution only overlaps with that of *P. tumidus*. Our data suggest that the tips of the dorsal papillae of *P. penangensis* gen. et sp. nov. tend to be paler yellow, while they tend to be brighter yellow in *P. tumidus*. However, the internal anatomy of *P. penangensis* gen. et sp. nov., especially the large penis inside the large penial sheath, is very distinct from that of all other species and reliably distinguishes it from *P. tumidus*.

Fig. 44. *Paromoionchis penangensis* gen. et sp. nov., habitats. **A**. Malaysia, Penang, open *Avicennia* mangrove with different types of mud (station 261, type locality). **B**. Western Peninsular Malaysia, *Rhizophora* and *Sonneratia* mangrove with soft mud, next to a landfill (station 17). **C**. India, Maharashtra, *Avicennia* mangrove with soft mud and a wall of large rocks (station 45). **D**. India, Maharashtra, *Avicennia* mangrove with a few small *Rhizophora*, soft mud and pools (station 47).

Distribution (Fig. 6)

Malaysia: Peninsular Malaysia, Strait of Malacca (type locality). India: Andaman Islands (Bay of Bengal), Maharashtra (W coast of India).

Habitat (Fig. 44)

Paromoionchis penangensis gen. et sp. nov. is found on soft and hard mud, in mangroves or in open areas near mangroves. This species was only found at three stations in the Strait of Malacca, three stations in the Andaman Islands (Bay of Bengal), and three stations in Maharashtra (W coast of India). However, at each station it was found to be quite abundant.

Paromoionchis goslineri Dayrat & Goulding gen. et sp. nov.
urn:lsid:zoobank.org:act:E375A628-4AE6-4E10-B424-D4BBF58F8941
Figs 45–51

Etymology

Paromoionchis goslineri gen. et sp. nov. is dedicated to Dr. Terry Gosliner, Senior Curator at the California Academy of Sciences, San Francisco, California, USA, who has been exploring the marine life of the Batangas region for many years, where this new species was found, and, more importantly, for years ago providing the first author with a great post-doctoral opportunity to focus on alpha-taxonomy.

Material examined

Holotype

PHILIPPINES • holotype (25/15 [3233] mm); Luzon, Calantagan, Batangas; 13°51.264′ N, 120°37.383′ E; 8 Jul. 2014; station 185; next to village, impacted narrow mangrove forest of *Avicennia* by the shore; PNM 041271.

Other material

INDONESIA – **Sulawesi** • 1 spec. (20/14 [2210] mm); Bahoi; 01°43.355′ N, 125°01.232′ E; 12 Mar. 2013; station 88; sand, small rocks and pieces of wood outside narrow coastal mangrove; UMIZ 00161 • 1 spec. (18/10 [2241] mm); Sondaken; 01°21.777′ N, 124°32.594′ E; 13 Mar. 2013; station 89; mostly *Rhizophora*, with sand, small rocks and pieces of wood outside narrow coastal mangrove; UMIZ 00153. – **Bali** • 3 spec. (22/15 [3060], 22/15 [3066] and 27/20 [3068] mm); Denpasar; 08°46.126′ S, 115°10.803′ E; 2 Apr. 2014; station 154; large mangrove by road, with shallow mud; UMIZ 00154 • 4 spec. (20/12 [3072], 17/10 [3074], 22/14 [3078] and 24/14 [3079] mm); Gilimanuk; 08°10.259′ S, 114°26.606′ E; 3 Apr. 2014; station 155; from high intertidal with water pools and many mounds up to shore with sand and rocks; UMIZ 00155 • 2 spec. (22/10 [3118] and 37/20 [3120] mm); Gilimanuk; 08°10.156′ S, 114°26.652′ E; 4 Apr. 2014; station 156; muddy mangrove with *Rhizophora* and *Avicennia* trees; UMIZ 00156. – **Timor** • 2 spec. (12/7 [5890] and 15/7 [5891] mm); Oesapa; 10°08.732′ S, 123°38.096′ E; 11 Jul. 2016; station 250; sandy part of mangrove, with *Sonneratia* and *Avicennia*; UMIZ 00157. – **Halmahera** • 2 spec. (24/16 [5072] and 32/23 [5073] mm); Dodinga; 00°51.348′ N, 127°38.504′ E; 9 Mar. 2015; station 206; back of mangrove, high intertidal, with ferns and mounds; UMIZ 00158 • 1 spec. (35/22 [5145] mm); Gamkonora; 01°26.911′ N, 127°31.625′ E; 21 Mar. 2015; station 219; mostly *Rhizophora*, with some sandy and open muddy areas; UMIZ 00159. – **Ambon** • 1 spec. (12/7 [3555] mm); Wai; 03°34.652′ S, 128°19.526′ E; 15 Feb. 2014; station 132; narrow band of old *Avicennia* trees on sandy mud, with old logs; UMIZ 00160.

PHILIPPINES – **Luzon** • 2 spec. (22/15 [3221] and 20/16 [6049] mm); Calantagan, Batangas; 13°53.278′ N, 120°37.124′ E; 8 Jul. 2014; station 184; narrow forest on the shore, with *Avicennia* and young *Rhizophora*; PNM 041272 • 1 spec. (28/20 [3232] mm); same data as for holotype; PNM 041273.

Color and morphology of live animals (Figs 45–46)

Live animals are most often covered with mud, in which case their dorsal color can hardly be seen. The background of the dorsal notum is gray-brown, mottled with darker and lighter areas. In addition, in some animals, the tip of dorsal papillae (with and without dorsal eyes) can be lighter (pale yellow or white). The foot and the hyponotum are dark or light gray. The color of both the foot and the hyponotum of an individual can change rapidly, especially when disturbed. The ocular tentacles are gray-brown and may or may not be speckled with white dots, like the head. The ocular tentacles are short (just a few millimeters long). The tip of dorsal papillae is usually white or pale yellow, but not always (in any case generally covered with mud).

Digestive system (Figs 47A, 48A, 49–50)

Radulae measure up to 2.6 mm (unit #1) and 2.2 mm (unit #2) in length. Examples of radular formulae are presented in Table 4.

Reproductive system (Figs 47B–C, 48B–C)

The male anterior organs consist of the penial complex (penis, penial sheath, vestibule, deferent duct, retractor muscle). An accessory penial gland is absent. The penial sheath is narrow and elongated. In unit #1, the retractor muscle is very short (much shorter than the penial sheath), inserting on the body

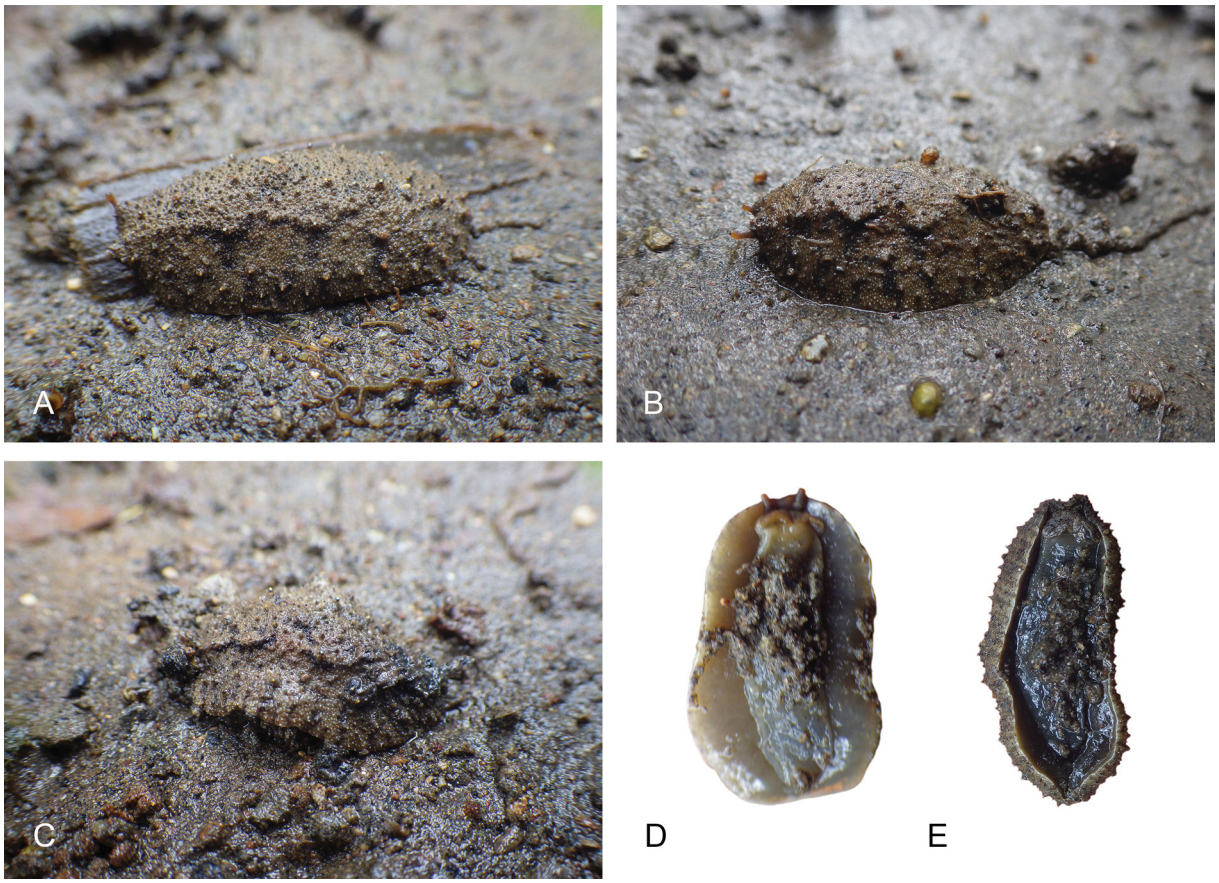

Fig. 45. *Paromoionchis goslineri* gen. et sp. nov. unit #1, live animals, Philippines, Luzon. **A**. Dorsal view, 30 mm long [3232] (PNM 041273). **B**. Dorsal view, 22 mm long [3221] (PNM 041272). **C**. Holotype, dorsal view, 25 mm long [3233] (PNM 041271). **D**. Ventral view, same as B. **E**. Ventral view, same as A.

wall near the nervous system, or vestigial (its distal end being free in the visceral cavity, with no clear insertion). In unit #2, the retractor muscle is long (as long as the penial sheath), inserting near the heart. The deferent duct is also highly convoluted, with many loops. Inside the penial sheath, the penis is a narrow, elongated, soft, smooth (no hooks) and hollow tube of approximately 200 µm in diameter.

Distinctive diagnostic features

Externally, *Paromoionchis goslineri* gen. et sp. nov. cannot be distinguished from other species of *Paromoionchis* gen. nov. The ventral side (foot and hyponotum) is gray, i.e., never yellow or orange. Unfortunately, a gray ventral side can occasionally be found in all other species of the genus, so the use of that color trait is not fully reliable for identification. However, the internal anatomy of *P. goslineri*

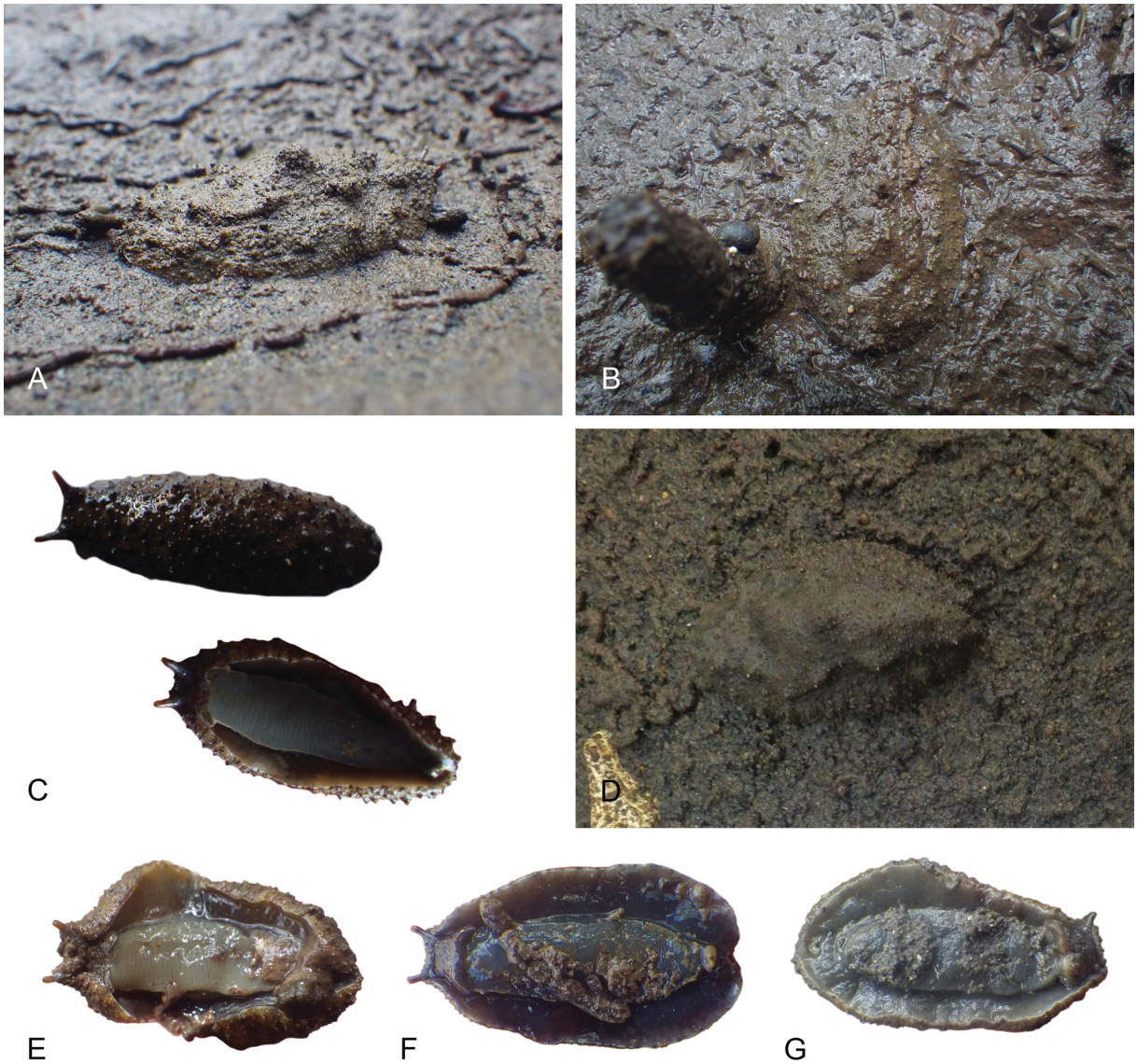

Fig. 46. *Paromoionchis goslineri* gen. et sp. nov. unit #2, live animals. **A**. Dorsal view, 33 mm long [3120], Indonesia, Bali (UMIZ 00156). **B**. Dorsal view, 32 mm long [5073], Indonesia, Halmahera (UMIZ 00158). **C**. Dorsal and ventral views, 18 mm long [2241], Indonesia, Sulawesi (UMIZ 00153). **D**. Dorsal view, 24 mm long [3079], Indonesia, Bali (UMIZ 00155). **E**. Ventral view, 26 mm long [5072], Indonesia, Halmahera (UMIZ 00158). **F**. Ventral view, 16 mm long [5891], Indonesia, Timor (UMIZ 00157) **G**. Ventral view, 26 mm long [3066], Indonesia, Bali (UMIZ 00154).

gen. et sp. nov. (no accessory penial gland, thin penis with no hooks) is very distinctive and can be used for a fully reliable identification. The only other species of *Paromoionchis* gen. nov. without an accessory penial gland, *P. penangensis* gen. et sp. nov., differs greatly from *P. goslineri* gen. et sp. nov. anatomically because its penis is very large. Units #1 and #2 of *P. goslineri* gen. et sp. nov. differ slightly with respect to the penial retractor: it is short and thin, inserting near the nervous system, or even vestigial in unit #1, while it is as long as the penial sheath, inserting near the heart in unit #2. However, given that only four specimens could be dissected in unit #1, it is very possible that intermediates may be found in the future, especially considering that units #1 and #2 are widely distant geographically.

Distribution (Fig. 6)

Philippines (unit #1): Luzon (type locality). Indonesia (unit #2): Ambon, Bali, Halmahera, Sulawesi and Timor.

Habitat (Fig. 51)

Paromoionchis goslineri gen. et sp. nov. unit #1 is found on mud, in *Avicennia* forests near the shore and is rare (only four specimens are known from two stations). Unit #2 is found on soft and hard mud, in mangroves or in open areas near mangroves and is rare (except in Bali, where several specimens were found at a few stations).

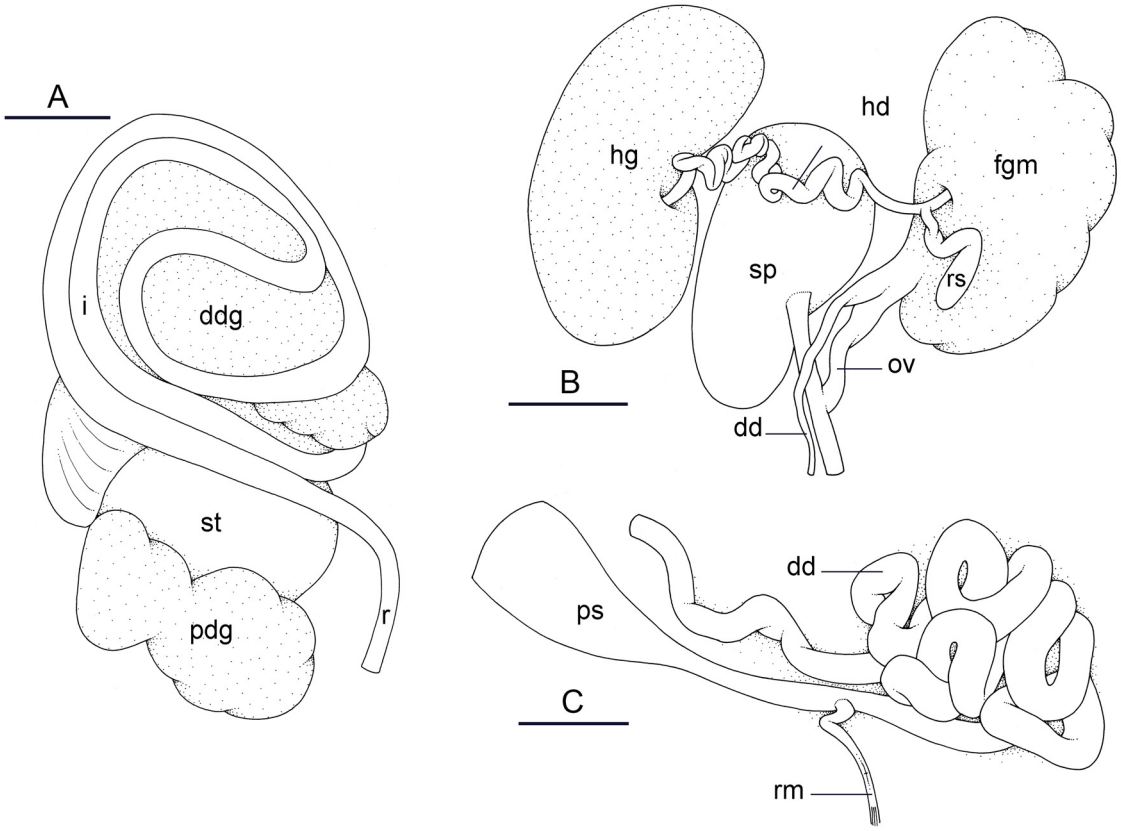

Fig. 47. *Paromoionchis goslineri* gen. et sp. nov. unit #1, holotype, Philippines, Luzon [3233] (PNM 041271). **A**. Digestive system. **B**. Posterior hermaphroditic (female) reproductive system. **C**. Male copulatory organs. Abbreviations: dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath; r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach. Scales: A–B = 2 mm; C = 1 mm.

Discussion

Nomenclature

Five species names are regarded as names of doubtful application (nomina dubia) for a variety of reasons (the type locality is too vague, the original description is not informative enough, the type material is destroyed or lost): *Onchidium griseum* Plate, 1893, *O. lixii* Labbé, 1934, *O. palaense* Semper, 1880, *O. papuanum* Semper, 1880 and *O. straelenii* Labbé, 1934.

Onchidium palaense Semper, 1880 could belong to *Paromoionchis* gen. nov., but its application is doubtful and it is regarded as a nomen dubium. The publication date for *O. palaense* is 1880 because it is the year in which Semper's plate 23 was published. ICZN Article 12.2.7 applies and Semper's fig. 8 on plate 23 is an indication accompanying the name. The written description of *O. palaense* was published two years later (Semper 1882: 275–276, pl. 21, fig. 8). Its type locality is Aibukit, Palau Islands, in the western Pacific. However, the type material (two syntypes) could not be located, which makes it impossible to determine some key characters not described by Semper. Semper indicated the absence of a rectal gland and of an accessory penial gland, but *O. palaense* cannot be reliably assigned to a genus without information on its digestive system type (type I or type II), because slugs without a rectal gland or an accessory penial gland are found in more than one clade. The position of the male aperture (between the two eye tentacles) seems to suggest that *O. palaense* could belong to *Paromoionchis* gen. nov. However, the position of the male aperture cannot be verified here and Semper did not always describe it accurately (see our remarks on *P. daemelii* and *P. tumidus* above). That the

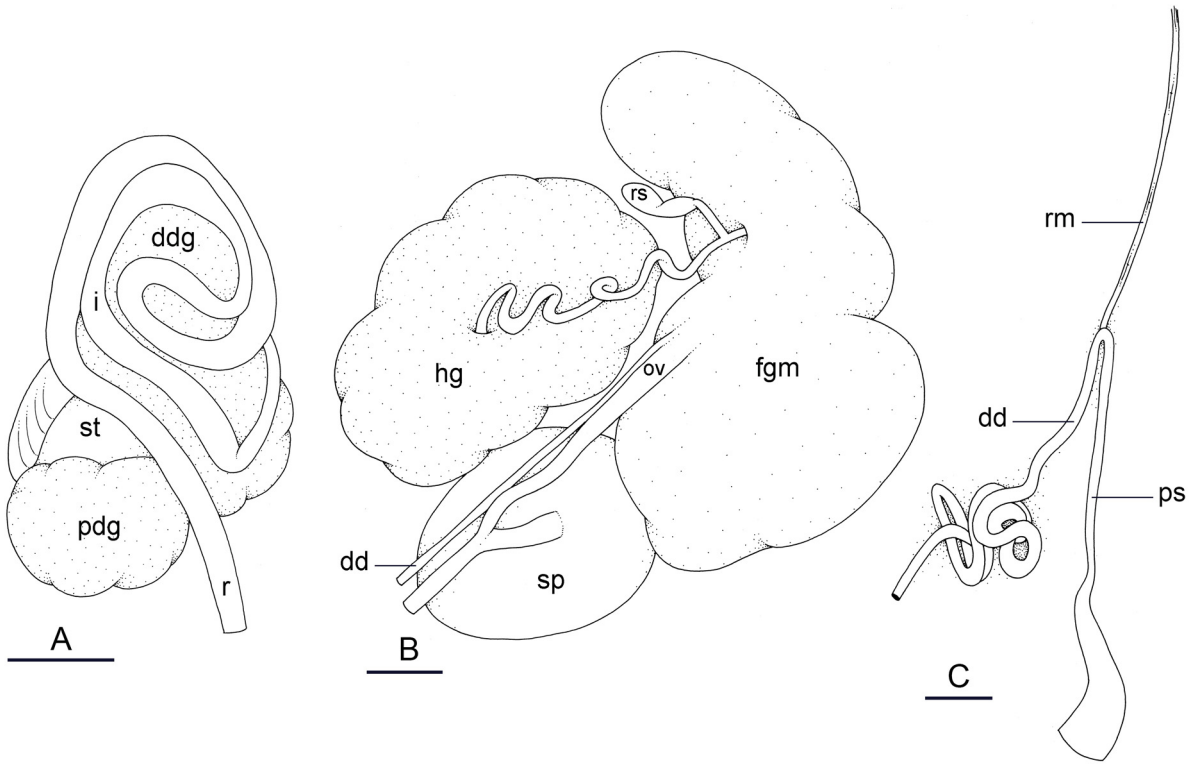

Fig. 48. *Paromoionchis goslineri* gen. et sp. nov. unit #2, Indonesia, Sulawesi [2241] (UMIZ 00153). **A**. Digestive system. **B**. Posterior hermaphroditic (female) reproductive system. **C**. Male copulatory organs. Abbreviations: dd = deferent duct; ddg = dorsal lobe of digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior lobe of digestive gland; ps = penial sheath; r = rectum; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach. Scales: A = 2 mm; B–C = 1 mm.

original description of *Onchidium palaense* by Semper does not provide enough information to decide on a generic placement is demonstrated by the fact that Hoffmann (1928: 82) thought that *O. palaense* and *O. gracile* Stantschinsky, 1907 were synonyms because of a "striking agreement" in their anatomy. However, *O. gracile* belongs to a different genus characterized by a digestive system of type I and is now known as *Wallaconchis gracilis* (see Goulding *et al.* 2018c). When the type material is lost and the original description is incomplete, a name can apply to basically anything! Therefore, it is more reasonable to regard *O. palaense* as a nomen dubium. Even if a distinct species of *Paromoionchis* gen. nov. were to be found one day in Palau, there is no guarantee that it would actually belong to Semper's species. Finally, Plate (1893: 180) reported *O. palaense* from Ambon based on a single specimen (with intestinal loops of type I). However, Plate acknowledged that the identification of that specimen was uncertain.

Onchidium papuanum Semper, 1880 could belong to *Paromoionchis* gen. nov., but is regarded as a nomen dubium because the type locality is too vague and because the type material is lost. Since Semper's plate 23 was published in 1880, ICZN Article 12.2.7 applies and Semper's fig. 9 on plate 23 is an indication accompanying the name. The written description of *O. papuanum* was published two years later (Semper 1882: 276–277, pl. 21, fig. 17). The type locality ("New Guinea") is too vague because it could be anywhere on the shore of the entire island of New Guinea (i.e., Indonesia and Papua New Guinea). Also, the type material could not be located and is likely lost. As a result, important characters cannot be checked, such as the type of the digestive system, which Semper does not mention. Slugs with no rectal gland and no accessory penial gland are found in more than one clade, so *O. papuanum* may or may not belong to *Paromoionchis* gen. nov. Even if *O. papuanum* was assumed to belong to

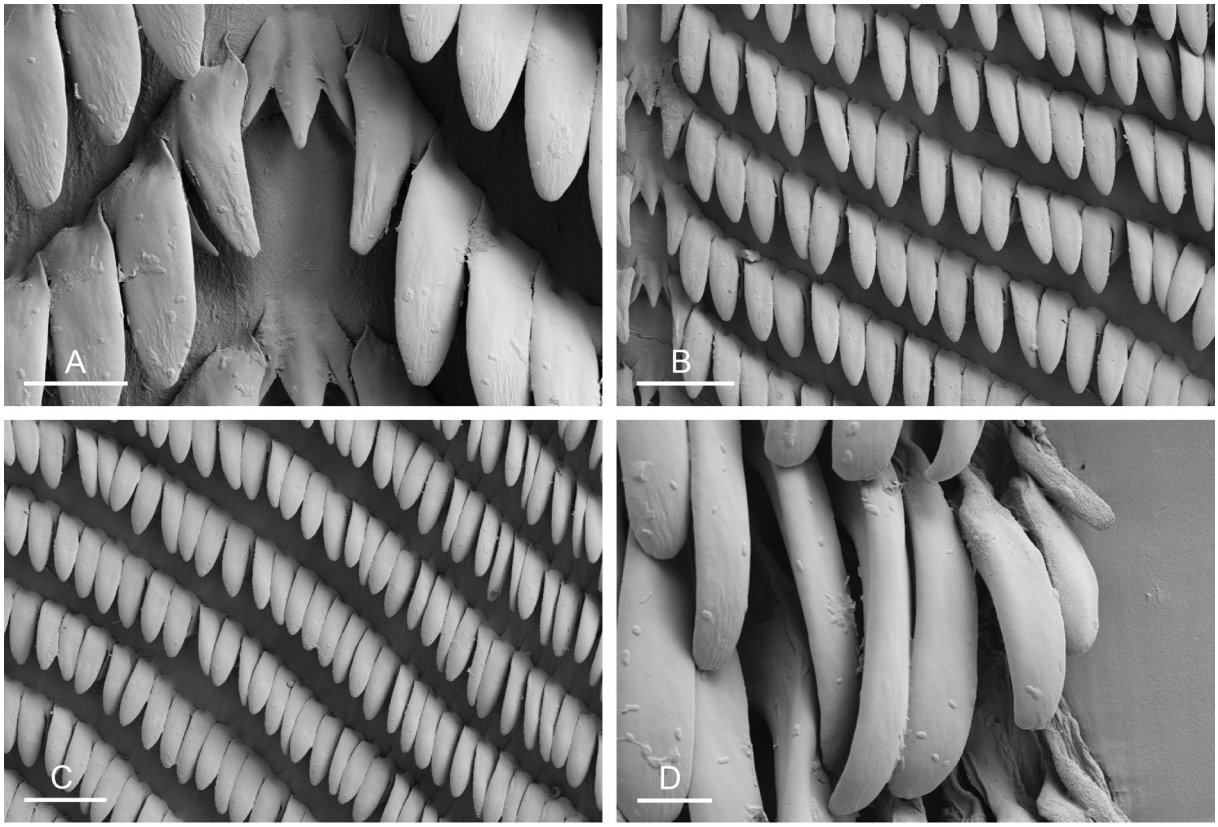

Fig. 49. *Paromoionchis goslineri* gen. et sp. nov. unit #1, radula, Philippines, Luzon [6049] (PNM 041272). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A = 20 µm; B–C = 50 µm; D = 10 µm.

Paromoionchis gen. nov., its male anatomy (penis with a large spherical vestibule) does not match that of any of the species described here. Previous authors have struggled with this species. Tapparone-Canefri (1883: 215) transferred *O. papuanum* to *Peronia*, as *Peronia papuana*, with no justification. Bretnall (1919: 317) commented on the anatomy of *O. papuanum*, which he regarded as valid, but without examining any new material. Based on two non-type specimens from New Guinea, Labbé (1934a: 230) transferred *O. papuanum* to his genus *Paraoncidium* (which is actually a junior synonym of *Onchidina* Semper, 1882), but acknowledged that the identification of those two specimens as *Paraoncidium papuanum* was only probable.

Onchidium griseum Plate, 1893 belongs to *Paromoionchis* gen. nov., but is regarded as a nomen dubium because the type locality is uncertain. In the original description (Plate 1893: 179), the specimens are said to be "of unknown origin, probably from one of the Polynesian islands." Also, no locality is indicated on the labels of the four syntypes (ZMB 45657). However, given its anatomy (digestive system of type II, no rectal gland, presence of an accessory penial gland and a male opening left of the right eye tentacle), we know that *O. griseum* belongs to *Paromoionchis* gen. nov.

Onchidium straelenii Labbé, 1934 may or may not belong to *Paromoionchis* gen. nov., but is regarded as a nomen dubium. The two syntypes used by Labbé were located (RBINS) and an examination of them revealed that his description is seriously erroneous regarding several important characters. For instance, Labbé (1934b: 76, our translation) described "numerous, small and very ramified gills" on the dorsal notum, which explains why Labbé (1934a) later transferred that species to *Scaphis*, a genus he created for onchidiids with dorsal gills. However, there are no gills at all on the notum of the two

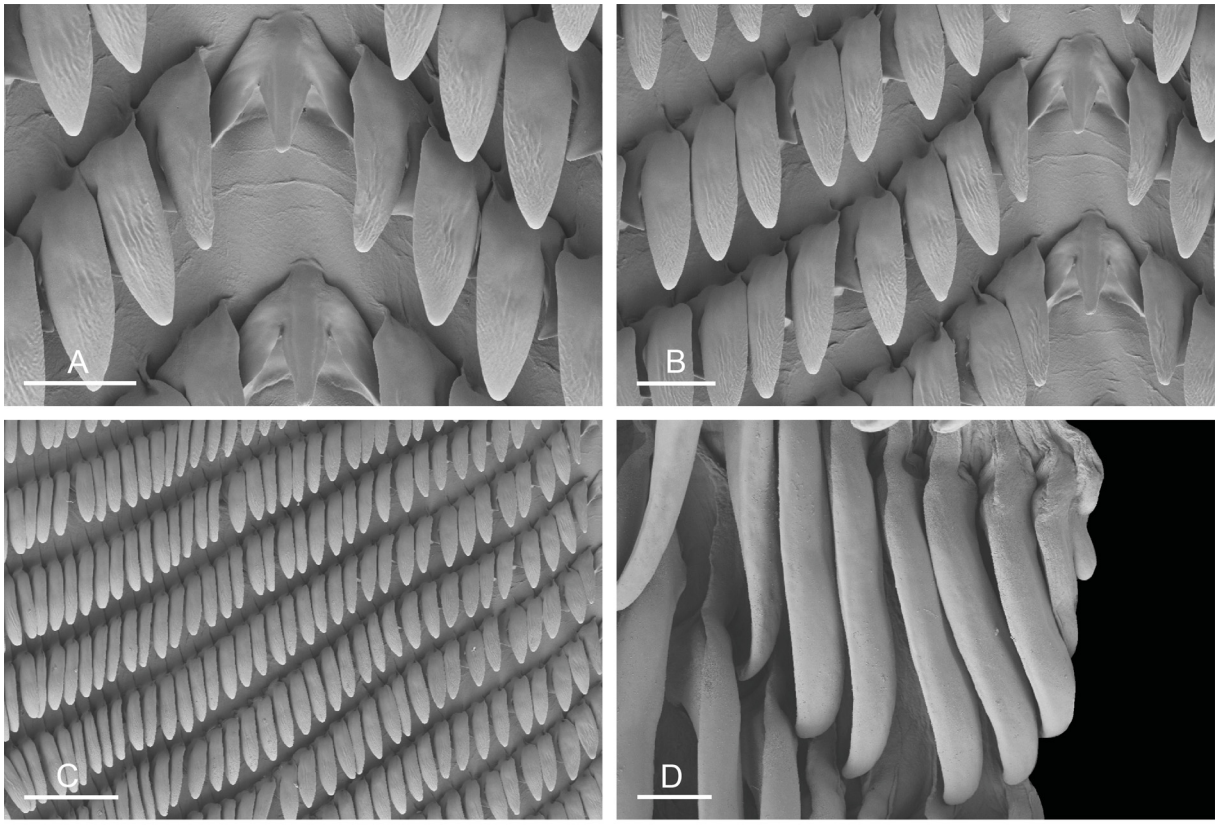

Fig. 50. *Paromoionchis goslineri* gen. et sp. nov. unit #2, radula, Indonesia, Bali [3078] (UMIZ 00155). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scales: A–B = 20 μm; C = 30 μm; D = 10 μm.

Fig. 51. *Paromoionchis goslineri* gen. et sp. nov., habitats. **A**. Philippines, Luzon, impacted mangrove next to a village, narrow band of *Avicennia* by the shore (station 185, type locality). **B**. Indonesia, Sulawesi, mostly *Rhizophora*, with sand, small rocks and pieces of wood outside narrow coastal mangrove (station 89). **C**. Indonesia, Bali, short mangrove shrubs, high intertidal, muddy area with pools (station 155). **D**. Indonesia, Bali, short mangrove shrubs high in intertidal, muddy area with pools (station 156). **E**. Indonesia, Halmahera, *Rhizophora* trees in open mangrove with sandy and muddy areas (station 219).

syntypes of *O. straelenii*. Furthermore, Labbé described a digestive system of type I, but it is clearly of type II. Sadly, these kinds of mistakes are not unusual in Labbé's work. Consequently, these mistakes make it impossible to trust any of the other features he described for the anatomy of the male apparatus (accessory penial gland present and penis with hooks), which cannot be checked because the male parts are missing in both syntypes. The characters of the syntypes (digestive system of type II, male aperture clearly on the left of the right eye tentacle, no rectal gland) suggest that *O. straelenii* belongs to *Paromoionchis* gen. nov. However, its application remains doubtful, although it is clear that *O. straelenii* does not belong to *Peronia*, the clade including all onchidiids with dorsal gills.

Onchidium lixii Labbé, 1934 likely belongs to *Paromoionchis* gen. nov. but it is regarded as a nomen dubium because the original description is confusing and the type locality ("New Guinea") is too vague. The four syntypes used by Labbé were located (MNHN Malacologie 22955). An examination of them revealed that the original description is based on specimens that belong to two species. Three syntypes were fully dissected by Labbé. In two of these syntypes (both 27/22 mm long), the male parts are completely missing, so we cannot verify the presence of an accessory penial gland (present according to Labbé's original description). The digestive system of one of these syntype is of type II (as described by Labbé); the digestive type of the second syntype could not be checked because it was destroyed by Labbé. In the third syntype dissected by Labbé (25/20 mm), the male parts are still inside the specimen, there is no accessory penial gland, and it does not seem that this gland was removed by Labbé. Thus, the presence of an accessory penial gland cannot be confirmed in that syntype. Its digestive system is of type II. Finally, a fourth syntype was left almost intact by Labbé, who only cut a small square of the dorsal notum but did not open it (and so none of its internal organs were touched by Labbé). Some characters of that fourth syntype are consistent with Labbé's original description: dorsum with no gills, digestive system of type II, and no rectal gland. However, an accessory penial gland is clearly absent. All four syntypes must belong to some species of *Paromoionchis* gen. nov., because they share a unique combination of two traits which characterizes this genus (a digestive system of type II and no rectal gland). However, those four syntypes may not all belong to the same species. If Labbé did really see an accessory penial gland in two (or three) syntypes, then they belong to a different species than the fourth syntype (in which the accessory penial gland is absent). If Labbé made a mistake and described an accessory penial gland that did not exist, then all those syntypes could belong to the same species. The fact that Labbé actually illustrated an accessory penial gland and its spine (Labbé 1934a: fig. 67) is not a guarantee that he actually saw it. We know for a fact that he illustrated various structures that he could not have seen. For instance, Labbé (1934a: 206) erroneously described dorsal gills and an accessory penial gland in the syntypes of *Onchidium ater*. Because of the uncertainty regarding the accessory penial gland, the application of the name *O. lixii* remains doubtful. One could designate the syntype which Labbé did not open as a lectotype. However, this would not help with the fact that the type locality ("New Guinea") is too vague; the syntypes could have been collected anywhere in West Papua (Indonesia), Papua (Indonesia) or mainland Papua New Guinea. So, in conclusion, *Onchidium lixii* is regarded as a nomen dubium.

Diversity

The analysis of three distinct data sets (comparative anatomy, mitochondrial DNA sequences and nuclear DNA sequences) provides invaluable insight on species boundaries. The mitochondrial units within *P. tumidus*, *P. boholensis* gen. et sp. nov. and *P. goslineri* gen. et sp. nov. are found to be reciprocally monophyletic and are separated by a wide gap in genetic divergences using mitochondrial DNA sequences (Figs 1–2, 5). However, they are not regarded as species for two main reasons: 1) nuclear markers suggest that there still is gene flow between mitochondrial units (because units are not recovered as reciprocally monophyletic in analyses based on nuclear markers) and 2) mitochondrial units are not distinct anatomically, especially for the male copulatory apparatus, which is essential for maintaining or preventing interbreeding. Naturally, one cannot completely exclude the hypothesis that

nuclear markers are not variable enough to distinguish species and that the least-inclusive units based on mitochondrial DNA sequences (especially COI) should be regarded as species. However, it seems easier to interpret those mitochondrial units as divergent haplotypes that have been maintained due to maternal inheritance. Studies on land snails and slugs (Stylommatophora), to which onchidiids are closely related, have shown that very old (20 million years) distinct haplotypes can co-occur within a single population (e.g., Thomaz *et al.* 1996; Pinceel *et al.* 2005). Because of the multiple changes in sea levels in South-East Asia, especially during the glacial-interglacial cycles in the Quaternary (e.g., Bowen *et al*. 2016), there were many opportunities for small populations to be isolated in refuges at regular periods. Furthermore, the results from nuclear sequences suggest that isolation has not always led to speciation, because gene flow is still happening between individuals representing old, distinct mitochondrial haplotypes. The present study shows the critical importance of using nuclear DNA sequences in addition to mitochondrial DNA sequences because, had we used mitochondrial DNA sequences alone, we could have erroneously postulated the existence of nine species of *Paromoionchis* gen. nov., including several cryptic species.

Prior to the present study, only two species of *Paromoionchis* gen. nov. were known: *P. tumidus*, for which there are three junior synonyms, and *P. daemelii*, described once. These two species were originally classified in *Onchidium*, traditionally used by default for most Indo-West Pacific onchidiids. However, *Onchidium* refers to a small clade of only three species (Dayrat *et al.* 2016) from which species of *Paromoionchis* gen. nov. highly differ anatomically (for example, the latter slugs lack a rectal gland). Also, molecular phylogenetics strongly supports the monophyly of *Paromoionchis* gen. nov., with respect to all other onchidiids. Both *P. tumidus* and *P. daemelii* were known exclusively from the types, showing that it has remained very difficult for authors to re-identify them. Here, dozens of new records are provided for *P. tumidus*, from the Andaman Islands (Bay of Bengal) all the way to the subtropical waters of Japan (33° N) and southeastern Australia (33° S). It is not surprising that *P. tumidus* was described four different times, because it is a very common species across its geographic distribution. New records are provided for *P. daemelii* (in Queensland) and it is shown to be endemic to eastern Australia.

The three other species of *Paromoionchis* gen. nov. are new to science. One might wonder how those species of large slugs have remained unnoticed for so long. However, it is not so surprising considering that the mangroves of South-East Asia have been very poorly explored and that these new species tend to be rare and found at only a few of the numerous stations that were visited (more than 260 stations across the Indo-West Pacific).

Species of *Paromoionchis* gen. nov. all live on mud, in or near mangroves. They are mostly found directly on the mud surface, which is their preferred habitat, but they can also be found on old logs covered with mud. Most species live on both soft mud (saturated in water) and hard mud (not saturated in water). Occasionally, some species (*P. tumidus*, *P. daemelii*, *P. boholensis* gen. et sp. nov.) can also be found on muddy sand (sand that is slightly muddy, usually with a few *Avicennia* trees). It is interesting to notice that some onchidiid genera seem to be more or less specialized to a particular habitat: for instance, *Peronina* is specialized to very soft mud, *Melayonchis* to tree roots and trunks, *Platevindex* to tree trunks and old logs covered with mud and *Peronia* to the rocky intertidal. We have never found *Paromoionchis* gen. nov. in the rocky intertidal and only very occasionally have we found it on old logs (mostly *P. tumidus*).

Each onchidiid genus is characterized by a distinct combination of anatomical characters. Thus, all onchidiids can easily be identified at the generic level as long as some key anatomical characters are known (presence or absence of dorsal gills, type of intestinal loops, position of the male opening, absence or presence of rectal gland, absence or presence of an accessory penial gland). Members of *Paromoionchis* gen. nov. are characterized by lacking dorsal gills and a rectal gland, and by having a male opening below and to the left of the right eye tentacle and intestinal loops of type II. Furthermore,

the monophyly of each genus is strongly supported by molecular data. Within each onchidiid genus, however, it is common for species of to be indistinguishable externally, although in most cases species differ internally, especially for the male copulatory apparatus. Species of *Paromoionchis* gen. nov. are cryptic externally due to their similar color patterns and to high individual variation, but they are distinct internally (Table 3).

Identification key

A key is provided here to help identify the five species of *Paromoionchis* gen. nov. Because species cannot be distinguished externally, the key is based on internal characters of reproductively mature specimens.

1. Accessory penial gland absent 2
– Accessory penial gland present 3

2. Penis large, within large penial sheath .....***P. penangensis*** gen. et sp. nov. (W India to Malacca Strait)
– Penis thin, within thin penial sheath .....***P. goslineri*** gen. et sp. nov. (Indonesia and Philippines)

3. Penial retractor muscle reaches heart; thin penis with hooks ....***P. tumidus*** (Semper, 1880) (Andaman Islands to subtropical waters of SE Australia and S Japan)
– Penial retractor muscle very short, vestigial, or absent; thin penis with no hooks 4

4. Accessory penial gland spine < 1.8 mm in length ....***P. boholensis*** gen. et sp. nov. (Indonesia and Philippines)
– Accessory penial gland spine > 2.5 mm in length .....***P. daemelii*** gen. et sp. nov. (SE Australia)

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