M o n o g r a p h

urn:lsid:zoobank.org:pub:FE4ED74A-3FE6-4CA6-A116-CB3AF46826F7

Systematic revision of *Platevindex* Baker, 1938 (Gastropoda: Euthyneura: Onchidiidae)

Tricia C. GOULDING [1], Adam J. BOURKE [2], Joseph COMENDADOR [3],
Munawar KHALIL [4], Ngo Xuan QUANG [5], Shau Hwai TAN [6],
Siong Kiat TAN [7] & Benoît DAYRAT [8,*]

[1,8] Department of Biology, Pennsylvania State University, University Park, PA 16802, USA.
[1] Current address: Smithsonian Institution, National Museum of Natural History,
PO Box 37012, MRC 163, Washington, DC, 20013, USA.
[2] College of Engineering, Information Technology and the Environment,
Charles Darwin University, Ellengowan Dr., Casuarina, NT 0810, Australia.
[3] National Museum of the Philippines, Taft Ave., Ermita, Manila, 1000 Metro Manila, Philippines.
[4] Department of Marine Science, Faculty of Agriculture, Universitas Malikussaleh,
Reuleut Main Campus, Kecamatan Muara Batu, North Aceh, Aceh, 24355, Indonesia.
[5] Institute of Tropical Biology, Vietnam Academy of Science and Technology,
85 Tran Quoc Toan Street, District 3, Ho Chi Minh City, Vietnam.
[5] Graduate University of Science and Technology, Vietnam Academy of Science and Technology,
18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam.
[6] Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia.
[6] Marine Science Laboratory, School of Biological Sciences,
Universiti Sains Malaysia, 11800 Minden Penang, Malaysia.
[7] Lee Kong Chian Natural History Museum, 2 Conservatory Dr,
National University of Singapore, 117377, Singapore.

[*] Corresponding author: bad25@psu.edu
[1] Email: tc.goulding@gmail.com
[2] Email: adamjohn.bourke@gmail.com
[3] Email: joseph.comendador@gmail.com
[4] Email: khalil@unimal.ac.id
[5] Email: ngoxuanq@gmail.com
[6] Email: aileen@usm.my
[7] Email: nhmtsk@nus.edu.sg

[1] urn:lsid:zoobank.org:author:6009A165-E73E-4124-96C6-C143FC51B18F
[2] urn:lsid:zoobank.org:author:AAF38199-57BF-4E7E-A888-468A9B01720C
[3] urn:lsid:zoobank.org:author:0EAAEF74-7E54-47BA-9A3A-D3A4ED40AD85
[4] urn:lsid:zoobank.org:author:6D38234D-0DE1-4CDE-9F7E-603070C9B27D
[5] urn:lsid:zoobank.org:author:AD2EB983-517E-435A-BEDB-B51BC442D42C
[6] urn:lsid:zoobank.org:author:6E9B8F28-EFCC-42F1-A7C4-3957C92995AA
[7] urn:lsid:zoobank.org:author:1BFA4D8E-30CE-4DC4-A6C2-64E0281996DF
[8] urn:lsid:zoobank.org:author:192B0AF4-A4B0-4129-8422-DEF8D0FB4A45

Abstract. In the Indo-West Pacific, intertidal slugs of the genus *Platevindex* Baker, 1938 are common in mangrove forests, where they typically live on the roots and trunks of mangrove trees. These slugs are easily distinguished from most onchidiids by their hard notum and narrow foot, but despite their large size and abundance, species diversity and geographic distributions have remained a mystery. With the aid of new collections from across the entire Indo-West Pacific, the taxonomy of *Platevindex* is revised using an integrative approach (natural history field observations, re-examination of type specimens, mitochondrial and nuclear DNA sequences, and comparative anatomy). In this monograph, nine species of *Platevindex* are recognized, including one new to science: *P. amboinae* (Plate, 1893), *P. applanatus* (Simroth, 1920) comb. nov., *P. aptei* Goulding & Dayrat sp. nov., *P. burnupi* (Collinge, 1902) comb. nov., *P. coriaceus* (Semper, 1880), *P. latus* (Plate, 1893), *P. luteus* (Semper, 1880), *P. martensi* (Plate, 1893) and *P. tigrinus* (Stoliczka, 1869) comb. nov. Five species names are recognized as junior synonyms, four of which are new, and two *Platevindex* names are regarded as *nomina dubia*. One new subspecies is also recognized: *P. coriaceus darwinensis* Goulding & Dayrat subsp. nov. Most species were previously known only from the type material and many new geographic records are provided across the Indo-West Pacific, from South Africa to the West Pacific (Japan, New Ireland and New Caledonia).

Keywords. Biodiversity, Indo-West Pacific, integrative taxonomy, revisionary systematics, South-East Asia.

Table of Contents

Introduction

In the tropics and subtropics, mangrove forests are home to a diverse array of invertebrates, fish and birds, and provide important ecosystem services (Dorenbosch *et al*. 2005; Lee 2008; Luther & Greenberg 2009; Vo *et al*. 2012). Mangrove forests were once widespread across South-East Asia, but forest coverage has declined substantially since the beginning of the 21st century due to land reclamation for development, agriculture, aquaculture and logging (Spalding *et al*. 1997; Valiela *et al*. 2001; Long *et al*. 2014; Richards & Friess 2016). These forests are further threatened by rising sea levels due to climate change (Lovelock *et al*. 2015). Mangroves host much higher plant and animal diversity in the tropical Indo-West Pacific than in the Americas (Ellison *et al*. 1999; Hoeksema 2007), but this diversity remains poorly known, especially for invertebrates. As a dominant component of mangrove ecosystems, molluscs play an important role in food webs through nutrient cycling (Kristensen *et al*. 2008) and serve as prey for other molluscs, crustaceans and fish (Hill 1976; Hughes 1984; Cannicci *et al*. 1998; Tan & Oh 2002). In order to conserve healthy mangrove ecosystems, it is imperative to understand the diversity, biogeography and natural history of mangrove molluscs.

Even though onchidiid slugs are one of the dominant groups of gastropods in the mangrove forests of South-East Asia and Australia, they have often been overlooked in surveys of mangrove invertebrates. This is likely due to their camouflage with mud and tree bark, but also because many species, even from different genera, are extremely difficult to distinguish (e.g., slugs of the genera *Paromoionchis* Dayrat & Goulding, 2019 and *Laspionchis* Dayrat & Goulding, 2019; Dayrat *et al*. 2019a, 2019b). Some of the challenges with onchidiid taxonomy are those that taxonomists often face: few specimens from mangroves available in museum collections, type material often destroyed or lost, and difficulty in identifying informative characters (Dayrat 2009). In spite of those difficulties, the taxonomy of the onchidiids is being revised systematically, genus by genus, based on an unprecedented effort in collecting fresh material worldwide (Dayrat *et al*. 2016, 2017, 2018, 2019a, 2019b, 2019c, 2019d, 2020; Dayrat & Goulding 2017; Goulding *et al.* 2018a, 2018b, 2018c).

The genus *Onchidium* Buchannan, 1800, which previously was used by default for many unrelated onchidiid species in the Indo-West Pacific, has been shown to include only four species restricted to mangroves (Dayrat *et al*. 2016, 2019d). Three genera have been described over the last few years for species formerly included in the genus *Onchidium* as well as species newly discovered; these include *Wallaconchis* Goulding & Dayrat, 2018, found in sandy mangroves and coral rubble (Goulding *et al*. 2018b), *Marmaronchis* Dayrat & Goulding, 2018, found on rocky shores (Dayrat *et al*. 2018) and *Paromoionchis* from muddy mangrove forests (Dayrat *et al*. 2019a). Three additional genera of mangrove onchidiids were described based entirely on new species: *Melayonchis* Dayrat & Goulding, 2017 (Dayrat *et al*. 2017, 2019c), *Laspionchis* (Dayrat *et al*. 2019b), and *Alionchis* Goulding & Dayrat, 2018 (Goulding *et al*. 2018). Two other existing genera of onchidiids associated with mangroves have also been revised: *Onchidina* Semper, 1882 (Dayrat & Goulding 2017) and *Peronina* Plate, 1893 (Goulding *et al*. 2018c). *Platevindex* Baker, 1938, one of the most diverse onchidiid genera, is revised here, with numerous new geographic records that reveal the broad distributions of most species. Most *Platevindex* slugs live on wood in muddy mangrove forests, either on the roots and trunks of mangrove trees or on logs, and they are generally abundant in estuarine mangrove forests.

Platevindex slugs can easily be recognized in the field due to their dorso-ventrally flattened body, their hard notum and their narrow foot (usually less than one third of the total width). Unlike other mangrove onchidiids, *Platevindex* slugs were recognized early on as distinct from other onchidiids and were first classified in the genus *Oncis* Plate, 1893. However, this name is a junior objective synonym of *Onchis* Férussac, 1822 (see our remarks on the generic name), and the valid generic name for the genus revised here is *Platevindex*, established by Baker (1938) with *Onchidium coriaceum* Semper, 1880 as the type species, by original designation. The diversity of *Platevindex* is revised using an integrative approach based on fresh material from the entire Indo-West Pacific (including most type localities of existing species names), a re-examination of all onchidiid type specimens available, a review of all original descriptions, and species delineations combining comparative anatomy, mitochondrial (COI and 16S) and nuclear (ITS2, 28S and H3) DNA sequences. Because the taxonomy of *Platevindex* has never been revised, the anatomy of many of the species is described in detail here for the first time (most original descriptions were brief and based on few specimens) and many new geographical records are provided (most species were known only from their type localities).

Nine species are recognized in *Platevindex*, one of which was undescribed: *P. amboinae* (Plate, 1893) comb. nov., *P. applanatus* (Simroth, 1920) comb. nov., *P. aptei* Goulding & Dayrat sp. nov., *P. burnupi* (Collinge, 1902) comb. nov., *P. coriaceus* (Semper, 1880), *P. latus* (Plate, 1893) comb. nov., *P. luteus* (Semper, 1880) comb. nov., *P. martensi* (Plate, 1893) comb. nov. and *P. tigrinus* (Stoliczka, 1869) comb. nov. One new subspecies is also described here: *P. coriaceus darwinensis* Goulding & Dayrat subsp. nov.

Material and methods

Field collecting and sampling

All specimens used in this study were collected by at least one of the authors, with the exception of 14 specimens from Papua New Guinea (Madang and Kavieng), Vanuatu, and New Caledonia collected during expeditions led by Philippe Bouchet and borrowed from the Muséum national d'histoire naturelle, 5 specimens from South Africa collected by Mary Cole and borrowed from the East London Museum, South Africa, 3 specimens of *P. latus* from the Zoologisches Museum Hamburg, 28 specimens of *P. coriaceus* from the Western Australian Museum, as well as the many type specimens borrowed from various institutions. Collecting parties were led by Benoît Dayrat in the Andaman Islands and West Bengal (India), Brunei, Malaysia, Northern Territory (Australia), the Philippines and Singapore, by Tricia Goulding in Queensland (Australia), Madagascar, Mauritius, Maharashtra and Tamil Nadu (India) and Vietnam, and by Munawar Khalil in Indonesia.

Specimens were collected by hand at low tide. GPS coordinates are available for all stations. At each site, photographs were taken to document the habitat (e.g., dense or open mangrove forest, sediment type, plant species) as well as the exact microhabitats where specimens were collected (e.g., mud surface, tree trunk, old log). In the field, specimens were individually numbered and photographed. At each site, individuals were chosen to represent variation in color and size. A notum piece was cut from most specimens for DNA extractions (in 95% ethanol) so that each DNA sequence corresponds to a particular preserved specimen and a series of field photographs. After those cuts for DNA extractions, animals were relaxed in magnesium chloride ($MgCl_2$) for approximately 24 hours and then preserved in 70% ethanol for comparative anatomy. Relaxed specimens from Sumatra, Sulawesi and Queensland were fixed in formalin prior to being transferred into 70% ethanol.

In total, 229 specimens of *Platevindex* are included in this study, not counting the many type specimens of existing nominal species. DNA sequences are provided for 184 specimens of *Platevindex* (Table 1). Specimens with no DNA sequences are marked in the list of material examined as "[no DNA]" or with a number in brackets (i.e. "[#1]") if the specimen is illustrated. Specimens with no DNA sequences include

Table 1 (continued on next 7 pages). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences. Details about specimens corresponding to individual (DNA) numbers are included in the material examined sections. All sequences of *Platevindex* Baker, 1938 are new, except for sequences from China downloaded from GenBank. Sequences for *Alionchis* Goulding & Dayrat, 2018, *Marmaronchis* Dayrat & Goulding, 2018, *Melayonchis* Dayrat & Goulding, 2017, *Onchidella* Gary, 1850, *Onchidium* Buchannan, 1800, *Onchidina* Semper, 1882, *Paromoionchis* Dayrat & Goulding, 2019, *Peronia* Fleming, 1822, *Peronina* Plate, 1893 and *Wallaconchis* Goulding & Dayrat, 2018 used as outgroups have previously been published by the authors (references in Material and methods).

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. coriaceus (unit 1)	1029	Brunei	BDMNH	MN807062	–	MN808983	–	–
	1031	Brunei	BDMNH	MN807063	–	MN808984	–	–
	–	China	–	JN543138	JN543074	–	–	–
	1731	Sumatra, Indonesia	UMIZ 00076	MN807064	–	MN808985	–	–
	1735	Sumatra, Indonesia	UMIZ 00076	MN807065	MN808829	MN808986	MN808919	–
	1772	Sumatra, Indonesia	UMIZ 00075	MN807066	–	MN808987	–	–
	2190	Sulawesi, Indonesia	UMIZ 00078	MN807067	MN808830	MN808988	MN808920	MN795323
	3000	Lombok, Indonesia	UMIZ 00079	MN807068	–	MN808989	MN808921	–
	3001	Lombok, Indonesia	UMIZ 00079	MN807069	MN808831	MN808990	–	–
	918	Peninsular Malaysia	USMMC 00026	MN807056	MN808827	MN808979	MN808917	MN795321
	935	Peninsular Malaysia	USMMC 00027	MN807057	–	–	–	–
	937	Peninsular Malaysia	USMMC 00026	MN807058	–	MN808980	–	–
	940	Peninsular Malaysia	USMMC 00026	MN807059	–	MN808981	–	–
	941	Peninsular Malaysia	USMMC 00025	MN807060	–	–	–	–
	998	Singapore	ZRC.MOL.10475	MN807061	MN808828	MN808982	MN808918	MN795322
	5625	Vietnam	ITBZC IM 00012	MN807070	–	–	–	–
	5629	Vietnam	ITBZC IM 00014	MN807071	MN808832	MN808991	MN808922	–
	5657	Vietnam	ITBZC IM 00014	MN807072	–	–	–	–
P. coriaceus (unit 2)	3245	Bohol, Philippines	PNM 041237	MN807076	MN808835	MN808994	–	–
	3247	Bohol, Philippines	PNM 041237	MN807077	MN808836	MN808995	–	–
	3248	Bohol, Philippines	PNM 041237	MN807078	MN808837	MN808996	MN808925	MN795326
	3256	Bohol, Philippines	PNM 041238	MN807079	–	MN808997	–	–
	3257	Bohol, Philippines	PNM 041238	MN807080	MN808838	MN808998	MN808926	MN795327
	3290	Bohol, Philippines	PNM 041239	MN807081	–	MN808999	–	–

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. coriaceus (unit 2, cont.)	3293	Bohol, Philippines	PNM 041239	MN807082	MN808839	MN809000	MN808927	MN795328
	3356	Bohol, Philippines	PNM 041240	MN807083	–	–	–	–
	3170	Luzon, Philippines	PNM 041236	MN807073	MN808833	MN808992	MN808923	MN795324
	3193	Luzon, Philippines	PNM 041236	MN807074	MN808834	MN808993	MN808924	MN795325
	3194	Luzon, Philippines	PNM 041236	MN807075	–	–	–	–
P. coriaceus (unit 3)	–	China	–	GU166575	–	–	–	–
	–	China	–	GU166577	–	–	–	–
	–	Japan	–	LC390406	–	–	–	–
	–	Japan	–	LC390408	–	–	–	–
P. coriaceus darwinensis subsp. nov.	1700	N. Territory, Australia	NTM P.57601	MN807084	MN808840	MN809001	MN808928	MN795329
	1663	N. Territory, Australia	NTM P.57602	MN807085	–	MN809002	–	–
	1672	N. Territory, Australia	NTM P.57602	MN807086	–	MN809003	–	–
	1674	N. Territory, Australia	NTM P.57602	MN807087	MN808841	MN809004	–	–
	1677	N. Territory, Australia	NTM P.57603	MN807088	–	MN809005	–	–
	1633	N. Territory, Australia	NTM P.57604	MN807089	MN808842	MN809006	MN808929	–
	1690	N. Territory, Australia	NTM P.57606	MN807090	–	–	–	–
	1701	N. Territory, Australia	NTM P.57608	MN807091	–	MN809007	–	–
	2549	Queensland, Australia	MTQ	MN807092	–	MN809008	–	–
	2590	Queensland, Australia	MTQ	MN807093	MN808843	MN809009	–	–
	2679	Queensland, Australia	MTQ	MN807094	MN808844	–	–	–
	2689	Queensland, Australia	MTQ	MN807095	MN808845	MN809010	MN808930	MN795330
	5021	Halmahera, Indonesia	UMIZ 00080	MN807096	MN808846	MN809011	MN808929	MN795331
	5071	Halmahera, Indonesia	UMIZ 00080	MN807097	–	–	–	–
	5109	Halmahera, Indonesia	UMIZ 00081	MN807098	MN808847	MN809012	–	–
	5110	Halmahera, Indonesia	UMIZ 00081	MN807099	–	MN809013	–	–
	5111	Halmahera, Indonesia	UMIZ 00081	MN807100	–	–	–	–
	5112	Halmahera, Indonesia	UMIZ 00081	MN807101	MN808848	MN809014	–	–
P. tigrinus	1030	Brunei	BDMNH	MN807119	MN808858	MN809022	MN808935	MN795335
	1032	Brunei	BDMNH	MN807120	–	MN809023	–	–
	1033	Brunei	BDMNH	MN807121	–	–	–	–

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. tigrinus (cont.)	–	China	–	JN543141	JN543077	–	–	–
	–	China	–	JN543139	JN543075	–	–	–
	–	China	–	GU166504	–	–	–	–
	–	China	–	GU166506	–	–	–	–
	–	China	–	GU166507	–	–	–	–
	–	China	–	GU166508	–	–	–	–
	–	China	–	GU166509	–	–	–	–
	1066	Sundarbans, India	BNHS 18-1066	MN807102	MN808849	–	–	–
	1065	Sundarbans, India	BNHS 18-1065	MN807103	MN808850	–	–	–
	1094	Andaman, India	BNHS 2-1094	MN807104	MN808851	–	–	–
	1114	Andaman, India	BNHS 12-1114	MN807105	MN808852	–	–	–
	1123	Andaman, India	BNHS 1-1123	MN807106	–	–	–	–
	1140	Maharashtra, India	BNHS 35-1140	MN807107	–	–	–	–
	1160	Maharashtra, India	BNHS 104-1160	MN807108	MN808853	–	–	–
	1178	Maharashtra, India	BNHS 33-1178	MN807109	–	–	–	–
	936	Peninsular Malaysia	USMMC 00024	MN807110	MN808854	MN809015	MN808932	MN795332
	939	Peninsular Malaysia	USMMC 00023	MN807111	MN808855	MN809016	–	–
	953	Peninsular Malaysia	USMMC 00022	MN807112	–	MN809017	–	–
	955	Peninsular Malaysia	USMMC 00022	MN807113	–	–	–	–
	956	Peninsular Malaysia	USMMC 00022	MN807114	–	–	–	–
	5522	Peninsular Malaysia	USMMC 00023	MN807115	–	MN809018	–	–
	992	Singapore	ZRC.MOL.10472	MN807116	–	MN809019	–	–
	993	Singapore	ZRC.MOL.10473	MN807117	MN808856	MN809020	MN808933	MN795333
	994	Singapore	ZRC.MOL.10474	MN807118	MN808857	MN809021	MN808934	MN795334
P. luteus	2551	Queensland, Australia	MTQ	MN807144	MN808868	MN809037	MN808944	MN795340
	2597	Queensland, Australia	MTQ	MN807145	–	–	–	–
	2678	Queensland, Australia	MTQ	MN807146	–	MN809038	–	–
	1039	Brunei	BDMNH	MN807124	MN808861	MN809026	MN808938	MN795338
	2837	Ambon, Indonesia	UMIZ 0008	MN807129	–	–	–	–
	2858	Ambon, Indonesia	UMIZ 00188	MN807130	MN808864	MN809030	MN808940	–

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. luteus (cont.)	3040	Bali, Indonesia	UMIZ 00095	MN807137	–	–	–	–
	3044	Bali, Indonesia	UMIZ 00095	MN807138	–	MN809034	–	–
	3046	Bali, Indonesia	UMIZ 00095	MN807139	–	–	–	–
	5022	Halmahera, Indonesia	UMIZ 00098	MN807140	–	–	–	–
	5041	Halmahera, Indonesia	UMIZ 00099	MN807141	MN808867	MN809035	MN808943	–
	2906	Kei, Indonesia	UMIZ 00091	MN807132	–	MN809032	–	–
	2915	Kei, Indonesia	UMIZ 00092	MN807133	–	–	–	–
	2916	Kei, Indonesia	UMIZ 00092	MN807134	–	–	–	–
	2922	Kei, Indonesia	UMIZ 00093	MN807135	MN808866	MN809033	MN808942	MN795339
	2958	Lombok, Indonesia	UMIZ 00094	MN807136	–	–	–	–
	2886	Seram, Indonesia	UMIZ 00189	MN807131	MN808865	MN809031	MN808941	–
	2335	Sulawesi, Indonesia	UMIZ 00191	MN807127	MT015968	MN809028	MN808939	–
	2364	Sulawesi, Indonesia	UMIZ 00086	MN807128	MN808863	MN809029	–	–
	1789	Sumatra, Indonesia	UMIZ 00082	MN807125	–	–	–	–
	1792	Sumatra, Indonesia	UMIZ 00082	MN807126	MN808862	MN809027	–	–
	5051	Ternate, Indonesia	UMIZ 00097	MN807142	–	–	–	–
	5939	Timor, Indonesia	UMIZ 00190	MN807143	MN808864	MN809036	–	–
	6344	New Caledonia	MNHN-IM-2019-1474	MN807160	MN808871	MN809047	–	–
	6361	New Caledonia	MNHN-IM-2019-1475	MN807161	MN808872	MN809048	–	–
	6367	New Caledonia	MNHN-IM-2019-1476	MN807162	MN808873	MN809049	–	–
	5429	Papua New Guinea	MNHN-IM-2013-10407	MN807154	MN808870	MN809043	MN808946	MN795342
	5431	Papua New Guinea	MNHN-IM-2013-10409	MN807155	–	–	–	–
	6101	New Ireland, PNG	MNHN-IM-2013-55235	MN807156	–	MN809044	–	–
	6102	New Ireland, PNG	MNHN-IM-2013-55239	MN807157	–	MN809045	–	–
	3280	Bohol, Philippines	PNM 041244	MN807150	–	MN809040	–	–
	3281	Bohol, Philippines	PNM 041244	MN807151	–	MN809041	–	–
	3367	Bohol, Philippines	PNM 041246	MN807152	–	MN809042	–	–
	3428	Bohol, Philippines	PNM 041248	MN807153	–	–	–	–
	3198	Luzon, Philippines	PNM 041242	MN807147	–	–	–	–
	3224	Luzon, Philippines	PNM 041243	MN807148	–	–	–	–

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. luteus (cont.)	3225	Luzon, Philippines	PNM 041243	MN807149	MN808869	MN809039	MN808945	MN795341
	997	Singapore	ZRC.MOL.10477	MN807122	MN808859	MN809024	MN808936	MN795336
	1000	Singapore	ZRC.MOL.10476	MN807123	MN808860	MN809025	MN808937	MN795337
	5613	Vietnam	ITBZC IM 00016	MN807158	–	MN809046	–	–
	5668	Vietnam	ITBZC IM 00016	MN807159	–	–	–	–
P. applanatus	2736	Ambon, Indonesia	UMIZ 00100	MN807167	MN808878	MN809054	MN808950	MN795345
	2750	Ambon, Indonesia	UMIZ 00101	MN807168	MN808879	MN809055	MN808951	MN795346
	2754	Ambon, Indonesia	UMIZ 00101	MN807169	–	–	–	–
	2755	Ambon, Indonesia	UMIZ 00101	MN807170	–	–	–	–
	2757	Ambon, Indonesia	UMIZ 00101	MN807171	–	–	–	–
	2892	Kei, Indonesia	UMIZ 00102	MN807174	MN808882	MN809058	–	–
	2893	Kei, Indonesia	UMIZ 00102	MN807175	MN808883	MN809059	MN808954	MN795347
	2894	Kei, Indonesia	UMIZ 00102	MN807176	–	–	–	–
	2895	Kei, Indonesia	UMIZ 00102	MN807177	–	–	–	–
	2900	Kei, Indonesia	UMIZ 00102	MN807178	–	–	–	–
	2904	Kei, Indonesia	UMIZ 00103	MN807179	MN808884	MN809060	MN808955	MN795348
	2925	Kei, Indonesia	UMIZ 00104	MN807180	MN808885	MN809061	–	–
	3563	Kei, Indonesia	UMIZ 00102	MN807181	–	–	–	–
	2877	Seram, Indonesia	UMIZ 00090	MN807172	MN808880	MN809056	MN808952	–
	2880	Seram, Indonesia	UMIZ 00090	MN807173	MN808881	MN809057	MN808953	–
	2160	Sulawesi, Indonesia	UMIZ 00083	MN807163	MN808874	MN809050	MN808947	–
	3152	Mauritius	MNHN-IM-2019-1393	MN807164	MN808875	MN809051	–	–
	3442	Mauritius	MNHN-IM-2019-1394	MN807165	MN808876	MN809052	MN808948	MN795343
	3604	Mauritius	MNHN-IM-2019-1392	MN807166	MN808877	MN809053	MN808949	MN795344
	6094	New Ireland, PNG	MNHN-IM-2013-53534	MN807188	MN808889	MN809066	MN808958	–
	6096	New Ireland, PNG	MNHN-IM-2013-54161	MN807189	–	–	–	–
	6097	New Ireland, PNG	MNHN-IM-2013-54163	MN807190	–	–	–	–
	6098	New Ireland, PNG	MNHN-IM-2013-54164	MN807191	MN808890	MN809067	MN808959	–
	5420	Papua New Guinea	MNHN-IM-2013-13765	MN807182	–	MN809062	–	–
	5424	Papua New Guinea	MNHN-IM-2013-14043	MN807183	MN808886	MN809063	MN808956	MN795349

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. applanatus (cont.)	5437	Papua New Guinea	MNHN-IM-2013-12493	MN807184	MN808887	–	–	–
	5450	Papua New Guinea	MNHN-IM-2013-14051	MN807185	–	MN809064	–	–
	5457	Papua New Guinea	MNHN-IM-2013-15867	MN807186	–	–	–	–
	5462	Papua New Guinea	MNHN-IM-2013-15908	MN807187	MN808888	MN809065	MN808957	MN795350
	5491	Vanuatu	MNHN-IM-2013-62402	MN807192	MN808891	–	–	MN795351
	5493	Vanuatu	MNHN-IM-2013-62404	MN807193	MN808892	MN809068	MN808960	MN795352
P. burnupi	6146	South Africa	ELM W04105	MN807194	MN808893	MN809069	MN808961	–
	6148	South Africa	ELM W04109	MN807195	–	–	–	–
	6149	South Africa	ELM W04108	MN807196	–	–	–	–
	6153	South Africa	ELM W04106	MN807197	MN808894	MN809070	MN808962	MN795353
	6154	South Africa	ELM W04107	MN807198	MN808895	MN809071	MN808963	MN795354
	3150	Madagascar	MNHN-IM-2019-1398	MN807200	MN808896	MN809073	MN808964	MN795355
	3151	Madagascar	MNHN-IM-2019-1399	MN807201	MN808897	MN809074	MN808965	MN795356
	3599	Madagascar	MNHN-IM-2019-1396	MN807202	MN808898	MN809075	MN808966	MN795357
	3602	Madagascar	MNHN-IM-2019-1397	MN807203	MN808899	MN809076	MN808967	MN795358
	3603	Madagascar	MNHN-IM-2019-1395	MN807204	MN808900	MN809077	MN808968	MN795359
	729	Mozambique	NHMUK 20060274	MN807199	HQ659917	MN809072	–	–
P. martensi	1707	N. Territory, Australia	NTM P.57611	MN807212		MN809084	–	–
	1709	N. Territory, Australia	NTM P.57611	MN807213		MN809085	–	–
	1710	N. Territory, Australia	NTM P.57611	MN807214	MN808906	MN809086	MN808972	MN795363
	1711	N. Territory, Australia	NTM P.57611	MN807215	–	MN809087	–	–
	1040	Brunei	BDMNH	MN807211	MN808905	MN809083	MN808971	MN795362
	–	China	–	JN543144	JN543080	–	–	–
	–	China	–	JN543142	JN543078	–	–	–
	1748	Sumatra, Indonesia	UMIZ 00109	MN807216	MN808907	MN809088	–	–
	1767	Sumatra, Indonesia	UMIZ 00107	MN807217		–	–	–
	1776	Sumatra, Indonesia	UMIZ 00108	MN807218	–	MN809089	–	–
	2333	Sulawesi, Indonesia	UMIZ 00111	MN807219	–	–	–	–
	2334	Sulawesi, Indonesia	UMIZ 00111	MN807220	–	MN809090	–	–
	930	Peninsular Malaysia	USMMC 00033	MN807205	MN808901	MN809078	MN808969	MN795360

Table 1 (continued). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
P. martensi (cont.)	933	Peninsular Malaysia	USMMC 00077	MN807206	–	MN809079	–	–
	934	Peninsular Malaysia	USMMC 00030	MN807207	–	MN809080	–	–
	964	Peninsular Malaysia	USMMC 00029	MN807208	MN808902	MN809081	–	–
	3336	Bohol, Philippines	PNM 041250	MN807221	–	MN809091	–	–
	3342	Bohol, Philippines	PNM 041250	MN807222	MN808908	MN809092	MN808973	MN795364
	3358	Bohol, Philippines	PNM 041251	MN807223	–	–	–	–
	3362	Bohol, Philippines	PNM 041251	MN807224	–	–	–	–
	3364	Bohol, Philippines	PNM 041251	MN807225	–	MN809093	–	–
	3365	Bohol, Philippines	PNM 041251	MN807226	–	–	–	–
	987	Singapore	ZRC.MOL.10481	MN807209	MN808903	MN809082	MN808970	MN795361
	988	Singapore	ZRC.MOL.10480	MN807210	MN808904	–	–	–
P. aptei sp. nov.	1092	Andaman, India	BNHS 8-1092	MN807232	MN808912	–	–	–
	1093	Andaman, India	BNHS 8-1093	MN807233	–	–	–	–
	1111	Andaman, India	BNHS 3-1111	MN807234	MN808913	–	–	–
	1112	Andaman, India	BNHS 3-1112	MN807235	–	–	–	–
	1121	Andaman, India	BNHS 14-1121	MN807236	–	–	–	–
	917	Peninsular Malaysia	USMMC 00037	MN807227	MN808909	–	–	–
	932	Peninsular Malaysia	USMMC 00036	MN807228	MN808910	MN809094	MN808974	MN795365
	5955	Peninsular Malaysia	USMMC 00078	MN807229	MN808911	MN809095	MN808975	MN795366
	5967	Peninsular Malaysia	USMMC 00078	MN807230	–	MN809096	–	–
	5968	Peninsular Malaysia	USMMC 00078	MN807231	–	MN809097	–	–
P. amboinae	2883	Seram, Indonesia	UMIZ 00105	MN807237	MN808914	MN809098	MN808976	MN795367
	5043	Halmahera, Indonesia	UMIZ 00106	MN807238	MN808915	MN809099	MN808977	MN795368
	5843	Halmahera, Indonesia	UMIZ 00106	MN807239	MN808916	MN809100	MN808978	MN795369

11

Table 1 (conclusion). GenBank accession numbers for COI, 16S, ITS2, 28S and H3 DNA sequences.

Species	Individual (DNA #)	Locality	Catalog number	GenBank COI	GenBank 16S	GenBank ITS2	GenBank 28S	GenBank H3
Melayonchis eloisae	1011	Singapore	ZRC.MOL.6499	KX240026	KX240050	MK122904	MK125515	MK122936
Melayonchis siongkiati	1002	Singapore	ZRC.MOL.6501	KX240020	KX240044	MK122905	MK122920	MK122937
Onchidium typhae	965	Peninsular Malaysia	USMMC 00005	KX179509	KX179525	MG958720	MG971210	MK122943
Peronina tenera	960	Peninsular Malaysia	USMMC 00039	MG958740	MG958796	MG958840	MG958874	MK122946
Peronina zulfigari	924	Peninsular Malaysia	USMMC 00048	MG958760	MG958816	MG958853	MG958876	MN795370
Onchidina australis	1523	NSW, Australia	AM C468918.002	KX240039	KX240039	MG958719	MG971209	MK122941
Marmaronchis vaigiensis	1183	Singapore	ZRC.MOL.3007	MK122812	MK122854	MK122877	MK122910	MK122925
Marmaronchis marmoratus	5409	Papua New Guinea	MNHN IM-2013-15764	MK122838	MK122859	MK122893	MK122915	MK122930
Peronia okinawensis	696	Okinawa, Japan	UF 352288	HQ660043	HQ659911	MG958871	MG958883	MK122945
Peronia platei	706	Hawaii, USA	UF 303653	HQ660038	HQ659906	MG958722	MG971212	MK122944
Paromoionchis tumidus	963	Peninsular Malaysia	USMMC 00057	MH054946	MH055101	MH055194	MH055266	MN795371
Paromoionchis penangensis	957	Peninsular Malaysia	USMMC 00061	MH055078	MH055137	MH055255	MH055293	MN795372
Wallaconchis ater	3272	Bohol, Philippines	PNM 041222	MG970809	MG970910	MG971132	MG971185	MN795373
Wallaconchis sinanui	2740	Ambon, Indonesia	UMIZ 00059	MG970713	MG970881	MG971093	MG971161	MG971093
Alionchis jailoloensis	5137	Halmahera, Indonesia	UMIZ 00117	MG953528	MG953538	MG953548	MK122918	MK122933
Onchidella celtica	5013	France	MNHN-IM-2014-6891	MG958715	MG958717	MK122906	MK122921	MK122938
Onchidella patelloidis	1524	NSW, Australia	AM C.468921.002	MG970878	MG970944	MK122908	MK122923	MK122940

material collected by the authors and which could be confidently identified based on their anatomy: *P. coriaceus darwinensis* subsp. nov. (3 specs), *P. tigrinus* (2 specs), *P. martensi* (5 specs) and *P. aptei* sp. nov. (4 specs). Specimens with no DNA sequences also include old, non-type material from museum collections which could not be sequenced: *P. latus* (3 specs) and *P. coriaceus* (28 specs). DNA sequences could not be obtained from the old type specimens of existing nominal species.

Type material, museum vouchers and collections

All the types available for the Onchidiidae were examined in the context of a taxonomic revision of all onchidiid genera (types were borrowed on loan, except for a few which could not be exported and were examined by the last author during visits to museum collections). Several species of *Platevindex* were originally described based on a single specimen. In the case of syntypes, it was often necessary to designate a lectotype in order to clarify the application of species names. Fresh material was used for DNA sequencing, comparative anatomy and natural history observations. Individual DNA extraction numbers are indicated on phylogenetic trees, in the lists of material examined, as well as in figure captions (DNA extraction numbers are in square brackets). Animal sizes are based on the maximum length and width of specimens when preserved, and are indicated in millimeters (as length/width).

All specimens freshly collected were deposited as vouchers in institutions in the countries where they were collected, except for specimens from Mauritius and Madagascar deposited at the MNHN. Acronyms of collections are:

AM   = Australian Museum, New South Wales, Australia
BNHS   = Bombay Natural History Society, Mumbai, India
BDMNH   = Brunei Darussalam Museum of Natural History, Brunei
ELM   = East London Museum, East London, East Cape, South Africa
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
NHMUK   = Natural History Museum, London, United Kingdom
NMSA   = KwaZulu-Natal Museum, Pietermaritzburg, South Africa
NTM   = Museum and Art Gallery of the Northern Territory, Darwin, Northern Territory, Australia
PNM   = National Museum of the Philippines, Manila, Philippines
SMF   = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany
SMNH   = Swedish Museum of Natural History, Stockholm, Sweden
UMIZ   = Universitas Malikussaleh, North Aceh, Sumatra, Indonesia
USMMC   = Universiti Sains Malaysia Mollusc Collection, Penang, Malaysia
WAM   = Western Australia Museum, Welshpool, Western Australia
ZMB   = Museum für Naturkunde, Berlin, Germany
ZMH   = Zoologisches Museum Hamburg, Hamburg, Germany
ZRC   = Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore

Animal preparation and anatomical description

Both the external morphology and the internal anatomy were examined 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, sputter-coated with gold-palladium and examined by SEM. Soft parts (penis and penial hooks) were dehydrated in 95% ethanol and critical point dried before coating. Radulae and the male parts were extracted from 3 specimens per species. Radulae and male parts were extracted from additional specimens in the three species with

Table 2. Types of intestinal loops in species of *Platevindex* Baker, 1938.

Taxon	Type I		Type II	Type III	
	12–3 o'clock	3–6 o'clock	6–9 o'clock	12–3 o'clock	3–6 o'clock
P. applanatus	✓(1 to 2)				
P. luteus		✓ (3 to 6)	✓ (6 to 8)		
P. burnupi			✓ (~7)		
P. coriaceus coriaceus (unit #1)			✓ (6 to 9)		
P. coriaceus coriaceus (unit #2)			✓ (7 to 9)		
P. coriaceus darwinensis subsp. nov.			✓ (6 to 8)		
P. tigrinus			✓ (6 to 9)		
P. martensi			✓ (6 to 9)		
P. aptei sp. nov.			✓ (7 to 9)		
P. amboinae				✓ (1 to 3)	✓ (~6)
P. latus				✓ (12 to 2)	

high intraspecific genetic diversity: 9 specimens of *P. coriaceus* (3 for *P. coriaceus coriaceus* unit #1, 3 for unit #2 and 3 for *P. coriaceus darwinensis* subsp. nov.), 9 specimens of *P. applanatus* (including 3 specimens from Mauritius) and 5 specimens of *P. burnupi*. Exceptionally, only 2 radulae were extracted for *P. latus*, as only a few specimens of this species are known in museum collections. Specimens were dissected from across the geographic distribution of each species, including 22 specimens of *P. coriaceus coriaceus*, 11 specimens of *P. coriaceus darwinensis* subsp. nov., 8 specimens of *P. tigrinus*, 21 specimens of *P. luteus*, 17 specimens of *P. applanatus*, 6 specimens of *P. burnupi*, 16 specimens of *P. martensi*, 6 specimens of *P. aptei* sp. nov., 4 specimens of *P. amboinae* and 3 specimens of *P. latus*. The number of dorsal eyes was counted in all specimens examined.

The anatomy of *P. coriaceus*, 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 repeating the information eight times. Thus, any feature that is only mentioned for *P. coriaceus* is identical in the other eight species. As expected, differences between species are mostly found in the male copulatory apparatus, which is described and illustrated in detail for each species.

Types of intestinal loops

In onchidiid slugs, the types of intestinal loops are based on the dorsal pattern of the intestine. Plate (1893: pl. 8, figs 29–32) first distinguished four types of intestinal loops (types I to IV) and Labbé (1934: 178, fig. 3) later added a type V. The intestinal types I, II and III are found in *Platevindex* (Figs 1–3, Table 2). It is necessary to define intestinal types clearly because they have often been confused. For that purpose, three different sections are recognized in intestinal loops and colored differently (Dayrat *et al.* 2019b, 2019c, 2019d, 2020): a clockwise loop is colored in blue, a counterclockwise loop in yellow, and a transitional loop between them in green (Figs 1–3).

The intestine first appears dorsally on the right side. In a type I (Fig. 1), the intestine starts by forming a clockwise (blue) loop. This clockwise loop does not form a full circle and soon transitions into a counterclockwise (yellow) loop. As a result, the transitional (green) loop between clockwise and counterclockwise loops is oriented to the right, typically at 3 o'clock (horizontal red arrow, Fig. 1A–B). In intestinal loops of type I, the transitional (green) loop is oriented to the right, but not always at 3 o'clock: it can vary from an orientation close to 12 o'clock (Fig. 1C) all the way down to an orientation at 6 o'clock (Fig. 1D). However, the intraspecific variation is usually limited to a range of

approximately 90° around a mean axis (i.e., 45° on either side of the mean axis). In *Platevindex*, a type I with a transitional loop oriented between 12 and 3 o'clock is found only in *P. applanatus* (Fig. 1C, Table 2) and a type I with a transitional loop oriented between 3 and 6 o'clock is found only in *P. luteus* (Fig. 1B, D, Table 2).

In a type II (Fig. 2), the clockwise (blue) loop is longer and rotates more than in a type I. As a result, the transitional (green) loop is oriented to the left, typically at 9 o'clock (horizontal red arrow, Fig. 2A–C). However, because of intraspecific variation, the transitional loop is not always oriented at 9 o'clock. A type II with a transitional loop oriented between 6 and 9 o'clock is found in six species of *Platevindex* (Fig. 2B–H, Table 2): *P. aptei* sp. nov., *P. burnupi*, *P. coriaceus*, *P. luteus*, *P. martensi* and *P. tigrinus*. The intraspecific variation of the intestinal loops in *P. luteus* is unusually high (Figs 1B, D, 2E): the orientation of its transitional loop covers a range of nearly 180°, between 3 o'clock (type I) and 8 o'clock (type II).

In a type III (Fig. 3), the clockwise (blue) loop is longer and rotates more than in a type II. As a result, the transitional (green) loop is oriented to the right, typically at 3 o'clock (horizontal red arrow, Fig. 3A). However, as in types I and II, there is some individual variation (Fig. 3). In *Platevindex*, two closely-related species are characterized by intestinal loops of type III (Tables 2, 4): *P. amboinae* and *P. latus*. In *P. amboinae*, the orientation of the transitional loop covers a range of nearly 180° (Fig. 3C–E). A type III with a transitional loop oriented between 12 and 2 o'clock is found in *P. latus* (Fig. 3B), but the limited variability in the orientation of the transition loop in *P. latus* may be due to limited sampling (see the remarks on that species).
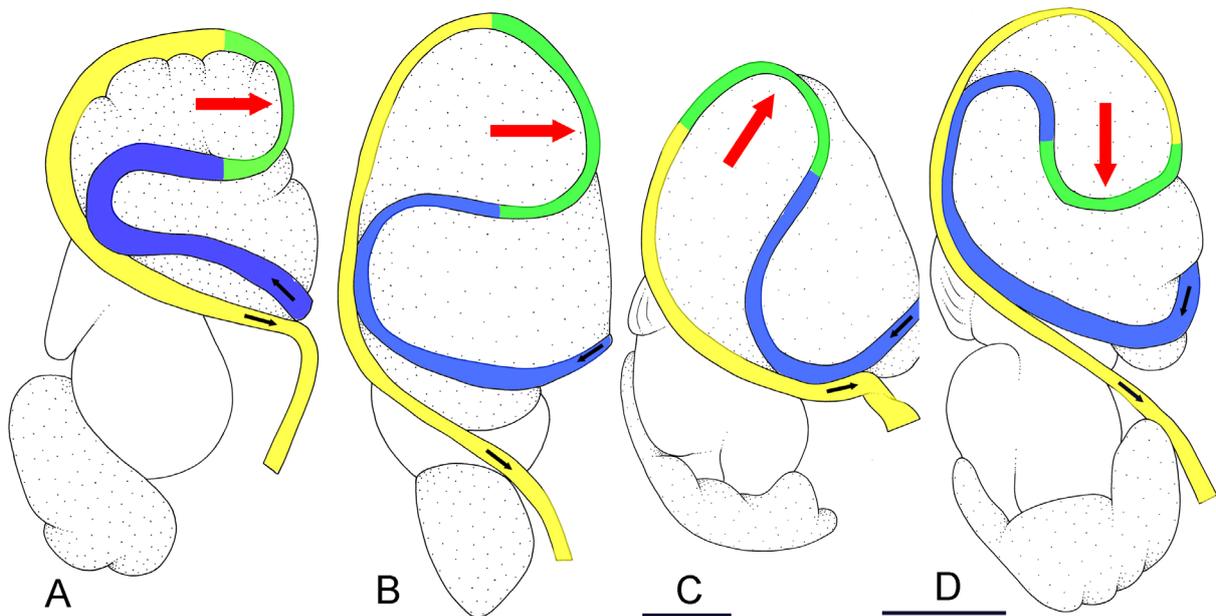
Fig. 1. Intestinal loops of type I. Small black arrows show the direction of the intestinal transport. The clockwise loop is in blue. The counterclockwise loop is in yellow. The transitional loop (between clockwise and counterclockwise loops) is in green. Red arrows indicate the orientation of the transitional loop. **A**. Type I (as defined by Plate 1893), with a transitional loop oriented at 3 o'clock, redrawn from Plate (1893: pl. 8, fig. 29). **B**. Type I, with a transitional loop oriented at 3 o'clock, *Platevindex luteus* (Semper, 1880) [5613] (ITBZC IM 00016), Vietnam. **C**. Type I, with a transitional loop oriented at 1 o'clock, *P. applanatus* (Simroth, 1920) [5420] (MNHN IM-2013-13765), Papua New Guinea. **D**. Type I, with a transitional loop oriented at 6 o'clock, *P. luteus* [2837] (UMIZ 00089), Ambon, Indonesia. Scale bars: B–C = 2 mm; D = 3 mm.
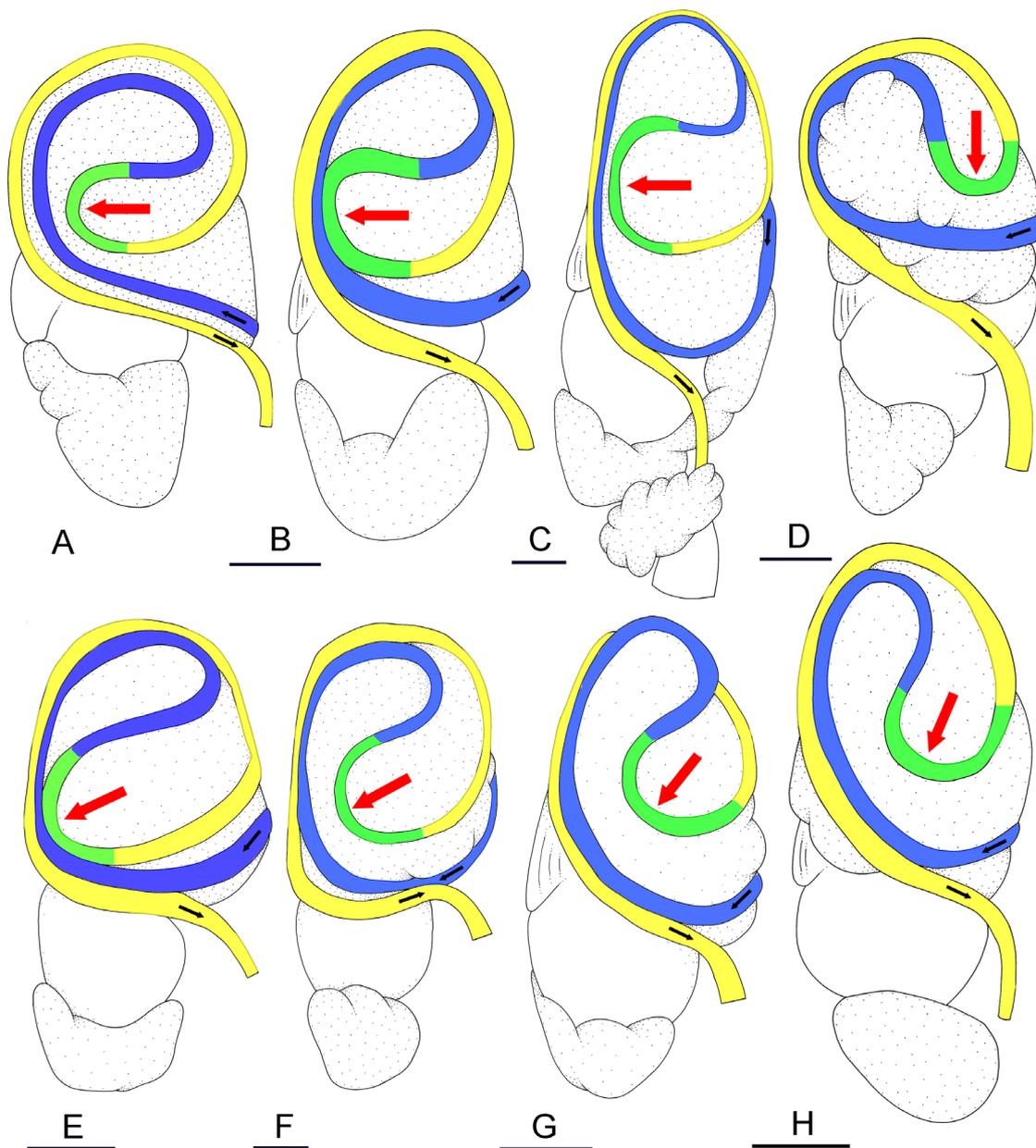
Fig. 2. Intestinal loops of type II. Small black arrows show the direction of the intestinal transport. The clockwise loop is in blue. The counterclockwise loop is in yellow. The transitional loop (between clockwise and counterclockwise loops) is in green. Red arrows indicate the orientation of the transitional loop. **A**. Type II (as defined by Plate 1893), with a transitional loop oriented at 9 o'clock, redrawn from Plate (1893: pl. 8, fig. 31). **B**. Type II, with a transitional loop oriented at 9 o'clock, *Platevindex coriaceus coriaceus* (Semper, 1880) unit #2 [3170] (PNM 041236), Luzon, Philippines. **C**. Type II, with a transitional loop oriented at 9 o'clock, *P. martensi* (Plate, 1893) [2333] (UMIZ 00111), Sulawesi, Indonesia. **D**. Type II, with a transitional loop oriented at 6 o'clock, *P. martensi* [964] (USMMC 00029), Peninsular Malaysia. **E**. Type II, with a transitional loop oriented at 8 o'clock, *P. luteus* (Semper, 1880) [3367] (PNM 041246), Bohol, Philippines. **F**. Type II, with a transitional loop oriented at 8 o'clock, *P. aptei* Goulding & Dayrat sp. nov., [5955] (USMMC 00078), Peninsular Malaysia. **G**. Type II, with a transitional loop oriented at 7 o'clock, *P. burnupi* (Collinge, 1902) [3150] (MNHN-IM-2019-1398), Madagascar. **H**. Type II, with a transitional loop oriented at 7 o'clock, *P. coriaceus coriaceus* unit #2 [3256] (PNM 041238), Bohol, Philippines. Scale bars: B–H = 2 mm.

DNA extraction and PCR amplification

DNA was extracted using a phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB). Portions of two mitochondrial genes (COI and 16S) and three nuclear loci (ITS2, 28S and H3) were amplified. The cytochrome oxidase I region (COI) was amplified using the universal primers (all primers indicated as 5′-3′): LCO1490 GGT CAA CAA ATC ATA AAG ATA TTG G, and HCO2198 TAA ACT TCA GGG TGA CCA AAR AAY CA (Folmer *et al*. 1994), except in *P. luteus*, for which modified Folmer primers were used: jgLCO1490 TIT CIA CIA AYC AYA ARG AYA TTG G, and jgHCO2198 TAI ACY TCI GGR TGI CCR AAR AAY CA (Geller *et al*. 2013). Other universal primers used for 16S, ITS2, 28S and H3 were: 16Sar CGC CTG TTT ATC AAA AAC AT
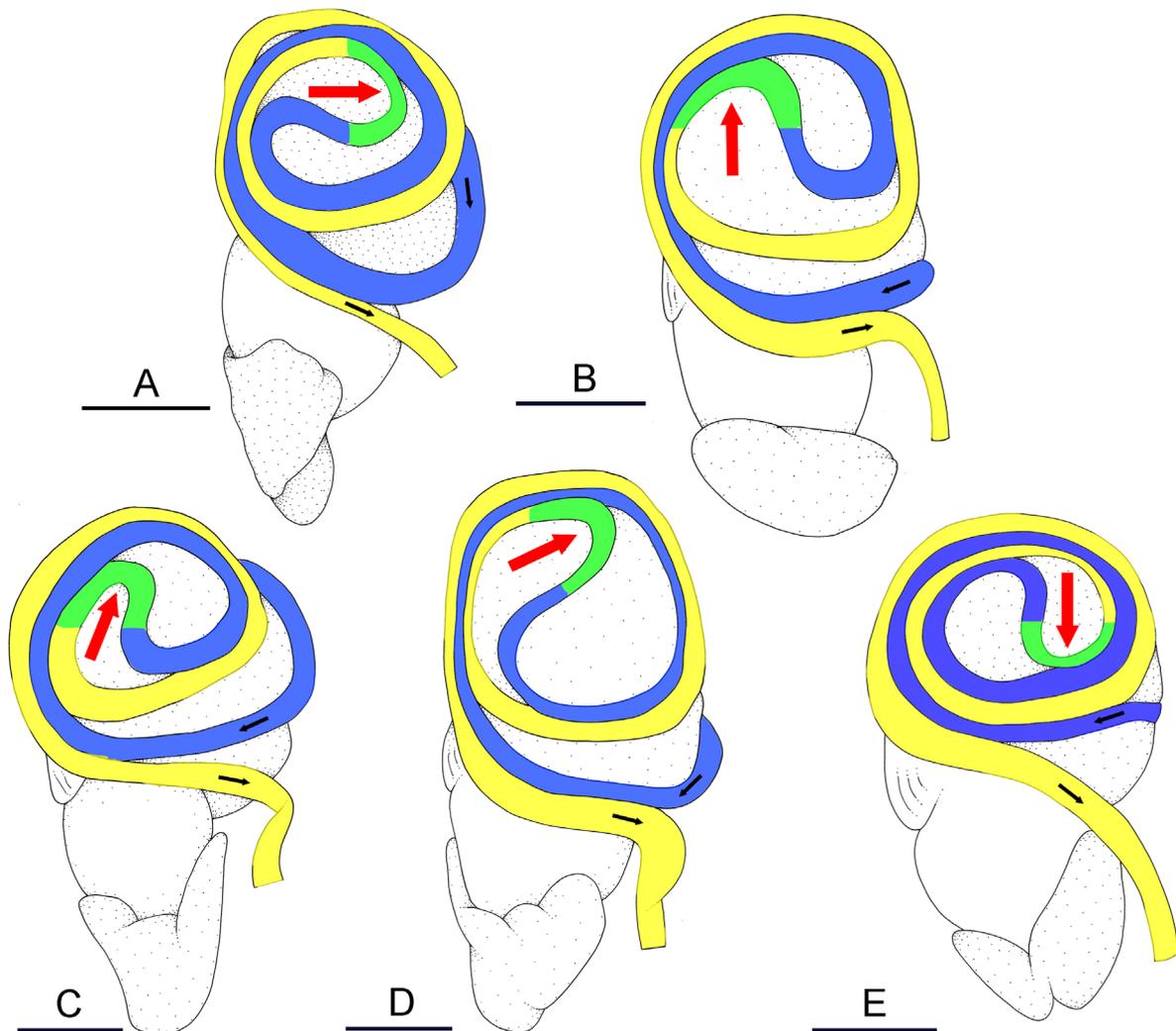
Fig. 3. Intestinal loops of type III. Small black arrows show the direction of the intestinal transport. The clockwise loop is in blue. The counterclockwise loop is in yellow. The transitional loop (between clockwise and counterclockwise loops) is in green. Red arrows indicate the orientation of the transitional loop. **A**. Type III, with a transitional loop oriented at 3 o'clock, *Onchidium stuxbergi* (Westerlund, 1883) (from Dayrat *et al*. 2016: fig. 11b). **B**. Type III, with a transitional loop oriented at 12 o'clock, *Platevindex latus* (Plate, 1893) (ZMH 27511, #1), Papua New Guinea. **C**. Type III, with a transitional loop oriented at 1 o'clock, *P. amboinae* (Plate, 1893), lectotype (ZMB/Moll 11621a), Ambon, Indonesia. **D**. Type III, with a transitional loop oriented at 2 o'clock, *P. amboinae* [2883] (UMIZ 00105), Seram, Indonesia. **E**. Type III, with a transitional loop oriented at 6 o'clock, *P. amboinae* (SMF 333602, #1), Sulawesi, Indonesia. Scale bars: A–B = 5 mm; C–E = 4 mm.

(Palumbi 1996), 16S 972R CCG GTC TGA ACT CAG ATC ATG T (Dayrat *et al.* 2011), ITS2-LSU1 CTAGCTGCGAGAATTAATGTGA, ITS2-LSU-3 ACTTTCCCTCACGGTACTTG (Wade & Mordan 2000), 28SC1 ACC CGC TGA ATT TAA GCA T (Hassouna *et al.* 1984), 28SD3 GAC GAT CGA TTT GCA CGT CA (Vonnemann *et al.* 2005), H3F ATG GCT CGT ACC AAG CAG ACV GC and H3R ATA TCC TTR GGC ATR ATR GTG AC (Colgan *et al.* 2000). PCRs for COI and 16S were each done in a total reaction volume of 25 µl containing 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 (Clontech, Cat No. R001A), 1 µl of 20 ng/µl template DNA and 1 µl of 100 × BSA (bovine serum albumin). PCRs for ITS2 used the reagents in the same amounts as for COI and 16S, except that water was reduced to 14.8 µl, the amount of 100 × BSA was increased to 2 µl and the amount of template DNA reduced to 0.5 µl. PCRs for 28S contained 14.3 µl of water, 0.5 µl of 10× PCR buffer, 5 µl of Q solution (QIAGEN, ID: 201203), 0.5 µl of each 10 µM primer, 1 µl of dNTPs, 0.2 µl (1 unit) of TaKaRa Taq and 0.5 µl of 20 ng/µl template DNA. PCR reactions for H3 were done in 25 µl reactions containing 14.8 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, 2 µl of 100 × BSA and 1 µl of 20 ng/µl template DNA. The thermoprofile used for COI and 16S was: 5 min at 94°C; 30 cycles of 40 s at 94°C, 1 min at 46°C and 1 min at 72°C; and 10 min at 72°C. The ITS2 thermoprofile was: 1 min at 96°C; 35 cycles of 30 s at 94°C, 30 s at 50°C and 1 min at 72°C; and a final extension of 10 min at 72°C. The 28S thermoprofile was: 4 min at 94°C; 38 cycles of 30 s at 94°C, 50 s at 52°C and 2 min 30 s at 72°C; and 10 min at 72°C. The H3 thermoprofile was: 5 min at 93°C; 30 cycles of 1 min at 93°C, 2 min at 55 °C and 1 min at 73°C; and a final extension of 10 min at 73°C. Sequenced fragments represented approximately 680 bp (COI), 530 bp (16S), 650 bp (ITS2, including parts of 5.8S and 28S), 1000 bp (28S) and 340 bp (H3).

Phylogenetic analyses

Chromatograms were consulted to resolve rare ambiguous base calls. Consensus sequences for 28S and (when necessary) ITS2 were produced by aligning forward and reverse sequences in Geneious ver. 9.1.8 (Kearse *et al.* 2012). Alignments of COI and 28S sequences were each obtained using MUSCLE in MEGA 7 (Kumar *et al.* 2016). 16S and ITS2 sequences were aligned separately using MAFFT ver. 7 (Katoh *et al.* 2002). The iterative refinement method E-INS-I was selected for sequences with multiple conserved domains and long gaps. COI DNA 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).

DNA sequences for 184 specimens were submitted to GenBank and vouchers deposited in museum collections (Table 1). All sequences of *Platevindex* in this study are new, with the exception of 14 previously published sequences from China and Japan, which were downloaded from GenBank. Seventeen onchidiid species were selected as outgroups representing other onchidiid genera. All outgroup sequences are from our recent taxonomic studies (Dayrat *et al.* 2011, 2016, 2017, 2018, 2019a, 2019b, 2019c, 2019d; Dayrat & Goulding 2017; Goulding *et al.* 2018a, 2018b, 2018c): *Alionchis jailoloensis* Goulding & Dayrat, 2018, *Marmaronchis marmoratus* (Lesson, 1831), *Marmaronchis vaigiensis* (Quoy & Gaimard, 1825), *Melayonchis eloisae* Dayrat, 2017, *Melayonchis siongkiati* Dayrat & Goulding, 2017, *Onchidella celtica* (Cuvier *in* Audouin & Milne-Edwards, 1832), *Onchidella nigricans* (Quoy & Gaimard, 1832), *Onchidina australis* (Semper, 1880), *Onchidium typhae* Buchannan, 1800, *Paromoionchis penangensis* Dayrat & Goulding, 2019, *Paromoionchis tumidus* (Semper, 1880), *Peronia platei* (Hoffmann, 1928), *Peronia okinawensis* Dayrat & Goulding, 2020, *Peronina tenera* (Stoliczka, 1869), *Peronina zulfigari* Goulding & Dayrat, 2018, *Wallaconchis ater* (Lesson, 1831) and *Wallaconchis sinanui* Goulding & Dayrat, 2018.

The ends of each alignment were trimmed. The concatenated mitochondrial alignment included 1047 nucleotide positions: 609 (COI) and 438 (16S). The concatenated nuclear alignment included 1768

positions: 758 (ITS2, including gaps) and 1010 (28S, including gaps) — the insertion of gaps in nuclear alignments is largely due to the comparison with outgroups. The alignment of H3, used in the partitioned multi-locus analysis, included 294 positions.

DNA sequences were used to test species limits within *Platevindex*, relationships between species, as well as the monophyly of *Platevindex*. Mitochondrial and nuclear sequences were first analyzed independently to determine whether different markers yielded different results. Then, mitochondrial and nuclear sequences were concatenated and analyzed using partitions. So, in total, five sets of phylogenetic analyses were performed (the number of individuals for each analysis does not include the outgroups): 1) maximum likelihood and Bayesian analyses with just COI sequences, performed with 198 individuals; 2) maximum likelihood and Bayesian analyses with concatenated COI and 16S sequences, performed with 96 individuals; 3) maximum parsimony analyses with ITS2 sequences, performed with 46 unique haplotypes representing 122 individuals; 4) maximum parsimony analyses with concatenated ITS2 and 28S sequences, performed with 62 individuals; and 5) maximum likelihood and Bayesian analysis of partitioned COI (all 3 codons partitioned separately), 16S, ITS2, 28S and H3 sequences, performed with 62 individuals.

Prior to phylogenetic analyses, the best-fitting evolutionary model was selected using the Model Selection option from Topali ver. 2.5 (Milne *et al.* 2004). Maximum likelihood analyses for mitochondrial COI and 16S were performed using PhyML (Guindon & Gascuel 2003) and Bayesian analyses were performed using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003), both implemented in Topali. Node support in maximum likelihood analyses was evaluated using bootstrapping with 100 replicates; here, bootstrap values greater than 70% are considered moderately supported, and greater than 95% are considered highly supported (Soltis & Soltis 2003). Bayesian analyses were performed with five simultaneous runs of 1.5×10^6 generations each, sample frequency of 100 and burn-in of 25%; posterior probabilities, or PP, were also calculated. Posterior probabilities greater than 0.95 are considered highly supported. Topali did not detect any issue with respect to convergence. Analyses of the internal transcribed spacer (ITS2) were carried out using maximum parsimony conducted in PAUP ver. 4.0 (Swofford 2002), with gaps coded as a 5th character state. Although both indels and shared nucleotide positions in nuclear sequences are informative for phylogenetic inference, indel characters are less likely to be homoplastic than nucleotide positions and are informative for phylogenetic analyses (Lloyd & Calder 1991; Simmons *et al.* 2001; Ashkenazy *et al.* 2014). Including indels in phylogenetic analyses has been shown to increase support for phylogenetic relationships (Nagy *et al.* 2012; Yuri *et al.* 2013). One hundred bootstrap replicates were conducted using a full heuristic search. Maximum likelihood analyses of partitioned loci were conducted in RAxML ver. 7.2.8 (Stamatakis 2014) using the General Time Reversible + Gamma (GTR + G) model as implemented in Geneious ver. 9.1.8 (Kearse *et al.* 2012). Node support was evaluated using bootstrapping with 100 replicates. For the Bayesian partitioned analyses, the best-fit model of nucleotide substitution was identified for each sequence partition by means of user-defined partition schemes evaluated with the corrected Akaike information criterion (AICc) in PartitionFinder ver. 2.1.1 (Lanfear *et al.* 2012). Six partitions were designated in the analyses: each codon position of COI partitioned separately, 16S, ITS2, 28S and H3. Bayesian analyses of partitioned data were performed in MrBayes ver. 3.2.6 on the CIPRES Science Gateway (Miller *et al.* 2010). Each MrBayes run consisted of four simultaneous runs of 10^7 generations each, sample frequency of 500, burn-in of 25%. Quality and ESS values (effective sampling size) of each run were checked in Tracer ver. 1.7 (Rambaut *et al.* 2018). All analyses were run several times and yielded similar results.

Pairwise p-distances between individual COI sequences were calculated in MEGA 7 (Kumar *et al.* 2016). Automatic Barcode Gap Discovery (Puillandre *et al.* 2011) was used to delimit molecular units based on the presence of a barcode gap in genetic divergence. Pairwise genetic distances summarized for each molecular unit delimited with the barcode gap analysis (ABGD) are presented in Table 3.

Table 3. Pairwise genetic p-distances for COI sequences within and between the 11 molecular mitochondrial units identified with Automatic Barcode Gap Discovery analysis (Table 1), in which *Platevindex luteus* (Semper, 1880) and *P. applanatus* (Simroth, 1920) comb. nov. were delineated together as a single unit. Pairwise distances for *P. luteus* and *P. applanatus* are also reported as two separate units. Ranges of minimum to maximum distances are indicated (as percentages) within and between each molecular clade. For example, within *P. tigrinus* (Stoliczka, 1869), individual sequences are between 0.0% and 2.7% divergent, and between *P. tigrinus* and *P. luteus* sequences are minimally 11.4% and maximally 15.6% divergent (the "barcode gap" between intraspecific and interspecific distances is illustrated in Fig. 9).

Units	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *P. coriaceus coriaceus* (unit #1)	0.0–1.9												
2. *P. coriaceus coriaceus* (unit #2)	8.5–10.0	0.0–3.1											
3. *P. coriaceus coriaceus* (unit #3)	8.7–10.2	7.0–8.7	0.2–1.1										
4. *P. coriaceus darwinensis* subsp. nov.	5.4–7.7	8.7–10.6	9.7–11.0	0.0–4.0									
5. *P. tigrinus*	10.5–12.7	12.2–14.0	12.2–13.8	10.5–14.9	0.0–2.7								
6. *P. luteus* + *P. applanatus*	11.9–15.3	13.7–16.2	13.3–16.7	11.7–16.7	10.8–15.6	0.0–7.7							
7. *P. luteus*	12.1–15.3	13.7–16.2	13.7–16.7	12.1–16.7	11.4–15.6	N/A	0.0–5.0						
8. *P. applanatus*	11.9–14.6	13.0–15.3	13.3–16.3	11.7–15.8	10.8–13.6	N/A	2.5–7.7	0.0–6.0					
9. *P. burnupi* (southern clade)	14.1–15.0	14.3–15.0	13.4–14.2	13.7–15.3	12.3–14.2	10.3–13.1	10.5–13.1	10.3–11.6	0.0–0.2				
10. *P. burnupi* (northern clade)	12.6–13.9	13.9–15.3	12.3–13.5	12.1–13.9	10.1–12.3	9.7–12.7	9.7–12.7	9.9–12.0	5.4–6.0	0.0–0.9			
11. *P. martensi*	20.2–22.2	23.1–25.2	20.0–21.8	19.7–22.5	19.9–22.9	20.5–24.0	20.5–24.0	20.7–23.5	21.4–22.4	19.9–21.2	0.0–2.1		
12. *P. aptei* sp. nov.	19.2–21.1	21.1–22.9	19.6–20.9	19.0–21.4	18.6–21.4	19.4–23.3	19.4–23.3	19.7–22.6	19.1–20.9	19.3–21.7	12.2–13.9	0.2–3.5	
13. *P. amboinae*	17.4–19.6	18.9–21.4	19.0–20.3	17.0–18.9	17.0–18.7	16.0–20.5	17.5–20.5	16.0–20.2	17.2–19.9	16.5–17.8	19.3–20.6	19.5–21.9	04–4.8

Results

Molecular phylogenetic analyses

The number of parsimony-informative sites in our alignments is reported without outgroups; thus, the number of sites is smaller than the number of sites in the alignments used for phylogenetic analyses (because outgroup sequences add many sites to the alignments). The ITS2 alignment includes 77 parsimony-informative sites out of 699 sites. The 28S alignment includes 20 parsimony-informative sites out of 986 sites. The best substitution model for mitochondrial loci was the GTR+G+I model, while the best substitution model for nuclear loci was HKY+G as determined by Topali. For partitioned analyses in MrBayes, the best substitution models selected for COI were GTR+G+I for the first codon position, GTR+I for the second position and GTR+G for the third position. The best fit model for 16S, ITS2, 28S and H3 as determined by PartitionFinder was GTR+G+I, implemented separately for each locus. For partitioned RAxML analyses, a GTR model is used by default, but the GTR+G+I search option was used to incorporate substitution rate heterogeneity and estimate the proportion of invariable sites for the same partitions used in the Bayesian analysis.

The monophyly of *Platevindex* is strongly supported in the partitioned multi-locus analysis (PP 0.96, bootstrap 87%, Fig. 4), as well as in analyses including nuclear sequences (Figs 5–6). Analyses of mitochondrial DNA sequences (COI, 16S) yield a similar topology for the deeper nodes (including the monophyly of *Platevindex*) but with lower support (Figs 7–8).

Seven well-supported clades in the partitioned analysis provide the foundation for *Platevindex* species relationships (clades labeled A to G, Fig. 4). That *P. amboinae* (clade B) is distantly related to all other *Platevindex* (clade A) is also recovered in the nuclear analyses (Figs 5–6) and is not contradicted by mitochondrial analyses (Figs 7–8). Clade B includes only *P. amboinae* in molecular analyses, but *P. latus* (for which no fresh material was available) likely belongs to clade B as well, because it shares several distinctive features with *P. amboinae* (Table 4). Clade A includes two clades (Fig. 4): clade D (*P. aptei* sp. nov. and *P. martensi*) and clade C (all *Platevindex* except *P. amboinae*, *P. martensi*, and *P. aptei* sp. nov.). The monophyly of clade D is strongly supported in all analyses (Figs 4–8), which is in agreement with morphology because both *P. martensi* and *P. aptei* sp. nov. share several distinctive features (Table 4). The monophyly of clade C is recovered in mitochondrial analyses of COI and 16S (Fig. 8) but is poorly supported (Figs 6–7) or unresolved (Fig. 5) in other analyses. Morphologically, clade C includes all the *Platevindex* species with dorsal eyes that are not close to the edge (> 2 mm) of the notum (Table 4), which could be a synapomorphy or a symplesiomorphy. Clade C includes two clades (Fig. 4): clade E (*P. burnupi*, *P. applanatus*, and *P. luteus*) and clade F (*P. coriaceus* and *P. tigrinus*). Clade E is unresolved in both nuclear analyses (Figs 5–6) and mitochondrial maximum likelihood analyses (Figs 7–8) but is supported in the Bayesian analysis of COI and 16S (Fig. 8, PP 1). Support for clade F is lower than for other clades but it is recovered in most analyses: in the partitioned analysis with all five markers (PP 0.7, bootstrap 64%, Fig. 4), in the nuclear analysis of ITS2 and 28S (bootstrap 57%, Fig. 6), as well as in the mitochondrial analysis of COI and 16S (bootstrap 51%, Fig. 8); it only is not recovered in the COI analyses, which is expected given that COI is much less useful for deeper nodes (Fig. 7). Although the monophyly of clade F (*P. tigrinus* and *P. coriaceus*) is not strongly supported by molecular data, both species are externally indistinguishable and share many anatomical features. Finally, clade E includes clade G (*P. applanatus* and *P. luteus*), which is sister taxon to *P. burnupi* (Fig. 4). Clade G is strongly supported in the combined, partitioned analyses (PP 1, bootstrap 100%, Fig. 4) as well as in the mitochondrial analyses (PP 0.99, bootstrap 91%, Fig.7; PP 1, bootstrap 99%, Fig. 8).

The monophyly of the eight species recognized here is well supported in the partitioned analysis with all five markers (Fig. 4). The monophyly of the ninth species, *P. latus*, could not be tested because no fresh material was available. These eight species are also supported in nuclear maximum parsimony analyses
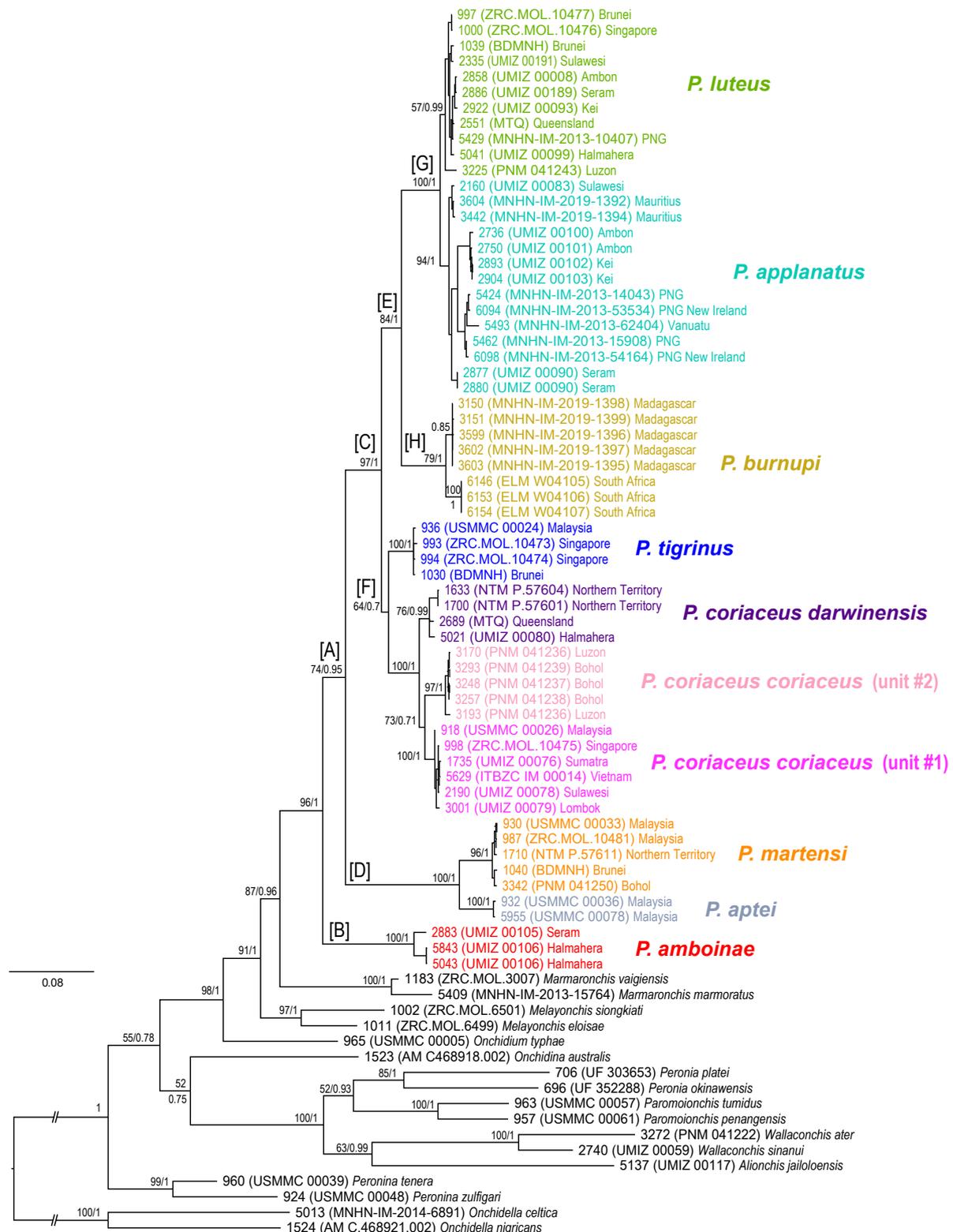
Fig. 4. Phylogenetic relationships of species of *Platevindex* based on partitioned COI, 16S, ITS2 and 28S sequences. Support values are reported above each branch with bootstrap values (maximum likelihood) listed first, followed by posterior probabilities (Bayesian analysis).

Table 4 (continued on next page). Summary of internal and external traits in species of *Platevindex* Baker, 1938. Traits are described in the corresponding species descriptions and vary among individuals. External traits include the length of the animal, number of dorsal eyes, color of the foot and other distinguishing characters such as the color of the hyponotum. Internal traits include the insertion of the retractor muscle (RM), the length of the retractor muscle compared to that of the penial sheath (PS), the length of the region with penial hooks and the type of the intestinal loops.

Species (clades in Figs 1–5)	Maximum length (mm)	Foot color	Hyponotum color	Appearance of dorsal notum	Number of dorsal eyes (present < 2mm from notum edge or not)	Intestinal type	Distribution
P. coriaceus coriaceus (clade A)	49	light yellow	light grey to dark blue-grey	bumpy and granular	17–68 (no)	II	Brunei, China, Indonesia, Malaysia, Philippines, Singapore, Vietnam
P. coriaceus darwinensis subsp. nov. (clade A)	57	light yellow	light grey	bumpy and granular	20–36 (no)	II	Australia, Halmahera (Indonesia)
P. tigrinus (clade A)	40	dark blue-grey or light yellow	light grey to blue-grey	bumpy and granular	25–50 (no)	II	Brunei, China, India, Malaysia, Singapore
P. luteus (clade A)	28	light yellow	white, light grey or dark blue-grey	distinctly-raised papillae, dome-shaped if disturbed	10–35 (no)	I and II	Australia, Brunei, Indonesia, Papua New Guinea, Philippines, Vietnam
P. applanatus (clade A)	22	light to bright yellow	light grey to semi-translucent	distinctly-raised papillae, dome-shaped if disturbed, bright yellow markings	2–26 (no)	I	Ambon, Kei and Aru Islands (Indonesia), Mauritius, Papua New Guinea, Vanuatu
P. burnupi (clade A)	24	yellow	light grey	bumpy and granular	12–38 (no)	II	Madagascar, Mozambique, South Africa
P. martensi (clade B)	52	bright to dark orange	yellow with dark spots (many spots = black)	bumpy and granular with elongated (longitudinal) ridges	20–65 (yes)	II	Northern Australia, Brunei, China, Indonesia, Myanmar, Philippines, Thailand
P. aptei sp. nov. (clade B)	60	black	yellow or tan with dark spots (many spots = almost black)	bumpy and granular with elongated (longitudinal) ridges	35–50 (yes)	II	Andaman Islands (India), Malaysia
P. amboinae (clade C)	38	yellow-grey or dark grey	light to dark grey	bumpy and granular with raised papillae if disturbed	absent	III	Ambon, Halmahera (Indonesia)
P. latus (clade C)	33	yellow (preserved)	grey (preserved)	large conical papillae	absent	III	New Britain (Papua New Guinea)

Table 4 (continued). Summary of internal and external traits in species of *Platevindex* Baker, 1938: reproductive system.

Species (clade in Figs 1–5)	Insertion of penial retractor	Length of RM/PS	Penial hooks, length (µm)	Region with penial hooks (mm)	Deferent duct and oviduct attached	Coiled deferent duct on (or near) oviduct	Width of oviduct/deferent duct (up to)	Length of distal/proximal oviduct (up to)	Distribution
P. coriaceus coriaceus (clade A)	posterior end of visceral cavity	#1: ⅛ to 1 #2: ⅛ to ⅓	60–130	4–8	closely	highly	×3	×4	Brunei, China, Indonesia, Malaysia, Philippines, Singapore, Vietnam
P. coriaceus darwinensis subsp. nov. (clade A)	posterior end of visceral cavity	¼ to 1	60–110	2–8	closely	highly	×5	×2	Australia, Halmahera (Indonesia)
P. tigrinus (clade A)	near heart	¼ to 1	60–100	1–1.5	closely	almost straight	×3	×3	Brunei, China, India, Malaysia, Singapore
P. luteus (clade A)	near heart	½ to 3	40–70	1–1.5	loosely	loosely	×2	×1	Australia, Brunei, Indonesia, Papua New Guinea, Philippines, Vietnam
P. applanatus (clade A)	near heart to posterior end of visceral cavity	⅕ to 1	20–90	1–3	closely	highly	×2	×2	Ambon, Kei and Aru Islands (Indonesia), Mauritius, Papua New Guinea, Vanuatu
P. burnupi (clade A)	¾ of visceral cavity to posterior end of visceral cavity	½ to 2	25–70	1–1.5	loosely	highly/loosely	×2	×1	Madagascar, Mozambique, South Africa
P. martensi (clade B)	½ to ¾ of visceral cavity	½ to 1	35–55	2–2.5	no	highly	×2	×2	Northern Australia, Brunei, China, Indonesia, Myanmar, Philippines, Thailand
P. aptei sp. nov. (clade B)	posterior end of visceral cavity	⅙ to 1	30–40	2.5–5	no	highly/loosely	×2	×2	Andaman Islands (India), Malaysia
P. amboinae (clade C)	Within anterior ½ of visceral cavity	½ to 1	N/A	N/A	no	highly	×1	×1	Ambon, Halmahera (Indonesia)
P. latus (clade C)	Within anterior ½ of visceral cavity	½ to ¾	N/A	N/A	no	highly	×1	×1	New Britain (Papua New Guinea)
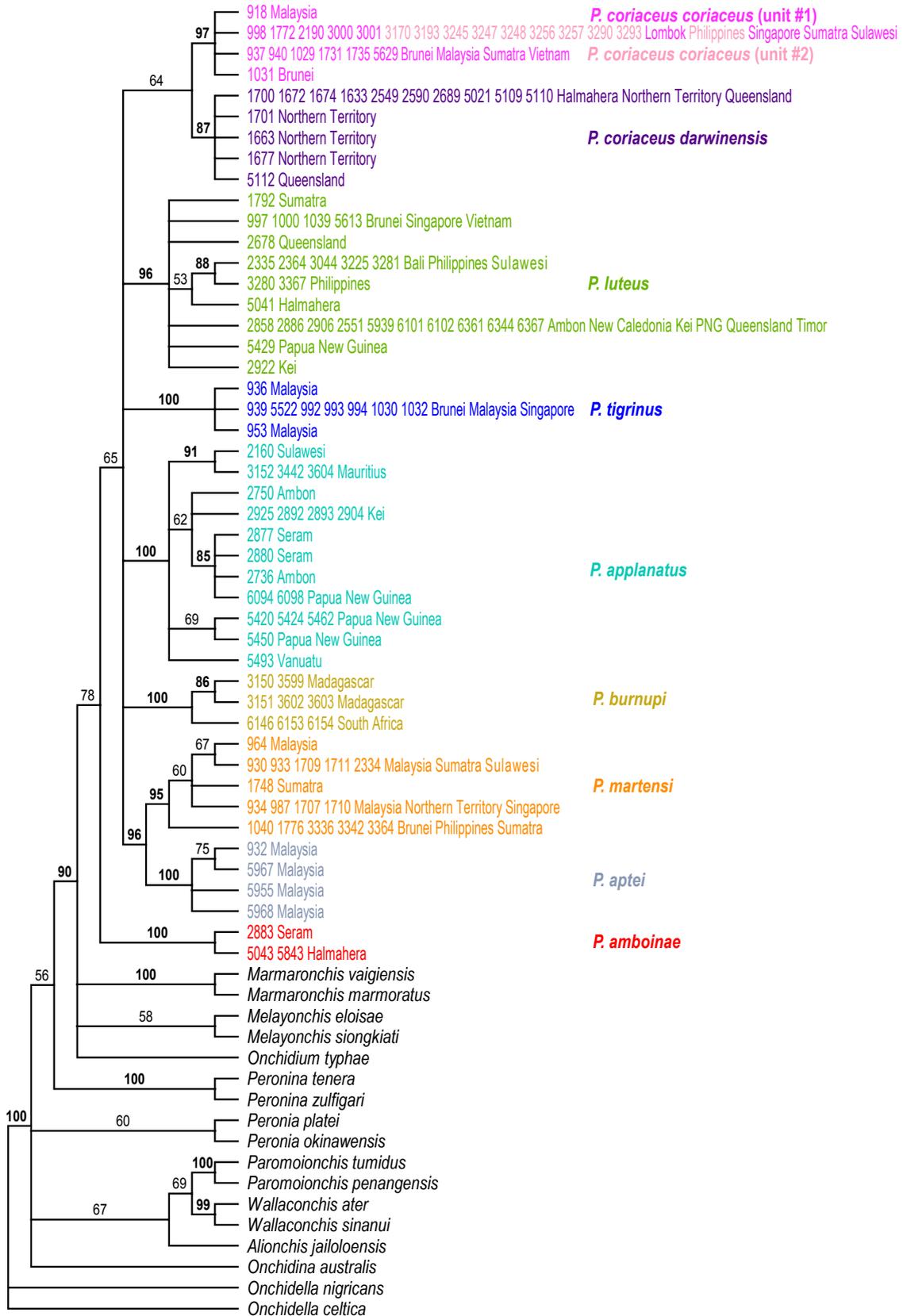
Fig. 5. Maximum parsimony consensus tree of species of *Platevindex* based on unique ITS2 haplotypes. Numbers above the branches are bootstrap values.
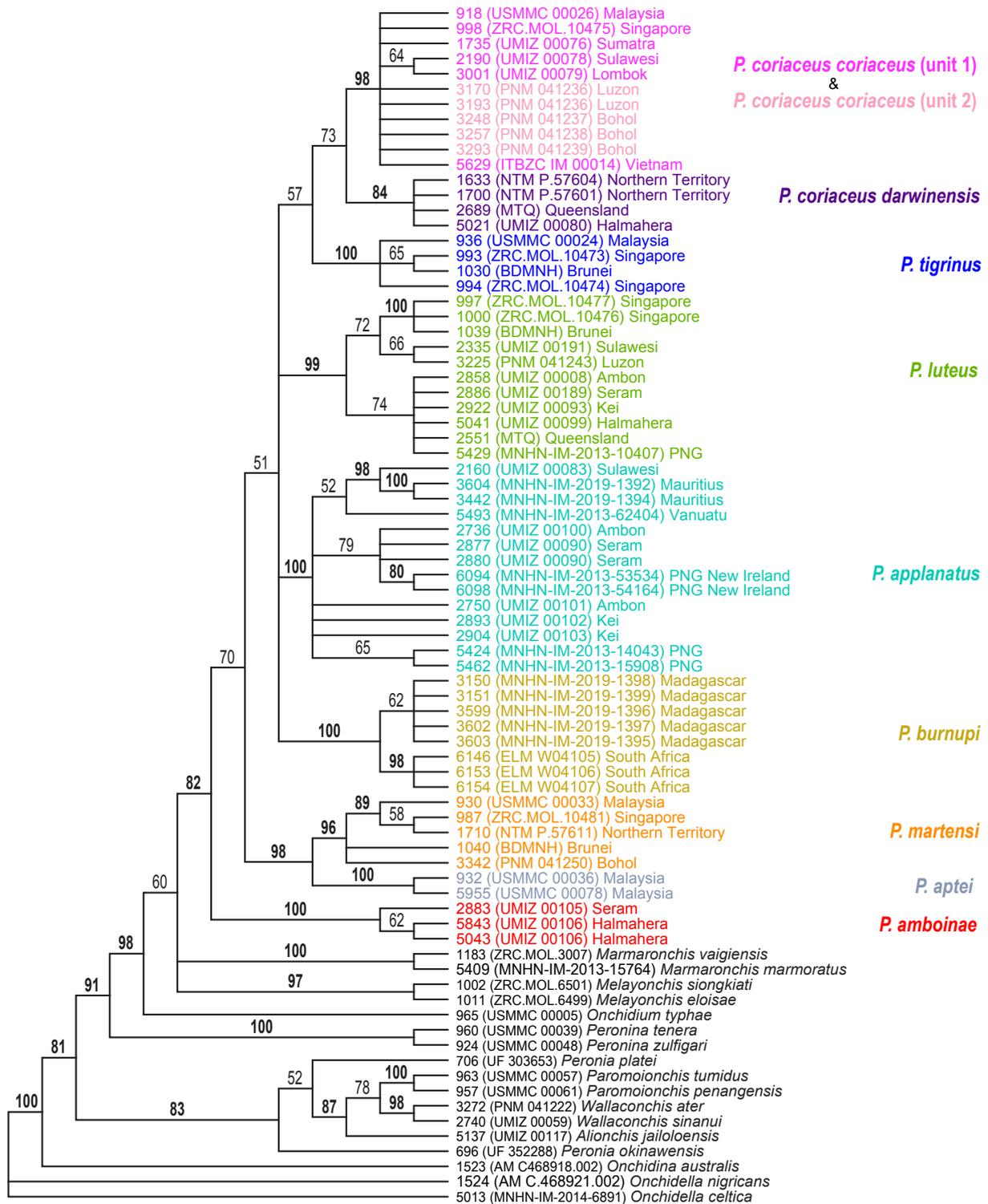
Fig. 6. Maximum parsimony consensus tree of species of *Platevindex* based on ITS2 and 28S sequences. Numbers above the branches are bootstrap values.
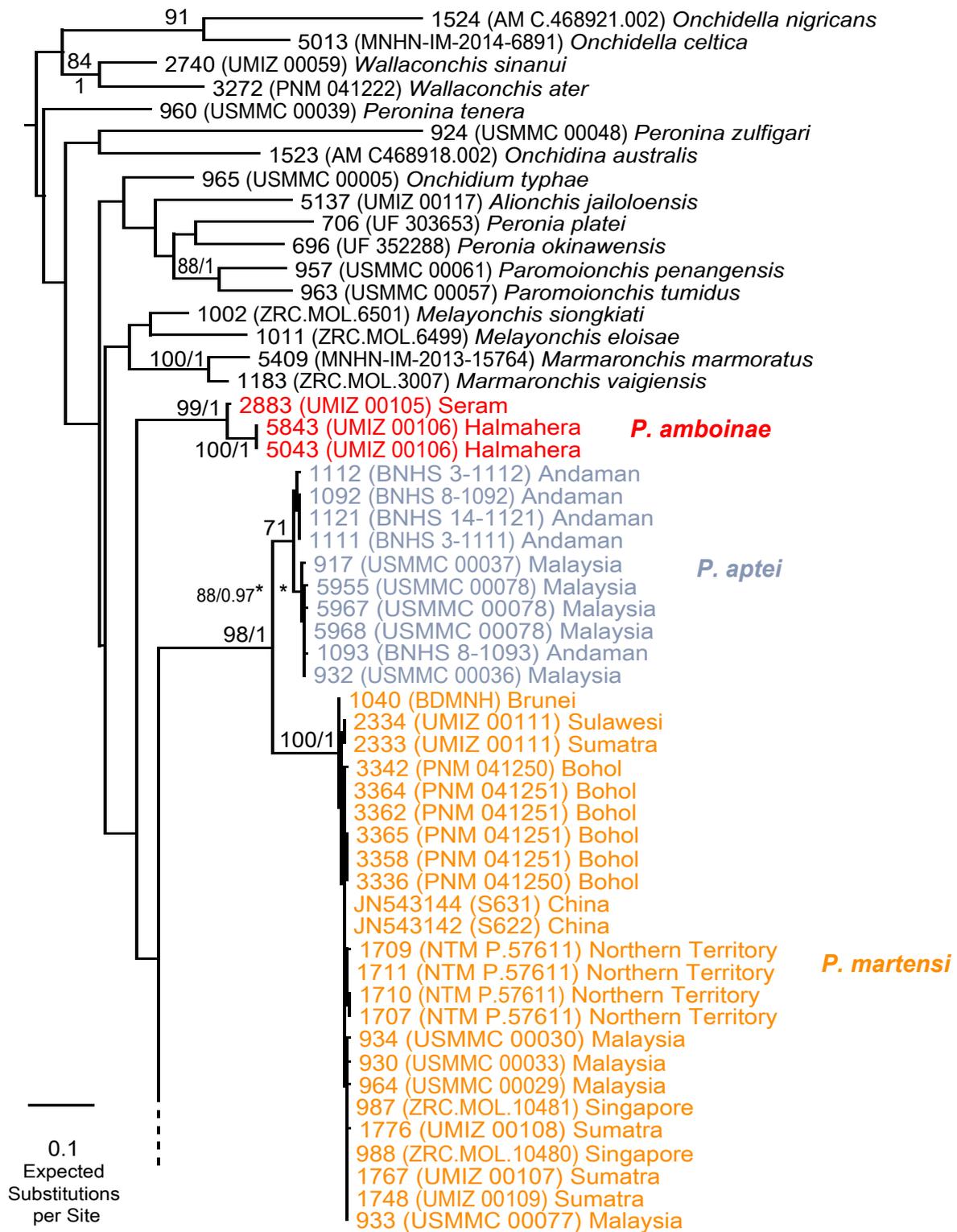
Fig. 7 (part 1 of 3). Phylogenetic tree based on COI sequences for 195 individuals (plus outgroups). Only bootstrap values > 60% (maximum likelihood) and posterior probabilities > 0.9 (Bayesian analysis) are indicated. Some outgroups sequences are from previous studies (Dayrat *et al*. 2011a, 2016, 2017, 2018, 2019a, 2019b, 2019c, 2019d; Goulding *et al*. 2018a, 2018b, 2018c). Information on specimens can be found in the lists of material examined and in Table 1. All sequences of specimens of *Platevindex* are new, except sequences obtained from GenBank for specimens from China.
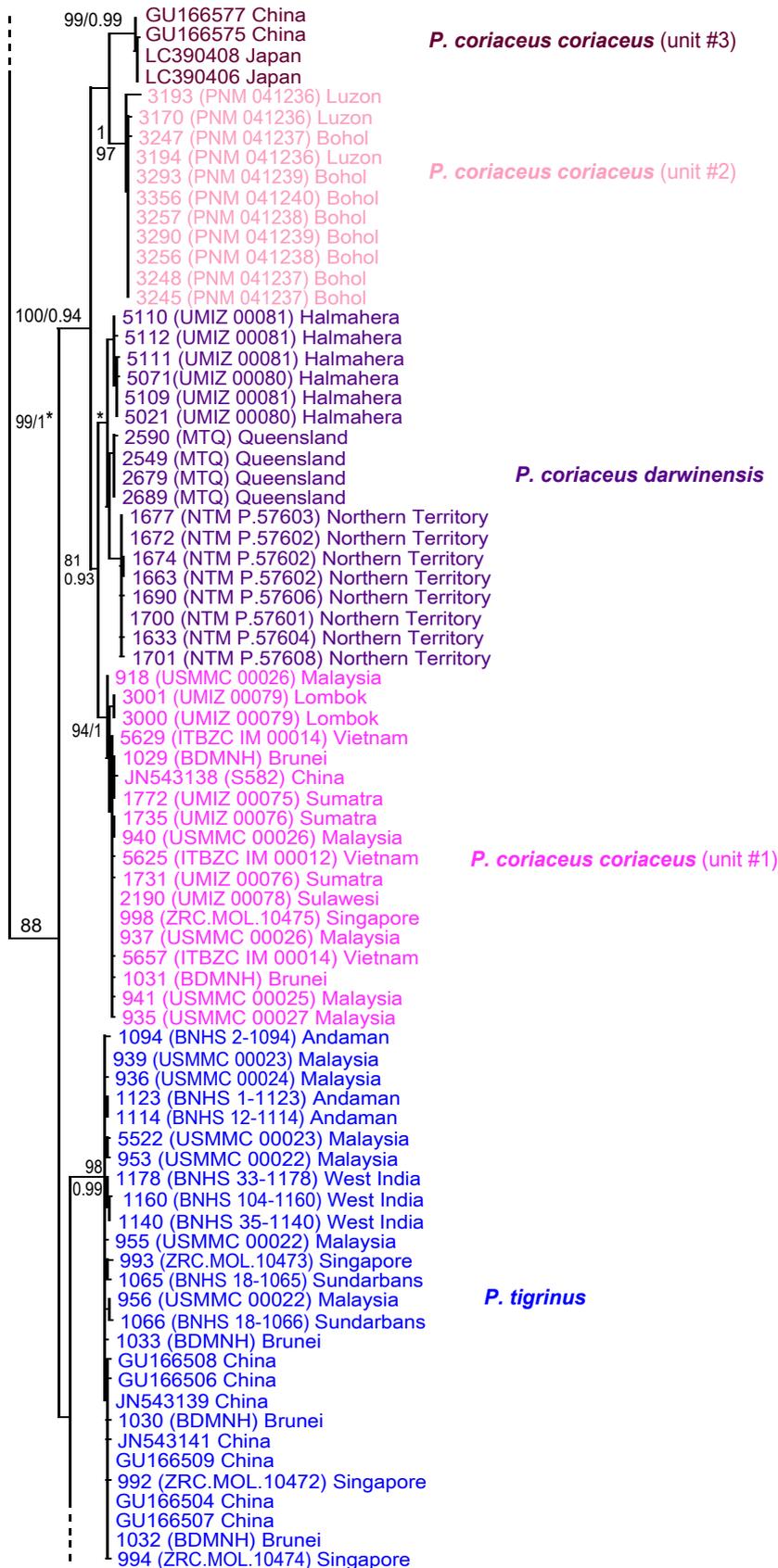
Fig. 7 (part 2 of 3). Phylogenetic tree based on COI sequences for 195 individuals (plus outgroups).
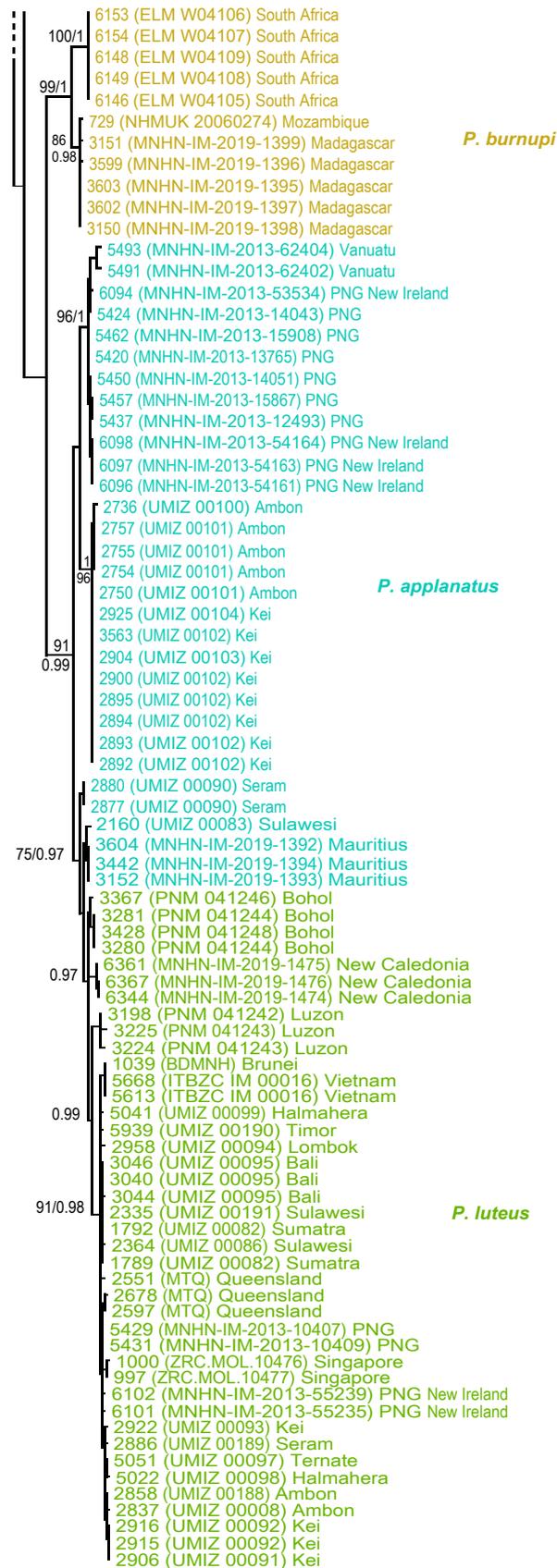
Fig. 7 (part 3 of 3). Phylogenetic tree based on COI sequences for 195 individuals (plus outgroups).
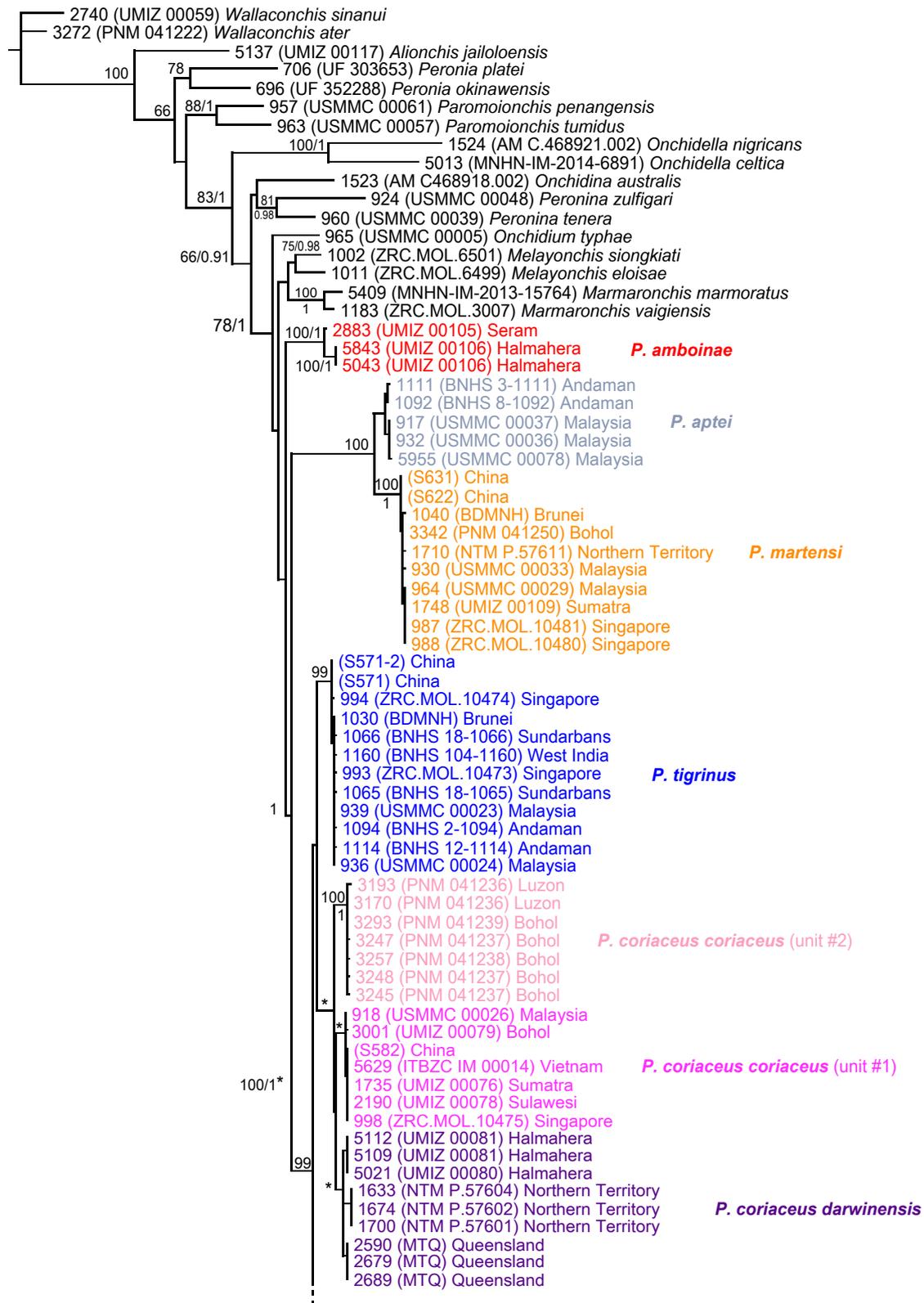
Fig. 8 (part 1 of 2). Phylogenetic tree of species of *Platevindex* based on mitochondrial COI and 16S sequences. Support values are reported above each branch with bootstrap values (maximum likelihood analysis) followed by posterior probabilities (Bayesian analysis); only values > 60% and > 0.9, respectively, are indicated.

(Figs 5–6). Overall, mitochondrial data show remarkable congruence with nuclear data regarding species limits. Trees from mitochondrial analyses (Figs 7–8) only differ with respect to *P. luteus* and *P. applanatus*, two species which are well supported in the combined partitioned analyses (Fig. 4) as well as in the nuclear analyses (Figs 5–6). Based on mitochondrial sequences, individuals of *P. applanatus* from Mauritius ([3152], [3442], 3604), Seram ([2877], [2880]), and Sulawesi ([2160]) are sister-group to *P. luteus*. As a result, *P. luteus* is nested within *P. applanatus* (Figs 7–8) and *P. applanatus* is paraphyletic based on mitochondrial DNA. Unlike nuclear DNA, mitochondrial loci are uniparentally inherited and do not undergo recombination. Thus, mitochondrial DNA can introgress from one species into another as a linked block following hybridization and backcrossing (Smith 1992; Funk & Omland
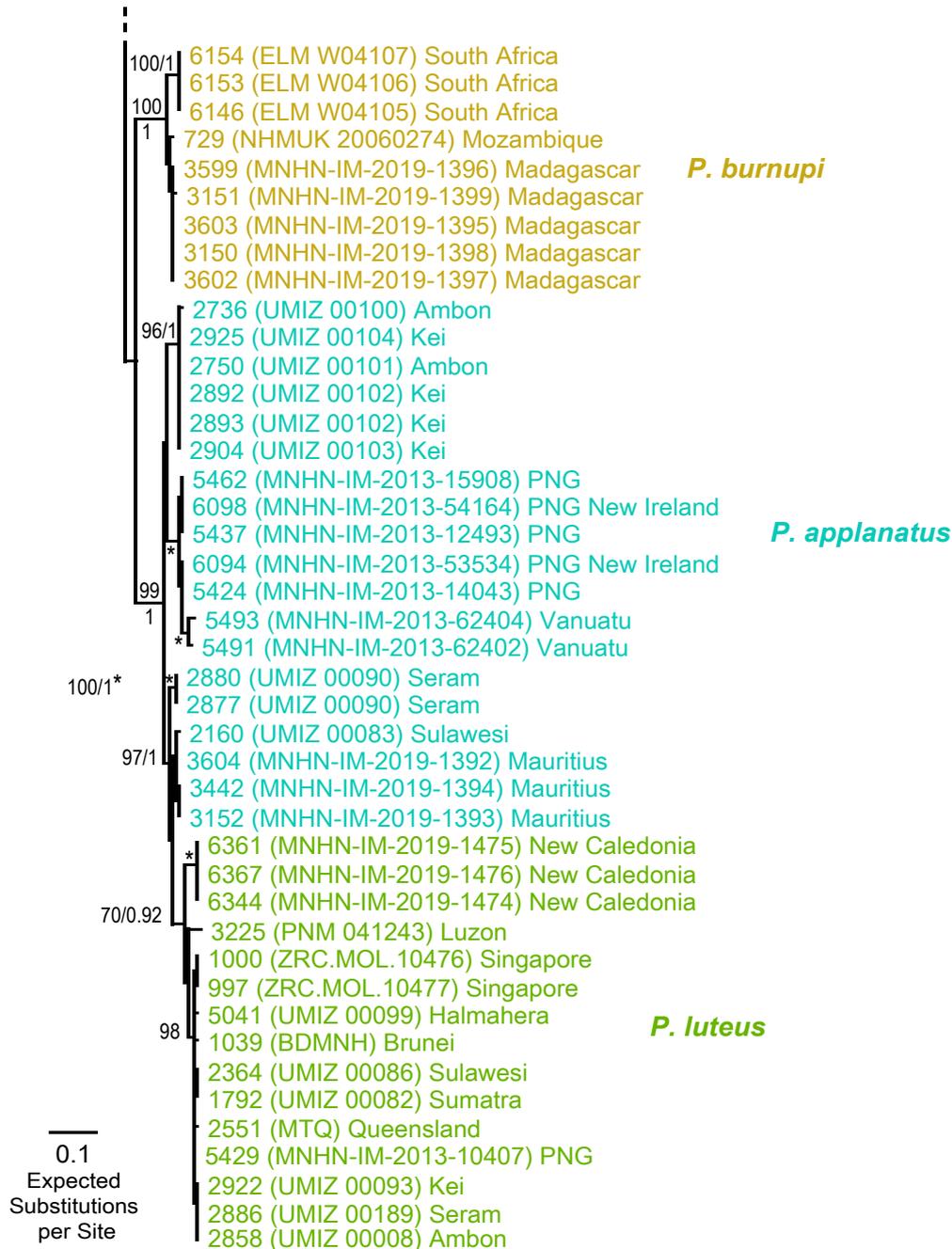
Fig. 8 (part 2 of 2). Phylogenetic tree of species of *Platevindex* based on mitochondrial COI and 16S sequences.

2003). *Platevindex luteus* and *P. applanatus* are regarded as distinct species (see 'Species delineation' below) because they differ anatomically and the two groups are genetically divergent clades based on nuclear DNA data (Figs 5–6). The incongruence between mitochondrial and nuclear data is addressed in the discussion.

Four clades are recovered in the species *P. coriaceus* based on mitochondrial COI sequences (Fig. 7): these four least-inclusive, monophyletic, mitochondrial units are referred to as units #1, #2, #3 and #4. Units #1 and #2 are not recovered as distinct clades with nuclear data (i.e., specimens from unit #1 and unit #2 cluster together in a single clade) and the reciprocal monophyly of the mitochondrial unit #4 is confirmed with nuclear data (Figs 5–6); mitochondrial unit #3 (China and Japan) is only represented in COI analyses because no 16S sequences and no nuclear sequences were available in GenBank for those individuals. The reciprocal monophyly between unit #4 and all other units in nuclear analyses and the fact that the specimens from unit #4 differ slightly from the rest of the species both serve to recognize two subspecies within *P. coriaceus*: *P. coriaceus coriaceus* (units #1, #2 and #3) and *P. coriaceus darwinensis* subsp. nov. (unit #4). The three units in *P. coriaceus coriaceus* have allopatric distributions: *P. coriaceus coriaceus* unit #1 is found from the Strait of Malacca to Lombok and southeastern China, unit #2 is found in the Philippines and unit #3 is found in eastern China and southern Japan. *Platevindex coriaceus darwinensis* sp. nov. is present in Halmahera, Queensland, and Northern Territory, and therefore is also allopatric with *P. coriaceus coriaceus*.

Pairwise genetic divergences

Pairwise p-distances were calculated between the 11 least-inclusive units identified through the barcode gap analysis (ABGD) of our COI data set (Fig. 8). Because *P. luteus* and *P. applanatus* are regarded as one single unit by ABGD based on COI sequences, distances were also calculated for those two species separately. As a result, pairwise distances and barcode gaps between intra-unit and inter-unit distances
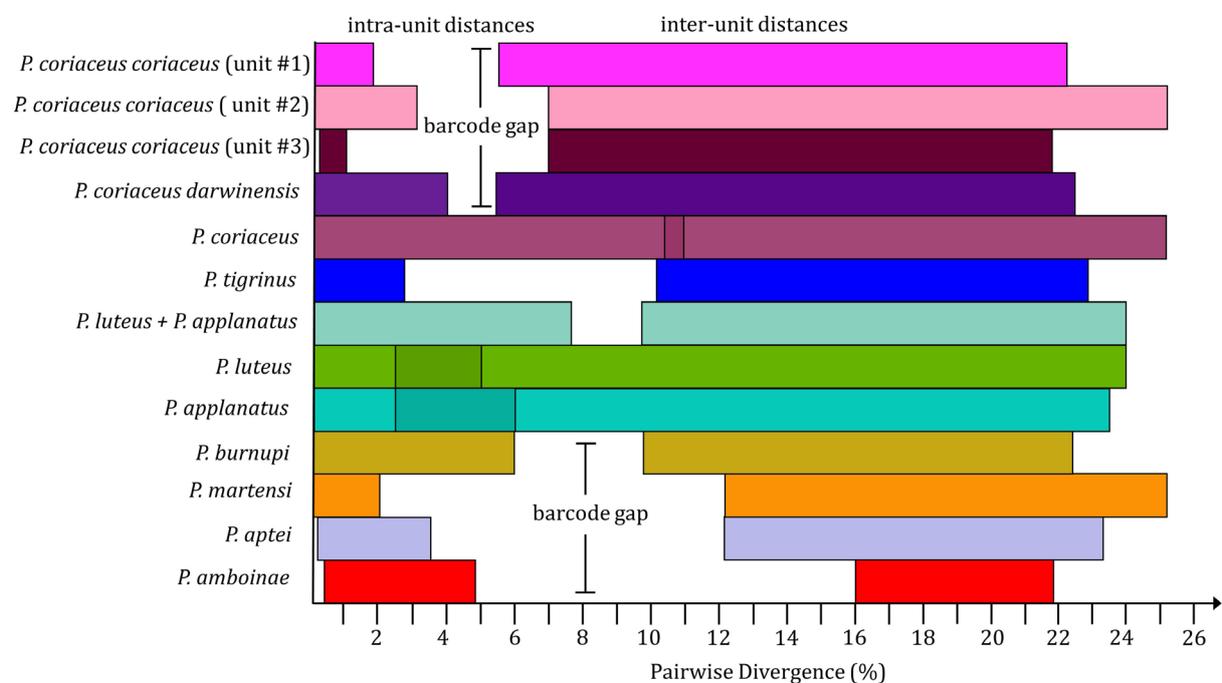
Fig. 9. Diagram illustrating pairwise genetic p-distances between COI sequences within and between mitochondrial molecular units in *Platevindex* delineated by Automatic Barcode Gap Discovery. Colored bars show intraspecific and interspecific genetic distances (in percent) and the "barcode gap" between these.

are presented for a total of 13 units, including *P. luteus* and *P. applanatus* taken together as a single unit and considered separately (Fig. 9, Table 3).

As might be expected, barcode gaps are not strictly identical across the genus. Large barcode gaps between intra-unit and inter-unit distances are found for species that are strongly supported in all three (morphological, mitochondrial and nuclear) data sets: *P. amboinae* (barcode gap from 4.8 to 16.0%), *P. aptei* sp. nov. (gap from 3.5 to 12.2%), *P. martensi* (gap from 2.1 to 12.2%) and *P. tigrinus* (gap from 2.7 to 10.1%). There also is a large barcode gap between the three units of *P. coriaceus coriaceus* (e.g., from 3.1 to 7.0% for *P. coriaceus coriaceus* unit #2) as well as for the southern clade of *P. burnupi* (gap from 0.2 to 5.4%) and the northern clade (gap from 0.9 to 5.4%). However, no barcode gap applies to *P. luteus* or *P. applanatus*, even though they are regarded as species based on further evidence from anatomy and nuclear data (see below). When *P. luteus* and *P. applanatus* are considered separately, genetic distances within *P. luteus* (0.0 to 5.0%) overlap with the interspecific distances between *P. luteus* and *P. applanatus* (2.5 to 7.7%). In fact, based on COI sequences, a few individuals of *P. applanatus* are within the *P. luteus* clade (Fig. 7). As a result, these two species are not reciprocally monophyletic and are regarded as a single unit by ABGD. When they are taken together as a single unit, intraspecific genetic distance is between 0.0 and 7.7%, and thus the barcode gap for the two species grouped together is between 7.7 and 9.7% (Fig. 9, Table 3).

Comparative anatomy

All *Platevindex* slugs share some traits that are not found in any other onchidiids. In particular, they are characterized by a dorso-ventrally flattened body and a very narrow foot which make them relatively easy to identify to the genus level in the field. In addition, species of *Platevindex* differ both internally and externally (Table 4) and their differences can be combined for species identification (see the identification key provided after the Discussion).

The dorsal color of most species of *Platevindex* is similar (generally shades of brown and black), with the notable exception of bright yellow longitudinal markings often observed in *P. applanatus*. The ventral color (foot and hyponotum) is similar in most species except in *P. martensi*, the only species with an orange foot, and *P. aptei* sp. nov., the only one with a black foot. Other external traits differ between species (Table 4). Prominent dorsal papillae (with or without dorsal eyes) and a nearly hemispherical body when the animal is contracted are only found in *P. luteus* and *P. applanatus*. The very large papillae found in *P. latus* are also different from those found in *P. luteus* and *P. applanatus*. Longitudinal ridges are only found on the dorsal notum of *P. martensi* and *P. aptei* sp. nov. And, finally, dorsal eyes can be absent (*P. amboinae* and *P. latus*) or present (all other species) and, when present, they are very close (<2 mm) to the notum edge (*P. martensi* and *P. aptei* sp. nov.) or not (all other species with dorsal eyes).

Species also differ with respect to several internal traits (Table 4). Some of those traits are fairly easy to observe, such as the type of intestinal loops (types I, II and III) and the insertion of the retractor muscle of the penis (e.g., near the heart in the middle of the visceral cavity or at the posterior end of the visceral cavity), as these structures are within the body cavity of the slug and can be checked after cutting open the notum. However, some expertise is required to observe some other traits, such as the length of the flexible portion of the penis (with or without hooks) and the penial hooks (present or absent), which cannot be examined without the dissection of the reproductive parts.

Species delineation

Species are delineated based on three lines of evidence: morphological differences, analyses of mitochondrial DNA sequences and analyses of nuclear DNA sequences. There is complete congruence between morphological and nuclear data. The 9 least-inclusive units obtained in trees based on nuclear

data are exactly those that are distinct morphologically, possibly with the exception of *P. coriaceus coriaceus* and *P. coriaceus darwinensis* subsp. nov., which are hard to distinguish morphologically (Figs 5–6). Mitochondrial COI sequences yield 11 least-inclusive units, most of which are the same as those supported by morphology and nuclear data. In all those cases where all three lines of evidence are in agreement, it is easy to decide what least-inclusive units should be recognized as taxa and properly named. For instance, *P. martensi* and *P. aptei* sp. nov. are recovered as two closely-related, reciprocally-monophyletic, least-inclusive units in all nuclear and mitochondrial analyses, they are separated by a large gap between intra- and interspecific genetic (COI) distances, they differ anatomically, they can be distinguished externally, and they are even sympatric in Peninsular Malaysia, indicating that they must be reproductively isolated (otherwise nuclear haplotypes would be similar between both species). Two least-inclusive units within *P. burnupi* are considered a single species, based on similar anatomy; the high intraspecific genetic distance is likely influenced by the geographic distance between sampling localities (5.4–6.0%).

Incongruence between mitochondrial data, on one side, and nuclear and anatomical data, on the other side, is exclusively limited to two cases: the distinction between *P. luteus* and *P. applanatus*, and to the distinction between *P. coriaceus coriaceus* units #1 and #2. In those cases, it is considered that two congruent lines of evidence (anatomical and nuclear data) should have priority over a single line of evidence (mitochondrial data). Mitochondrial DNA is still used in the delineation of species of *Platevindex* but is interpreted in conjunction with other data, as introgression in mitochondrial DNA has been shown to be common across diverse taxa (Funk & Omland 2003). In onchidiids, nuclear loci have been critically important in delineating species, as high intraspecific mitochondrial divergence occurs in many species, including *Paromoionchis tumidus* (up to 7.2%; Dayrat *et al.* 2019a), *Laspionchis bourkei* Dayrat & Goulding, 2019 (up to 7.8%; Dayrat et al. 2019b) and *Peronina zulfigari* (up to 9.9%; Goulding *et al*. 2018c), but is not accompanied by any morphological differences or genetic divergence in nuclear sequences. According to mitochondrial trees (Figs 7–8), *P. applanatus* is paraphyletic at the base of *P. luteus*, while nuclear DNA sequences recover *P. applanatus* and *P. luteus* as monophyletic, although the relationship between the two species is unclear due to an unresolved polytomy (Figs 5–6). Because *P. applanatus* is anatomically distinct and a highly-supported clade with ITS2 and 28S sequences (Fig. 6), it is regarded as a distinct species (see the Discussion). Units #1 and #2 of *P. coriaceus coriaceus* are reciprocally-monophyletic in mitochondrial analyses (Figs 5–6), while individuals of those two units (which are anatomically indistinguishable) are mixed with each other in nuclear analyses (Figs 7–8), suggesting that there is still gene flow between populations of those two mitochondrial units (because the mitochondrial genome is maternally-inherited while the nuclear genome is inherited from both parents). As a result, the mitochondrial units #1 and #2 of *P. coriaceus coriaceus* are not named and recognized as distinct taxa. Note that we did not have access to fresh material and nuclear sequences for mitochondrial unit #3 of *P. coriaceus coriaceus*, from eastern China and southern Japan. It may or may not be a distinct subspecies of *P. coriaceus*.

Two subspecies are recognized in *P. coriaceus*: *P. coriaceus darwinensis* subsp. nov. and *P. coriaceus coriaceus* (units #1, #2 and #3), which are recovered as distinct in all analyses. They differ by seven consecutive base pairs in the ITS2 sequence, a low level of divergence compared to the other species recognized here. Also, they only differ anatomically in minute details of the reproductive system. Thus, *P. coriaceus coriaceus* and *P. coriaceus darwinensis* subsp. nov. are ranked as subspecies (see the Discussion). Two least-inclusive, reciprocally-monophyletic clades are also consistently recovered within *Platevindex burnupi*, and there is greater genetic divergence between these two units of *P. burnupi* than between the units of *P. coriaceus*. However, due to the limited geographic sampling for *P. burnupi*, these two clades may not represent two distinct molecular groups. *Platevindex burnupi* is considered a single species, but further study is needed to understand dispersal and population connectivity.

Systematics and anatomical descriptions

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

Genus ***Platevindex*** Baker, 1938

Type species

Onchidium coriaceum Semper, 1880, by original designation (Baker 1938: 88).

Diagnosis

Body dorso-ventrally flattened. Notum hard. No dorsal gills. Dorsal eyes present (in most species) or absent (only in two species). Dorsal eyes occur individually, never in groups. Eyes at the tip of short ocular tentacles. Foot narrow, approximately ¼ to ⅓ of total width. Pneumostome median, on ventral hyponotum. Intestinal loops of types I, II or III. Accessory penial gland absent. Male opening below two ocular tentacles, almost centered, but slightly to right side (in dorsal view). Rectal gland present. Penis composed of two regions: rigid proximal region and flexible distal region. Penial hooks in distal region present (in most species) or absent.

Gender

The gender is masculine (ICZN Article 30.1.1). The generic name *Platevindex* was formed from the family name of the German zoologist Dr. Ludwig H. Plate (1862–1937), professor at Jena, who described several onchidiid species. No gender was specified in Baker's (1938) original publication of the generic name *Platevindex*. However, Baker (1938: 88) changed the ending of the specific name *coriacea* (combined with the generic name *Oncis* Plate, 1893) to *coriaceus*, indicating that he considered *Platevindex* to be of masculine gender. Also, the Latin word '*vindex*', meaning 'protector' or 'champion', is masculine. As a result, the ending of all specific names transferred to *Platevindex* must become masculine (e.g., *Onchidium luteum* becomes *Platevindex luteus*).

Distinctive diagnostic features

Platevindex slugs can easily be identified in the field by their dorso-ventrally flattened body, firm notum and very narrow foot (one third of the total width or less when the animal is not active). However, no combination of internal characters is unique to *Platevindex*. Slugs with a rectal gland and no accessory penial glands are also found in *Melayonchis* and *Onchidina*. Also, among *Platevindex*, *Melayonchis* and *Onchidina* slugs, intestinal loops of type I are found only in *Platevindex*, but intestinal loops of type II are found in all three genera and intestinal loops of type III are found in both *Platevindex* and *Melayonchis*. The lateral radular teeth of *Platevindex* are characterized by a slight protuberance on their inner lateral margin (e.g., see arrows on Figs 18B, 34C, 48C, 57C, 66C). This kind of radular protuberance is unusual among onchidiids. Apart from in *Platevindex*, it has been observed only in *Marmaronchis*, in which the protuberance is also slight (Dayrat *et al.* 2018), and in *Melayonchis*, where it is much more conspicuous and sharp (Dayrat *et al.* 2019c).

Remarks

Several of the species that belong to *Platevindex* were classified in Plate's genus *Oncis*. Baker (1938) established the generic name *Platevindex* as a replacement name for *Oncis* Plate, 1893, which he treated as a junior homonym of *Oncis* Herrmannsen, 1847. However, *Oncis* Herrmannsen, 1847 was a mere

nomenclator entry ("*Oncis* - vid. *Onchis*") which referred to *Onchis* Férussac, 1822, an available generic name, and which Herrmannsen treated as a full entry. Because *Oncis* was not treated as the valid name of a taxon by Herrmannsen (1847), it is not an available name under ICZN Article 11.5.

Regardless of the nomenclatural status of *Oncis* Herrmannsen, 1847, the generic name *Oncis* Plate, 1893 is not available because it is a junior objective synonym of *Onchis* Férussac, 1822. Indeed, under ICZN Article 33.2.1, one reason for a change in the original spelling of a name to be interpreted as "demonstrably intentional" is "when two or more names in the same work are treated in a similar way." In his revision of the onchidiids, Plate (1893) changed the original spelling of *Onchidium* to *Oncidium*, that of *Onchidina* to *Oncidina*, and that of *Onchidella* Gray, 1850 to *Oncidiella*. It is thus obvious that Plate (1893) considered that *Oncis* was a "demonstrably intentional" spelling change from *Onchis*. The generic name *Oncis* Plate, 1893 is thus an emendation of *Onchis* Férussac, 1822, but it is an unjustified emendation because Plate's (1893) correction was not made in accordance with Article 32.5. As an unjustified emendation, *Oncis* Plate, 1893 is a junior objective synonym of *Onchis* Férussac, 1822 and it enters in homonymy (Article 33.2.3). The fact that Plate (1893: 164) claimed that *Oncis* was a new generic name does not change the fact that, according to the Code, it is treated as an unjustified emendation of *Onchis* Férussac, 1822. Interestingly, several authors already treated *Oncis* Plate, 1893 as a junior objective synonym of *Onchis* Férussac, 1822. For instance, according to Woodward (1894: 57), *Oncis* Plate, 1893 is a "*nom.* preocc. *Onchis* (*i.e .,* *Oncis*), Fér., = *Peronia*, Blainv.". Also, Woodward (1894: 57) designated *Oncis coriacea* as the type species of *Oncis*. Regardless, being a junior objective synonym of *Onchis* Férussac, 1822, *Oncis* Plate, 1893 is objectively invalid. *Oncis* Plate, 1893 actually refers to the taxon of which the type species is *Onchidium peronii* Cuvier, 1804 (i.e., the type species of *Onchis* Férussac, 1822), and thus refers to the genus *Peronia* Fleming, 1822, not *Platevindex* (Dayrat *et al.* 2020). As a result, the valid generic name for the genus revised here is *Platevindex*, which Baker (1938) rightly established as a new generic name to refer to the taxon erroneously named *Oncis* by Plate (1893), even though the justification provided by Baker was not completely appropriate. Finally, Baker (1938: 87) correctly pointed out that the generic name *Semperella* Labbé, 1934 was a junior homonym of *Semperella* Gray, 1868 (Porifera). Baker (1938: 87) considered *Semperella* Labbé as a subjective synonym of *Platevindex* but provided no explanation; *Semperella* Labbé was later replaced by *Semperoncis* Starobogatov, 1976, which refers to a genus of terrestrial onchidiids (Dayrat 2009, 2010).

Distribution

Platevindex is broadly distributed in the Indo-West Pacific from the eastern coast of South Africa (~32° South) to New Ireland, Papua New Guinea and eastern Australia in the Pacific (~21° South). It has been documented up to 33° North in southern Japan (Takagi *et al.* 2019). The known geographic range of each species is illustrated in Fig. 10.

Platevindex coriaceus coriaceus (Semper, 1880)
Figs 11–21

Onchidium coriaceum Semper, 1880: pl. 19, figs 1, 16, pl. 23, fig. 12.
Onchidella condoriana Rochebrune, 1882: 67. **Syn. nov.**
Oncis semperi Plate, 1893: 192–193. **Syn. nov.**

Onchidium coriaceum – Semper 1882: 271–273, pl. 21, fig. 7.
Oncis coriacea – Plate 1893: 190–191. — Stantschinsky 1907: 395.
Oncis semperi – Stantschinsky 1907: 395.
Platevindex coriaceus – Baker 1938: 88.
Platevindex mortoni – Sun *et al*. 2014: 63 [non *Platevindex mortoni* Britton, 1984].

Material examined

Lectotype of *Onchidium coriaceum*
PHILIPPINES • lectotype (here designated; 20/16 mm); ZMB/Moll 39028a.

Paralectotypes of *Onchidium coriaceum*
MALAYSIA • 1 paralectotype; Penang; ZMB/Moll 39029.

PHILIPPINES • 6 paralectotypes; ZMB/Moll 39028b.

SINGAPORE • 2 paralectotypes; Semper leg.; ZMB/Moll 39030.

Holotype of *Onchidella condoriana*
VIETNAM • holotype (23/16 mm), by monotypy; Poulo-Condor [Côn Son, the largest island of the Côn Đảo archipelago, off the coast of southern Vietnam]; 1876; Dr Harmand leg.; MNHN-IM-2000-22952.
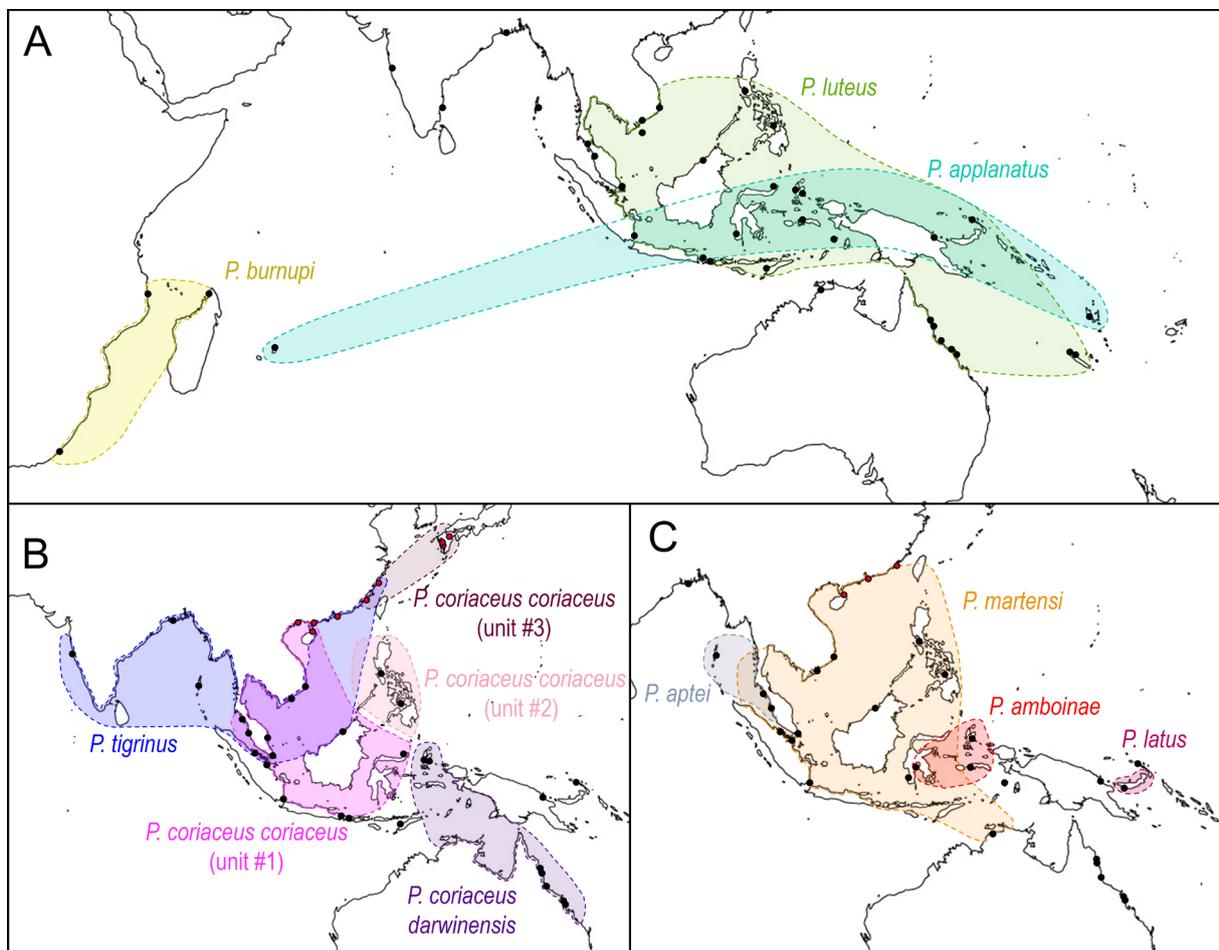
Fig. 10. Geographic distributions of species of *Platevindex*. Colored areas correspond to hypothetical ranges proposed based on all known records, and the colors are the same as those used for each species in the phylogenetic trees (Figs 1–5). Distinct colors are used for each subspecies and mitochondrial unit in *P. coriaceus* (Semper, 1880) as well as for each subspecies of *P. burnupi* (Collinge, 1902). Black dots show sites sampled for this study and red dots (China and Japan) show localities of previously published genetic sequences included in the phylogenetic analyses. **A**. *Platevindex luteus* (Semper, 1880), *P. applanatus* (Simroth, 1920), *P. burnupi*. **B**. *Platevindex tigrinus* (Stoliczka, 1869), *P. coriaceus coriaceus* (units #1, #2, and #3) and *P. coriaceus darwinensis* subsp. nov. **C**. *Platevindex martensi* (Plate, 1893), *P. aptei* Goulding & Dayrat sp. nov., *P. amboinae* (Plate, 1893) and *P. latus* (Plate, 1893).

Syntypes of *Oncis semperi*
PHILIPPINES • 2 syntypes (25/20 and 21/20 mm); Mindanao; ZMB/Moll 45661.

Notes on type material
Onchidium coriaceum. According to the original description, the lectotype and paralectotypes from the Philippines were collected from Bohol, Manila (Luzon) and Zamboanga (Mindanao). However, they are all mixed together in the same jar and nothing allows us to assign them to Bohol, Manila or Zamboanga. Thus, the type locality is simply "Philippines". The lectotype is selected because it is well preserved and was dissected for the present study (all internal organs remain in the specimen); the anatomy of the lectotype matches perfectly the characters observed in our recently-collected material (retractor muscle inserting at the posterior end of the visceral cavity, penis almost as long as the visceral cavity, intestinal loops of type II, deferent duct attached to the surface of the oviduct and tightly coiled with many U-turns). All other syntypes become paralectotypes. All six paralectotypes (30/22 to 23/16 mm) from the Philippines (ZMB/Moll 39028b) were dissected previously, likely by Semper himself or Plate (1893). Three of these paralectotypes (30/22, 28/28 and 23/16 mm) are missing most of the reproductive and digestive systems, but parts of the oviduct, intestine and rectal gland remain; one paralectotype (23/16 mm) corresponds to only the left half of a slug with some organs remaining; two paralectotypes (27/26 and 20/16 mm) were previously dissected but all organs remain. The large (22/10 mm) paralectotype from Singapore (ZMB/Moll 39030) was previously dissected and its penial apparatus is missing; the notum of a small (20/17 mm) paralectotype from Singapore (ZMB/Moll 39030) was cut open for the present study to check several characters. The paralectotype (27/25 mm) from Penang (ZMB/Moll 39029) was previously dissected and the penial complex is missing; the deferent duct in its posterior reproductive system is not attached to the oviduct, indicating that this paralectotype is not part of the species described here but, instead, is a misidentification of *P. martensi*. Semper (1882: 272) also mentioned some material (likely only one specimen) collected in Brisbane (Queensland, Australia) which could not be located. While Queensland is part of the geographic distribution of the species described here, that material from Brisbane could belong to *P. luteus*. Finally, Semper (1882: 272) mentioned two specimens from "des Wiener Museums" (the Vienna Museum) but from an unknown locality. Due to the presence of at least two species of *Platevindex* in the type material (certainly *P. coriaceus* and *P. martensi*, and possibly *P. luteus*; see Remarks for more details), it is necessary to designate a lectotype to clarify the application of the name *P. coriaceus*.

Onchidella condoriana. The radula, the penial complex and most of the posterior (female) reproductive parts were all previously removed and are missing from the holotype. Some parts remain though (digestive gland, intestine, oviduct of the posterior reproductive parts). It is unclear how many specimens were used by Rochebrune (1882) for the original description, but only one specimen is present at the MNHN and it is regarded as the holotype (there is no evidence suggesting that Rochebrune examined more than one specimen).

Oncis semperi. Both syntypes were previously emptied of all their internal organs, likely by Plate himself. Two stomachs and some pieces of digestive glands remain in the jar but the type of intestinal loops could not be checked. Plate's description of intestinal loops of type I (Plate 1893) is inconsistent with *P. coriaceus* but it was most likely a mistake (see our remarks below). The designation of a lectotype would be pointless because the two syntypes are externally similar and it is unclear whether Plate's description was mostly based on the largest specimen or both specimens.

Other material
BRUNEI • 1 spec. (30/27 [1031] mm); Pulau Kaingara; 04°57.020′ N, 115°01.785′ E; 28 Jul. 2011; station 33; open mangrove with *Rhizophora* trees and logs, by the river; BDMNH • 1 spec. (25/20 [1029] mm); near Batu Marang; 04°59.131′ N, 115°01.820′ E; 29 Jul. 2011; station 34; old mangrove with tall *Rhizophora* trees with high roots and *Thalassina* mounds; BDMNH.

INDONESIA – **Sumatra** • 1 spec. (38/29 [1772] mm); Pulau Sinaboi; 02°18.145′ N, 100°59.309′ E; 8 Oct. 2012; station 73; some small *Avicennia* and *Rhizophora* near shore; UMIZ 00075 • 2 specs (30/19 [1735] and 24/20 [1731] 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 00076. – **Sulawesi** • 1 spec. (49/34 [2190] mm); Wawontulap; 01°19.275′ N, 124°31.053′ E; 11 Mar. 2013; station 86; *Rhizophora* mangrove with some *Avicennia* and dead logs; UMIZ 00078. – **Lombok** • 2 specs (35/23 [3000] and 29/18 [3001] mm); Kayangan Bay, Bajo Village; 08°29.491′ S, 116°39.719′ E; 28 Mar. 2014; station 151; mangrove of small, sparse *Avicennia* trees, and a few older trees; UMIZ 00079.

MALAYSIA – **Peninsular Malaysia** • 1 spec. (30/26 [941] mm); Sungai Ular; 03°56.512′ N, 103°22.320′ E; 14 Jul. 2011; station 20; dense forest of mostly *Rhizophora*, higher intertidal; USMMC 00025 • 3 specs (35/21 [937], 28/21 [940] and 25/29 [918] mm); Merbok; 05°39.035′ N, 100°25.782′ E; 18 Jul. 2011; station 21; deep *Rhizophora* forest with old, tall trees, hard mud, many small creeks and dead logs; USMMC 00026 • 1 spec. (24/18 [935] mm); Matang, close to Crocodile River; 04°49.097′ N, 100°37.37′ E; 19 Jul. 2011; station 28; old and open *Rhizophora* forest with tall trees, hard mud, creeks, and many dead logs; USMMC 00027.

PHILIPPINES – **Luzon** • 3 specs (44/26 [3193], 31/17 [3170] and 21/14 [3194] mm); Nasugbu, Batangas; 14°10.714′ N, 120°36.817′ E; 6 Jul. 2014; station 182; dense forest of *Avicennia* and *Rhizophora*; PNM 041236. – **Bohol** • 3 specs (30/29 [3247], 28/18 [3245] and 26/15 [3248] mm); Inabanga; 10°00.389′ N, 124°03.522′ E; 12 Jul. 2014; station 186; rehabilitated fish ponds with mostly young *Rhizophora*; PNM 041237 • 2 specs (33/17 [3256] and 27/19 [3257] mm); Inabanga; 10°04.432′ N, 124°04.691′ E; 13 Jul. 2014; station 188; old forest of mostly *Avicennia* with many dead logs; PNM 041238 • 2 specs (37/25 [3293] and 34/24 [3290] mm); Mabini; 09°51.532′ N, 124°31.685′ E; 17 Jul. 2014; station 194; narrow mangrove on the edge of fish ponds, tall *Rhizophora* and *Avicennia*, many dead logs; PNM 041239 • 1 spec. (34/22 [3356] mm); Mabini; 09°51.402′ N, 124°30.982′ E; 18 Jul. 2014; station 195; narrow *Rhizophora* and *Avicennia* mangrove by the sea with fish ponds built on landward side, cement ditches between the mangrove patches and the ponds; PNM 041240.

SINGAPORE • 1 spec. (28/20 [998] mm); Lim Chu Kang; 01°26.785′ N, 103°42.531′ E; 2 Apr. 2010; station 7; mud outside mangrove on sun-exposed mudflat; ZRC.MOL.10475.

VIETNAM • 1 spec. (32/15 [5625] mm); Can Gio mangrove forest; 10°24.430′ N, 106°53.878′ E; 11 Jul. 2015; station 222; *Avicennia* and *Rhizophora* mangrove patch by road; ITBZC IM 00012 • 2 specs (38/16 [5629] and 27/23 [5657] mm); Can Gio mangrove forest; 10°27.804′ N, 106°53.289′ E; 16 Jul. 2015; station 228; open forest of tall *Rhizophora*, hard mud; ITBZC IM 00014.

Description

Color and morphology of live animals (Fig. 11)

Live animals are not usually covered with mud, and their natural color can be observed without washing. The dorsal notum is typically dark brown, dark grey or black and often has some lighter brown longitudinal bands or mottling. The dorsal surface is typically bumpy, granular and not smooth. The color of the hyponotum in unit #1 (from Peninsular Malaysia to China and Sulawesi) is grey or blue-grey, or occasionally light grey (Fig. 11J–K), while in unit #2 (Philippines) it is generally dark grey or dark blue (Fig. 11D–E). The margin of the hyponotum may be bright white, which is especially common in unit #2. No specimens or pictures of the hyponotum were available for unit #3 from China or Japan (only a photo of the dorsal notum was published by Takagi *et al.* 2019). The foot is light yellow in units #1 and #2. The ocular tentacles are frequently retracted when animals are observed in the field, but extended ocular tentacles are brown and short (up to 4 mm long). Inferior to the ocular tentacles, superior to the mouth, the head bears a pair of oral lobes. On each oral lobe, there is an elongated bump or protuberance, likely with sensitive receptors.
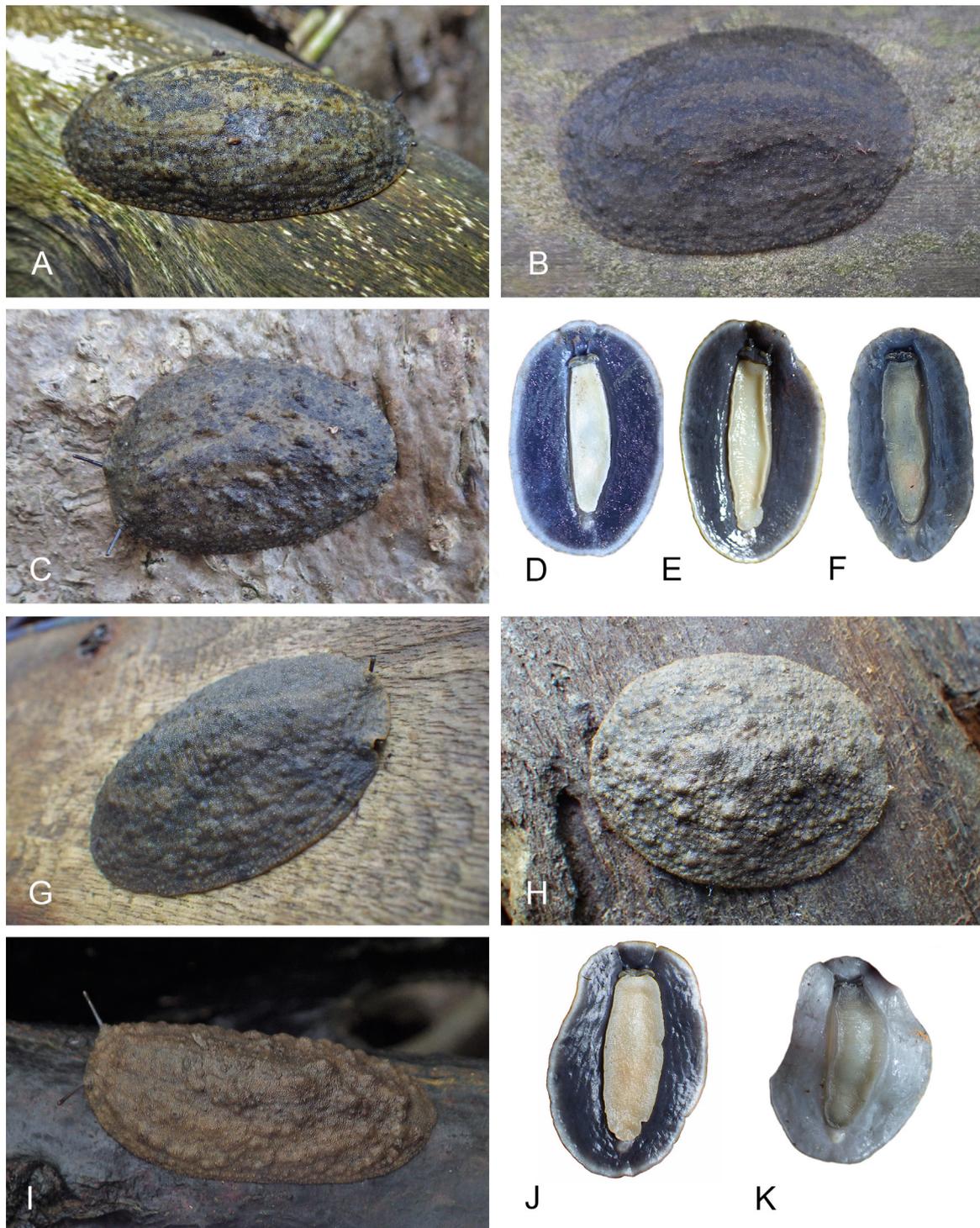
Fig. 11. *Platevindex coriaceus coriaceus* (Semper, 1880), live animals. **A–F**. Mitochondrial unit #2. **A**. Dorsal view, 44 mm long [3193], Philippines, Luzon (PNM 041236). **B**. Dorsal view, 34 mm long [3356], Philippines, Bohol (PNM 041240). **C**. Dorsal view, 37 mm long [3293], Philippines, Bohol (PNM 041239). **D**. Ventral view, same as B. **E**. Ventral view, same as A. **F**. Ventral view, 33 mm long [3256], Bohol (PNM 041238). **G–K**. Mitochondrial unit #1. **G**. Dorsal view, 49 mm long [2190], Indonesia, Sulawesi (UMIZ 00078). **H**. Dorsal view, 38 mm long [1772], Indonesia, Sumatra (UMIZ 00075). **I**. Dorsal view, 38 mm long [5629], Vietnam, Can Gio (ITBZC IM 00014). **J**. Ventral view, same as G. **K**. Ventral view, 27 mm long [5657], Vietnam, Can Gio (ITBZC IM 00014).

Dorsal gills are absent. Papillae with dorsal eyes are present. The exact number of papillae bearing dorsal eyes is variable (between 20 and 68 in unit #1 and between 17 and 45 in unit #2), with the largest animals bearing the largest numbers of eyes. The number of eyes on each papilla is one. The dorsal eyes are distributed across the notum but are absent on the margin (are never <2 mm from the notum edge).

External morphology (Fig. 12A–C)
The notum is oval and the body is dorso-ventrally flattened (Fig. 12A). The foot is narrow in proportion to the hyponotum and is approximately ¼ to ⅓ of the total width. The anus is posterior, median, close to the edge of the pedal sole. The pneumostome is median and is near the anus (closer to the anus than to the posterior margin of the hyponotum) (Fig. 12C). On the right side (to the left in ventral view), a peripodial groove is present at the junction between the pedal sole and the hyponotum, running longitudinally from the buccal area to the posterior end and ending with the female opening. The female opening is approximately 1 to 3 mm from the anus in most individuals but may be up to 6 mm away in large specimens (observed in unit #1). The male aperture is below the ocular tentacles, almost centered between them, but slightly to the right side (Fig. 12B).

Visceral cavity and pallial complex
The heart is enclosed in the pericardium, on the right side of the visceral cavity, slightly posterior to the middle. The large, anterior ventricle becomes a large aorta that branches into smaller vessels delivering blood to the visceral organs. The auricle, significantly smaller than the ventricle, is posterior. The pericardium communicates through a small hole with the right portion of the renal-pulmonary complex. The kidney is intricately attached to the pulmonary cavity, which is slightly asymmetrical, the right part being slightly larger than the left part.

Digestive system (Figs 2B, H, 13–17A)
There is no jaw. The left and right salivary glands have numerous branches and join the buccal mass dorsally on either side of the esophagus. The radula is located between two large postero-lateral muscular masses. Radulae measure up to 6.1 mm in length (unit #1) and 4.7 mm (unit #2). Each radular row contains a central rachidian tooth and two, left and right, half rows of lateral teeth. Examples of radular formulae are presented in Table 5. The half rows of lateral teeth form an angle of 45° with the rachidian axis. The rachidian teeth are unicuspid: a median cusp is always present; there are no distinct lateral cusps (Figs 13A, 14A). The lateral aspect of the base of the rachidian teeth is straight (neither concave nor convex). The length of the cusp of each rachidian tooth is approximately 15–35 µm, significantly smaller than that of the lateral teeth. The hook of the lateral teeth is extended posteriorly by a tail-like structure attaching to the radular membrane and making the hook look longer. The tail-like structure (posterior hook extension, Fig. 13D) is most noticeable in the outermost lateral teeth. The lateral teeth are unicuspid with a flattened hook. The tip of the hook may be rounded or pointed, which varies between individuals and even within a particular radula. Lateral teeth are approximately 35 to 75 µm long, and their length gradually increases along the half row, excluding the few innermost lateral teeth and outermost lateral teeth which are significantly smaller (Fig. 13B, D). The lateral teeth bear an outer pointed spine on the lateral expansion of the base. In most cases, the basal lateral spine cannot be observed because it is hidden below the hook of the adjacent lateral tooth. It can only be observed when the teeth are not too close together or when the teeth are turned in an unusual position (Fig. 13E–F). The inner lateral aspect of the hook of the lateral teeth is not straight. It is marked by a moderate protuberance placed over the inner adjacent tooth. That protuberance is slight and rounded (not pointed) and makes the inner aspect of the hook look wavy. The protuberance diminishes in the outermost teeth, and, as a result, their lateral aspect is almost straight.

The esophagus, narrow and straight, enters the stomach anteriorly. The stomach is located on the left, dorsal side of the visceral mass. In dorsal view, only a portion of the stomach can be seen 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 (Fig. 15C–D). The first chamber, just distal to the esophagus, is delimited by a thin layer of tissue, and receives the ducts of the dorsal and left lateral lobes of the digestive gland. The second chamber is delimited by a thick, muscular layer of tissue and receives the duct of the posterior lobe of the digestive gland. In the third chamber of the stomach, thick ridges extend towards the middle of the chamber. The fourth chamber is externally similar to the third chamber but is characterized by much lower and thinner internal ridges. The intestine is long and narrow, with intestinal loops of type II. The transitional loop is oriented between 7 and 9 o'clock in unit #1 (Fig. 16), and between 6 and 9 o'clock in unit #2 (Figs 2B, H, 16–17). A rectal gland is present.
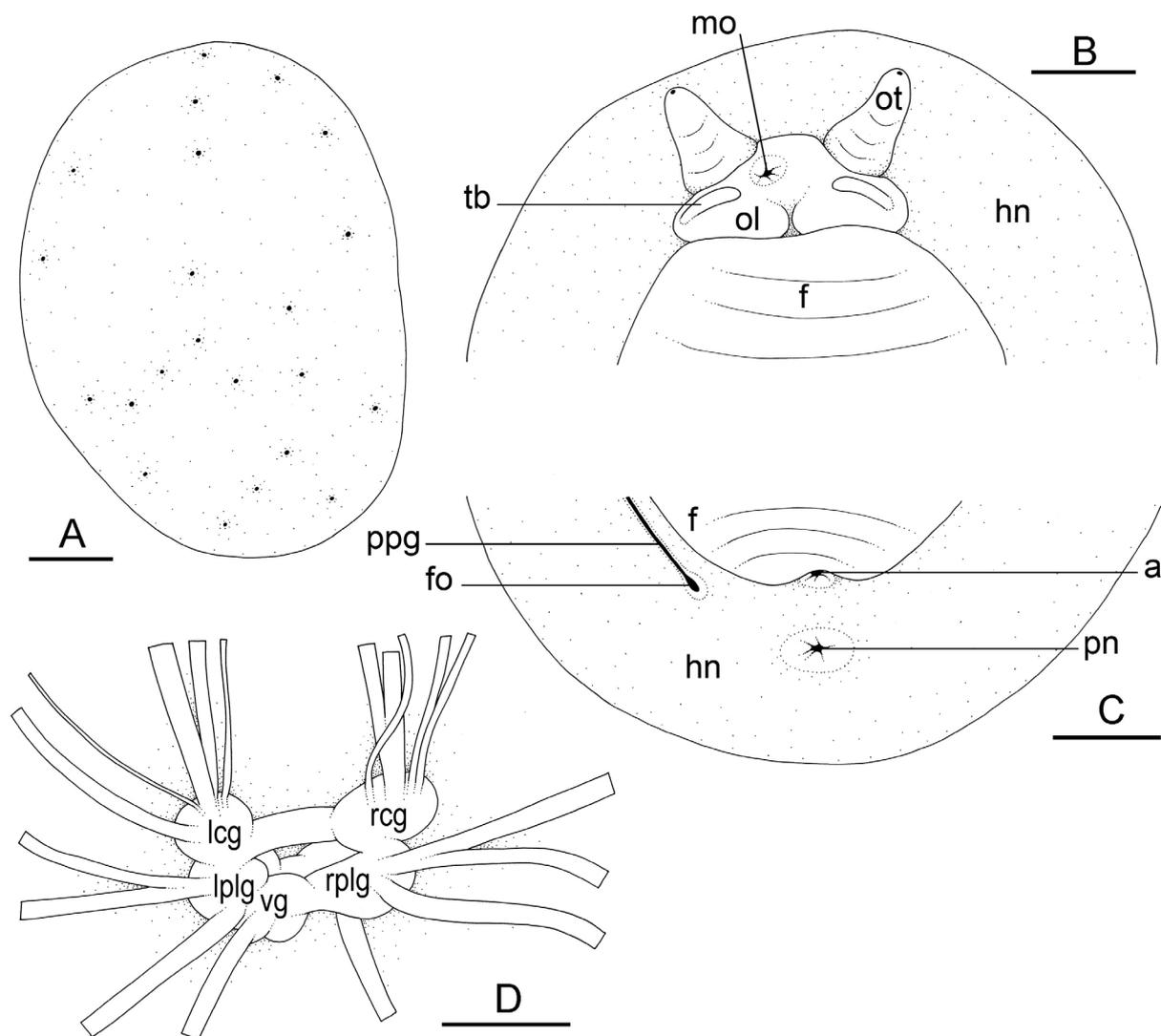
Fig. 12. *Platevindex coriaceus coriaceus* (Semper, 1880) unit #2, external morphology and nervous system, Bohol, Philippines. **A**. Dorsal view [3290] (PNM 041239). **B**. Anterior, ventral view [3256] (PNM 041238). **C**. Posterior, ventral view, same as B. **D**. Nervous system, dorsal view [3257] (PNM 041238). Abbreviations: a = anus; f = foot; fo = female opening; hn = 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; tb = transverse protuberance; vg = visceral ganglion. Scale bars: A = 5 mm; B–C = 2 mm; D = 1 mm.

Table 5. Radular formulae in species of *Platevindex* Baker, 1938.

Species	Radular formula	Specimen length (mm)	Catalog Number	DNA extraction number
P. coriaceus coriaceus (unit #1)	82 × (120-1-120)	49	UMIZ 00078	2190
	70 × (90-1-90)	28	ZRC.MOL.10475	998
	70 × (100-1-100)	38	ITBZC IM 00014	5629
P. coriaceus coriaceus (unit #2)	58 × (70-1-70)	21	PNM 041236	3194
	65 × (80-1-80)	33	PNM 041238	3256
	63 × (85-1-85)	34	PNM 041240	3356
P. coriaceus darwinensis subsp. nov.	90 × (115-1-115)	23	MTQ stn 123	#1
	62 × (80-1-80)	28	UMIZ 00080	5021
	59 × (70-1-70)	22	UMIZ 00081	5111
P. tigrinus	68 × (75-1-75)	19	USMMC 00022	955
	67 × (85-1-85)	26	USMMC 00023	5522
	62 × (70-1-70)	23	BDMNH	1030
P. luteus	47 × (50-1-50)	22	MTQ stn 108	2597
	41 × (35-1-35)	28	UMIZ 00089	2837
	43 × (40-1-40)	22	PNM 041246	3367
P. applanatus	35 × (35-1-35)	9	MNHN-IM-2019-1393	3152
	30 × (23-1-23)	7	MNHN-IM-2019-1394	3442
	30 × (26-1-26)	6.5	MNHN-IM-2019-1392	3604
	40 × (35-1-35)	22	UMIZ 00101	2754
	46 × (55-1-55)	18	UMIZ 00101	2755
	54 × (65-1-65)	16	UMIZ 00102	2893
	52 × (60-1-60)	16	MNHN-IM-2013-14043	5424
	49 × (60-1-60)	13	MNHN-IM-2013-14051	5450
	36 × (35-1-35)	12	MNHN-IM-2013-62402	5491
P. burnupi	56 × (70-1-70)	32	ELM W04105	6146
	50 × (60-1-60)	19	ELM W04109	6148
	50 × (60-1-60)	20	ELM W04107	6149
	55 × (65-1-65)	22	ELM W04108	6153
	41 × (50-1-50)	12	MNHN-IM-2019-1397	3602
	47 × (60-1-60)	16	MNHN-IM-2019-1395	3603
P. martensi	75 × (95-1-95)	30	USMMC 00029	964
	75 × (100-1-100)	39	NTM P.57611	1711
	48 × (65-1-65)	14	PNM 041250	3336
P. aptei sp. nov.	81 × (95-1-95)	35	USMMC 00078	5955
	76 × (115-1-115)	42	USMMC 00078	5967
	77 × (105-1-105)	37	USMMC 00078	5968
P. amboinae	80 × (120-1-120)	38	UMIZ 00105	2883
	85 × (120-1-120)	32	UMIZ 00106	5043
	87 x (110-1-110)	32	UMIZ 00106	5843
P. latus	98 × (145-1-145)	32	ZMB/Moll 45656	N/A (spm #1)
	93 × (145-1-145)	30	ZMB/Moll 45656	N/A (spm #2)

Nervous system (Fig. 12D)

The circum-esophageal nerve ring is post-pharyngeal and pre-esophageal. The cerebral commissure between the paired cerebral ganglia is short but its length varies among individuals. The paired pleural and pedal ganglia are also all distinct. The visceral commissure is short but distinctly present and the visceral ganglion is approximately median. Cerebro-pleural and pleuro-pedal connectives are very short,
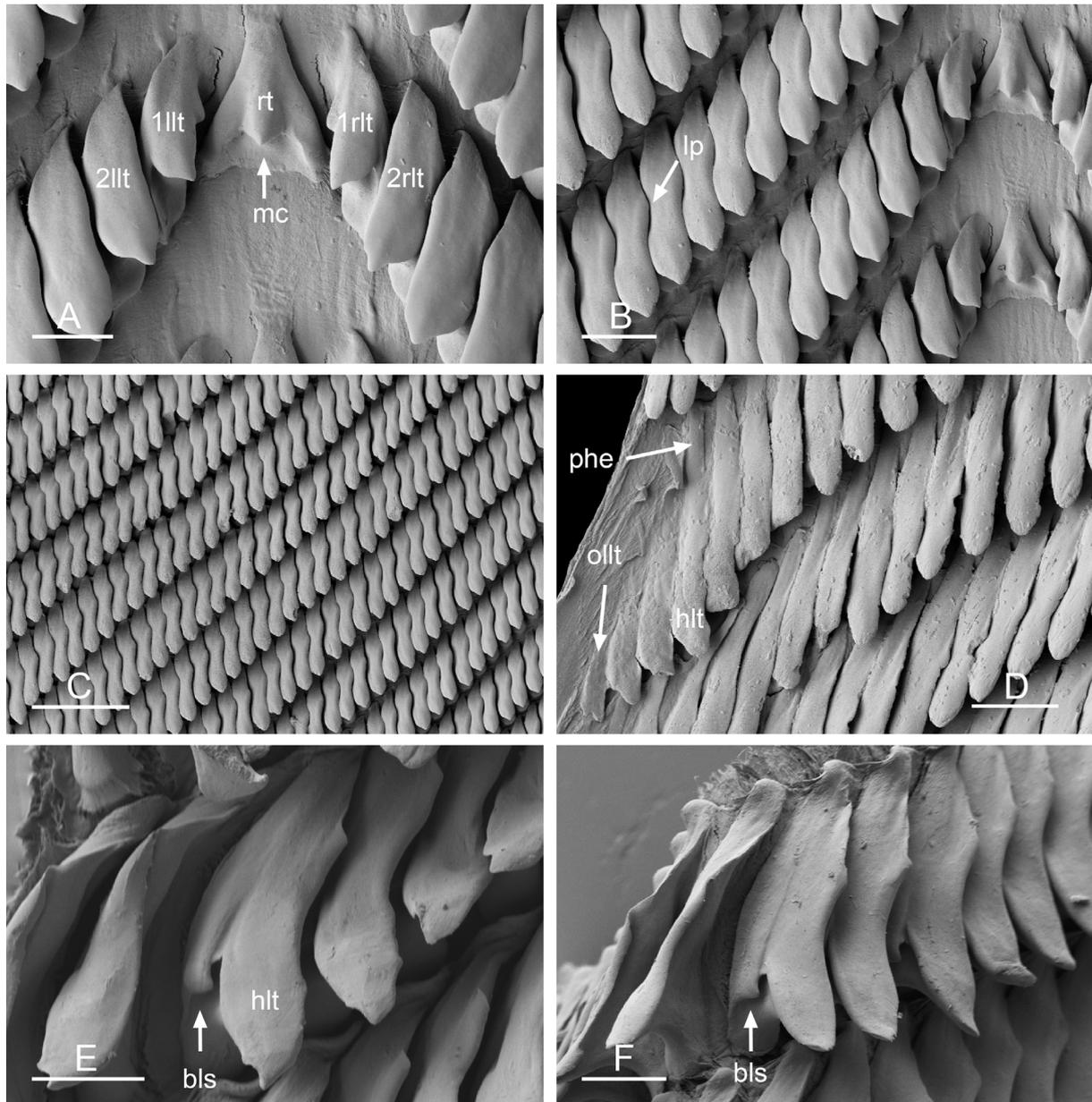
Fig. 13. *Platevindex coriaceus coriaceus* (Semper, 1880) unit #2, radula, Philippines. **A–D**. Bohol [3356] (PNM 041240). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. **E–F**. Luzon [3170] (PNM 041236). **E**. Close up of separated lateral teeth and basal lateral spine. **F**. Lateral teeth separated to reveal basal lateral spine. 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 (of lateral tooth); hlt = hook of lateral tooth; lp = lateral protuberance; mc = median cusp of rachidian tooth; ollt = outermost, left, lateral tooth; phe = posterior hook extension; rt = rachidian tooth. Scale bars: A = 20 μm; B, D = 30 μm; C = 100 μm; E–F = 20 μm.

and pleural and cerebral ganglia touch each other. 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 ganglion innervate the visceral organs.

Reproductive system (Figs 18–19)

Sexual maturity is correlated with animal length. Mature individuals have large, posterior, female (hermaphroditic) organs and fully-developed, anterior, male copulatory parts. Immature individuals (<22 mm long) may have small or simply no posterior female organs, and rudimentary male parts. Hermaphroditic organs are located at the posterior end of the visceral cavity and consist of the female parts mixed with some male parts (Fig. 18). The hermaphroditic gland is a single mass. A hermaphroditic duct conveys the eggs and the autosperm from the hermaphroditic gland to the fertilization chamber, which connects to a large receptaculum seminis (caecum). The receptaculum seminis is generally elongated but its shape varies and it may be oval-shaped or almost spherical. The female gland mass contains various glands (mucus and albumen) of which the exact connections remain uncertain. The spermoviduct (for autosperm, exosperm and eggs) is embedded within the female gland mass, at least proximally. Distally, the spermoviduct branches into the deferent duct (which conveys the autosperm to the anterior region, running through the body wall) and the oviduct. The latter conveys the eggs up to the female opening and the exosperm from the female opening to the fertilization chamber. The section of the oviduct distal to the spermatheca is long, up to three or four times the length of the proximal section
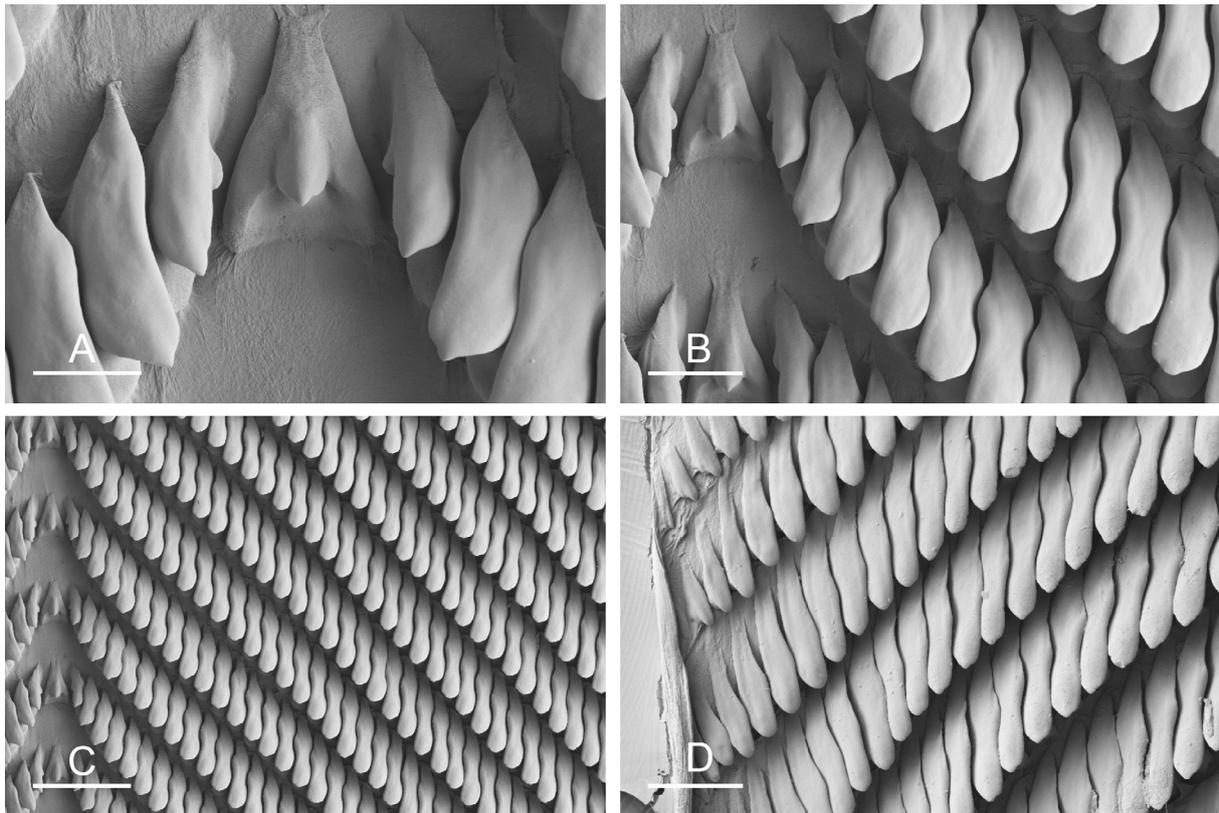
Fig. 14. *Platevindex coriaceus coriaceus* (Semper, 1880) unit #1, radula. **A**. Rachidian and innermost lateral teeth, Vietnam, Can Gio [5629] (ITBZC IM 00014). **B**. Lateral teeth with rachidian teeth, same as A. **C**. Lateral teeth, same as A. **D**. Outermost lateral teeth, Singapore, Lim Chu Kang [998] (ZRC MOL.10475). Scale bars: A = 20 μm; B = 30 μm; C = 100 μm; D = 50 μm.

(from the female gland mass to the spermatheca). The oviduct is much wider (at least two or three times wider) than the deferent duct. The latter is closely attached to the surface of the oviduct, and is highly coiled, with U-shaped turns back and forth. The spherical spermatheca connects to the distal portion of the oviduct through a short duct.

The male anterior organs include the penial complex (penis, vestibule, deferent duct, retractor muscle) (Fig. 19). There is no accessory penial gland. The penial sheath protects the penis for its entire length. The vestibule is continuous with the distal part of the penial sheath. The vestibule is cylindrical. Short muscle fibers connect the distal part of the penial sheath, near the vestibule, to the anterior wall of the visceral cavity. Inside the penial sheath, the penis is a narrow, thin, elongated, hollow tube. Its proximal region is rigid. Its distal region is flexible and bears hooks measuring from 80 to 130 μm (Fig. 20). The flexible region of the penis with hooks is generally between 4 and 8 mm long and approximately 160 to 190 μm wide. The hooks are inside the tube-like penis when it is inside the penial sheath (but can be
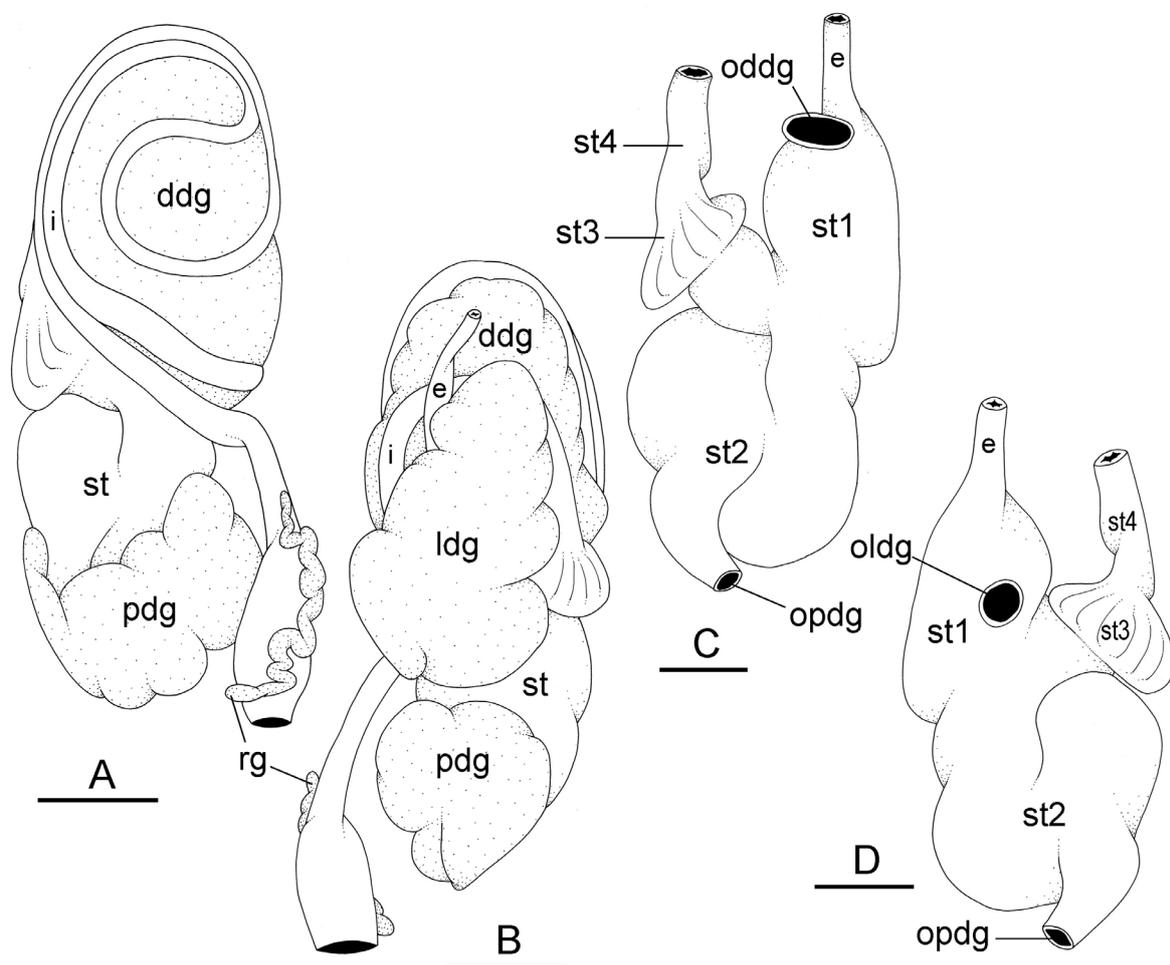
Fig. 15. *Platevindex coriaceus coriaceus* (Semper, 1880) unit #2, digestive system, [3356] (PNM 041240), Bohol, Philippines. **A**. Dorsal view. **B**. Ventral view. **C**. Stomach, dorsal view. **D**. Stomach, ventral view. Abbreviations: ddg = dorsal digestive gland; e = esophagus; i = intestine; ldg = lateral digestive gland; oddg = opening of the dorsal lobe of the digestive gland; oldg = opening of the lateral lobe of the digestive gland; opdg = opening of the posterior lobe of the digestive gland; pdg = posterior digestive gland; rg = rectal gland; st = stomach; st1 = stomach chamber 1; st2 = stomach chamber 2; st3 = stomach chamber 3; st4 = stomach chamber 4. Scale bars: A–B = 3 mm; C–D = 2 mm.

seen by transparency) and are outside when the penis is evaginated like the finger of a glove. The penial sheath measures from approximately ⅔ the length of the visceral cavity to nearly the entire length of the visceral cavity. The beginning of the retractor muscle marks the separation between the penial sheath and the deferent duct. The retractor muscle inserts at the posterior end of the body cavity near the rectum (in mature specimens). The length of the retractor muscle is variable. In unit #1, the retractor muscle is either shorter than the penial sheath (as short as ⅛ of its length) to almost equal to it. In unit #2, the retractor muscle is shorter than the penial sheath (between ⅓ and ⅛ of its length). The deferent duct is highly convoluted, with many loops, though it is less convoluted in immature specimens.
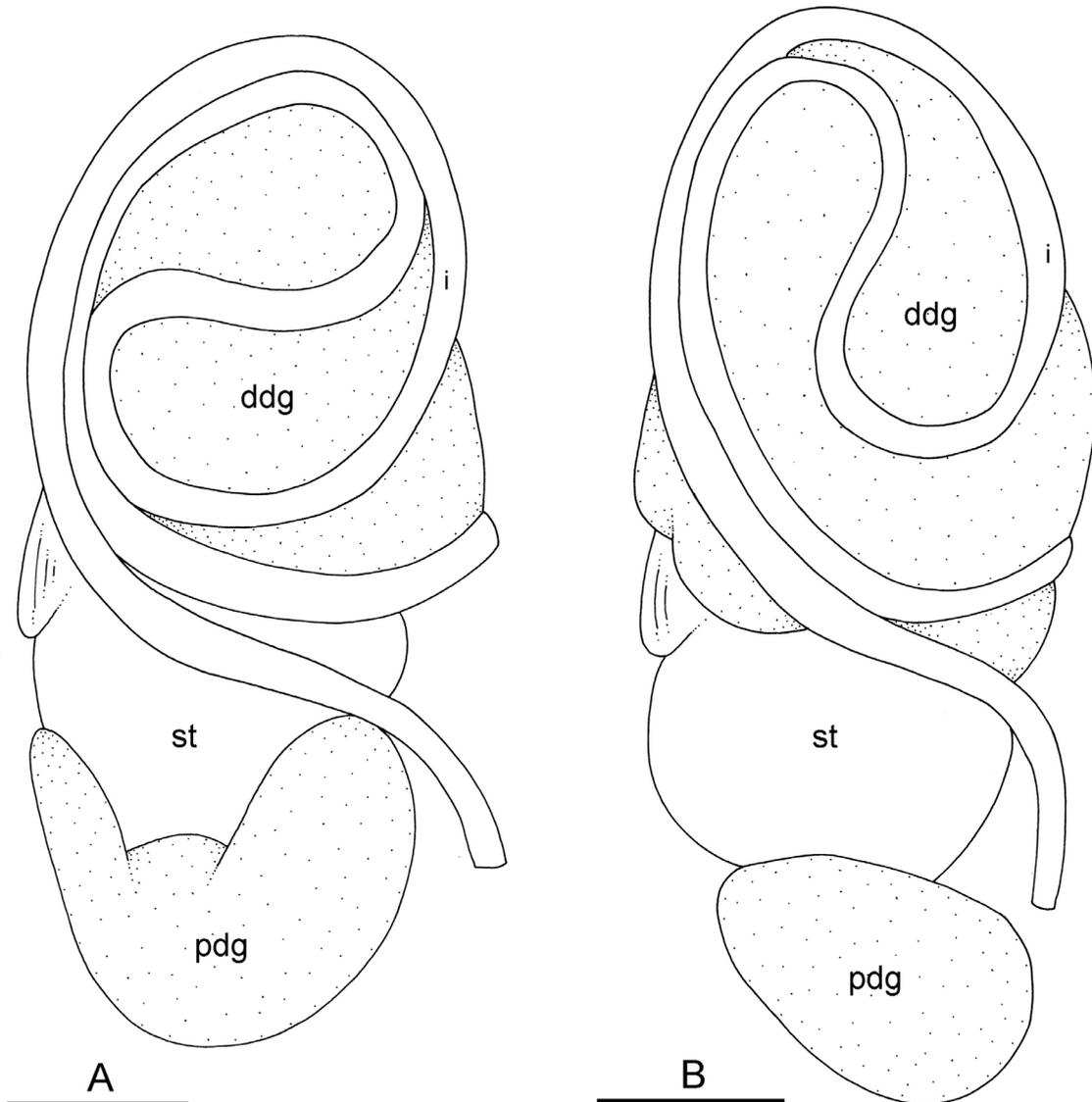
Fig. 16. *Platevindex coriaceus* (Semper, 1880), digestive system. **A**. Dorsal view of intestinal loops of type II, with a transitional loop oriented at 9 o'clock, *Platevindex coriaceus coriaceus* unit #1, Vietnam [5629] (ITBZC IM 00014). **B**. Dorsal view with no digestive glands, type II, with a transitional loop oriented at 7 o'clock, *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., Northern Territory, Australia [1663] (NTM P.57602). Abbreviations: ddg = dorsal digestive gland; i = intestine; oddg = opening of the dorsal lobe of the digestive gland; opdg = opening of the posterior lobe of the digestive gland; pdg = posterior digestive gland; rg = rectal gland; st = stomach. Scale bars = 3 mm.

Distinctive diagnostic features (Table 4)

Externally, *P. coriaceus coriaceus* cannot be confused with the only two species of *Platevindex* which lack dorsal eyes (*P. amboinae* and *P. latus*). Externally, the blue-grey hyponotum and light yellow foot differentiate *P. coriaceus coriaceus* from *P. martensi* (orange foot) and *P. aptei* sp. nov. (black foot). *Platevindex coriaceus coriaceus* can generally be distinguished from *P. luteus* and *P. applanatus* by the presence of distinctly-raised dorsal papillae in the two latter species (which are absent in *P. coriaceus*).
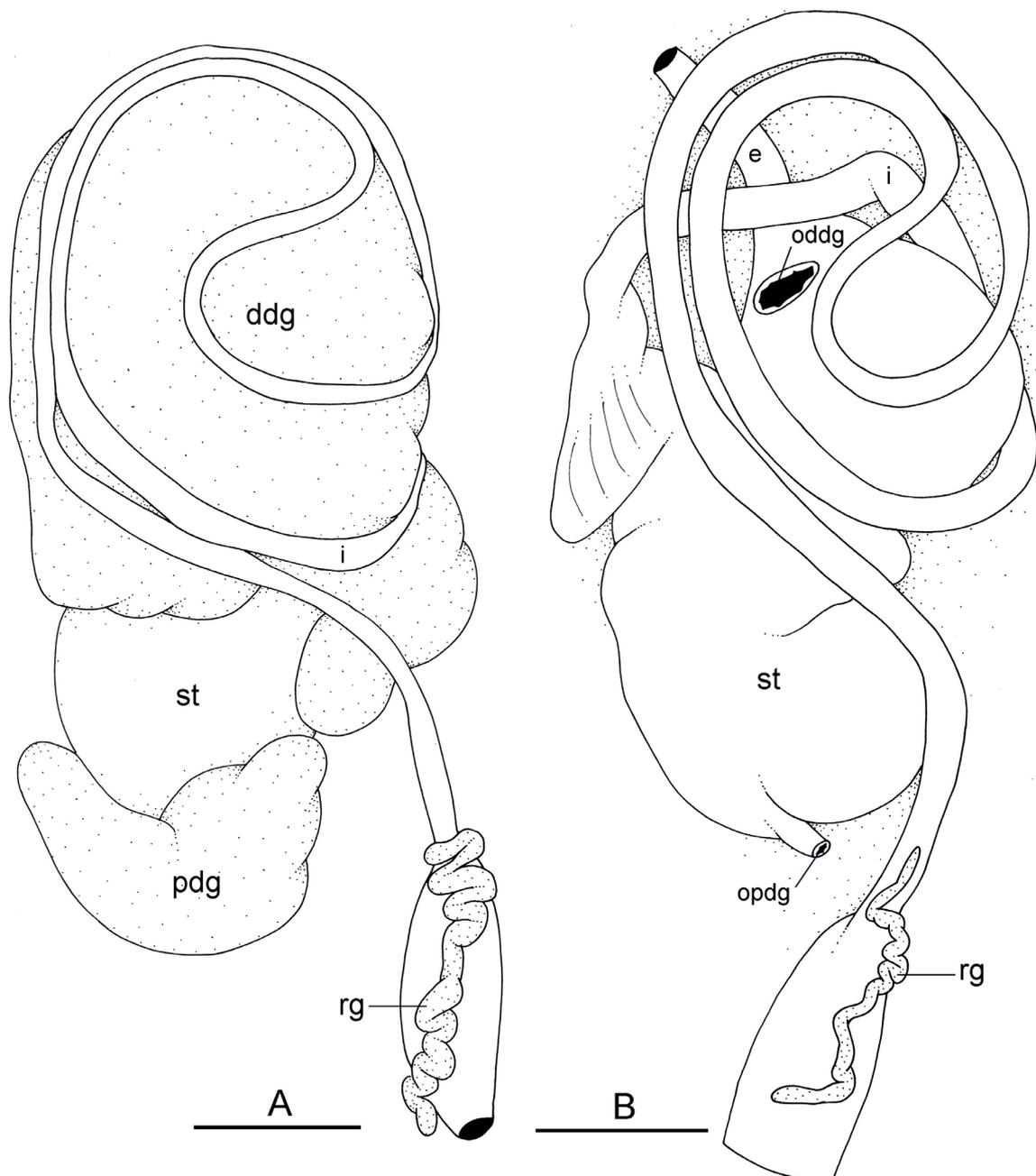
Fig. 17. *Platevindex coriaceus coriaceus* (Semper, 1880) unit #2, digestive system, dorsal view, intestinal loops of type II. **A**. Transitional loop oriented at 9 o'clock, Luzon, Philippines [3170] (PNM 041236). **B**. Transitional loop oriented at 7 o'clock, Bohol, Philippines [3256] (PNM 041238). Abbreviations: ddg = dorsal digestive gland; i = intestine; pdg = posterior digestive gland; rg = rectal gland; st = stomach. Scale bars = 2 mm.
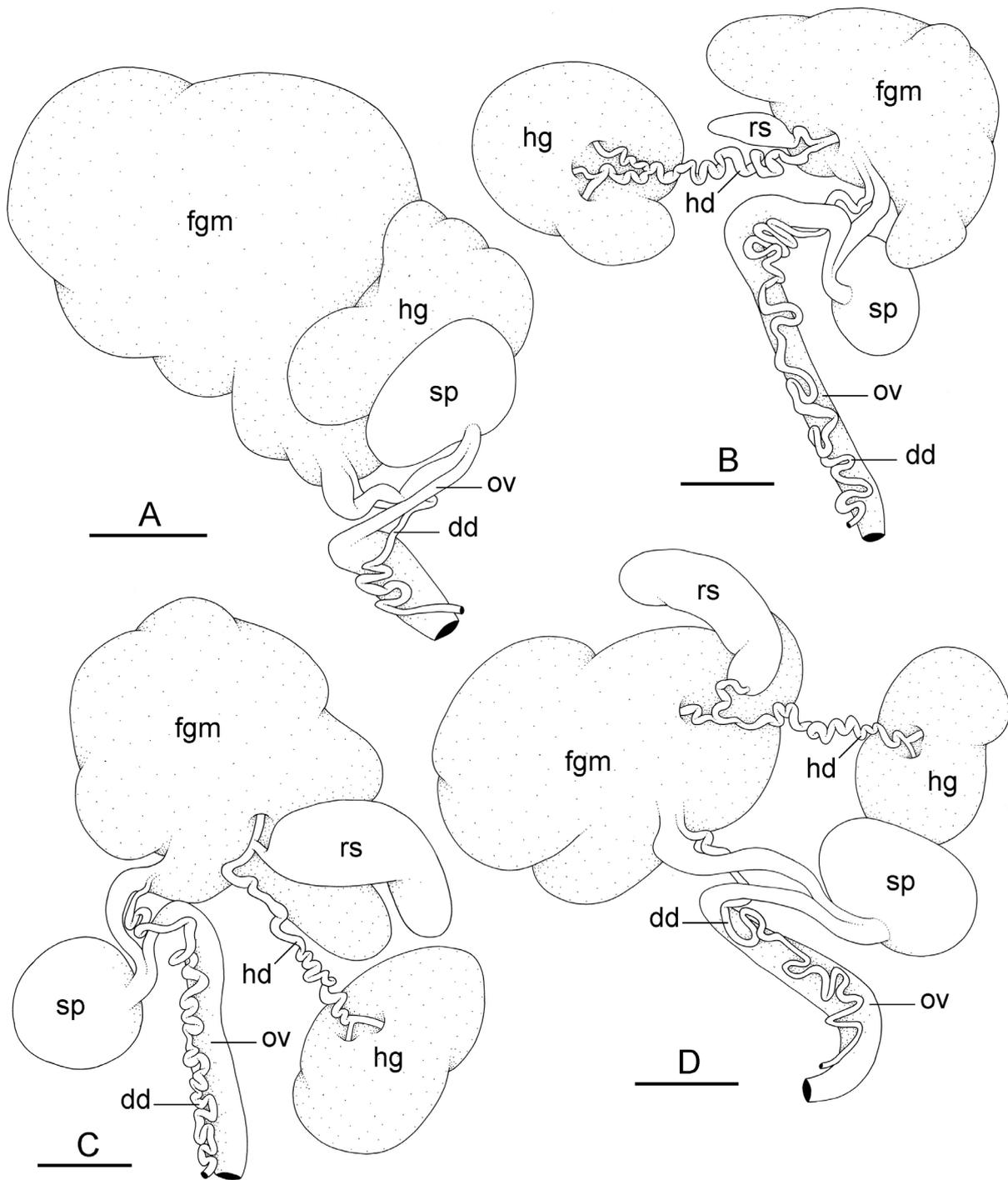
Fig. 18. *Platevindex coriaceus* (Semper, 1880), posterior reproductive system. **A**. *Platevindex coriaceus coriaceus* unit #2, Philippines, lectotype (ZMB/Moll 39028a). **B**. *Platevindex coriaceus coriaceus* unit #2, Bohol, Philippines [3356] (PNM 041240). **C**. *Platevindex coriaceus coriaceus* unit #1, Vietnam [5629] (ITBZC IM 00014). **D**. *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., Northern Territory, Australia [1690] (NTM P.57606). Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; rs = receptaculum seminis; sp = spermatheca. Scale bars = 2 mm.

Large individuals of *P. coriaceus coriaceus* (>40 mm long) can be distinguished from *P. luteus*, *P. applanatus* and *P. burnupi* (<30 mm) by their size. Small individuals of *P. coriaceus coriaceus* could potentially be confused with individuals of *P. burnupi* (which, unlike *P. luteus* and *P. applanatus*, lack distinctly-raised dorsal papillae). However, note that based on current data, *P. burnupi* is only found in the western Indian Ocean and does not overlap geographically with *P. coriaceus coriaceus*. In addition, *P. coriaceus coriaceus* is distinct from *P. luteus*, *P. applanatus* and *P. burnupi* based on several details of the reproductive and digestive systems (Table 4). For instance, the deferent duct is closely attached to the oviduct in *P. coriaceus coriaceus* while it is not (or only loosely) attached to it in *P. luteus* and *P. burnupi*. Internally, also, the intestinal loops are of type II in *P. coriaceus coriaceus* and of type I in *P. applanatus*.

The only species with which *Platevindex coriaceus coriaceus* overlaps geographically and cannot be distinguished externally is *P. tigrinus*, due to a similar foot color (variants of grey and yellow) and hyponotum color (variants of blue and grey). Internally, however, *P. coriaceus coriaceus* can easily be distinguished from *P. tigrinus*: the retractor muscle of the penis inserts at the posterior end of the visceral
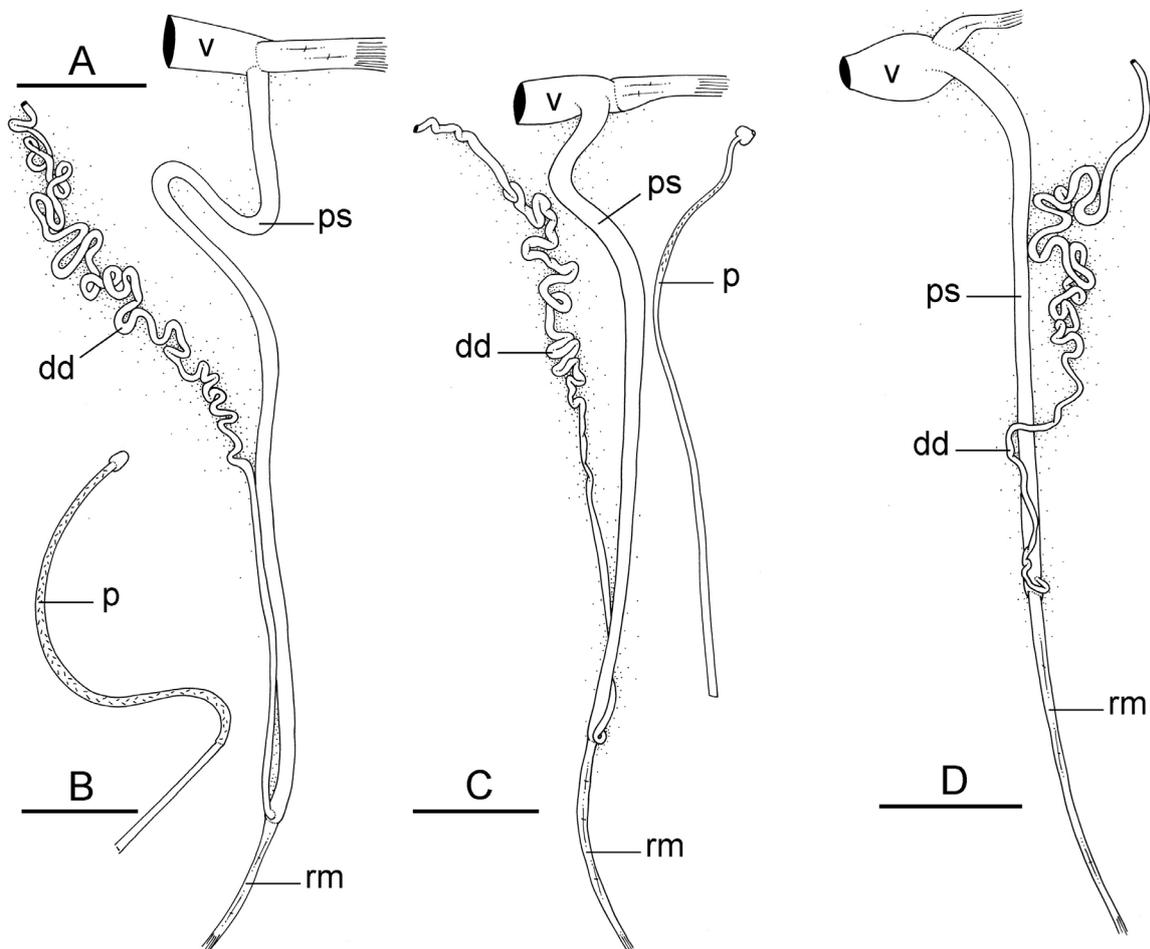
Fig. 19. *Platevindex coriaceus* (Semper, 1880), anterior, male copulatory apparatus. **A**. *Platevindex coriaceus coriaceus* unit #2, Bohol, Philippines [3356] (PNM 041240). **B**. Penis (extracted from the penial sheath), same as A. **C**. *Platevindex coriaceus coriaceus* unit #1, Vietnam [5629] (ITBZC IM 00014). **D**. *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., Northern Territory, Australia [1663] (NTM P.57602). Abbreviations: dd = deferent duct; p = penis; ps = penial sheath; rm = retractor muscle; v = vestibule. Scale bars: A, C–D = 3 mm; B = 2 mm.

cavity in *P. coriaceus coriaceus* and near the heart in *P. tigrinus*; the distal, flexible region of the penis with hooks is >4 mm long in *P. coriaceus coriaceus* and <1.5 mm long in *P. tigrinus*; in the posterior part of the reproductive system, the deferent duct (closely attached to the oviduct) is tightly convoluted in *P. coriaceus coriaceus* while it is almost straight in *P. tigrinus*.

Distribution (Fig. 10B)

Mitochondrial unit #1. Brunei. China: Qinzhou and Guangxi (Sun *et al*. 2014, misidentified as *P. mortoni*). Indonesia: Lombok, Sumatra and Sulawesi. Peninsular Malaysia. Singapore (paralectotypes of *P. coriaceus* and newly collected specimens). Vietnam (type locality of *O. condoriana* and newly collected specimens).

Mitochondrial unit #2. Philippines (type locality of *O. coriaceum*): Luzon, Bohol, and Mindanao. Fresh specimens were collected from Luzon and Bohol, but not from Mindanao. It could not be determined whether the lectotype selected here was from Manila (Luzon), Bohol, or Zamboanga (Mindanao).

Mitochondrial unit #3. China: Fujian Province (Sun *et al*. 2014, misidentified as *P. mortoni*). Japan (Takagi *et al*. 2019, identified as *Platevindex* sp. A).

All records are new, except for the localities of some of the type material. Note that the paralectotype(s) of *O. coriaceum* from Brisbane are not included in the distribution of *P. coriaceus coriaceus*.

Habitat (Fig. 21)

Platevindex coriaceus coriaceus is found in mangrove forests, on tree roots and trunks, and on dead logs, but not directly on mud. The logs and trees may be in silty mud saturated with water or on harder mud. It does not live on rocky shores. *Platevindex coriaceus coriaceus* is very common across its range, except in central Indonesia where it seems less common. Few specimens were found in Lombok and Sulawesi and it was not found in Maluku (Ambon, Seram and Kei Islands).

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 coriaceum* was first published with three figures illustrating the external morphology, dorsal eyes and penial hooks (Semper 1880: pl. 19, figs 1, 16, pl. 23, fig. 12) and no written description. Because *Onchidium coriaceum* was published before 1931, ICZN Article 12.2.7 applies and Semper's figures are regarded as an indication accompanying the new name *Onchidium coriaceum*. The text of the description and the illustration of the radula (pl. 21, fig. 7) were published in 1882. However, not everything in the written description refers to the subspecies described here (see below for more details). The illustrations of the dorsal surface (pl. 19, fig. 1), the dorsal eyes (pl. 19, fig. 16) and the radular teeth (pl. 21, fig. 7) could apply to any almost any species of *Platevindex*, so there is no reason to consider
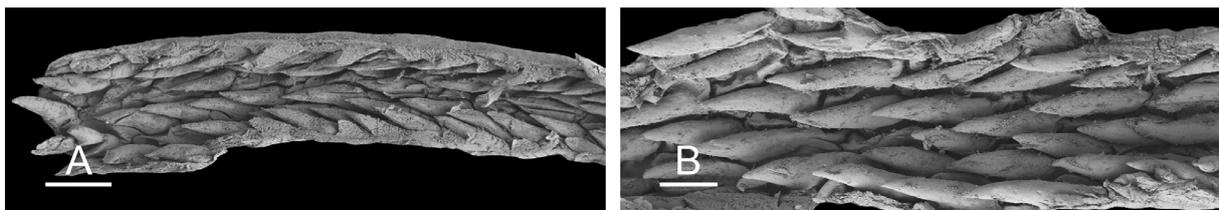
Fig. 20. *Platevindex coriaceus coriaceus* (Semper, 1880), penial hooks. **A**. Unit #1, Vietnam, Can Gio [5629] (ITBZC IM 00014). **B**. Unit #2, Philippines, Bohol [3248] (PNM 041237). Scale bars: A = 100 µm; B = 50 µm.

that they do not refer to the subspecies described here. The illustration of the male apparatus (pl. 23, fig. 12) could refer to the subspecies described here (if Semper illustrated one of the paralectotypes from Singapore or the Philippines) or *P. coriaceus darwinensis* subsp. nov. (if Semper illustrated the paralectotype from Brisbane, both subspecies being anatomically cryptic), even though his written description of the insertion of the retractor muscle (near the heart) matches that of *P. tigrinus* instead of the subspecies described here (insertion near the posterior end of the visceral cavity).

Semper (1880) originally described *Onchidium coriaceum* based on syntypes from Brisbane (Australia), Penang (Malaysia), Singapore, and Manila (Luzon), Bohol and Zamboanga (Mindanao) in the Philippines. Our sampling across the Indo-West Pacific shows that multiple species of *Platevindex* are present across the region encompassing these countries. A re-examination of the type material and a critical analysis of the original description reveal that, when describing *O. coriaceum*, Semper used specimens that were part of at least two distinct species.

The lectotype from the Philippines (ZMB/Moll 39028a) designated here clarifies the application of the name *Platevindex coriaceus* because it was dissected for the present study and it displays all the diagnostic features of the nominotypical subspecies described here. Two paralectotypes (27/26 and 20/16 mm) from the Philippines (ZMB/Moll 39028b) are also part of *P. coriaceus coriaceus*. The other paralectotypes from the Philippines, however, cannot be identified to the species level because the male reproductive parts were previously removed by Semper. Even though they seem to be part of *P. coriaceus coriaceus*, they potentially could belong to *P. luteus* or *P. martensi*, both of which are found in the Philippines.

Semper mentioned that the paralectotype (27/25 mm) from Penang (ZMB/Moll 39029) had previously been misidentified as *Onchidium typhae* (there is only one dorsal eye on each of its papillae while there are 3 or 4 eyes per papilla in *O. typhae*). This paralectotype from Penang was dissected (likely by Semper) and its penial complex is missing; however, the deferent duct in its posterior reproductive system is not attached to the oviduct, indicating that this paralectotype is not part of the subspecies described here but is, instead, a misidentification of *P. martensi* (an undescribed species at that time). *Platevindex martensi* also differs from *P. coriaceus coriaceus* with respect to the insertion of the retractor muscle: in the posterior half of the visceral cavity (from ½ to ¾ its length) in *P. martensi* and near the end of the visceral cavity in *P. coriaceus coriaceus*. Also, in *P. martensi*, the length of the flexible portion of the penis with hooks does not exceed 2.5 mm, while it measures from 4 to 8 mm in *P. coriaceus coriaceus*. Finally, the position of 20 dorsal eyes on the edge of the mantle described by Semper is a character compatible with *P. martensi*, but not with *P. coriaceus coriaceus* or any related species within clade A (Figs 1, 5). Labbé (1934) considered that the paralectotype from Penang was part of *Onchidium tigrinum* rather than *O. coriaceum* (likely based on Semper's description because Labbé, who did not comment on the anatomy of that specimen, does not seem to have examined it).

The large (22/10 mm) paralectotype from Singapore (ZMB/Moll 39030) was previously dissected and its copulatory apparatus is missing. However, it seems to be part of the subspecies described here because even though its posterior reproductive system is largely destroyed, the highly-coiled deferent duct is attached to the distal part of the oviduct, which is characteristic of *P. coriaceus coriaceus*. The notum of the small (20/17 mm) paralectotype from Singapore (ZMB/Moll 39030) was cut open for the present study. It is partly immature (its posterior reproductive system is not developed) but is definitely part of the subspecies described here because its penis is almost as long as the visceral cavity.

Semper (1882: 272) also mentioned some material (likely only one specimen) collected in Brisbane (Queensland, Australia) which could not be located by us. Queensland is not part of the geographic distribution of *P. coriaceus coriaceus*, so Semper's material from Brisbane most likely did not belong

Fig. 21. Habitats of *Platevindex coriaceus coriaceus* (Semper, 1880). **A**. Peninsular Malaysia, Matang, old and open *Rhizophora* forest with tall trees, creeks, hard mud and many dead logs (station 28). **B**. Indonesia, Sumatra, high intertidal open mangrove with *Rhizophora* trees, mounds of *Thalassina* and dead logs (station 80). **C**. Vietnam, Can Gio, open mangrove with big *Avicennia* trees, soft mud and some dead logs (station 231). **D**. Indonesia, Lombok, mangrove next to village with small, sparse *Avicennia* in open mangrove with a few older trees (station 151). **E**. Philippines, Bohol, Inabanga, old forest of mostly *Avicennia* with many dead logs (station 188). **F**. Philippines, Bohol, Mabini, narrow mangrove on the edge of fish ponds, tall *Rhizophora* and *Avicennia*, many dead logs (station 194).

to *P. coriaceus coriaceus*. Instead, it could belong to *P. coriaceus darwinensis* subsp. nov. or *P. luteus*. Finally, Semper (1882: 272) mentioned two specimens at the Vienna Museum but from an unknown locality. It is not possible to determine which species of *Platevindex* Semper observed, which, thanks to the designation of the lectotype from the Philippines, is not an issue.

Semper (1882: 273) noted that the only character which differed between the descriptions of *O. coriaceum* and *O. tigrinum* was Stoliczka's description of a "supplementary albuminous gland" (i.e., accessory penial gland) (Stoliczka 1869: 107), and indicated that *O. coriaceum* could be a synonym of Stoliczka's *O. tigrinum*. Semper was not able to properly compare the anatomy of the two species without examining Stoliczka's specimens and stated and that he could not be sure about the synonymy. An accessory penial gland is actually absent in *Platevindex tigrinus*, which is anatomically and genetically distinct from *P. coriaceus coriaceus*.

Finally, Semper's description of the penial morphology in the original description of *O. coriaceum* needs to be commented on. The length of the flexible distal region of the penis with hooks was described by Semper as being 6 mm long, which is within the range observed here in *P. coriaceus coriaceus* (4 to 8 mm) but is incompatible with those of *P. tigrinus* (1 to 1.5 mm) or *P. martensi* (2 to 2.5 mm). However, Semper also described a retractor muscle inserting "at the height of the heart" (1882: 272, translated from German), which is compatible with *P. tigrinus* (the retractor muscle inserts near the heart), somewhat compatible with *P. martensi* (insertion in the posterior half of the visceral cavity), but not with *P. coriaceus coriaceus* (insertion at the posterior end of the visceral cavity). There are only two possible explanations. First, Semper's written description of the insertion of the retractor muscle is based on the paralectotype from Penang (which belongs to *P. martensi*), or, second, Semper made a mistake.

The description of *Onchidella condoriana* by Rochebrune did not include any information about the internal anatomy. Externally, *O. condoriana* was described as "granulous and sprinkled with whitish tubercles and grey underneath" (Rochebrune 1882: 67, translated from Latin). The holotype (23/16 mm) can readily be identified as a *Platevindex* by the hard, flattened notum, but it was previously dissected by someone who removed the penial complex (it is unclear who dissected it because the species was not mentioned by Plate and neither Hoffmann nor Labbé commented on the internal anatomy). Most of the posterior (female) reproductive system is missing but the oviduct, which remains, is similar to that of the subspecies described here (with the highly-coiled deferent duct attached to it). Thus, the holotype of *O. condoriana* belongs to *P. coriaceus coriaceus* and not *P. tigrinus* (in which the deferent duct is almost straight). Note that *P. tigrinus* is likely also present in Vietnam because it is known from western India all the way to China, even though we did not find it there. Because the type locality of *O. condoriana* (Côn Son Island, Côn Đảo Archipelago, Vietnam) is within the range of mitochondrial unit #1 (from Peninsular Malaysia to China and Sulawesi), the name *Platevindex condorianus* could potentially apply to it, if it would ever need to be formally named. *Platevindex* slugs were not found at the type locality of *O. condoriana* (we explored the Côn Đảo Archipelago in 2015), but were found in mainland Vietnam, in the Can Gio mangrove forest protected area. All those *Platevindex* slugs from the Can Gio mangrove forest belonged to *P. coriaceus coriaceus*. Finally, *P. martensi* is likely also present in Vietnam (Fig. 10), but the lack of dorsal eyes at the margin of the notum and the deferent duct being attached to the oviduct indicate that Rochebrune's type of *O. condoriana* is not part of *P. martensi*.

Plate (1893: 190–191) re-described *P. coriaceus* based on Semper's original specimens from the Philippines. Semper did not indicate how many individuals he examined from the Philippines, but Plate listed ten specimens. Only seven of Semper's type specimens were located from the Philippines (ZMB/Moll 39028), suggesting that some specimens may have been previously destroyed. Plate's description of one single dorsal eye per papilla with papillae irregularly distributed is consistent with

a species of *Platevindex*. He also mentioned new details that were not included in Semper's original description, such as the granular notum, the male pore being above and to the left of the right oral lobe (i.e., below and to the left of the right oral tentacle) and intestinal loops of type II. The number of radular teeth per half row (120) described by Plate is within the range reported here (from 70 to 120), and it is expected that the number he observed would be at the high end of the range due to the large size of the specimens that he examined (up to 47 mm long).

Plate described *Oncis semperi* based on two syntypes (22/18 and 22/18 mm) from Mindanao (ZMB/Moll 45661). The width of the foot and the position of the male opening confirm that they belong to a species of *Platevindex*. According to Plate (1893: 193), the penis of *Oncis semperi* is extremely long (26 mm in a slug that was only 24.5 mm long), inserts at the posterior end of the body cavity, and its distal, flexible region with hooks is 8 mm long. This description is only consistent with *P. coriaceus* (Table 4). However, Plate's description of intestinal loops of type I is problematic because it is inconsistent with *P. coriaceus*. Two explanations are possible. Most likely, Plate's description of a type I was a mistake (his description of the intestinal loops in *P. amboinae* was a mistake). Alternatively, one of the syntypes could belong to *P. luteus* (in which the intestine can be of type I). Because Plate's description of the copulatory apparatus matches perfectly that of *P. coriaceus*, *P. semperi* is regarded as a synonym of *P. coriaceus* and it is assumed that Plate confused the types of intestinal loops.

Semper (1882: 272) questioned whether *Platevindex coriaceus* could be a synonym of *Onchidium marmoratum* Lesson, 1831, and noted that the original description was insufficient to separate it from *O. coriaceum*. Bretnall (1919: 323) also listed this potential synonymy with a question mark. The original description of *O. marmoratum* did not indicate any characters which would distinguish it from *P. coriaceus*, but the type specimens of *O. marmoratum* do not share the flattened shape of *Platevindex* slugs and clearly do not belong to this genus. *Onchidium marmoratum* was recently transferred to the genus *Marmaronchis* Dayrat & Goulding, 2018 (Dayrat *et al.* 2018). Hoffmann (1928: 88) suggested that *O. coriaceum*, *O. martensi* and *O. condoriana* were all synonyms of *Oncis stuxbergi* (Westerlund, 1883) but he did not describe the anatomy of *Oncis stuxbergi*. Westerlund (1883: 165) also did not describe the internal anatomy of this species (described as *Vaginulus stuxbergi*). Thus, neither Westerlund's description nor Hoffmann's remarks can be attributed to *Platevindex coriaceus*. The specific name *stuxbergi* applies to a species in the genus *Onchidium* as a result of the designation of a lectotype (Dayrat *et al.* 2016: 22). Note that Hoffmann (1928) thought that *Onchidium coriaceum* was a junior synonym of *Oncis stuxbergi* because he adopted 1885 as the date of publication for Semper's monograph in the *Reisen im Archipel der Philippinen* series (for a collation of Semper's monograph, see Johnson 1969). Labbé (1934: 235–236), who does not seem to have examined any specimens, followed Hoffmann in considering *Oncis coriacea* a synonym of *Oncis stuxbergi*. For unclear reasons, he indicated an insertion of the penial retractor near the heart, which is not consistent with *Platevindex coriaceus*.

DNA sequences of *P. coriaceus* from southern China were misidentified as *P. mortoni* by Sun *et al.* (2014). Recent COI DNA sequences by Wang *et al.* (unpublished, GenBank Accession GU166575 and GU166577) were also identified as *P. mortoni*, and are shown here to belong to *P. coriaceus*. Therefore, *P. coriaceus* is not restricted to southernmost China but is also present in the Fujian Province of China (the province facing Taiwan). *Platevindex coriaceus* should also be present around Hong Kong, which is south of Fujian province. Hong Kong is the type locality for *Platevindex mortoni*, a name which is regarded here as a nomen dubium (see our remarks on *P. tigrinus* and *P. luteus*). Additionally, DNA sequences published by Takagi *et al.* (2019) show that *P. coriaceus* is present in southern Japan, and is closely related to individuals from northern China, i.e., north of Taiwan (*P. coriaceus coriaceus* unit #3). Finally, a voucher specimen identified as *Platevindex* cf. *coriaceus* (Dayrat *et al.* 2011) in the collection of the Natural History Museum in London (NHMUK 20060274) actually belongs to *Platevindex burnupi*.

Von Martens (1897: 127) indicated that *Oncis coriacea* was identified from "Celebes: bei Luwu" [Luwu, Sulawesi, Indonesia] by M. Weber, from "Halmaheira: Dodinga" by himself, as well as from Java and "Nikobaren, Pulo Pinang und Philippinen" [Nicobar Islands; Penang, Malaysia; the Philippines] based on specimens in the Berlin Museum. Von Martens did not provide any details about how the specimens were identified. The specimens from Halmahera, Java, Malaysia, the Philippines and Sulawesi, Indonesia could be either *P. coriaceus* or *P. tigrinus*. *Platevindex coriaceus* was not found in the Andaman Islands, but could be present in the Nicobar Islands.

Platevindex coriaceus darwinensis Goulding & Dayrat subsp. nov.
urn:lsid:zoobank.org:act:A609EB85-101E-467E-AFD5-812043EDAFFE
Figs 16B, 18D, 19D, 22–25

Etymology

Platevindex coriaceus darwinensis subsp. nov. is named after Darwin, Northern Territory, Australia, which is the type locality.

Material examined

Type material
AUSTRALIA • holotype (28/26 [1700] mm); Northern Territory, Darwin, close to Tiger Brenan Rd; 12°28.782′ S, 130°54.750′ E; 19 Aug. 2012; station 69; high tidal *Ceriops* mangrove by small service road; NTM P.57601.

Other material
AUSTRALIA – **Northern Territory** • 3 specs (40/25 [1674], 29/21 [1663] and 20/14 [1672] mm); Darwin, Talc Head; 12°28.765′ S, 130°46.297′ E; 15 Aug. 2012; station 62; open forest of large *Sonneratia alba* with mud saturated with water; NTM P.57602 • 1 spec. (29/16 [1677] mm); Darwin, Near Berrimah; 12°28.786′ S, 130°54.750′ E; 16 Aug. 2012; station 63; *Sonneratia*, *Rhizophora* and *Ceriops* mangrove forest; NTM P.57603 • 1 spec. (32/17 [1633] mm); Darwin, near Channel Island Rd; 12°33.557′ S, 130°52.889′ E; 16 Aug. 2012; station 64; *Sonneratia*, *Rhizophora* and *Ceriops* mangrove forest; NTM P.57604 • 1 spec. (27/19 [1690] mm); Darwin, end of Channel Island Rd; 12°33.557′ S, 130°52.894′ E; 17 Aug. 2012; station 66; *Sonneratia*, *Rhizophora* and *Ceriops* mangrove forest; NTM P.57606 • 1 spec. (33/25 [1701] mm); Darwin, close to Tiger Brenan Rd; 12°28.782′ S, 130°54.750′ E; 19 Aug. 2012; station 69; high tidal *Ceriops* mangrove by small service road; NTM P.57608. – **Queensland** • 1 spec. (31/26 [2549] mm); Cairns; 16°52.972′ S, 145°45.665′ E; 15 Jun. 2013; station 98; *Rhizophora*, *Bruguiera* and *Ceriops*, not many dead logs; MTQ • 1 spec. (50/27 [no DNA] mm); Flying Fish Point; 17°30.001′ S, 146°04.295′ E; 20 Jun. 2013; station 104; mangrove by creek with sandy mud; MTQ • 1 spec. (24/18 [2590] mm); Magnetic Island; 19°10.096′ S, 146°49.366′ E; 23 Jun. 2013; station 106; mostly *Avicennia* mangrove with mounds of mud; MTQ • 1 spec. (34/25 [2679] mm); Campwin Beach; 21°22.455′ S, 149°18.753′ E; 5 Jul. 2013; station 121; narrow *Rhizophora* mangrove with watery mud and large rocks by creek; MTQ • 2 specs (48/34 [no DNA] and 23/17 [2689] mm); Armstrong Beach; 21°27.129′ S, 149°17.084′ E; 6 Jul. 2013; station 123; margin of *Rhizophora* and *Avicennia* mangrove with open mudflat; MTQ • 1 spec. (48/29 [no DNA] mm); Queensland, Pioneer River; 21°08.511′ S, 149°12.076′ E; 8 Jul. 2013; station 125; *Avicennia* & *Rhizophora* mangrove; MTQ.

INDONESIA – **Halmahera** • 2 specs (36/24 [5071] and 28/18 [5021] mm); Dodinga; 00°51.348′ N, 127°38.504′ E; 9 Mar. 2015; station 206; high intertidal back of mangrove with *Acrostichum* sp. and mounds of mud; UMIZ 00080 • 4 specs (34/19 [5112], 34/18 [5109], 22/17 [5111] and 19/13 [5110] mm); Buli; 00°55.446′ N, 128°20.612′ E; 16 Mar. 2015; station 212; logged area in front of old *Rhizophora* forest; UMIZ 00081.
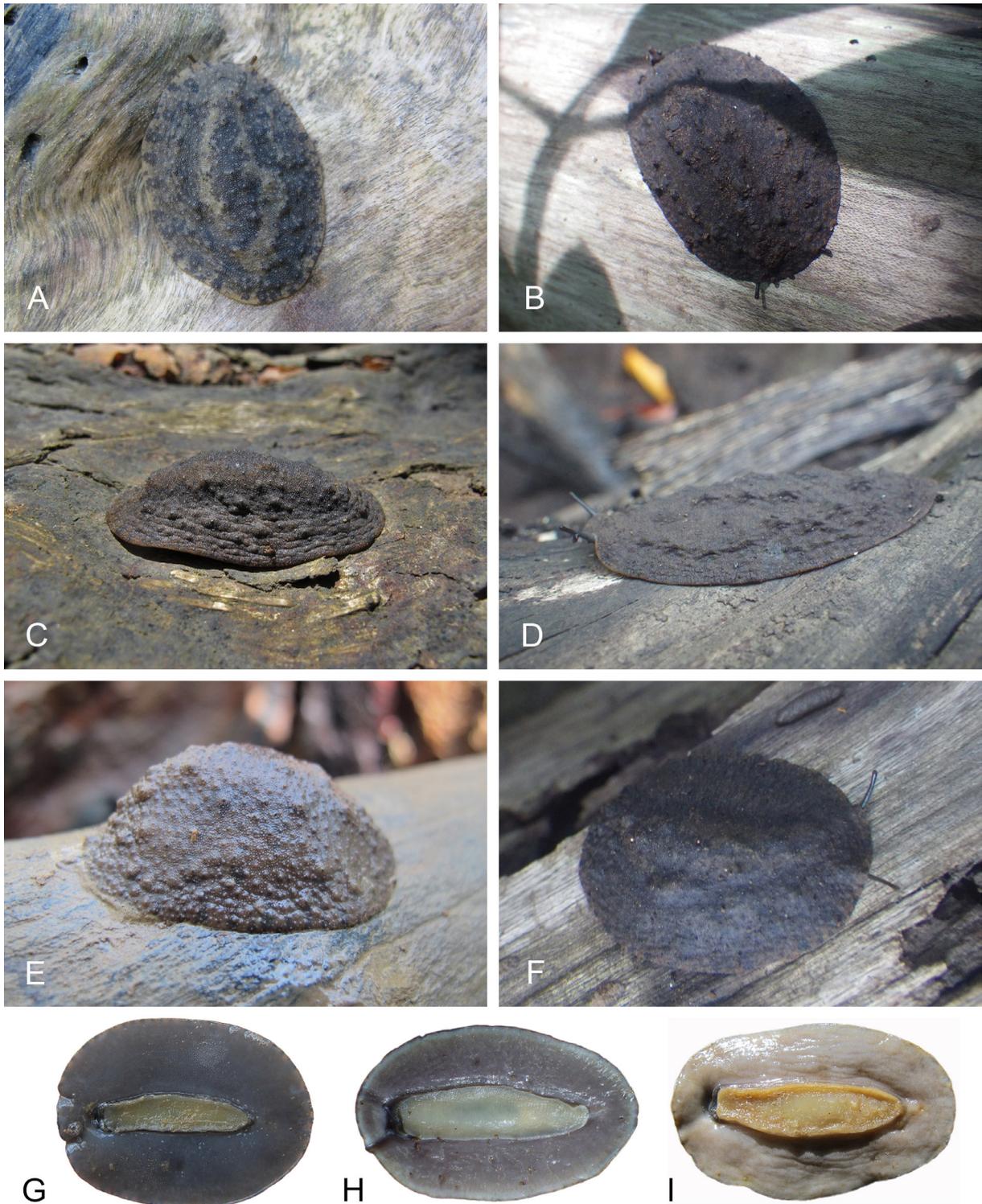
Fig. 22. *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., live animals. **A**. Dorsal view, 20 mm long [1672], Australia, Darwin (NTM P.57602). **B**. Dorsal view, 36 mm long [5071], Indonesia, Halmahera (UMIZ 00080). **C**. Dorsal view, 36 mm long [1674], Australia, Darwin (NTM P.57602). **D**. Dorsal view, 34 mm long [5109], Indonesia, Halmahera (UMIZ 00081). **E**. Dorsal view, holotype, 28 mm long [1700], Australia, Darwin (NTM P.57601). **F**. Dorsal view, 22 mm long [5111], Indonesia, Halmahera (UMIZ 00081). **G**. Ventral view, 33 mm long [1701], Australia, Darwin. **H**. Ventral view, same as B. **I**. Ventral view, same as C.

Other museum material without DNA sequences
AUSTRALIA – **Western Australia** • 13 specs (from 35/30 to 20/20 mm); Kimberley, Whirlpool Pass; 16°15. 81′ S, 123°29.88′ E; on mangroves; WAM S42812 • 6 specs (from 25/25 to 17/15 mm); Kimberley, Cambridge Gulf, Cape Domett; 14°49.78′ S, 128°23.20′ E; WAM S26581 • 4 specs (from 35/30 to 15/15 mm); Exmouth Gulf, Tubridgi Point Boat Channel; 21°50.0′ S, 114°39.90′ E; WAM S26772 • 5 specs (from 30/30 to 8/8 mm); Exmouth Gulf, NE of Tent Point; 22°00.0′ S, 114°30.5′ E to 22°00.4′ S, 114°32.1′ E; WAM S26777.

Description

Color and morphology of live animals (Fig. 22)
Identical to *P. coriaceus coriaceus* (see above), acknowledging some minor variations: the hyponotum is grey or light grey; the foot is light yellow; there are between 20 and 36 papillae with dorsal eyes, the largest animals bearing the largest numbers of eyes.

Digestive system (Figs 17B, 23)
Identical to that of *P. coriaceus coriaceus* (see above), acknowledging some minor variations: radulae measure up to 7.4 mm; examples of radular formulae are presented in Table 5; intestinal loops are of type II, with a transitional loop oriented between 6 and 8 o'clock (Fig. 17B).

Reproductive system (Figs 18–19, 24)
Identical to that of *P. coriaceus coriaceus* (see above), acknowledging some minor variations: the distal section of the oviduct (i.e., distal to the spermatheca) is long, up to two times the length of the proximal
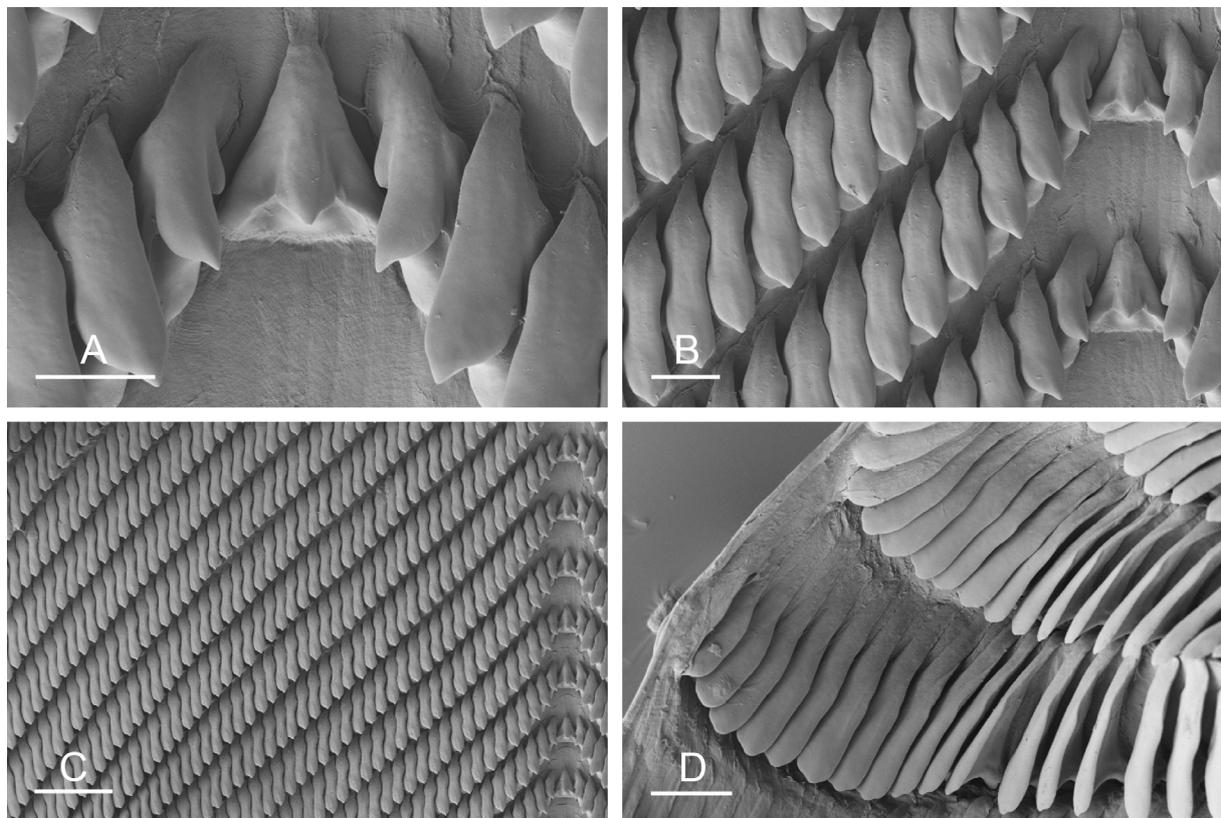
Fig. 23. *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., radula, Indonesia, Halmahera [5021] (UMIZ 00080). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scale bars: A = 50 μm; B = 10 μm; C = 100 μm; D = 30 μm.

section (from the female gland mass to the spermatheca); the oviduct is much wider (up to five times) than the deferent duct; penial hooks measure from 60 to 110 μm; the flexible region of the penis with hooks is between 2 and 8 mm long (Fig. 24); the retractor muscle varies from the length of the sheath to ¼ of its length.

Distinctive diagnostic features (Table 4)

Platevindex coriaceus coriaceus and *P. coriaceus darwinensis* subsp. nov. are indistinguishable externally. The only minor difference in color variation is that a dark blue-grey hyponotum was observed in *P. coriaceus coriaceus* (most commonly in the Philippines) but never in *P. coriaceus darwinensis* subsp. nov. Internally, both subspecies can hardly be distinguished either. The ratio between the oviduct width and the deferent duct width tends to be much higher in *P. coriaceus darwinensis* subsp. nov. than in *P. coriaceus coriaceus*, but a higher variation may be discovered in the future. However, based on current data, *P. coriaceus coriaceus* and *P. coriaceus darwinensis* subsp. nov. do not overlap geographically.

Distribution (Fig. 10B)

Australia: Northern Territory and Queensland. Indonesia: Halmahera.

Habitat (Fig. 25)

Platevindex coriaceus darwinensis subsp. nov. is found in the same habitat as the nominotypical subspecies, i.e., mangrove forests, on tree roots, tree trunks and logs. It is very common in the Northern Territory (Australia) and Halmahera (Indonesia). It seems to be less common in Queensland (Australia), with *Platevindex luteus* found in higher abundance.

Remarks

A new subspecific name is needed because no existing species-group name could apply with confidence to the taxon recognized here. *Platevindex cinereus* was described from Broome, Western Australia, by Odhner (1917) as *Oncis cinerea*, exclusively known from the holotype, by monotypy, which is a small (9/9 mm) and immature specimen (SMNH 945). There is no doubt that the holotype of *Oncis cinerea* belongs to a species of *Platevindex*, but, because it is immature, it is not possible to determine which one. *Platevindex cinereus* could apply to either of the two species sampled in the Northern Territory, Australia, *P. coriaceus darwinensis* subsp. nov. or *P. martensi*, and even to the widespread species *P. luteus*, although the latter has not been recorded from Northern Territory or Western Australia. Because it will remain impossible to confidently apply *P. cinereus* to any particular species of *Platevindex*, it is regarded here as a nomen dubium. Some onchidiid slugs from the collections of the Western Australia
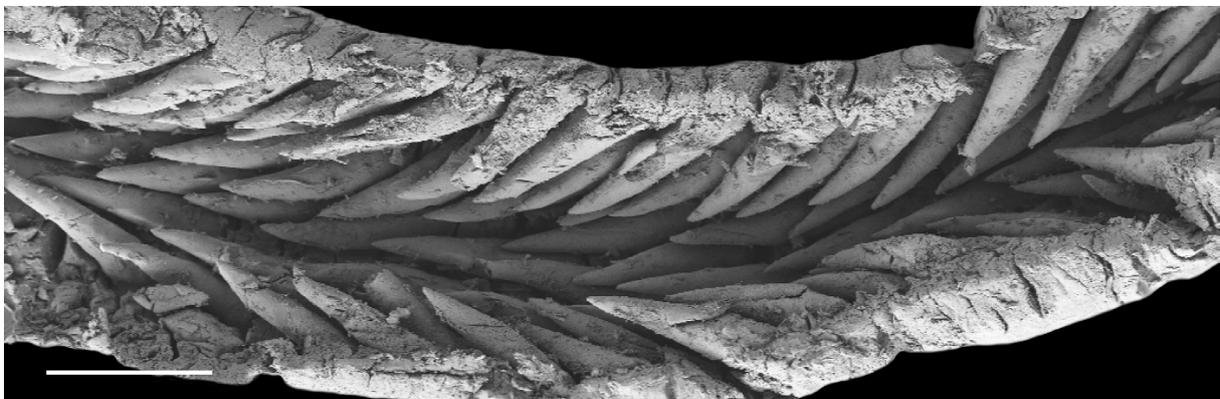
Fig. 24. *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov., penial hooks, Australia, Queensland, [no DNA] (MTQ). Scale bar = 100 μm.

Museum are identified here as *P. coriaceus* based on the position of their dorsal eyes and their reproductive anatomy. Whether populations of *P. coriaceus* from Western Australia belong to *P. coriaceus coriaceus*, *P. coriaceus darwinensis* subsp. nov., or even a distinct subspecies would have to be checked with fresh material from Western Australia.

Bretnall's (1919: 323) description of *Onchidium coriaceum* from Queensland does not appear to be based on *Platevindex* slugs: "short conical papillae" and a hyponotum "regularly yellowish" are not compatible with *P. coriaceus darwinensis* subsp. nov.

Platevindex tigrinus (Stoliczka, 1869) comb. nov.
Figs 26–30

Onchidium tigrinum Stoliczka, 1869: 105–107, pl. 15, fig. 2.

Platevindex mortoni – Sun *et al.* 2014: 63. — Zhang *et al.* 2017: fig. 1 [non *Platevindex mortoni* Britton, 1984].
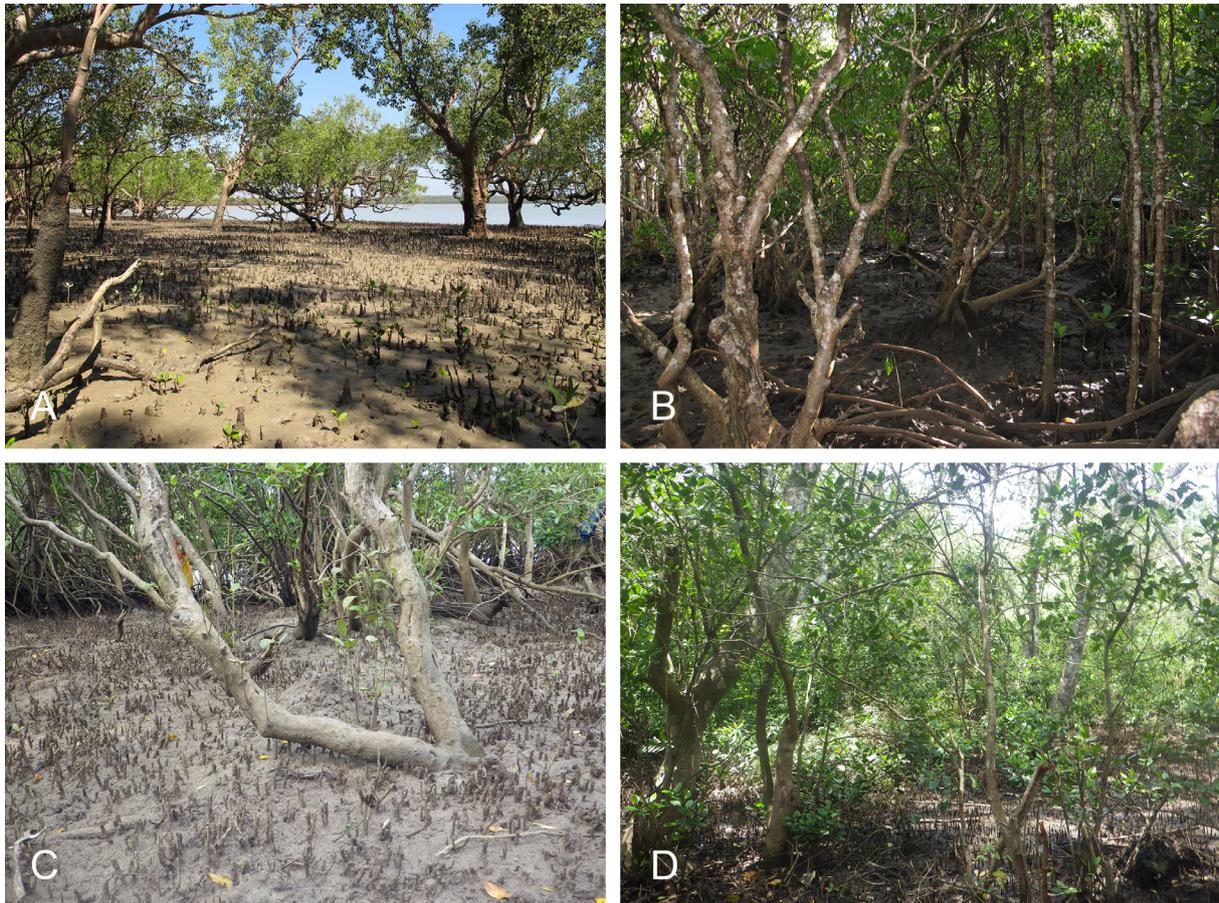
Fig. 25. Habitats of *Platevindex coriaceus darwinensis* Goulding & Dayrat subsp. nov. **A**. Australia, Darwin, large *Sonneratia alba*, open forest, soft mud by shore (station 62). **B**. Australia, Queensland, *Rhizophora*, *Bruguiera* and *Ceriops* by boardwalk, not many dead logs (station 98). **C**. Australia, Queensland, open forest with *Avicennia*, some *Rhizophora* and soft mud (station 124). **D**. Indonesia, Halmahera, high intertidal back of a mangrove, with *Acrostichum* ferns and mounds of mud (station 206).

Material examined

Neotype (here designated)
INDIA • neotype (28/18 [1066] mm); Sundarbans, Bali Island; 22°04.387′ N, 88°41.828′ E; 6 Jan. 2011; station 50; soft mud by the sea with a few mangrove trees and dead logs; BNHS 18-1066.

Notes on type material
The designation of a neotype is needed in order to clarify the application of the name *Onchidium tigrinum* (ICZN Article 75.3.1). The characters that differentiate *P. tigrinus* from other species of *Platevindex* are mentioned below in a section on 'Distinctive diagnostic features' (ICZN Article 75.3.2). The neotype is preserved separately and will be easily recognized (ICZN Article 75.3.3). The syntypes could not be located after an exhaustive search of museum collections (Dayrat 2009) (ICZN Article 75.3.4). What is known of the former syntypes, from the original description and illustrations, is consistent with the neotype (ICZN Article 75.3.5). The type locality is the banks of the Mutlah River at Port Canning [Matla River, Ganges Delta, India] and the neotype was collected as nearly as practicable from the original type locality in West Bengal (ICZN Article 75.3.6), and it is already the property of a scientific institution, the Bombay Natural History Society, in Mumbai, India (ICZN Article 75.3.7). The neotype was collected on soft mud by the sea with a few mangrove trees and dead logs. The designation of a neotype is exceptionally needed in order to make sure that the application of the name *Onchidium tigrinum* remains unambiguous (see Remarks below).

Other material
BRUNEI • 2 specs (29/18 [1033] and 15/14 [1032] mm); Sungai; 04°53.756′ N, 114°59.496′ E; 26 Jul. 2011; station 31; very large, tall *Rhizophora* mangrove with soft mud; BDMNH • 1 spec. (23/16 [1030] mm); Pulau Pyatan, Teluk Brunei; 04°55.246′ N, 115°02.764′ E; 27 Jul. 2011; station 32; open mangrove with a few sparse old trees and large old logs, by the river; BDMNH.

INDIA – **West Bengal** • 1 spec. (13/10 [1065] mm); same collection data as for neotype; BNHS 18-1065 • 1 spec. (22/15 [#1] mm); same collection data as for neotype; BNHS 18. – **Andaman Islands** • 1 spec. (40/30 [1094] mm); Shamkund, near Rangat; 12°29.448′ N, 92°50.620′ E; 11 Jan. 2011; station 57; by a large river, deep mangrove with tall trees, small creeks and old muddy logs, next to a road and a small cemented bridge across creek; BNHS 2-1094 • 2 specs (35/22 [#1] and 24/15 [1114] mm); Shantipur, Kadamtala; 02°19.844′ N, 92°46.377′ E; 12 Jan. 2011; station 58; open area with hard mud and many old logs, next to a mangrove; BNHS 12-1114 • 1 spec. (25/22 [1123] mm); Shoal Bay, by Bamboo Flat; 11°47.531′ N, 92°42.576′ E; 13 Jan. 2011; station 59; open mangrove with hard mud, old logs, next to a road and a small cemented bridge across creek; BNHS 1-1123. – **Maharashtra** • 1 spec. (25/16 [1140] mm); Khandra mangrove; 19°03.876′ N, 72°49.296′ E; 18 Dec. 2011; station 43; very small *Avicennia* trees in mud; BNHS 35-1140 • 1 spec. (36/26 [1160] mm); Vatad; 17°15.791′ N, 73°17.623′ E; 23 Dec. 2011; station 46; *Avicennia* mangroves by field with deep and very watery mud; BNHS 104-1160 • 1 spec. (29/16 [1178] mm); Areware mangrove; 17°04.404′ N, 73°17.747′ E; 24 Dec. 2011; station 47; mangrove of *Avicennia* and a few small *Rhizophora* with soft mud and areas with pooled water; BNHS 33-1178.

MALAYSIA – **Peninsular Malaysia** • 3 specs (23/17 [953], 21/18 [955] and 14/12 [956] mm); Matang, Crocodile River off Kuala Septang; 04°49.521′ N, 100°37.630′ E; 10 Jul. 2011; station 16; mangrove with tall *Rhizophora*; USMMC 00022 • 2 specs (27/18 [939] and 26/14 [5522] mm); Merbok; 05°39.035′ N, 100°25.782′ E; 18 Jul. 2011; station 21; deep *Rhizophora* forest with old, tall trees, hard mud, many small creeks and dead logs; USMMC 00023 • 1 spec. (14/13 [936] mm); Langkawi Island, Tanjung Rhu; 06°25.771′ N, 99°49.436′ E; 13 Jul. 2011; station 23; young *Rhizophora*, *Sonneratia* and *Avicennia* in a dense forest with small creeks; USMMC 00024.

SINGAPORE • 1 spec. (21/17 [992] mm); Lim Chu Kang; 01°26.785′ N, 103°42.531′ E; 2 Apr. 2010; station 7; open mangrove forest with tall trees and soft mud by river, ending on sun-exposed mudflat; ZRC.MOL.10472 • 1 spec. (18/17 [993] mm); Semakao Island; 01°12.083′ N, 103°45.585′ E; 3 Apr. 2010; station 8; landfill island with newly planted mangrove, very dense; ZRC.MOL.10473 • 1 spec. (19/13 [994] mm); Lim Chu Kang; 01°26.785′ N, 103°42.531′ E; 5 Apr. 2010; station 9; open mangrove forest with tall trees and soft mud by river, ending on sun-exposed mudflat; ZRC.MOL.10474.

Description

Color and morphology of live animals (Fig. 26)
The dorsal surface is bumpy, not smooth, and typically brown with dark brown or yellow-brown markings. The hyponotum color varies from bluish grey to light grey. The edge of the hyponotum may be slightly lighter, but there is no prominent light-colored line around the entire edge. The foot color varies from dark blue-grey to light yellow. The number of papillae with dorsal eyes is variable (generally between 25 and 50). Dorsal eyes are distributed across the notum but are absent from its margin (i.e., eyes are never <2 mm from the notum edge).

Digestive system (Figs 27A, 28)
Radulae measure up to 5 mm in length. Examples of radular formulae are presented in Table 5. The intestinal loops are of type II, with transitional loops oriented between 6 and 9 o'clock (Fig. 27A).

Reproductive system (Figs 27B–C, 29)
The oviduct is much wider than the deferent duct (approximately up to three times). Its distal section (distal to the spermatheca) is up to three times as long as its proximal section (Fig. 27B). The deferent duct is closely attached to the oviduct and almost straight (with only loose turns). The distal, flexible, hook-bearing section of the penis is 1 to 1.5 mm long. The penial hooks are approximately 60 to 100 µm long, and can be seen inside the semi-transparent penis. In mature specimens, the retractor muscle inserts on the right side of the visceral cavity near the heart. The retractor muscle is from one quarter as long as the penial sheath to equal to it in length (Fig 27C). The deferent duct is not highly convoluted, with only a few loops (and is even less convoluted in immature specimens).

Distinctive diagnostic features (Table 4)

Externally, the yellow foot of *Platevindex tigrinus* clearly distinguishes it from *P. martensi* (orange foot) and *P. aptei* sp. nov. (black foot). *Platevindex tigrinus* is very similar externally to *P. amboinae*, except that the notum of *P. tigrinus* bears many dorsal eyes which are absent in *P. amboinae*. *Platevindex tigrinus* can be distinguished from *P. latus* by its granular dorsal surface and the lack of large, thorny dorsal papillae. Its granular dorsal surface also helps to distinguish it from *P. luteus* and *P. applanatus*, which bear prominent dorsal papillae when disturbed, although it is still possible to confuse these three species. *Platevindex tigrinus* cannot be distinguished externally from *P. coriaceus*, which has been found in many of the same sites, except in India (where *P. coriaceus* has not been found so far).

Internally, the intestinal loops clearly distinguish *P. tigrinus* (type II) from *P. applanatus* (type I). Some individuals of *P. luteus* are characterized by intestinal loops of type II and cannot be distinguished from *P. tigrinus* based only on the digestive system. The reproductive system can also be used to differentiate *P. tigrinus* from *P. coriaceus*, *P. luteus* and *P. burnupi*. In *P. tigrinus*, the retractor muscle for the penis inserts near the heart on the right side of the visceral cavity (i.e., in the posterior half or third of the cavity) while it inserts at the posterior end of the cavity in *P. coriaceus*. In *P. tigrinus* the deferent duct is closely attached to the oviduct (in the posterior reproductive system), while it is only loosely attached to it in *P. luteus* and *P. burnupi*. This trait also differs slightly between *P. tigrinus* and *P. coriaceus*: the deferent duct, which is closely attached to the oviduct in both species, is almost straight in *P. tigrinus* and highly-convoluted, with tight, U-shaped turns in *P. coriaceus*.
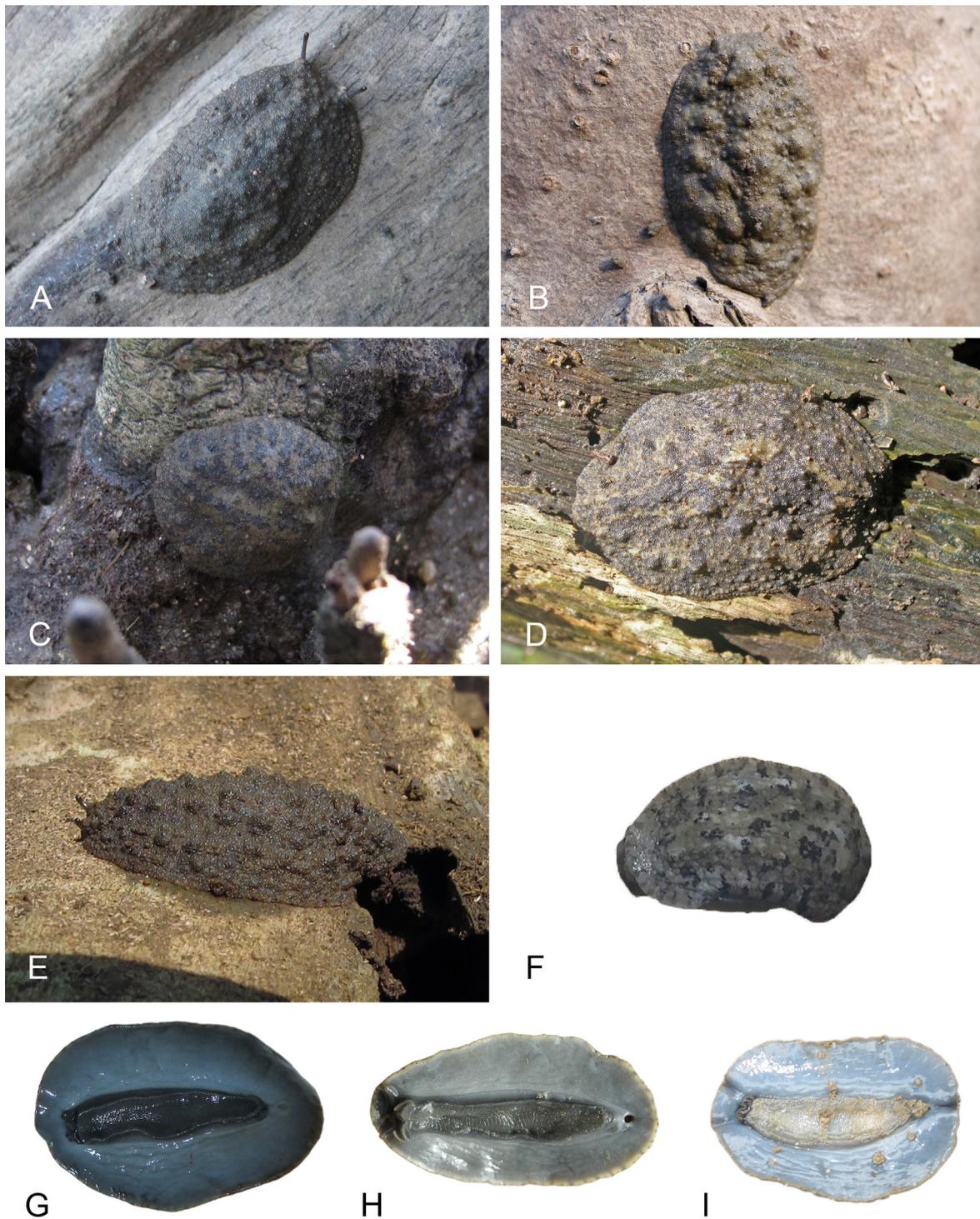
Fig. 26. *Platevindex tigrinus* (Stoliczka, 1869), live animals. **A**. Dorsal view, 35 mm long [#1], India, Andaman Islands, Shantipur, Kadamtala (BNHS 12). **B**. Dorsal view, 22 mm long [#1], India, Sundarbans, Bali Island (BNHS 18). **C**. Dorsal view, 25 mm long [1140], India, Maharashtra, Khandra mangrove (BNHS 35-1140). **D**. Dorsal view, 19 mm long [994], Singapore, Lim Chu Kang (ZRC.MOL.10474). **E**. Dorsal view, 29 mm long [1178], India, Maharashtra (BNHS 33-1178). **F**. Dorsal view, neotype, 28 mm long [1066], India, West Bengal, Sundarbans, Bali Island (BNHS 18-1066). **G**. Ventral view, 27 mm long [939], Malaysia, Merbok (USMMC 00023). **H**. Ventral view, same as B. **I**. Ventral view, same as A.

Distribution (Fig. 10B)

Brunei. India: Andaman Islands, Maharashtra and West Bengal (type locality and fresh specimens newly collected). Peninsular Malaysia. Singapore. Southern China (specimens misidentified as *Platevindex mortoni* in Sun *et al*. 2014 and Zhang *et al*. 2017). All records are new, except for the type locality.

Habitat (Fig. 30)

Platevindex tigrinus is found in mangroves, on tree trunks and roots and dead logs, but is not found directly on mud. Those logs and trees may be in silty mud saturated with water or in the mid-intertidal. It does not live on rocky shores. *Platevindex tigrinus* is common across most of its geographic range. It is one of the most abundant onchidiid species in the mangroves of India.

Remarks

Stoliczka's illustration of the external appearance of *O. tigrinum* clearly shows a *Platevindex* slug (Stoliczka 1869: fig. 2). In his description of *O. tigrinum*, Stoliczka emphasized the flattened shape of the slug, the narrow foot and the hardened notum, which are all diagnostic of *Platevindex*. Other aspects of the original description are also in agreement with *Platevindex*: a granular dorsal surface, a foot from one third to one fourth the total width of the body, dorsal eyes on papillae of the notum and a male opening above the right oral lobe. Therefore, *O. tigrinum* is transferred to *Platevindex*.
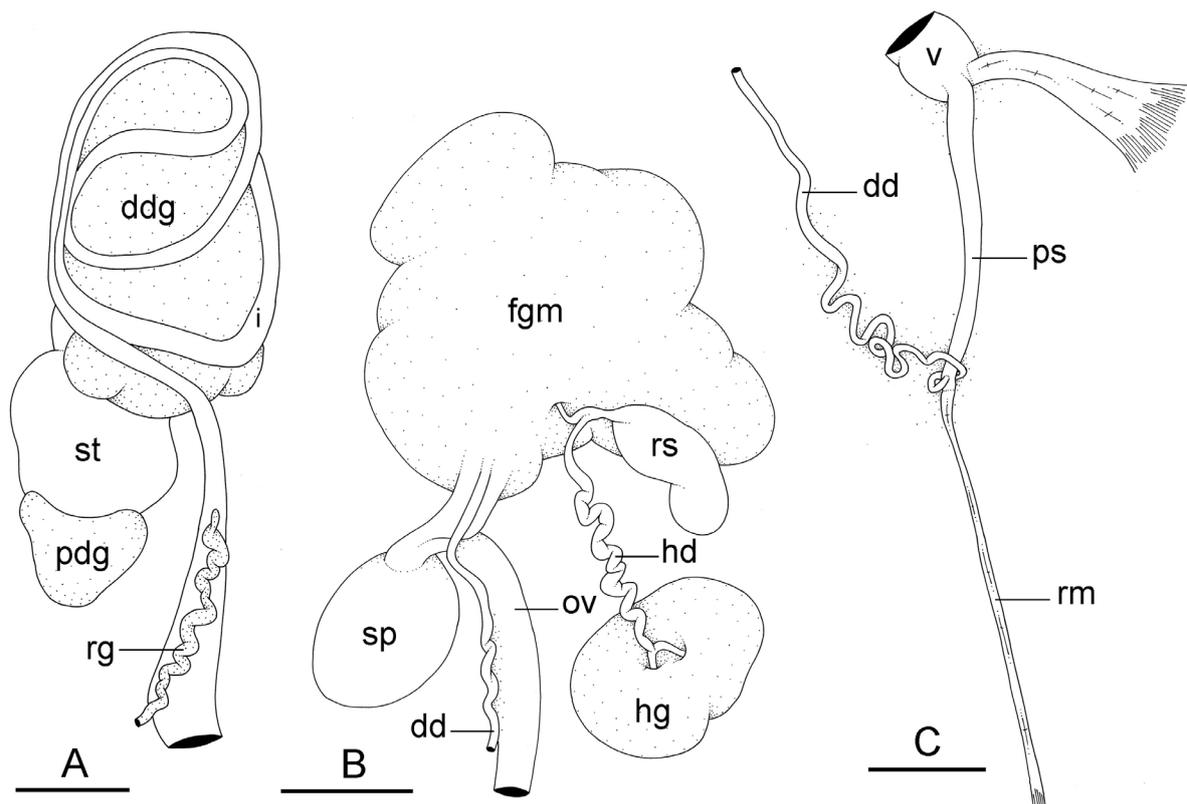
Fig. 27. *Platevindex tigrinus* (Stoliczka, 1869), digestive and reproductive systems, Peninsular Malaysia [5522] (USMMC 00023). **A**. Digestive system, dorsal view, type II with a transitional loop oriented at 9 o'clock. **B**. Posterior reproductive system. **C**. Anterior, male copulatory apparatus. Abbreviations: dd = deferent duct; ddg = dorsal digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior digestive gland; ps = penial sheath; rg = rectal gland; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scale bars: A = 3 mm; B–C = 2 mm.

Stoliczka's description of the color of the ventral surface is as follows: "Young specimens have the mantle below uniform light bluish with very numerous and white dots; large ones have occasionally a number of dark green or rusty, more or less confluent spots along the lateral margins, and the general colour is pale. The foot (...) is of a uniform dark bluish grey colour." (Stoliczka 1869: 106). The color of Stoliczka's young specimens perfectly matches the species described here and the color of the large ones is also within the observed color variation. The species treated here is the only one that we found at the type locality of *O. tigrinum* with a blue-grey ventral surface, strongly suggesting that the name *O. tigrinum* applies to the species described here. Also, Stoliczka mentioned that, at the type locality, *O. tigrinum* was common and found crawling on old wood, which is in complete agreement with our observations in the field, including at the type locality.

There is, however, a problem with Stoliczka's original description of *O. tigrinum*. Indeed, Stoliczka (1869: 107) stated that the "internal vas deferens is about 5 inches, and its supplementary albuminous string [Stoliczka's term for the accessory penial gland] about 8 inches long." An accessory penial gland is not present in any species of *Platevindex* and this strongly suggests that a species from another genus was part of the type material, although it cannot be excluded that he made a mistake. Thus, the designation of a neotype is needed because it allows us to ensure that, in the future, *O. tigrinum* will always apply to the species described here. The designation of a neotype is far more preferable to a lectotype designation based on an illustration or description. Indeed, even though the species described here is the only *Platevindex* we found at the type locality of *O. tigrinum*, it cannot be excluded that other species, especially *P. luteus*, will be found there in the future. Because *P. luteus* and *P. tigrinus* are hardly distinguishable externally, it is possible that Stoliczka also examined some specimens of *P. luteus*. For all the reasons above, the neotype designated here efficiently clarifies the application of *O. tigrinum*.
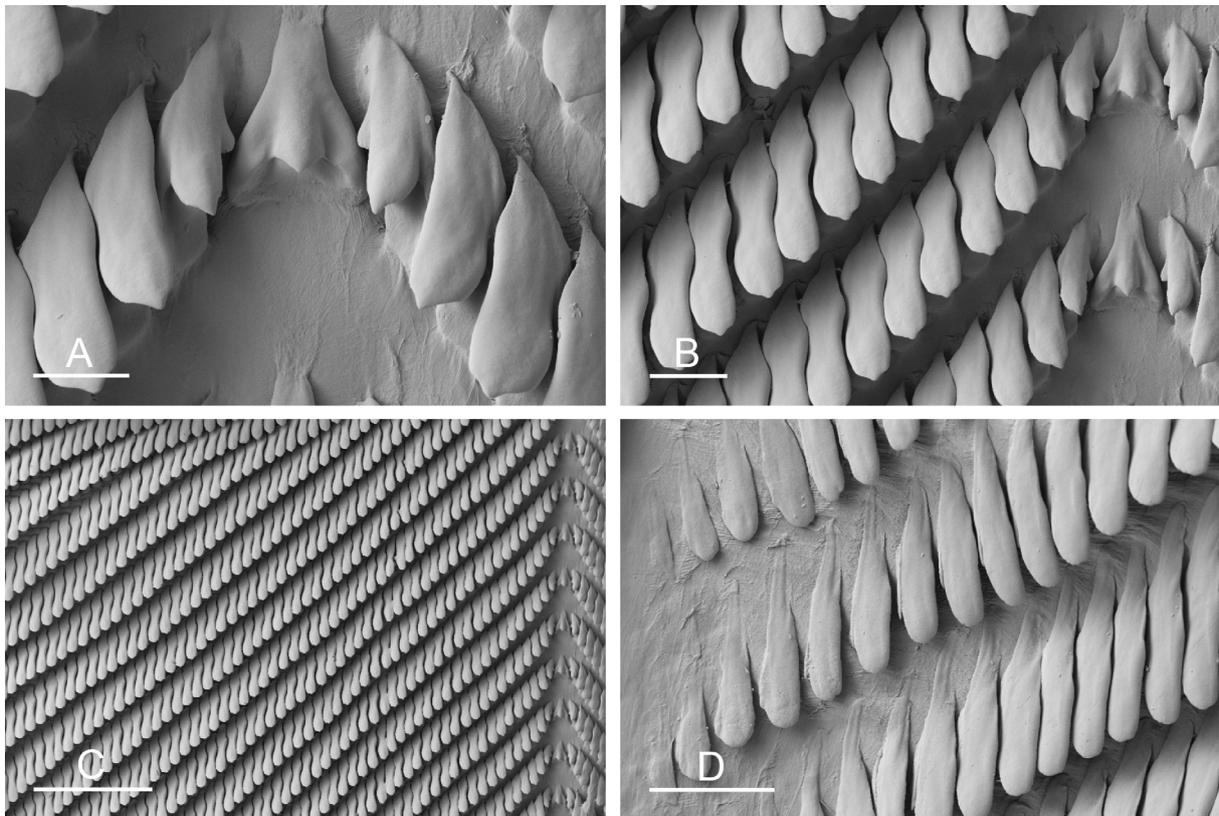
Fig. 28. *Platevindex tigrinus* (Stoliczka, 1869), radula, Peninsular Malaysia, Merbok [5522] (USMMC 00023). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scale bars: A = 20 μm; B = 30 μm; C = 200 μm; D = 50 μm.

In his remarks on *Onchidium coriaceum*, Semper (1882: 273) addressed the similarity between the species he described and Stoliczka's description of *Onchidium tigrinum*. Semper pointed out that the only difference between the two descriptions is the presence of an accessory penial gland in *O. tigrinum*, but doubted that one was actually present in Stoliczka's specimens of *O. tigrinum*. Semper considered *O. tigrinum* to be a synonym of *O. coriaceum* (although with a question mark), even though he was not able to properly compare the anatomy of the two species, and even though, strictly speaking, *O. tigrinum* had priority over *O. coriaceum*. *Platevindex tigrinus* is shown here to be genetically and anatomically distinct from *P. coriaceus*.

Hoffmann (1928: 77) noted Semper's comments on the similarity between *Onchidium tigrinum* and *Oncis stuxbergi*, but did not provide additional comments on the species or add new localities. Hoffmann's indication that the species was from "Port Canning (Penang, Malayische Halbinsel)" [Penang, Peninsular Malaysia] appears to be a mistake for Stoliczka's locality of Port Canning in West Bengal, India. Labbé (1934: 223) repeated Hoffmann's erroneous record but did not provide new information about the species.

The type material of *Platevindex mortoni*, a species originally described by Britton (1984) from Hong Kong, includes a holotype by original designation (NHMUK 1982288) and three paratypes (NHMUK 1982289/1,2 and NHMUK 1982289/3). The holotype (18/16 mm) is missing both the male and female reproductive parts, which were not described in detail by Britton. Also, its digestive system is largely destroyed (the intestinal loops cannot be observed) even though the radula remains. The two largest paratypes (22/18 and 15/15 mm) are empty of all internal organs. All organs remain in the smallest (9/9 mm) paratype but it is not fully mature (the posterior, female reproductive parts are only partly developed). The intestinal loops of the smallest paratype are clearly of type II. Britton did not describe the color of the ventral surface (foot and hyponotum) of live animals. He only mentioned that the preserved holotype and two preserved paratypes (NHMUK 1982289/1,2) were brown with a darker mantle rim, while the third paratype (NHMUK 1982289/3) was grey with darker mottling. However, the dorsal color is useless for identifying species of *Platevindex* and a brown dorsal surface with a darker mantle rim (color of the holotype) could apply to any species. Britton's description of the type of intestinal loops is also problematic. He described intestinal loops of type I in the holotype, of type II in what he called the "grey paratype" (NHMUK 1982289/3), which is the largest paratype, and intermediate between types I and II in the smallest paratype. Intestinal loops of type II are clearly present in the smallest paratype (the only type specimen with remaining intestinal loops) which Britton called the "smaller brown paratype." There are three possible explanations for that. First, Britton correctly described the intestinal loops of the holotype of *P. mortoni* (the only specimen with a name-bearing function) and the name *P. mortoni*
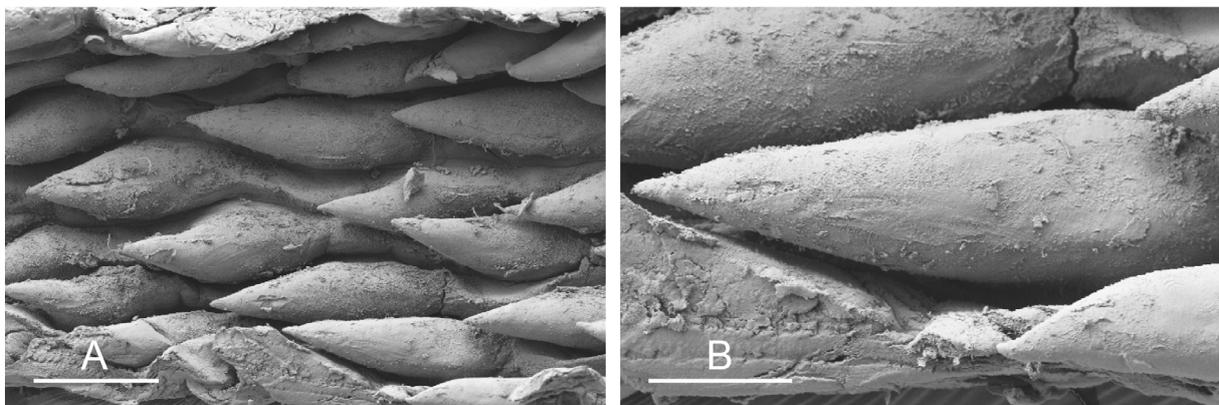
Fig. 29. *Platevindex tigrinus* (Stoliczka, 1869), penial hooks, Brunei [1030] (BDMNH). **A**. Penial hooks. **B**. Close up of penial hook. Scale bars: A = 50 μm; B = 20 μm.

cannot apply to *P. tigrinus* or *P. coriaceus*, two species with intestinal loops of type II and which are known to be present in Hong Kong (see below). However, the name *P. mortoni* could apply to *P. luteus*, a species with intestinal loops of type I, but which is not known from Hong Kong (although it is known from the Philippines and Vietnam, among other places). Second, it is also possible (and quite likely) that Britton simply made a mistake in identifying the type of the intestinal loops in the holotype of *P. mortoni* because he also misidentified the intestinal type in another onchidiid that he called *Paraoncidium reevesii* (J.E. Gray, 1850) (see Goulding *et al*. 2018b). If Britton misidentified the intestinal loops in the holotype of *P. mortoni*, the description would be compatible with *P. tigrinus*. Third, it is also possible that the original description of *P. mortoni* was based on specimens from two different species (one with a type I and one with a type II), even though, strictly speaking, only the holotype is the name-bearer. Because Britton's description of *P. mortoni* is confusing and since critical characters cannot be checked in the type material, *P. mortoni* is regarded as a nomen dubium. It does apply to a species of *Platevindex*, but which one cannot be confidently determined.

DNA sequences of onchidiids from China published by Sun *et al*. (2014) show that there are several species of *Platevindex* in China and at least two in Hong Kong. For unclear reasons, Sun *et al*. applied the name *P. mortoni* to all Chinese onchidiids with a bluish-grey hyponotum and foot. By comparing

Fig. 30. Habitats of *Platevindex tigrinus* (Stoliczka, 1869). **A**. Brunei, Sungai, very large, tall *Rhizophora* with soft mud, access by boat from river (station 31). **B**. Peninsular Malaysia, Merbok, old, tall *Rhizophora* trees with hard mud (station 21). **C**. India, Maharashtra, small *Avicennia* trees and some *Rhizophora* with soft mud, trees in clumps with open area in between (station 47). **D**. Singapore, Lim Chu Kang, *Avicennia* mangrove (station 7).

their DNA sequences with ours, we have determined that the sequenced specimens they called *P. mortoni* belong to *P. tigrinus* and *P. coriaceus*. The specimens called *P. mortoni* from southern China, east of Hainan (including Hong Kong), are here referred to *P. tigrinus,* while a specimen collected from southern China west of Hainan belongs to *P. coriaceus*.

Zhang *et al*. (2017) recently re-described a species they identified as *Platevindex mortoni* based on specimens from Hong Kong. This description did not address the inconsistency in the original description regarding the intestinal loops and appears to be based on multiple species of *Platevindex*. Despite the fact that COI sequences from Sun *et al*. (2014) showed that several species of this genus are present in China, including two in Hong Kong, Zhang *et al*. did not discuss how the species they re-described was different from other sympatric species of *Platevindex*. Photographs of live specimens by Zhang *et al*. clearly show that there are two different kinds of ventral coloration. The individual with a blue-grey foot and hyponotum (Zhang *et al*. 2017: fig. 1c) was either *P. tigrinus* or *P. coriaceus* (both could potentially be present in Hong Kong), and the individual with a bright orange foot (Zhang *et al*. 2017: fig. 1E) is identified here as *P. martensi*.

Platevindex tigrinus is distributed from western India to southern China (Hong Kong). It is one of few onchidiid species which is broadly distributed from the Indian Ocean to the South China Sea. It was not found in Tamil Nadu (southeastern India) during our recent (2016) survey in the mangroves of Pichavaram, but the diversity of mangrove molluscs was very low. Further exploration of southeastern India could reveal whether *Platevindex tigrinus* is present in low abundance, whether it varies in abundance seasonally, or is simply absent.

<center>

Platevindex luteus (Semper, 1880)
Figs 31–35

</center>

Onchidium luteum Semper, 1880: pl. 20, fig. 10, pl. 23, figs 2, 6.
Oncis schneideri Hoffmann, 1932: 135–137, fig. 1. **Syn. nov.**

Onchidium luteum – Semper 1882: 274–275, pl. 21, fig. 6. — Plate 1893: 181.
Oncis lutea – Stantschinsky 1907: 395. — Hoffmann 1928: 89–90.
Platevindex luteus – Dayrat 2009: 5. — Goulding *et al*. 2018a: 340; 2018b: 12; 2018c: 807. — Dayrat *et al*. 2019a: 6; 2019b: 38; 2019c: 560; 2019d: 30.

Material examined

Lectotype (here designated)
SINGAPORE • lectotype (14/11 mm); 1858; Semper leg.; ZMB/Moll 39031a.

Paralectotypes
SINGAPORE • 3 paralectotypes (15/11, 13/11 and 12/12 mm); 1858; Semper leg.; ZMB/Moll 39031b.

Holotype of *Oncis schneideri*
PAPUA NEW GUINEA • holotype (7/5 mm) by monotypy; Ostküste von Neu-Pommern [east coast of New Britain]; ZMB/Moll 114152.

Notes on type material
Onchidium luteum. The lectotype was selected because the male parts are present (although they were previously detached from the specimen). The posterior part of the lectotype is missing and the digestive system is not well preserved. The three paralectotypes were also previously dissected: the internal organs are missing in the two largest ones; the third and smallest paralectotype was cut longitudinally

in two halves and is largely destroyed. Semper listed five syntypes, suggesting that one of the original syntypes is missing.

Oncis schneideri. The holotype was previously dissected. The penial complex was drawn by Hoffmann and likely destroyed by him (it is missing), and the insertion of the retractor muscle cannot be checked. Some parts of the female (posterior) reproductive system are inside the holotype, but are largely destroyed. The digestive system is largely destroyed; the radula is present but the intestine is missing and the intestinal type cannot be verified.

Other material
AUSTRALIA – **Queensland** • 1 spec. (17/14 mm [2551]); Cairns; 16°52.972′ S, 145°45.665′ E; 15 Jun. 2013; station 98; *Rhizophora*, *Bruguiera* and *Ceriops* mangrove; MTQ • 1 spec. (22/16 mm [2597]); Magnetic Island; 19°09.733′ S, 146°48.625′ E; 24 Jun. 2013; station 108; dead log over pool of water in mangrove; MTQ • 1 spec. (20/14 mm [2678]); Armstrong Beach; 21°27.129′ S, 149°17.084′ E; 5 Jul. 2013; station 120; margins of mangrove and mudflat with *Rhizophora* and *Avicennia*; MTQ.

BRUNEI • 1 spec. (16/14 mm [1039]); Pulau Kaingara; 04°57.020′ N, 115°01.785′ E; 28 Jul. 2011; station 33; open mangrove with *Rhizophora* trees and logs, by the river; BDMNH.

INDONESIA – **Sumatra** • 2 specs (22/17 mm [1792] and 15/7 mm [1789]); Sungai Lubuk; 05°40.174′ S, 105°34.097′ E; 20 Oct. 2012; station 80; open mangrove with *Rhizophora* trees, *Thalassina* mounds and dead logs; UMIZ 00082. – **Lombok** • 1 spec. (11/9 mm [2958]); Seriwe Bay; 08°51.960′ S, 116°32.838′ E; 25 Mar. 2014; station 146; *Avicennia* mangrove with hard mud and rocks; UMIZ 00094. – **Bali** • 3 specs (19/16 mm [3046], 18/13 mm [3040] and 14/12 mm [3044]); Denpasar; 08°47.435′ S, 115°13.197′ E; 1 Apr. 2014; station 153; large mangrove by road, very soft mud; UMIZ 00095. – **Sulawesi** • 1 spec. (17/14 mm [2335]); Makassar City, Tallo; 05°06.117′ S, 119°26.777′ E; 21 Mar. 2013; station 92; small mangrove with outhouse in center; UMIZ 00191 • 1 spec. (23/16 mm [2364]); same locality as for preceding but 26 Mar. 2013; station 95; small mangrove with outhouse in center; UMIZ 00086. – **Ambon** • 1 spec. (28/18 mm [2837]); Lateri; 03°38.237′ S, 128°14.783′ E; 14 Feb. 2014; station 131; muddy mangrove with *Rhizophora*; UMIZ 00089 • 1 spec. (17/10 mm [2858]); Lateri; 03°38.261′ S, 128°14.716′ E; 16 Feb. 2014; station 133; low intertidal mangrove, slugs on mangrove trees underneath bark; UMIZ 00188. – **Seram** • 1 spec. (23/20 mm [2886]); Piru; 03°04.072′ S, 128°11.362′ E; 19 Feb. 2014; station 136; beach of palms and *Acrostichum* ferns behind *Sonneratia* mangrove; UMIZ 00189. – **Kei Islands** • 1 spec. (14/9 mm [2906]); Un; 05°38.273′ S, 132°45.738′ E; 25 Feb. 2014; station 140; in back of mangrove on rocks, mud, inside logs and under leaf litter; UMIZ 00091 • 2 specs (18/10 mm [2915] and 17/11 mm [2916]); Un; 05°38.282′ S, 132°45.669′ E; 26 Feb. 2014; station 141; *Bruguiera* and *Rhizophora* mangrove, slugs under the bark; UMIZ 00092 • 1 spec. (18/12 mm [2922]); Ohoi Ibra; 05°46.216′ S, 132°46.116′ E; 27 Feb. 2014; station 142; some old trees, others replanted, mud very soft; UMIZ 00093. – **Ternate** • 1 spec. (9/6 mm [5051]); Bastiong; 00°46.407′ N, 127°22.760′ E; 7 Mar. 2015; station 203; small mangrove patch and some rocks nearby a harbor; UMIZ 00097. – **Halmahera** • 1 spec. (17/12 mm [5022]); Dodinga; 00°51.348′ N, 127°38.504′ E; 9 Mar. 2015; station 206; back of a mangrove, high intertidal with *Acrostichum* ferns and mounds of mud; UMIZ 00098 • 1 spec. (17/15 mm [5041]); Saolat; 00°53.435′ N, 127°56.475′ E; 12 Mar. 2015; station 209; open *Rhizophora* mangrove with soft dark mud, many dead logs; UMIZ 00099. – **Timor** • 1 spec. (17/12 mm [5939]); Tablolong; 10°18.895′ S, 123°28.774′ E; 17 Jul. 2016; station 255; mangrove patch with very dark mud by a village; UMIZ 00190.

NEW CALEDONIA • 1 spec. (9/8 mm [6344]); Upper Diahot River; 20°20.564′ S, 164°21.842′ E; 6 Sep. 2018; Our Planet Reviewed Koumac 2018 expedition leg.; station KM505; lower, wet (and dry) trunks and roots of trees in a forest of *Rhizophora apiculata* and *Xylocarpus granatum* with a patchy understory

of *Acrostium* fern; MNHN-IM-2019-1474 • 1 spec. (12/8 mm [6361]); Diahot River; 20°19.435′ S, 164°19.195′ E; 8 Sep. 2018; Our Planet Reviewed Koumac 2018 expedition leg.; station KM510; firm sandy mud amongst prop roots in a *Rhizophora stylosa* forest fringing the river; MNHN-IM-2019-1475 • 1 spec. (15/11 mm [6367]); Hienghene, Hienghene River Bridge; 20°41.756′ S, 164°56.644′ E; 14 Sep. 2018; Our Planet Reviewed Koumac 2018 expedition leg.; station KM521; edge of *Rhizophora apiculta* mangrove forest near the high tide mark next to a bridge; MNHN-IM-2019-1476.

PAPUA NEW GUINEA – **Madang** • 1 spec. (9/8 mm [5429]); 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-2013-10407 • 1 spec. (9/7 mm [5431]); South Dumduman Island; 05°00.2′ S, 145°47.6′ E; 9 Nov. 2012; MNHN expedition Papua Niugini leg.; station PM12; limestone rocky intertidal; MNHN-IM-2013-10409. – **New Ireland** • 1 spec. (8/5 mm [6101]); Kavieng, Lisinung Island; 02°40.6′ S, 150°44.4′ E; 23 Jun. 2014; MNHN expedition Kavieng 2014 leg.; station KM60; platform with seagrass and mangrove; MNHN-IM-2013-55235 • 1 spec. (8/5 mm [6102]); same collection data as for preceding; MNHN-IM-2013-55239.

PHILIPPINES – **Luzon** • 1 spec. (10/9 mm [3198]); Batangas, Calantagan; 13°55.319′ N, 120°37.260′ E; 7 Jul. 2014; station 183; open forest with mix of *Avicennia* and *Rhizophora*, sandy and muddy areas; PNM 041242 • 2 specs (13/10 mm [3224] and 11/7 mm [3225]); Batangas, Calantagan; 13°53.278′ N, 120°37.124′ E; 8 Jul. 2014; station 184; very narrow forest on the shore, mixed *Avicennia* and young *Rhizophora*; PNM 041243. – **Bohol** • 2 specs (19/14 mm [3281] and 15/8 mm [3280]); Maribojoc; 09°43.806′ N, 123°51.234′ E; 15 Jul. 2014; station 192; pier at the beginning of Sabima boardwalk; PNM 041244 • 1 spec. (22/14 mm [3367]); Mabini; 09°51.402′ N, 124°30.982′ E; 18 Jul. 2014; station 195; narrow *Rhizophora* and *Avicennia* mangrove by the sea with fish ponds built on landward side, cement ditches between the mangrove patches and the ponds; PNM 041246 • 1 spec. (22/12 mm [3428]); Maribojoc; 09°44.280′ N, 123°49.389′ E; 20 Jul. 2014; station 202; uplifted, dead coral flat covered with sand and algae, near *Sonneratia* trees; PNM 041248.

SINGAPORE • 1 spec. (14/11 mm [1000]); Mandai; 01°26.237′ N, 103°45.730′ E; 1 Apr. 2010; station 6; followed river in the mangrove from railroad towards sea; ZRC.MOL.10476 • 1 spec. mm (12/8 [997]); Semakao Island; 01°12.083′ N, 103°45.585′ E; 3 Apr. 2010; station 8; artificial landfill island with low and very dense newly-planted *Rhizophora* trees, muddy areas in between *Rhizophora* patches and coral rubble close to the shore; ZRC.MOL.10477.

VIETNAM • 2 specs (18/13 mm [5668] and 14/11 mm [5613]); Can Gio mangrove forest; 10°24.157′ N, 106°53.950′ E; 19 Jul. 2015; station 233; rocks and gravel on side of *Avicennia* and *Rhizophora* mangrove; ITBZC IM 00016.

Description

   Color and morphology of live animals (Fig. 31)
The dorsal notum of live animals may be covered by dry mud (especially when found underneath logs and rocks). The notum is bumpy with prominent, distinctly-raised papillae (with or without dorsal eyes). Individuals are flattened but often become almost hemispherical when disturbed. The dorsal color is typically brown, dark brown or nearly black, and occasionally yellowish-brown. The hyponotum color varies greatly: it may be dark blue, medium grey, white or variants in between. Papillae with dorsal eyes are present, many of which are distinctly raised. The exact number of papillae bearing dorsal eyes is difficult to determine as papillae may be retracted, but is usually between 10 and 22, although up to 35 dorsal eyes have been observed. Papillae bear only one dorsal eye. Dorsal eyes may be distributed across the entire notum or only in the middle but are absent from the margin (eyes are never <2 mm from the notum edge).

Fig. 31. *Platevindex luteus* (Semper, 1880), live animals. **A**. Dorsal view, 28 mm long [2837], Indonesia, Ambon (UMIZ 00089). **B**. Dorsal view, 17 mm long [2880], Indonesia, Seram (UMIZ 00090). **C**. Dorsal view, 14 mm long [5613], Vietnam, Can Gio (ITBZC IM 00016). **D**. Dorsal view, 18 mm long [3040], Indonesia, Bali (UMIZ 00095). **E**. Dorsal view, 22 mm long [3367], Philippines, Bohol (PNM 041246). **F**. Dorsal view, 15 mm long [3280], Philippines, Bohol (PNM 041244). **G**. Ventral view, 19 mm long [3281], Philippines, Bohol (PNM 041244). **H**. Ventral view, same as A. **I**. Ventral view, 17 mm long [5939], Indonesia, Timor. **J**. Ventral view, 17 mm long [5041], Indonesia, Halmahera (UMIZ 00099).

Digestive system (Figs 1B, 1D, 2E, 32, 33A–E)
Radulae measure up to 3.7 mm in length. Examples of radular formulae are presented in Table 5. The intestinal loops are of type I, with a transitional loop oriented between 3 and 6 o'clock, and of type II, with a transitional loop oriented between 6 and 8 o'clock (Figs 1B, 1D, 2E, 32).

Reproductive system (Figs 33F, 34)
In the posterior part of the reproductive system, the oviduct is approximately twice as wide as the deferent duct. Its distal section (distal to the spermatheca) is shorter or equal to its proximal section. The deferent duct is not attached or only loosely attached to the oviduct, and generally loosely coiled (not with many tight, U-shaped loops), but individuals with a highly-coiled deferent duct exceptionally do exist. The position of the female pore varies from very close to the anus (< 1 mm) up to 3 mm away from the anus. The flexible region of the penis with hooks is approximately 1 to 1.5 mm long. Penial hooks are large, approximately 45 to 90 µm long, but between 20 to 60 µm long in smaller individuals from Mauritius. The penial hooks can be seen inside the semi-transparent penis. The posterior retractor muscle inserts near the heart on the right side of the visceral cavity. Its length varies from being half the length of the penial sheath to three times as long. The deferent duct is not particularly long or convoluted, displaying only a few loose loops (it is even less convoluted in immature specimens).

Distinctive diagnostic features (Table 4)

The yellow foot of *Platevindex luteus* easily distinguishes it from *P. martensi* (black foot) and *P. aptei* sp. nov. (orange foot). However, its hyponotum color is highly variable and does not help distinguish it from other species of *Platevindex* with a blue or grey hyponotum (e.g., *P. coriaceus*, *P. burnupi*
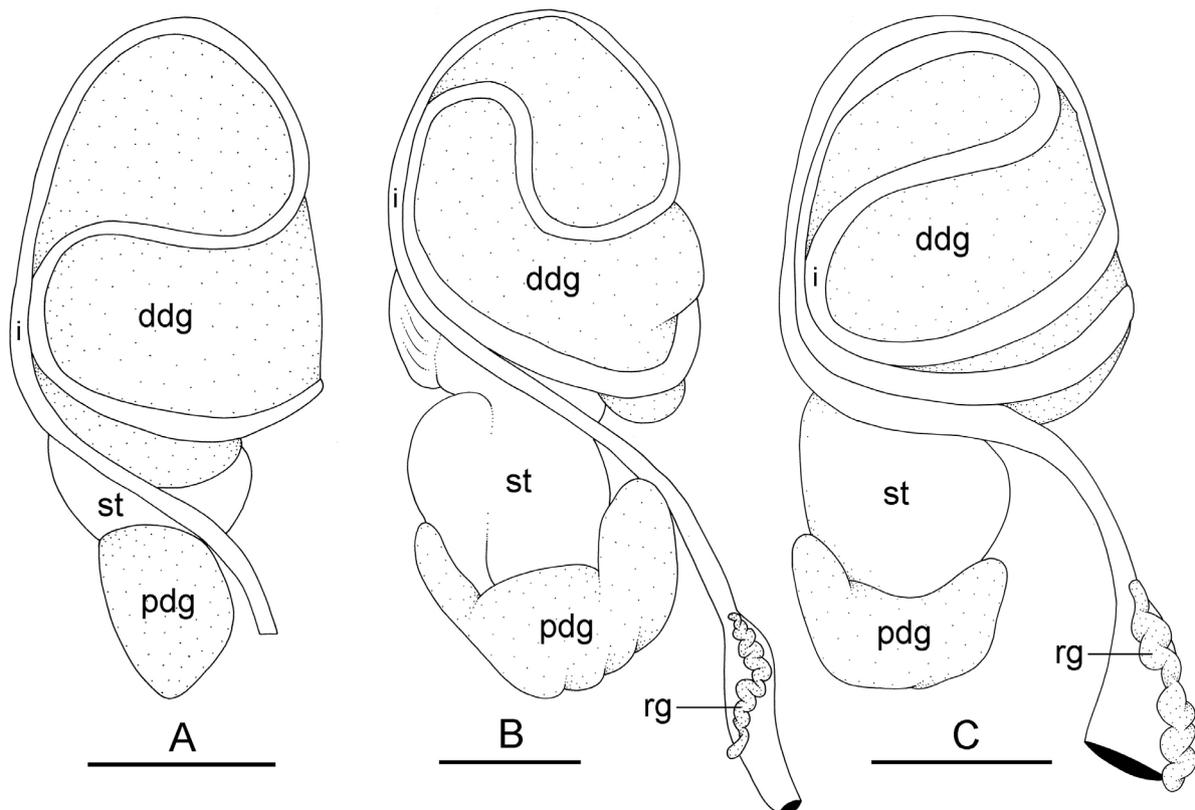
Fig. 32. *Platevindex luteus* (Semper, 1880), digestive system, dorsal view. **A**. Type I, with a transitional loop oriented at 3 o'clock, Vietnam [5613] (ITBZC IM 00016). **B**. Type I (or type II), with a transitional loop oriented at 6 o'clock, Ambon, Indonesia [2837] (UMIZ 00089). **C**. Type II, with a transitional loop oriented at 8 o'clock, Bohol, Philippines [3367] (PNM 041246). Scale bars = 3 mm.

and *P. applanatus*). Live individuals can be more hemispherical (especially when contracted) than in other species, but flattened individuals can easily be mistaken for small individuals of other species of *Platevindex*. *Platevindex luteus* reaches a smaller maximum size than other species with a similar ventral color, but the size range of all these species overlaps and cannot be used for identification. Finally, the notum of *P. luteus* bears prominent dorsal papillae, which are especially obvious when the animal is contracted, but these dorsal papillae are also present in *P. applanatus* and are thus not strictly diagnostic of *P. luteus*. The notum of *P. burnupi* is granular (i.e., not smooth), but does not bear prominent papillae, whether animals are disturbed or not.
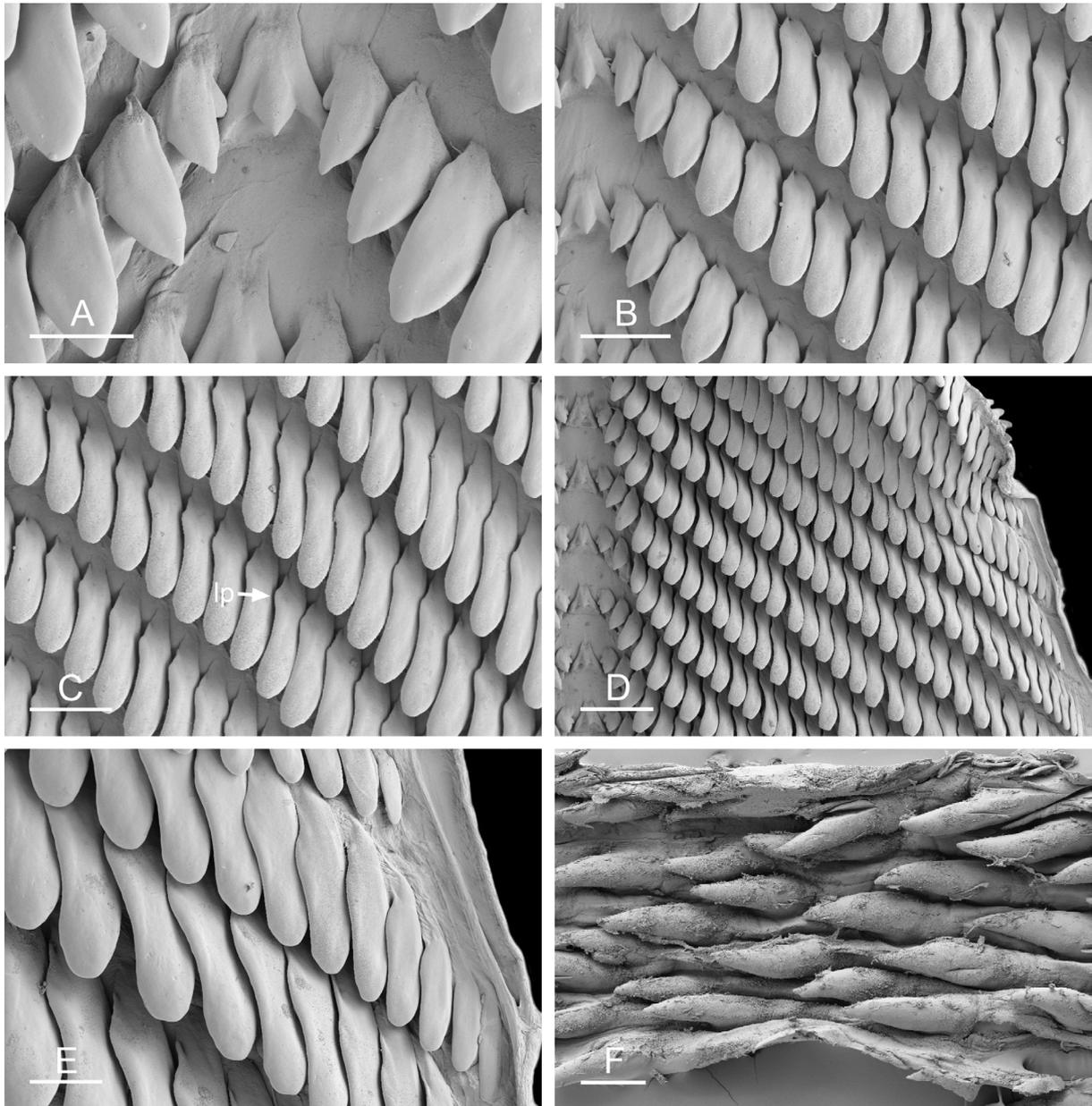
Fig. 33. *Platevindex luteus* (Semper, 1880). **A–E**. Radula. A. Rachidian and innermost lateral teeth, Philippines, Bohol [3367] (PNM 041246). B. Lateral teeth with rachidian teeth, same as A. C. Lateral teeth, same as A. D. Outermost lateral teeth, Indonesia, Ambon [2837] (UMIZ 00089). E. Outermost lateral teeth, same as D. **F**. Penial hooks, same specimen as D. Abbreviation: lp = lateral protuberance. Scale bars: A, E–F= 30 μm; B–C = 50 μm; D = 100 μm.

Internally, intestinal loops help to distinguish *P. luteus* from *P. applanatus*, *P. amboinae* and *P. latus* (Table 4). The latter two species share intestinal loops of type III, while the intestine of *P. luteus* is of type I or II. Further, even though the intestinal loops of *P. applanatus* are also of type I, their transitional loop is oriented between 1 and 2 o'clock, while the transitional loop of individuals of *P. luteus* with a type I is oriented between 3 and 6 o'clock. *Platevindex* slugs with similar intestinal loops of type II can be distinguished by other means, especially the length of the region of the penis with penial hooks: *P. luteus* (approximately 1 mm), *P. coriaceus* (2–8 mm), *P. martensi* (2–2.5 mm) and *P. aptei* sp. nov. (2.5–5 mm). Note that *P. amboinae* and *P. latus*, which both completely lack penial hooks, also differ from *P. luteus* in that respect. In the posterior reproductive system, the deferent duct is short, usually loosely coiled and only loosely attached to the oviduct, which helps to differentiate *P. luteus* from *P. coriaceus* and *P. tigrinus*, in which the deferent duct is tightly coiled and attached to the oviduct. The insertion of the retractor muscle of the penis near the heart in *P. luteus* also clearly distinguishes it from *P. coriaceus* and *P. aptei* sp. nov., in which it inserts at the posterior end of the visceral cavity.

Finally, individuals of *P. luteus* with intestinal loops of type I can also be distinguished from *P. burnupi* (intestinal loops of type II) but individuals of *P. luteus* with intestinal loops of type II cannot. However, *P. burnupi* and *P. luteus* do not overlap geographically, and can be reliably distinguished using both mitochondrial and nuclear DNA sequences.
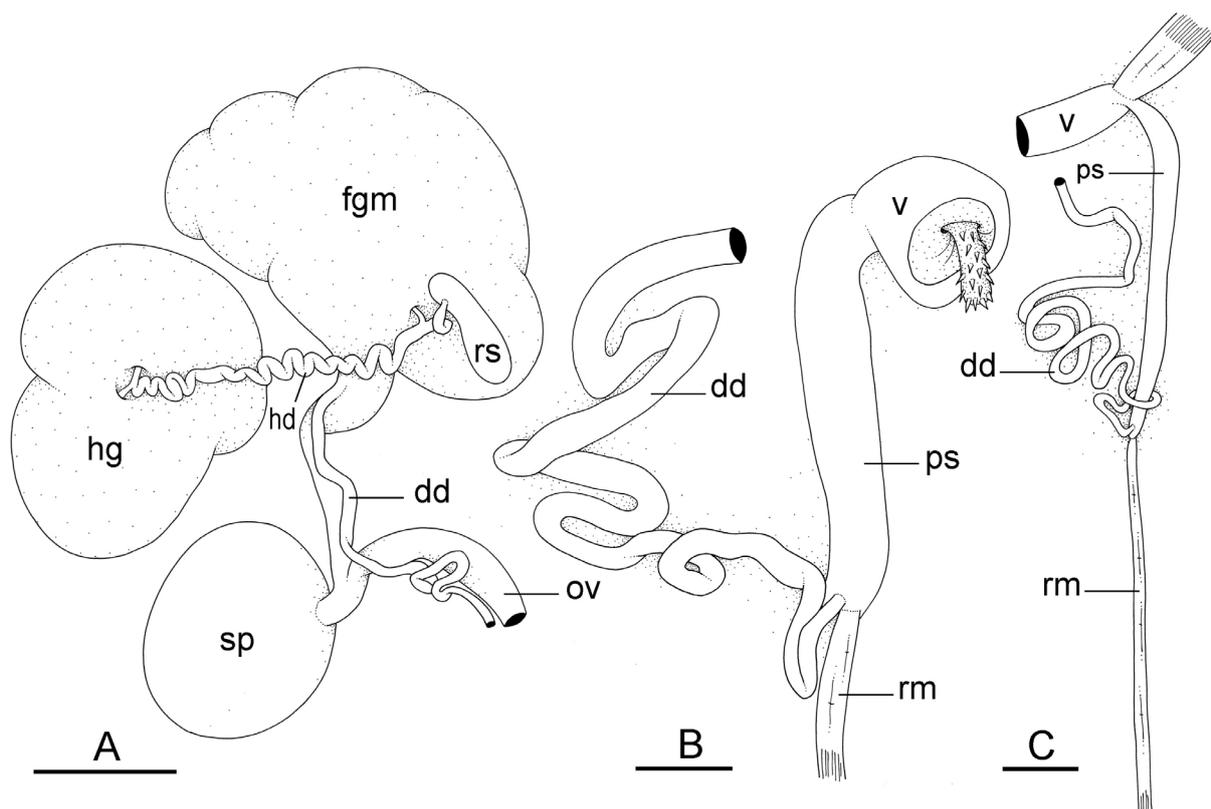
Fig. 34. *Platevindex luteus* (Semper, 1880), reproductive system. **A**. Posterior reproductive system, Ambon, Indonesia [2837] (UMIZ 00089). **B**. Anterior, male copulatory apparatus (ZMB/Moll 39031a). **C**. Anterior, male copulatory apparatus, same as A. Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; ps = penial sheath; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; v = vestibule. Scale bars: A = 2 mm; B–C = 1 mm.

Distribution (Fig. 10A)

Australia: Queensland. Brunei. Indonesia: Ambon, Bali, Halmahera, Kei Islands, Lombok, Seram, Sulawesi, Sumatra, Ternate and Timor. Papua New Guinea: New Britain (type locality of *O. schneideri*), New Ireland and Madang. Philippines: Bohol and Luzon. Singapore (type locality of *O. luteum* and newly-collected material). Vietnam. All records are new, except for the type localities.

Habitat (Fig. 31)

Platevindex luteus is found both within mangroves and at mangrove margins. It is typically found on dead logs or tree trunks and, occasionally, on tree roots or under the loose bark of dead logs. In Timor, some individuals were found on pieces of wood and other plant material, but also on very dark mud (individuals were found directly on mud nowhere else).

Remarks

The publication dates of the different sections of Semper's *Landmollusken* in the *Reisen im Archipel der Philippinen* series were clarified by Johnson (1969). Because *Onchidium luteum* was published before 1931, ICZN Article 12.2.7 applies: *Onchidium luteum* was made available in 1880 because Semper's figures (pl. 20, fig. 10, pl. 23, figs 2, 6) are regarded as an indication accompanying it, although the text of the description was not published until 1882.

The species treated here is common and broadly distributed in the Indo-West Pacific, and so many original descriptions had to be reviewed and many type specimens examined in order to determine which existing names apply to it. The lectotype of *Onchidium luteum* displays all the distinctive characteristics of a species of *Platevindex*: flattened shape, narrow foot and no accessory penial gland. Also, its male opening is slightly to the right of the midline between the oral tentacles, which agrees with Semper's (1882: 275) description and is perfectly compatible with *Platevindex*. Two main features indicate that the lectotype of *O. luteum* belongs to the species described here: the dorsal papillae on its notum as well as its penial anatomy, which is identical to what was observed in fresh material (Fig. 31C). Based on their dorsal notum (which also bears dorsal papillae) and Semper's description (1882: 275) of the internal anatomy, it is very likely that the paralectotypes also are part of the species described here. In particular, Semper described a short penis with a distal, flexible, hook-bearing region scarcely 1 mm long and a retractor muscle that inserts by the heart. Semper also described 16–25 dorsal eyes and noted that the dorsal eyes never reach the edge of the dorsal notum, which is in agreement with our observations and with all species of *Platevindex* in clade C (see Fig. 4).

Semper (1882) did not mention or illustrate the type of intestinal loops in the original description of *Onchidium luteum*, and it could not be checked for the present study because the intestine of the lectotype is not well preserved (and that of the paralectotypes could not be checked either). However, Plate (1893: 181) examined two of the former syntypes and indicated that intestinal loops are of type II, which is compatible with our observations on freshly-collected samples from Singapore.

The intraspecific variation in the type of intestinal loops observed in *Platevindex luteus* (type I, type II and intermediary between types I and II) is very unusual. Nearly all onchidiid species are characterized by only one type of intestinal loops. Another known exception is *Alionchis jailoloensis* characterized by intestinal loops of both types II and III (Goulding *et al.* 2018a; Dayrat *et al.* 2019c). The dissection of individuals for which the species identification was confirmed through DNA sequences allowed us to determine that intestinal types vary between individuals of *P. luteus* even at the exact same localities.

Platevindex schneideri was described by Hoffmann (1932: 135–137), as *Oncis schneideri*, from New Britain, Papua New Guinea, as a flat animal with a rectal gland, no accessory penial gland and a male pore to the left of the right eye tentacle. Combined, these features indicate that Hoffmann was correct in

Fig. 35. Habitats of *Platevindex luteus* (Semper, 1880). **A**. Philippines, Bohol, narrow mangrove on the edge of fish ponds, tall *Rhizophora* and *Avicennia*, many dead logs (station 194). **B**. Indonesia, Seram, palms and *Acrostichum* ferns behind a *Sonneratia* mangrove (station 136). **C**. Vietnam, Can Gio mangrove forest, *Avicennia* and *Rhizophora* with rocks and gravel on side of mangrove (station 233). **D**. Australia, Queensland, mangrove by creek with sandy mud (station 104). **E**. Singapore, Semakao Island, landfill island with newly planted mangrove, very dense (station 8). **F**. Indonesia, Kei Islands, very soft mud with some older trees and some replanted (station 142).

describing the species in Plate's genus *Oncis* (now *Platevindex*). Hoffmann (1932: 135) also described strong dorsal papillae (which he called 'Tuberkeln', or tubercles), a characteristic of *P. luteus*. The male parts of the holotype, now missing, were described and illustrated by Hoffmann (1932: 136), and the insertion of the retractor muscle at the level of the pericardium is compatible with *P. luteus*. The intestinal loops were described as of type II, which is compatible with the variation observed in *P. luteus*, but not with the sympatric species *P. applanatus* (in which intestinal loops are only of type I). For all the reasons above, *Platevindex schneideri* is regarded as a junior synonym of *P. luteus*.

Hoffmann (1932: 136) suggested that *Platevindex schneideri* might be a synonym of *P. amboinae* or *P. granulosa* (all as species of *Oncis*), but *P. granulosa* is a nomen dubium (see our species remarks on *P. latus*). However, since Hoffmann (1928: 36) considered *Platevindex latus* a synonym of *P. granulosa*, we can consider his comments on *P. schneideri* (Hoffmann 1932: 136) refer, in his mind, to *P. amboinae* and *P. latus*. Hoffmann's (1932: 136) description of *P. schneideri* includes penial hooks, which are not found in either *P. amboinae* or *P. latus* (Table 4). Hoffmann did not describe the dorsal eyes on the back of *O. schneideri*, but there are at least 18 eyes (one eye per papilla) on the dorsal notum of the holotype. The presence of dorsal eyes also precludes *P. schneideri* from being a synonym of *P. amboinae* or *P. latus*, which both lack dorsal eyes (Table 4).

Hoffmann (1932: 135) noted a similarity between *Platevindex schneideri* and *P. semperi* (Plate, 1893), but concluded that they could not refer to the same species because their intestinal loops differed (type II in the holotype of *P. schneideri* and type I in *P. semperi* according to Plate's original description). However, as mentioned above, *P. luteus* is an exception regarding intestinal loops, and both *P. schneideri* and *P. semperi* are compatible with the intraspecific variation in intestinal loops within *P. luteus*.

Plate's (1893) description of *Oncis semperi*, based on two syntypes (22/18 and 22/18 mm) from Mindanao (ZMB/Moll 45661), is only compatible with *P. coriaceus*, and *Platevindex semperi* is thus regarded as a junior synonym of *P. coriaceus*. The description of intestinal loops of type I suggests that one of the two syntypes could belong to *P. luteus* instead of *P. coriaceus*, but this is most likely simply a mistake (see our remarks on *P. coriaceus*).

Britton (1984) described *Platevindex mortoni* from Hong Kong based on four specimens with different intestinal types: two specimens (including the holotype) with intestinal loops of type I, one with intestinal loops of type II and one with intestinal loops of an intermediate type between types I and II. Only the latter could be checked here because the digestive system is missing in all other types (see our remarks on *P. tigrinus* for a detailed description of the type material of *P. mortoni*). If Britton was correct that the intestinal loops of the holotype of *P. mortoni* were of type I, then *P. mortoni* would be incompatible with *P. tigrinus*, *P. coriaceus* or *P. martensi* (which are all characterized by a digestive system of type II), and the holotype of *P. mortoni* could be part of *P. luteus*. However, it is unclear whether Britton's description of the intestinal loops of the holotype is correct (see our remarks on *P. tigrinus* for additional discussion of the status of *P. mortoni*). Also, *P. luteus* is not represented in the genetic sequences published by Sun *et al*. (2014) or other sequences available in GenBank from China. If *P. luteus* is later found in Hong Kong, then the name *P. mortoni* could be discussed as a possible synonym of *P. luteus*. For now, however, *P. mortoni* is regarded as a nomen dubium.

Von Martens (1897: 127) indicated that *Onchidium luteum* was found in "Celebes Djenemaedja bei Luwu" [Djenemaedja by Luwu, Sulawesi, Indonesia] by M. Weber, but did not provide any details with respect to identification. Hoffmann (1928: 89–90) noted that it was impossible to determine whether the specimens von Martens examined from Sulawesi were *O. luteum*, since only the external appearance was described.

In a study focusing on the relative abundance of onchidiids across a Malaysian mangrove forest, Sabri & Singh (2018) mentioned *P. luteus* from Selangor, western Peninsular Malaysia. Based on the small picture provided and the absence of any additional details regarding ventral coloration, anatomy or DNA sequences, it is unclear whether this identification is correct. We did not find *P. luteus* at any of the localities we visited in western Peninsular Malaysia. Thus, the presence of *P. luteus* in Selangor is regarded here as hypothetical.

Platevindex luteus is not a new combination because it was already used in our recent studies (Dayrat 2009: 5; Goulding *et al.* 2018a, 2018b, 2018c; Dayrat *et al.* 2019a, 2019b, 2019c, 2019d), even though the classification in *Platevindex* is demonstrated here for the first time. Note that Stantschinsky (1907: 395) and Hoffmann (1928: 89) had already moved *Onchidium luteus* to Plate's genus *Oncis*, based on information from the original description (Semper 1882).

Platevindex applanatus (Simroth, 1920) comb. nov.
Figs 36–45

Onchidium applanatum Simroth, 1920: 294, pl. 20, figs 40–42.

Material examined

Holotype
INDONESIA • holotype (15/12 mm), by monotypy; Aru Inseln, Strand von Manumbai, Kobroor [Manumbai Beach, Kobroor Island, Aru Islands, Moluccas, Indonesia]; 13 Mar. 1908; H. Merton leg.; ZMB/Moll 104630.

Notes on type material
The notum of the holotype was cut open for the present study to check internal characters; all organs remain in the specimen.

Other material
INDONESIA – **Ambon** • 1 spec. (15/12 [2736] mm); Pulau Haruku; 03°36.520′ S, 128°25.068′ E; 11 Feb. 2014; station 127; dead log high on beach above rocky *Sonneratia* mangrove; UMIZ 00100 • 4 specs (22/15 [2754], 18/14 [2755], 18/14 [2757] and 15/12 [2750] mm); Passo; 03°37.080′ S, 128°16.068′ E; 13 Feb. 2014; station 129; logs on rocky beach with coral rubble; UMIZ 00101. – **Seram** • 2 specs (24/20 [2877] and 17/11 [2880] mm); Piru; 03°04.072′ S, 128°11.362′ E; 19 Feb. 2014; station 136; beach of palms and *Acrostichum* ferns behind *Sonneratia* mangrove; UMIZ 00090. – **Kei Islands** • 6 specs (21/14 [2892], 17/11 [3563], 16/10 [2893], 16/10 [2895], 13/6 [2894] and 12/9 [2900] mm); Un; 05°38.273′ S, 132°45.738′ E; 23 Feb. 2014; station 137; *Bruguiera* and *Rhizophora* mangrove with coral rubble and thin layer of mud; UMIZ 00102 • 1 spec. (15/9 [2904] mm); Un; 05°38.273′ S, 132°45.738′ E; 25 Feb. 2015; station 140; back of mangrove with rocks, mud, dead logs, and leaf litter; UMIZ 00103 • 1 spec. (5/4 [2925] mm); Fiditan; 05°35.957′ S, 132°45.112′ E; 28 Feb. 2014; station 144; rocks with mat of algae behind dense *Rhizophora* mangrove; UMIZ 00104. – **Sulawesi** • 1 spec. (17/11 [2160] mm); Bahoi; 01°43.355′ N, 125°01.232′ E; 10 Mar. 2013; station 85; sand, rocks and pieces of wood outside a mangrove; UMIZ 00083.

MAURITIUS • 1 spec. (7/4 [3604] mm); Pointe Maurice; 20°15.447′ S, 57°47.670′ E; 8 Jun. 2014; station 174; *Rhizophora* mangrove with very dark mud, slug under piece of wood; MNHN-IM-2019-1392 • 1 spec. (9/7 [3152] mm); Mahebourg; 20°25.059′ S, 57°42.680′ E; 10 Jun. 2014; station 176; mangrove with dark brown mud, slugs on rotting petiole of palm frond; MNHN-IM-2019-1393 • 1 spec. (7/5 [3442] mm); same collection data as for preceding; MNHN-IM-2019-1394.
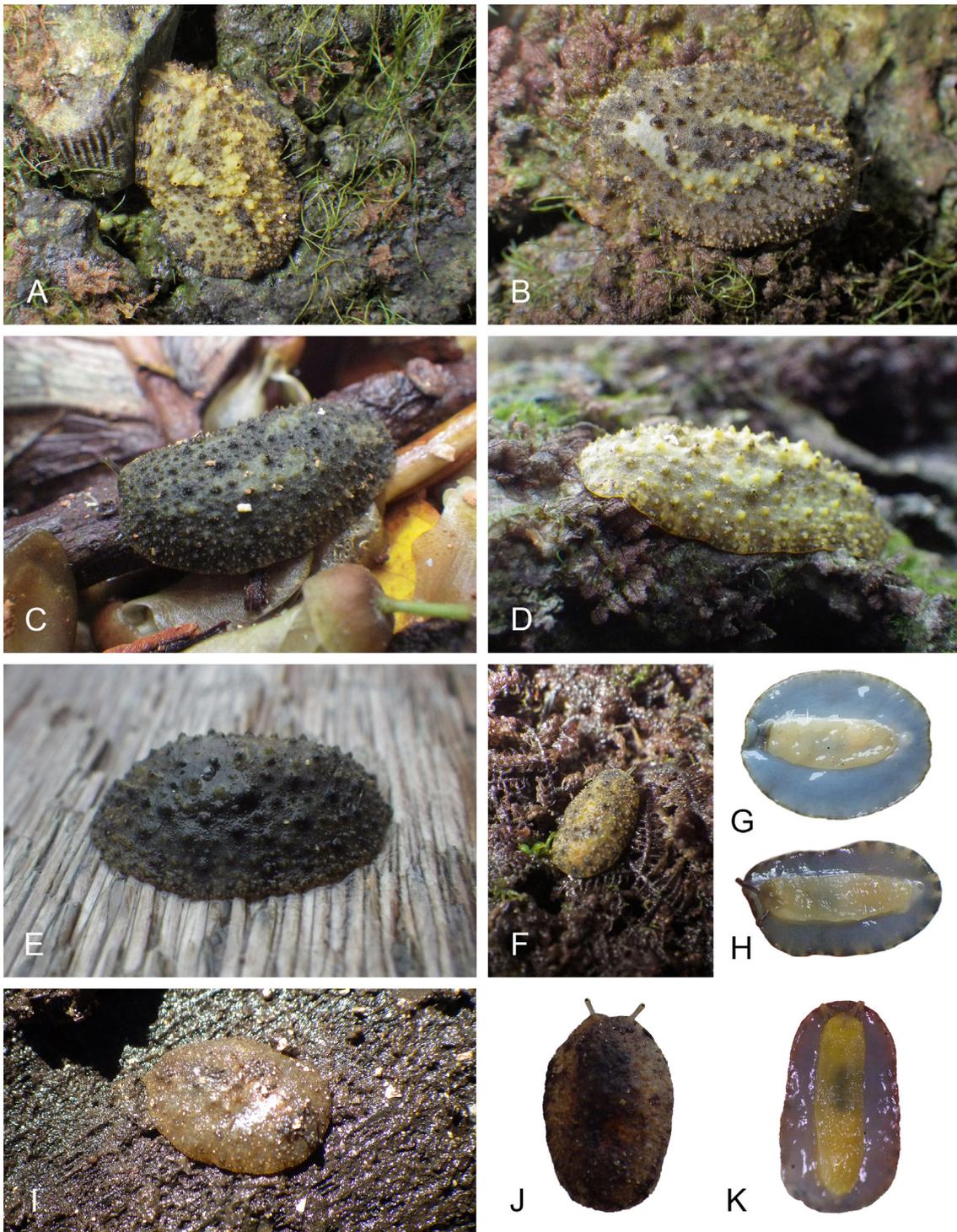
Fig. 36. *Platevindex applanatus* (Simroth, 1920) comb. nov., live animals. **A**. Dorsal view, 16 mm long [2893], Indonesia, Kei Islands (UMIZ 00102). **B**. Dorsal view, 16 mm long [2895], Indonesia, Kei Islands (UMIZ 00102). **C**. Dorsal view, 15 mm long [2904], Indonesia, Kei Islands (UMIZ 00103). **D**. Dorsal view, 16 mm long [3563], Indonesia, Kei Islands (UMIZ 00102). **E**. Dorsal view, 18 mm long [2757], Indonesia, Ambon (UMIZ 00101). **F**. Dorsal view, 5 mm long [2925], Indonesia, Kei Islands (UMIZ 00104). **G**. Ventral view, same as E. **H**. Ventral view, 12 mm long [2900], Indonesia, Kei Islands (UMIZ 00102). **I**. Dorsal view, 9 mm long [3152], Mauritius (MNHN-IM-2019-1393). **J**. Same as I. **K**. Ventral view, same as I.

PAPUA NEW GUINEA – **Madang** • 1 spec. (14/11 [5437] mm); South Dumduman Island; 05°00.2′ S, 145°47.6′ E; 9 Nov. 2012; MNHN expedition Papua Niugini leg.; station PM12; limestone rocky intertidal; MNHN-IM-2013-12493 • 1 spec. (16/16 [5424] mm); Hargun Island; 05°01.6′ S, 145°47.9′ E; 15, 20 Nov. 2012; MNHN expedition Papua Niugini leg.; station PM24; night tide; MNHN-IM-2013-14043 • 1 spec. (13/11 [5450] mm); same collection data as for preceding; MNHN-IM-2013-14051 • 1 spec. (18/15 [5420] mm); same collection data as for preceding; MNHN-IM-2013-13765 • 1 spec. (13/11 [5457] mm); Wonad Island; 05°08.1′ S, 145°49.3′ E; 27 Nov. 2012, 9 Dec. 2012; MNHN expedition Papua Niugini leg.; station PM41; sandy beach and intertidal rocks; MNHN-IM-2013-15867 • 1 spec. (13/10 [5462] mm); Tab Island; 05°10.2′ S, 145°50.4′ E; 28 Nov. 2012; MNHN expedition Papua Niugini leg.; station PM42; night tide, sandy beach and intertidal rocks; MNHN-IM-2013-15908. – **New Ireland** • 1 spec. (7/4 [6094] mm); Povalval, E coast of New Ireland; 02°41′ S, 150°57′ E; 11–13 Jun. 2014; MNHN expedition Kavieng 2014 leg.; station KM05; mixed hard platform and seagrass bed at outlet of rivulet; MNHN-IM-2013-53534 • 1 spec. (8/6 [6096] mm); Cape Jesehke, Manne Island; 02°43.1′ S, 150°37.8′ E; 15, 26 Jun. 2014; MNHN expedition Kavieng 2014 leg.; station KM32; *Rhizophora* mangrove; MNHN-IM-2013-54161 • 1 spec. (10/7 [6097] mm); same collection data as for preceding; MNHN-IM-2013-54163 • 1 spec. (8/6 [6098] mm); same collection data as for preceding; MNHN-IM-2013-54164.

VANUATU • 1 spec. (12/11 [5491] mm); Santo Rose Point; 15°34.9′ S, 167°02.4′ E; 10 Sep. 2006; MNHN expedition Santo 2006 leg.; station VM02; intertidal, coral sand; MNHN-IM-2013-62402 • 1 spec. (9/8 [5493] mm); same collection data as for preceding; MNHN-IM-2013-62404.
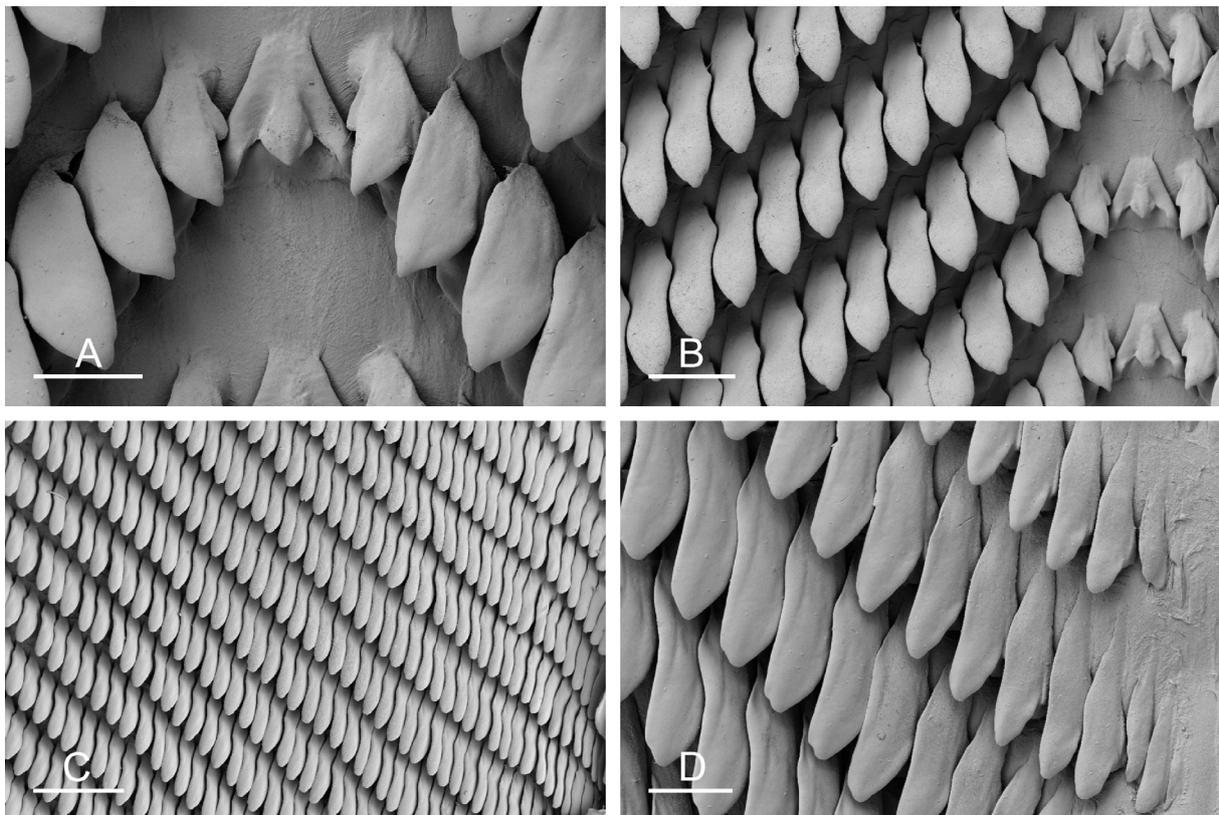
Fig. 37. *Platevindex applanatus* (Simroth, 1920) comb. nov., radula, Indonesia, Ambon. **A**. Rachidian and innermost lateral teeth [2754] (UMIZ 00101). **B**. lateral teeth with rachidian teeth, same as A. **C**. Lateral teeth [2755] (UMIZ 00101). **D**. Outermost lateral teeth, same as A. Scale bars: A, D = 30 μm; B = 50 μm; C = 100 μm.

Description

Color and morphology of live animals (Fig. 36)

Live animals are not covered with mud and their natural color can be seen without washing. The notum is bumpy with prominent, distinctly-raised papillae (with or without dorsal eyes). Live animals may become nearly hemispherical when disturbed. The dorsal color is variable although it is typically brown with yellow longitudinal (irregular) lines. Slugs with an entirely dark brown notum or a light beige notum also occur. The hyponotum is light grey and almost translucent in small specimens. The margin of the hyponotum is frequently translucent with the brown color of the notum showing through. The foot is light yellow.

Papillae with dorsal eyes are present. Their exact number is difficult to determine, as they are often retracted, but ranges approximately from 4 to 26, except in the case of very small specimens, in which as few as 2 dorsal eyes have been observed. Each papilla bears one dorsal eye. Dorsal eyes may be distributed across the notum or only present in the middle but are always absent on the margin (i.e., eyes are never <2 mm from the notum edge).

Digestive system (Figs 1C, 37–40)

Radulae measure up to 4.3 mm in length. Examples of radular formulae are presented in Table 5. Due to the high genetic divergence (in COI sequences) between populations of *P. applanatus*, radulae are figured from Indonesia, Mauritius and Papua New Guinea (Figs 37–39). Intestinal loops are of type I, with a transitional loop oriented between 1 and 2 o'clock (Figs 1C, 40A–C).
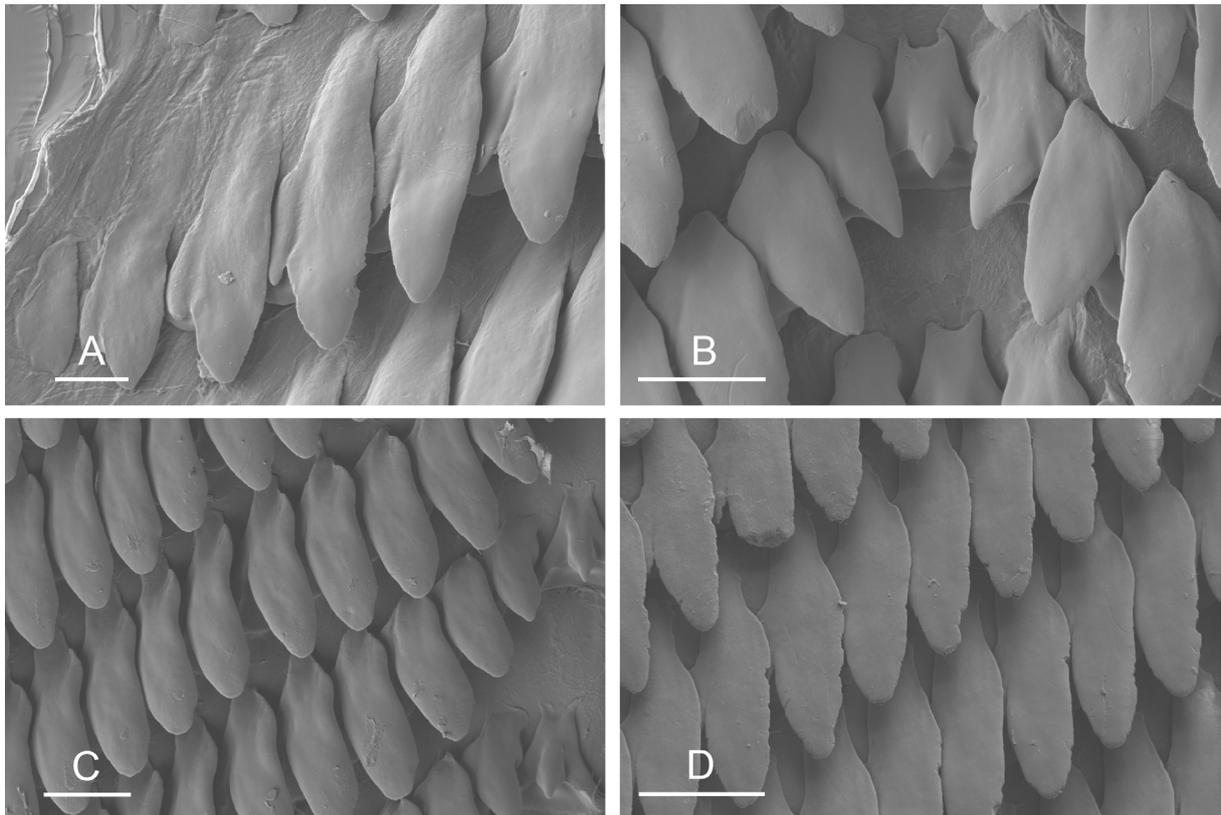
Fig. 38. *Platevindex applanatus* (Simroth, 1920) comb. nov., radula, Mauritius. **A**. Left, outermost, lateral teeth [3604] (MNHN-IM-2019-1392). **B**. Rachidian tooth and innermost lateral teeth, same as A. **C**. Rachidian tooth and left, innermost lateral teeth [3152] (MNHN-IM-2019-1393). **D**. Right, lateral teeth [3442] (MNHN-IM-2019-1394). Scale bars: A = 10 μm; B–D = 20 μm.

Reproductive system (Figs 41–44)

In the posterior part of the reproductive system, the oviduct is wider than the deferent duct (up to twice as wide). Its distal section (distal to the spermatheca) is slightly longer than its proximal section (up to two or three times as wide) or equal to it in length. The deferent duct is longer than the oviduct, loosely attached to it, and varies from slightly convoluted with a few loose loops to tightly coiled with U-shaped loops (Fig. 41). The position of the female pore varies from being adjacent to the anus to 4 mm away from it in large specimens. The flexible, distal region of the penis with hooks measures approximately 1.5 to 3 mm in length. In eastern Indonesia, the distal region is 2 to 3 mm long, while in Mauritius and Papua New Guinea it is approximately 1.5 to 2 mm long. The penial hooks are large and can be seen inside the semi-transparent penis. They are usually 45 to 90 µm long (Figs 43, 44A), but between 20 to 60 µm in smaller specimens from Mauritius (Fig. 44B–C). The insertion of the penial retractor muscle varies. It inserts at the posterior end of the visceral cavity in specimens from eastern Indonesia, except in a few specimens in which it inserts approximately ⅔ down the length of the visceral cavity. It inserts approximately halfway to ⅔ down the length of the visceral cavity in specimens from Papua New Guinea (and near the posterior end of the visceral cavity in one specimen). In Mauritius, it inserts at the posterior end of the visceral cavity in the largest specimen, and by the heart halfway down the visceral cavity in a smaller specimen. The length of the retractor muscle varies from much shorter than the penial sheath ($^1/_5$ to $^1/_3$ of its length) to as long as the penial sheath. The deferent duct is not particularly long and is only loosely convoluted (Fig. 42). It may even be nearly straight in immature specimens (Fig. 42C).
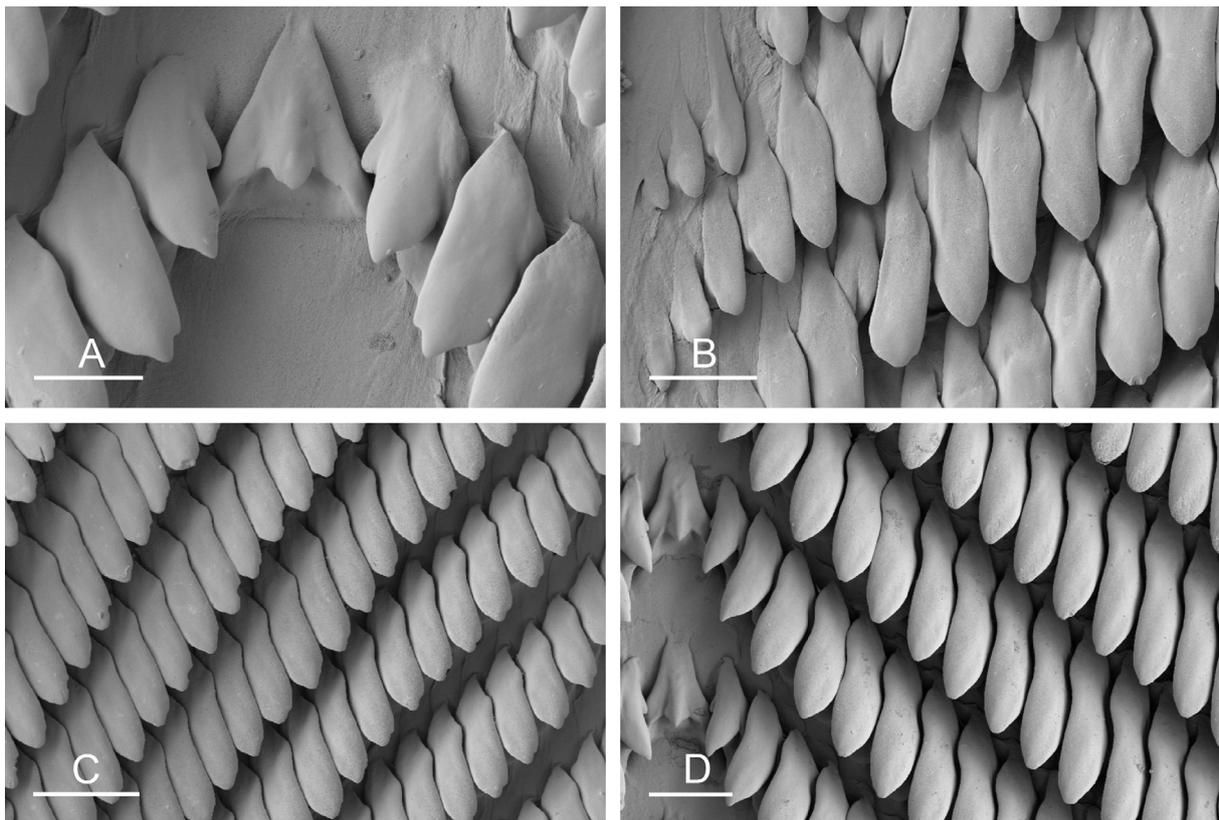
Fig. 39. *Platevindex applanatus* (Simroth, 1920) comb. nov., radula, Papua New Guinea. **A**. Rachidian and innermost lateral teeth [5450] (MNHN-IM-2013-14051). **B**. Outer lateral teeth, same as A. **C**. Inner lateral teeth, same as A. **D**. Rachidian and innermost lateral teeth [5424] (MNHN-IM-2013-14043). Scale bars: A = 20 µm; B, D = 30 µm; C = 50 µm.

Distinctive diagnostic features (Table 4)

Externally, *Platevindex applanatus* can be easily distinguished from *P. martensi* and *P. aptei* sp. nov. by the light yellow color of its foot. The presence of prominent dorsal papillae helps to distinguish *P. applanatus* from other species of *Platevindex*, except *P. luteus*, which is characterized by similar prominent dorsal papillae. The dorsal coloration of *Platevindex applanatus* is much more variable than in other species of *Platevindex*, and this variation prevents reliable separation from *P. luteus*. However, the dorsal notum of *P. applanatus* is frequently marked by bright yellowish-green markings or bands, which were very rarely observed in *P. luteus*. Individuals of *P. applanatus* also reach a smaller maximum size than individuals of *P. martensi* and *P. amboinae*, two species that are sympatric in eastern Indonesia,
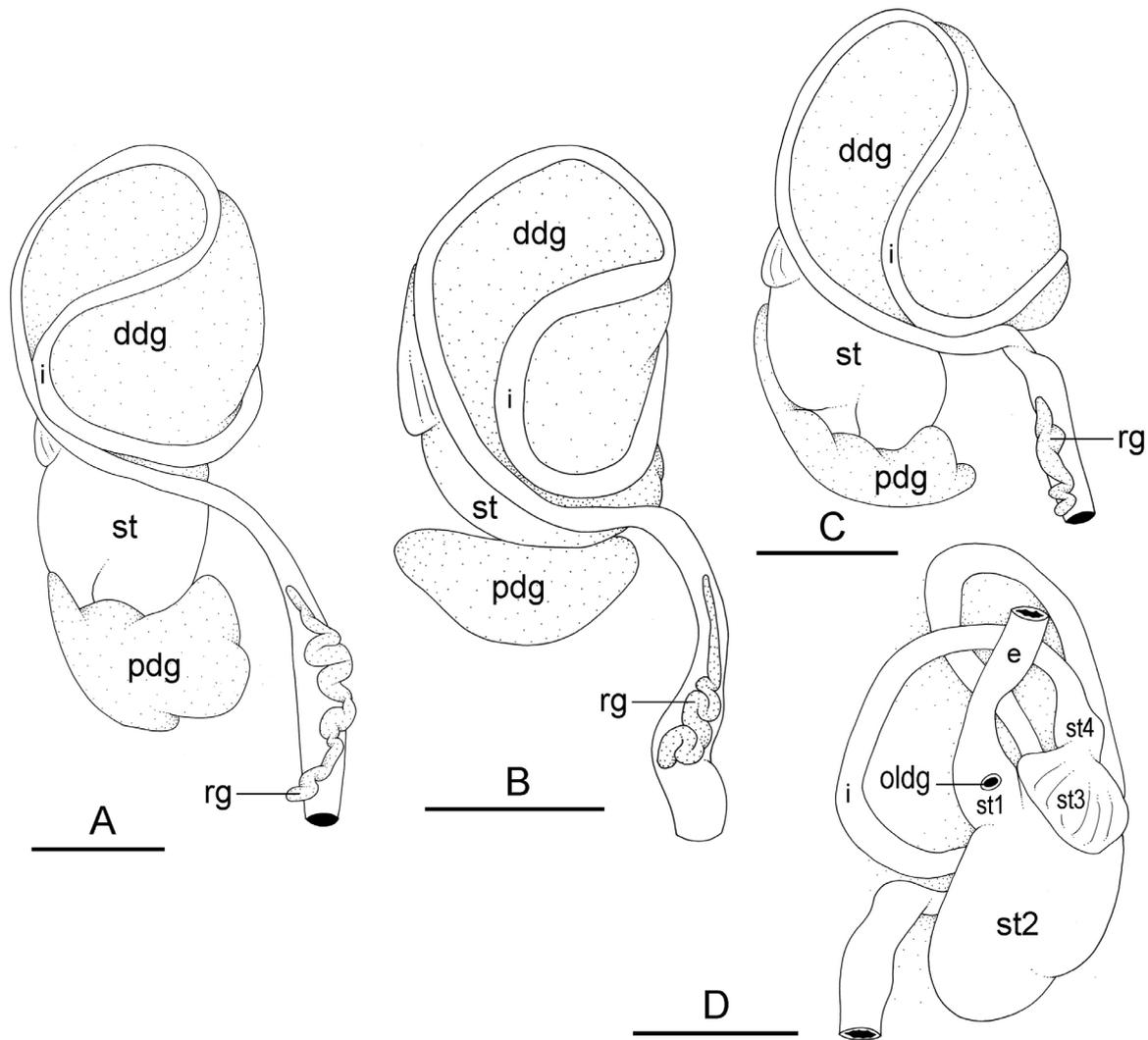
Fig. 40. *Platevindex applanatus* (Simroth, 1920) comb. nov., digestive system, intestinal loops of type I. **A**. Dorsal view, type I with a transitional loop oriented at 2 o'clock, Kei, Indonesia [2892] (UMIZ 00102). **B**. Dorsal view, type I with a transitional loop oriented at 2 o'clock, Mauritius [3152] (MNHN-IM-2019-1393). **C**. Dorsal view, type I with a transitional loop oriented at 1 o'clock, Papua New Guinea [5420] (MNHN-IM-2013-13765). **D**. Stomach, ventral view, same as C. Abbreviations: ddg = dorsal digestive gland; e = esophagus; i = intestine; oldg = opening of the lateral lobe of the digestive gland; pdg = posterior digestive gland; rg = rectal gland; st = stomach; st1 = stomach chamber 1; st2 = stomach chamber 2; st3 = stomach chamber 3; st4 = stomach chamber 4. Scale bars: A, D = 3 mm; B = 2 mm; C = 4 mm.

between the Halmahera Sea and the Banda Sea. However, animal sizes overlap between species and cannot be reliably used for identification.

Internally, the intestinal loops of *P. applanatus* (type I) distinguish it from all other species of *Platevindex*. The only other species with intestinal loops of type I is *P. luteus*. However, the orientation of the transitional loop can be used to reliably distinguish *P. applanatus* (between 1 and 2 o'clock) from *P. luteus* (between 3 and 8 o'clock). *Platevindex applanatus* can also be distinguished from *P. luteus* based on reproductive anatomy. The deferent duct in the posterior reproductive system is more closely attached to the oviduct, longer and more highly coiled in *P. applanatus* than in *P. luteus*. The
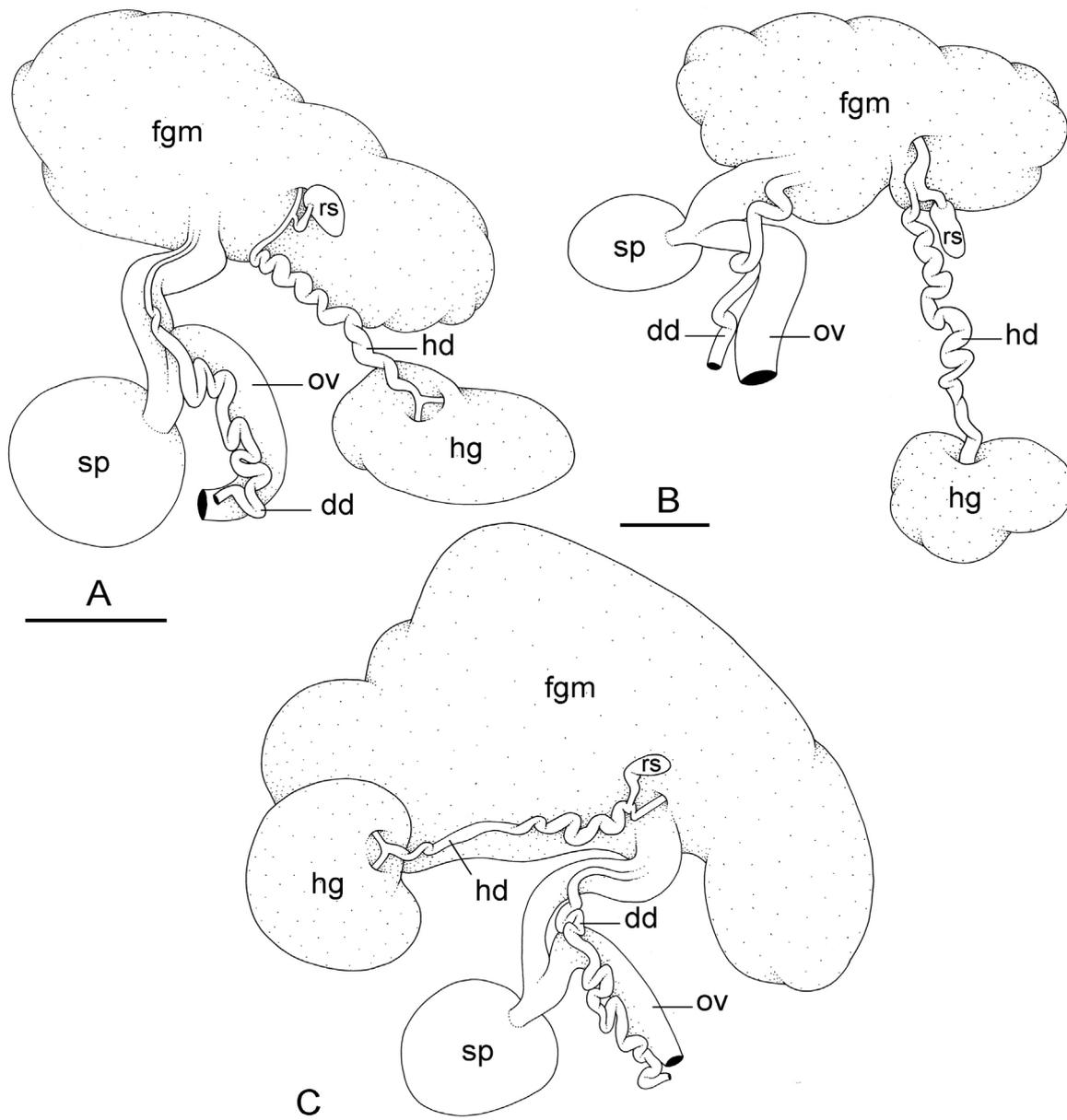
Fig. 41. *Platevindex applanatus* (Simroth, 1920) comb. nov., posterior reproductive system. **A**. Kei, Indonesia [2892] (UMIZ 00102). **B**. Mauritius [3152] (MNHN-IM-2019-1393). **C**. Papua New Guinea [5420] (MNHN-IM-2013-13765). Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; rs = receptaculum seminis; sp = spermatheca. Scale bars: A, C = 2 mm; B = 1 mm.

distal region of the oviduct (distal to the spermatheca) is also longer in *P. applanatus* than in *P. luteus*. Finally, the distal region of the penis with hooks is longer in *P. applanatus* (up to 3 mm) than in *P. luteus* (up to 1 mm). The insertion of the retractor muscle varies greatly within *P. applanatus* (it may insert at the posterior end of the visceral cavity or near the heart), so this character does not help to reliably distinguish it from *P. luteus*.

Distribution (Fig. 10A)

Indonesia: Ambon, Aru Islands (type locality), Kei Islands. Mauritius. Papua New Guinea: Madang and New Ireland. Vanuatu. All records are new, except for the type locality.

Habitat (Fig. 45)

Platevindex applanatus is primarily found in the high intertidal, including on limestone, on rocks covered with a thin layer of algae. In the Kei Islands, individuals were found on rocks at the upper margin of the intertidal near a mangrove. In Ambon, individuals were found on logs very high in the intertidal, including at one locality that was not near any mangrove. In mangroves, individuals were typically
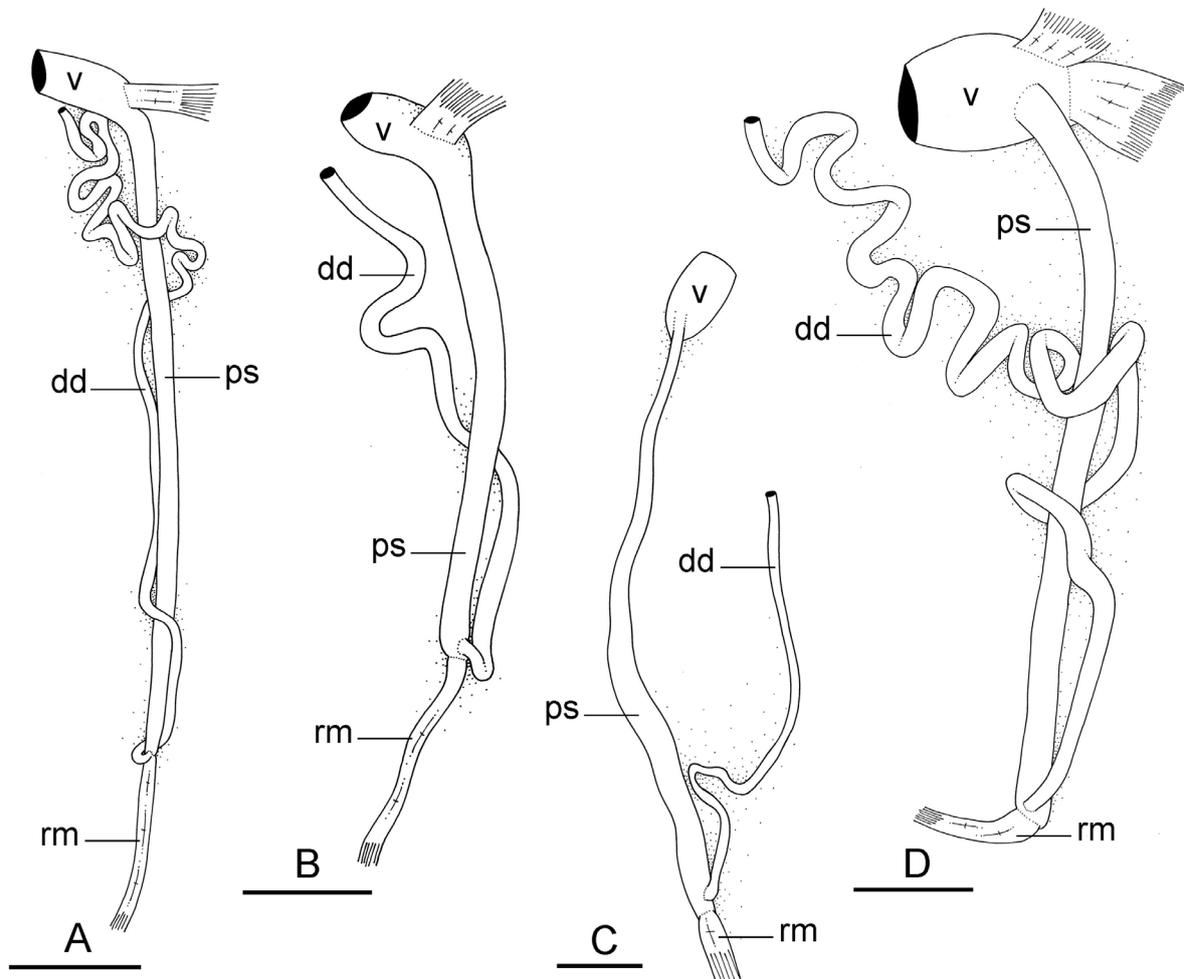
Fig. 42. *Platevindex applanatus* (Simroth, 1920) comb. nov., anterior reproductive system, male copulatory apparatus. **A**. Kei, Indonesia [2892] (UMIZ 00102). **B**. Mauritius [3152] (MNHN-IM-2019-1393). **C**. Mauritius [3604] (MNHN-IM-2019-1392). **D**. Papua New Guinea [5420] (MNHN-IM-2013-13765). Abbreviations: dd = deferent duct; ps = penial sheath; rm = retractor muscle; v = vestibule. Scale bars: A = 2 mm; B, D = 1 mm; C = 0.5 mm.
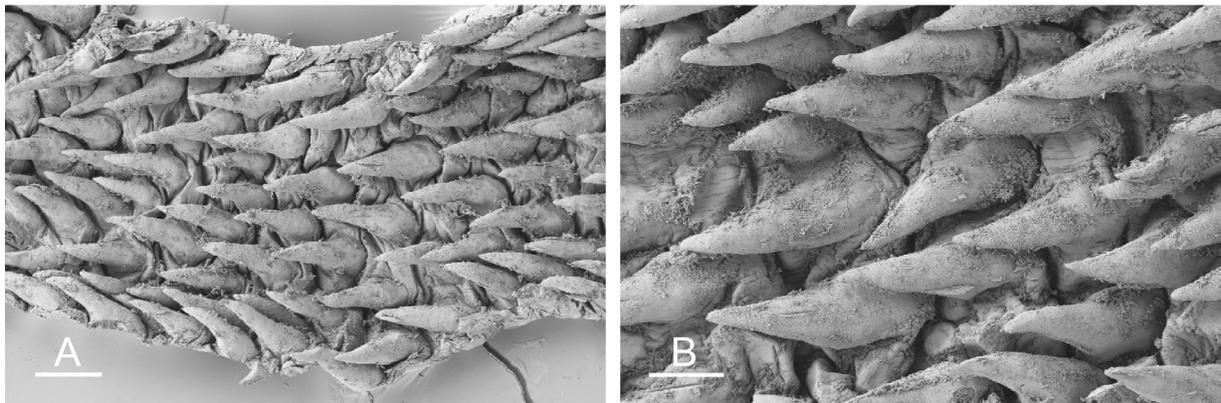
Fig. 43. *Platevindex applanatus* (Simroth, 1920) comb. nov., penial hooks. Indonesia, Ambon [2757] (UMIZ 00101). Scale bars: A = 50 μm; B = 60 μm.

collected on dead logs or tree trunks. In Mauritius, it was found in mangroves, on pieces of wood and wet petioles of palm leaves. *Platevindex applanatus* is not found directly on mud.

Remarks

Onchidium applanatum was originally described from the Aru Islands. Fresh material was collected from the Kei Islands, very close to Aru. The holotype of *Onchidium applanatum* is small (15/12 mm) but its flattened shape, the presence of a rectal gland and no accessory penial gland all indicate that it is a *Platevindex* slug. The prominent papillae on its dorsal notum and its digestive system of type I are compatible with the species described here as well as *P. luteus*. However, the retractor muscle of the
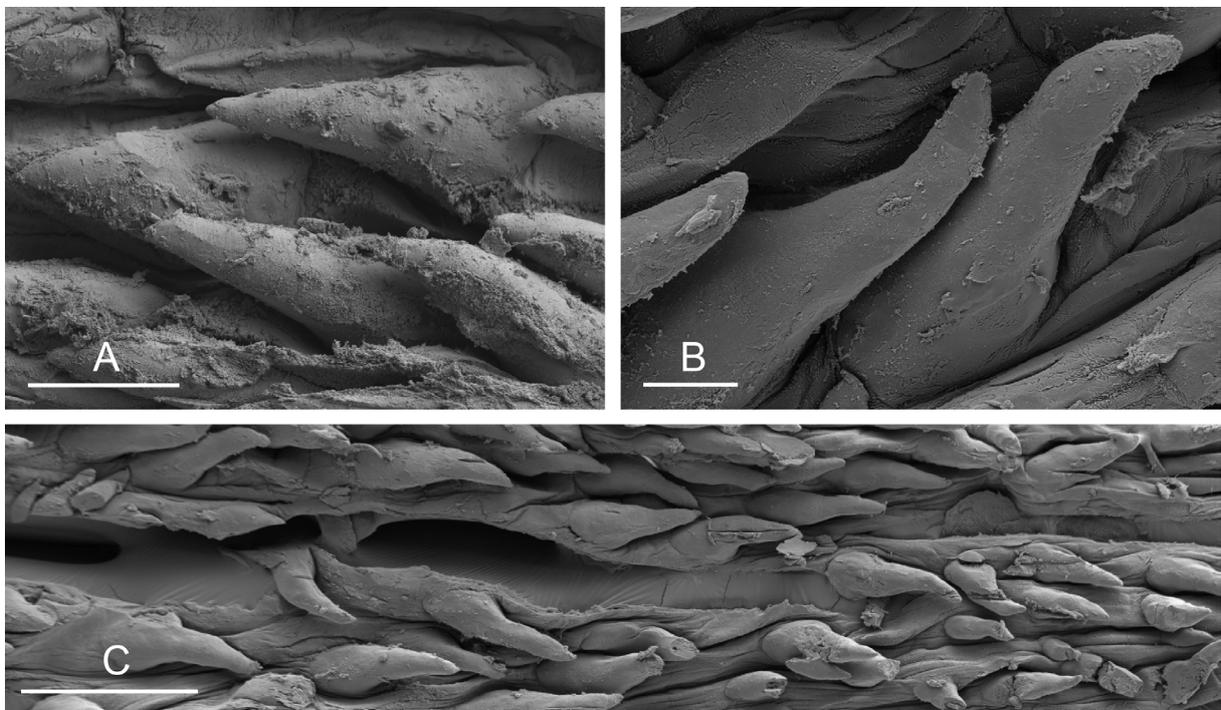
Fig. 44. *Platevindex applanatus* (Simroth, 1920) comb. nov., penial hooks. **A**. Papua New Guinea [5424] (MNHN-IM-2013-14043). **B–C**. Mauritius [3152] (MNHN-IM-2019-1393). Scale bars: A = 30 μm; B = 10 μm; C = 60 μm.
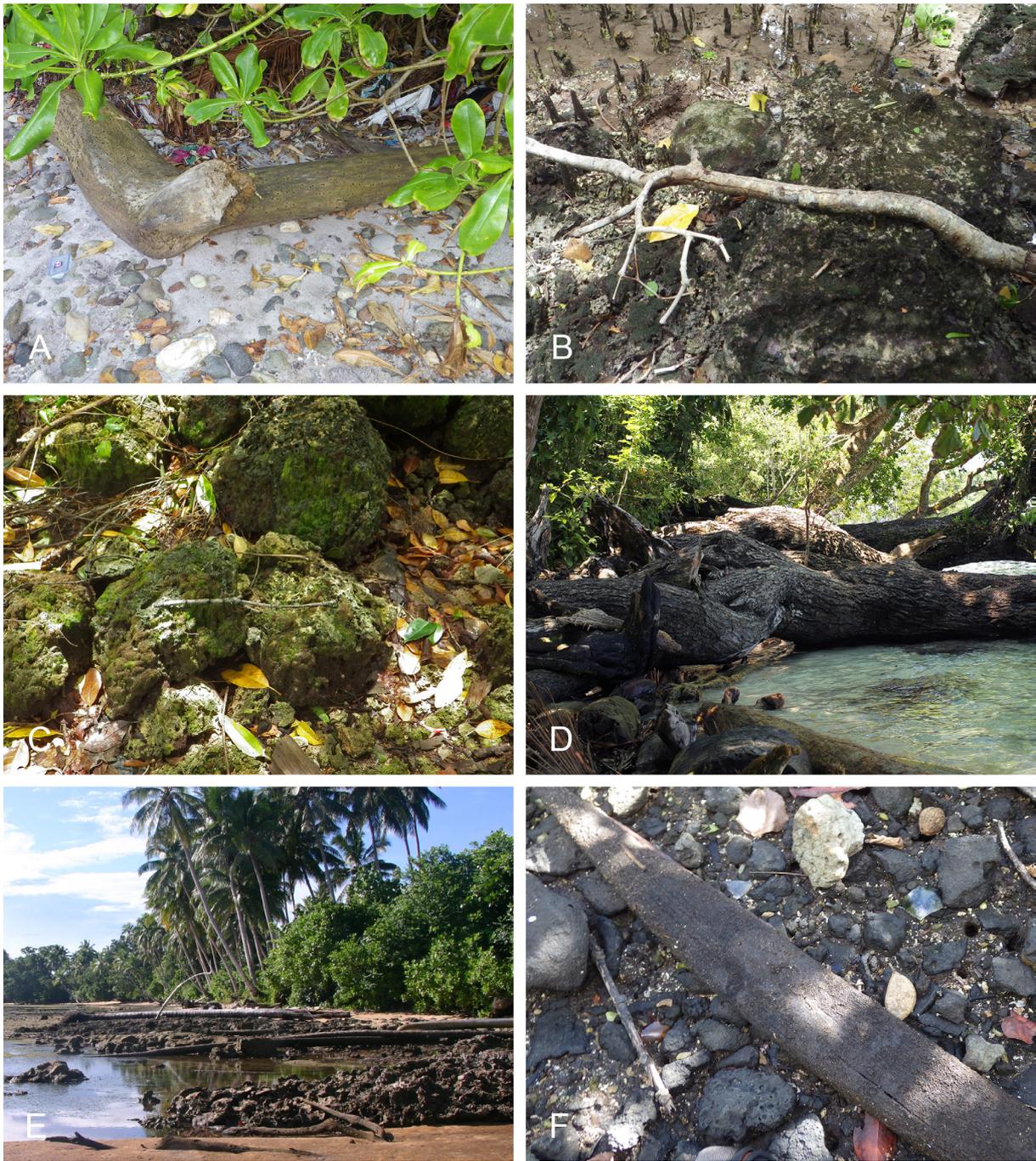
Fig. 45. Habitats of *Platevindex applanatus* (Simroth, 1920) comb. nov., Indonesia (A–C), Papua New Guinea (D–E) and Mauritius (F). **A**. Ambon, log behind a rocky mangrove in the very high intertidal, shaded by trees (station 127). **B**. Kei Islands, rocks with algae at the edge of the mangrove (station 137). **C**. Kei Islands, Un, rocks in the high intertidal behind a mangrove, surrounded by dry vegetation, algae growing on the rocks (station 137). **D**. Madang, Hargun Island, night tide (station PM24). **E**. New Ireland, Povalval, east coast of New Ireland, mixed hard platform and seagrass bed at outlet of rivulet (station KM05). **F**. Mahebourg, close up of rotting petiole of palm frond at margin of mangrove where juvenile onchidiids were found.

holotype of *O. applanatum* is very long and inserts near the posterior end of the visceral cavity, which is only compatible with the species described here (in *P. luteus*, the retractor muscle inserts near the heart). Therefore, *Platevindex applanatus* is applied to the species described here from the Kei Islands and Ambon.

Hoffmann (1928: 84–85) and Labbé (1934: 225–226) considered that *Onchidium applanatum* and *Onchidium tabularis* Tapparone-Canefri, 1883 were both junior synonyms of *Onchidium planatum* Quoy & Gaimard, 1825. *Onchidium planatum*, originally described from Guam, may not even refer to an onchidiid based on the brief written description. Two pieces of a notum were located recently at the MNHN which are part of the type series of *O. planatum* (MNHN-IM-2000-33706). However, these are so poorly preserved that it is not possible to determine whether they were part of an onchidiid slug. Tapparone-Canefri's (1883) description of *O. tabularis* from Wokam, Aru Islands, does not mention the internal anatomy, and the type specimens could not be located. As a result, both *Onchidium planatum* and *Onchidium tabularis* are considered here nomina dubia. Labbé's (1934: 225–226) specimens identified as *O. planatum* from Guam, New Caledonia and Mauritius (as île de France) cannot belong to *P. applanatus* or any other species of *Platevindex* due to the presence of a penial gland.

Platevindex burnupi (Collinge, 1902) comb. nov.
Figs 46–53

Onchidium burnupi Collinge, 1902: 17, figs 1–2.

Onchidium burnupi – Collinge 1910: 171–172. — Connolly 1912: 224; 1939: 456. — Hoffmann 1928: 84.

Material examined

Lectotype
SOUTH AFRICA • lectotype (here designated; 21/16 mm); Natal, Umlaas Lagoon [now the Umlazi River]; NHMUK 1905.4.12.33.

Paralectotype
SOUTH AFRICA • 1 paralectotype (18/12 mm); NHMUK 1905.4.12.34.

Notes on type material
The notum of the lectotype was cut open for the present study, with all internal organs remaining. The paralectotype was not dissected.

Other material
MADAGASCAR • 1 spec. (10/6 [3599] mm); Mangaoka area; 12°15.984′ S, 49°06.103′ E; 18 May 2014; station 160; mangrove of *Avicennia* and *Rhizophora*, many small trees in center of mangrove had been cut; MNHN-IM-2019-1396 • 1 spec. (16/9 [3150] mm); Madagascar, Ambaro Bay; 13°24.769′ S, 48°47.341′ E; 23 May 2014; Station 164; large, very dry mangrove of mostly *Avicennia*; MNHN-IM-2019-1398 • 1 spec. (14/9 [3151] mm); same collection data as for preceding; MNHN-IM-2019-1399 • 1 spec. (12/6 [3602] mm); same collection data as for preceding; MNHN-IM-2019-1397 • 1 spec. (16/10 [3603] mm); same collection data as for preceding; MNHN-IM-2019-1395.

MOZAMBIQUE • 1 spec. (13/10 [729] mm); Mecufi, 50 km S of Pemba, Cabo Delgado Province [about 13° S]; 13 Jul. 2006; D.G. Reid leg.; on base of *Ceriops* bush in landward zone of mangrove belt, 30 cm above firm mud; NHMUK 20060274.
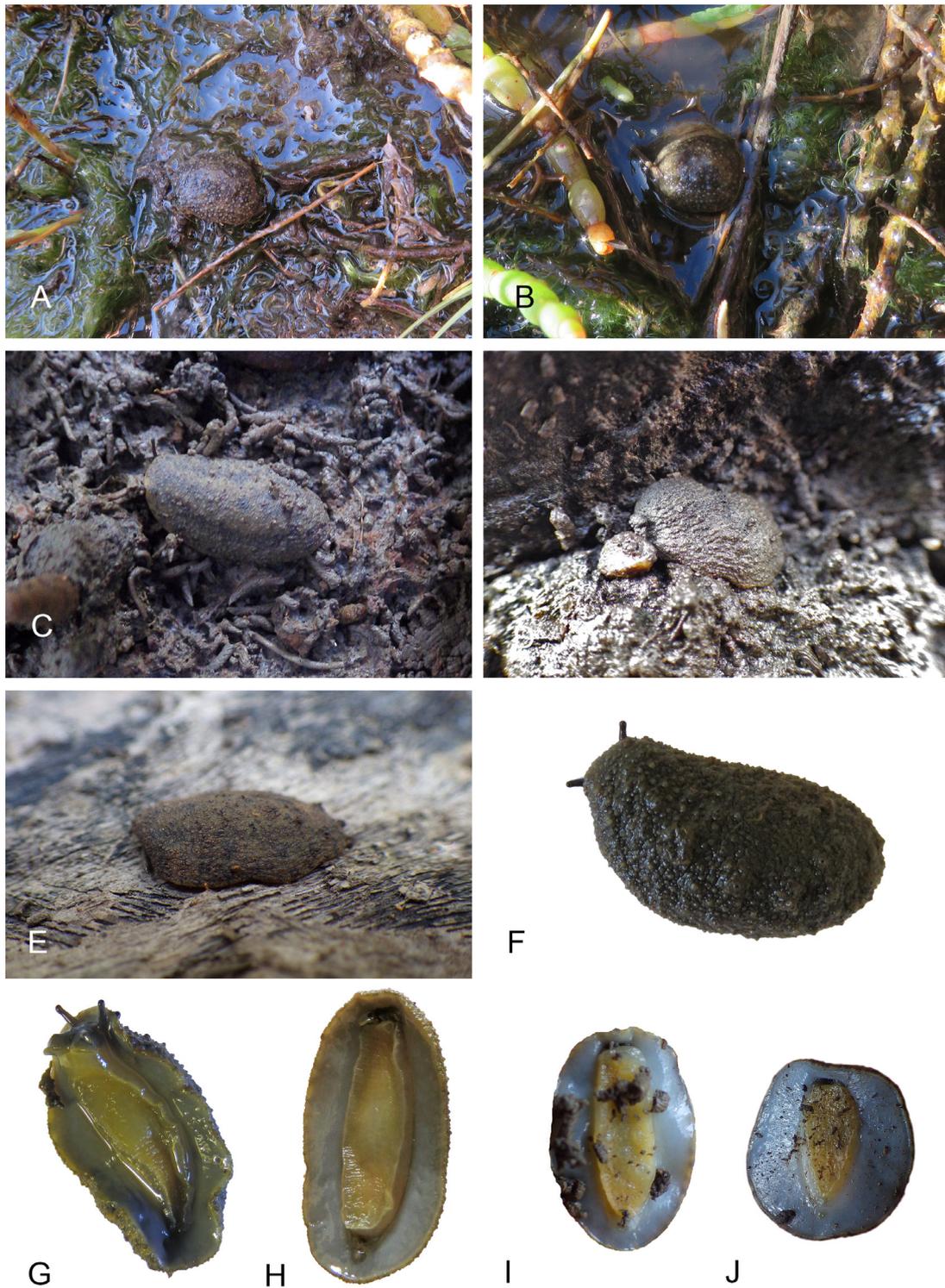
Fig. 46. *Platevindex burnupi* (Collinge, 1902) comb. nov., live animals. **A–B**. Dorsal view [unnumbered], South Africa, East London. **C**. Dorsal view, 16 mm long [3150], Madagascar, Ambaro Bay (MNHN-IM-2019-1398). **D**. Dorsal view, 10 mm long [3599], Madagascar, near Mangaoka (MNHN-IM-2019-1396). **E**. Dorsal view, 14 mm long [3151], Ambaro Bay (MNHN-IM-2019-1399). **F**. Dorsal view, 22 mm long [6153], South Africa, East London (ELM W04108). **G**. Ventral view, 20 mm long [6149], South Africa, East London (ELM W04107). **H**. Ventral view, same as F. **I**. Ventral view, same as C. **J**. Ventral view, same as D.

SOUTH AFRICA • 1 spec. (32/11 [6146] mm); East Cape, Kwelera River estuary; 32°54.169′ S, 28°03.954′ E; 23 Jun. 2017; M. Cole leg.; mud amongst plants in supratidal fringe; ELM W04105 • 1 spec. (23/9 [6154] mm); same collection data as for preceding; ELM W04107 • 1 spec. (22/10 [6153] mm); same collection data as for preceding; ELM W04106 • 1 spec. (20/10 [6149] mm); same collection data as for preceding; ELM W04108 • 1 spec. (19/7 [6148] mm); same collection data as for preceding; ELM W04109.

Description

Color and morphology of live animals (Fig. 46)

The dorsal notum of live animals can be covered with mud, in which case their color may be obscured until they are washed. The dorsal notum is brown with dark brown or black markings. The hyponotum is light blue-grey and the foot is yellow. Papillae with dorsal eyes are present. Their exact number is variable, approximately from 15 to 38 were observed in specimens from South Africa and between 12 and 20 were observed in specimens from Madagascar. Each papilla bears one dorsal eye. Eyes are distributed across the notum but are absent from the margin (i.e., eyes are never <2 mm from the notum edge).

Digestive system (Figs 2G, 47–48B, 53)

Radulae measure up to 3.3 mm in length. Examples of radular formulae are presented in Table 5. The intestinal loops are of type II, with a transitional loop oriented at approximately 7 o'clock (Figs 2G, 48A, 53).
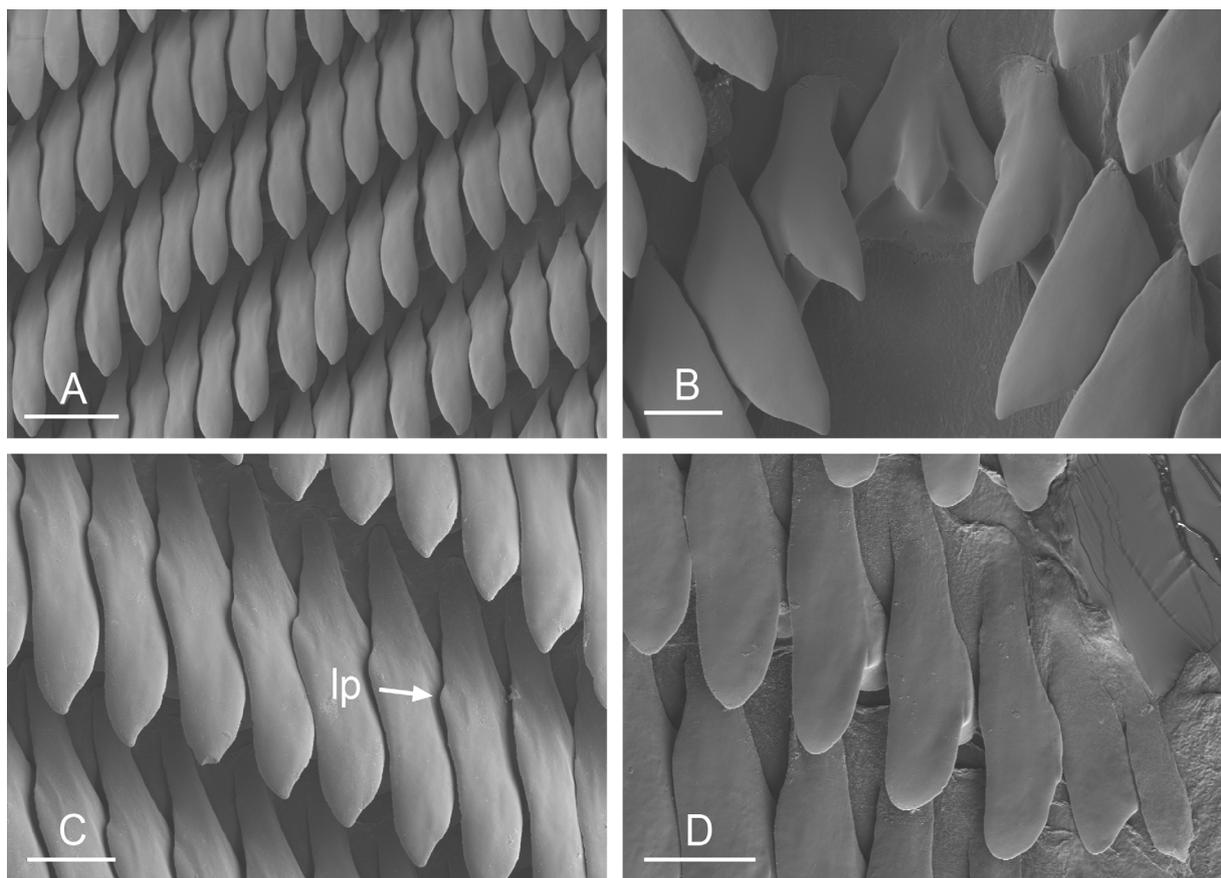
Fig. 47. *Platevindex burnupi* (Collinge, 1902) comb. nov., radula, South Africa. **A**. Left, lateral teeth [6153]. **B**. Rachidian tooth and innermost lateral teeth, same as A. **C**. Right, lateral teeth [6149]. **D**. Right, outermost, lateral teeth [6148]. Abbreviation: lp = lateral protuberance. Scale bars: A = 30 μm; B = 10 μm; C–D = 20 μm.

Reproductive system (Figs 49–51)

In the posterior (female) reproductive system, the oviduct is short, wider than the deferent duct (approximately twice as wide). The length of its distal section (distal to the spermatheca) is shorter than or equal to that of its proximal section. The deferent duct is slightly longer than the oviduct, is only loosely attached to it and varies from loosely to tightly coiled (Fig. 49). The female pore is approximately 0.5 to 2 mm from the anus. The distal, flexible region of the penis with hooks is 1 to 1.5 mm long. Penial hooks are large, between 25 to 70 µm long (Fig. 51A), and can be seen inside the semi-transparent penis. The retractor muscle of the penis inserts on the right side at the posterior end of the visceral cavity (from the posterior end of the heart, up to the posterior end of the visceral cavity). The length of the retractor muscle varies from half the length of the penial sheath to approximately two times its length (Fig. 50B). The deferent duct is highly convoluted.

Distinctive diagnostic features (Table 4)

Platevindex burnupi is the only known species of *Platevindex* from the western Indian Ocean. It can be distinguished from *P. martensi* and *P. aptei* sp. nov. by its grey hyponotum and yellow foot, and from *P. amboinae* and *P. latus* by the presence of dorsal eyes. *Platevindex burnupi* is similar in appearance to *P. luteus* and *P. applanatus*, but lacks distinctly raised dorsal papillae. Its dorsal surface can even be smooth. It is difficult to distinguish *P. burnupi* from *P. coriaceus* and *P. tigrinus* due to their similar coloration and granular dorsal appearance. Although individuals of *P. burnupi* tend to be shorter than those of *P. coriaceus* and *P. tigrinus*, animal sizes overlap and cannot be used for identification.
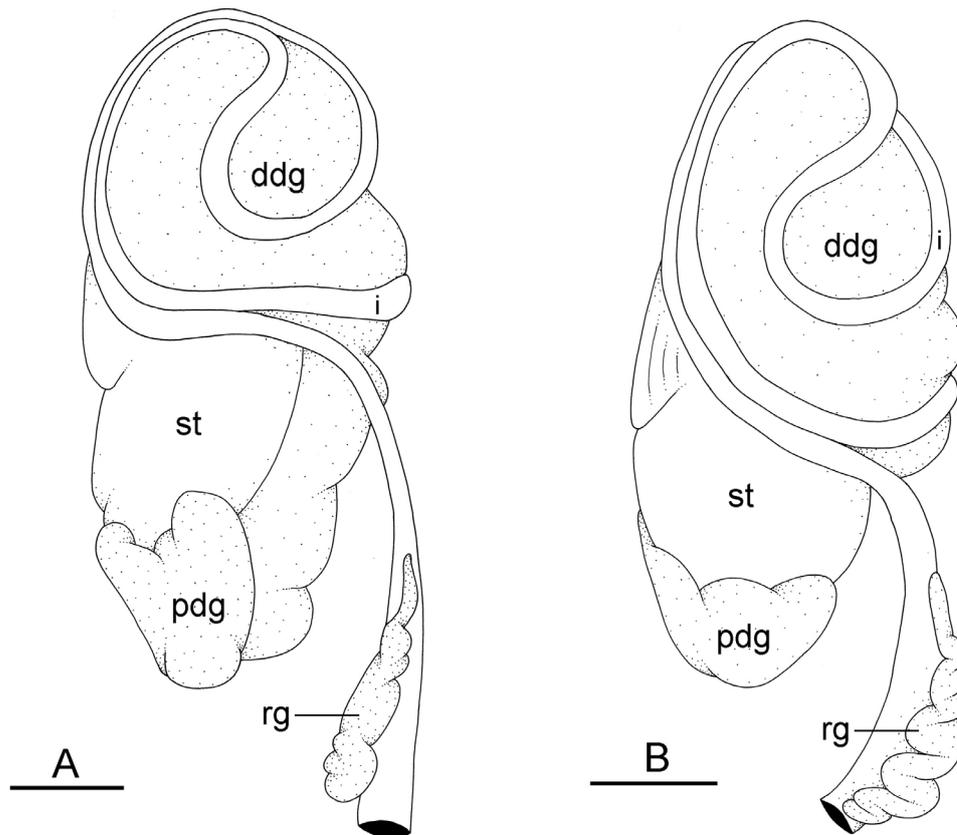
Fig. 48. *Platevindex burnupi* (Collinge, 1902) comb. nov., digestive system, dorsal view, intestinal loops of type II, with a transitional loop oriented at 7 o'clock. **A**. South Africa, lectotype (NHMUK 1905.4.12.33). **B**. Madagascar [3150] (MNHN-IM-2019-1398). Abbreviations: ddg = dorsal digestive gland; i = intestine; pdg = posterior digestive gland; rg = rectal gland; st = stomach. Scale bars = 2 mm.

Internally, the intestinal loops of type II differentiate *P. burnupi* from *P. amboinae*, *P. latus*, *P. applanatus* and some specimens (with intestinal loops of type I) of *P. luteus*. The reproductive system can be used to distinguish *P. burnupi* from all other species of *Platevindex*. The deferent duct in the posterior reproductive system is loosely attached to the oviduct in *P. burnupi*, which distinguishes it from *P. coriaceus* and *P. tigrinus* (deferent duct closely attached to the oviduct). The distal region of the penis with penial hooks is also much shorter in *P. burnupi* (1–1.2 mm) than in *P. coriaceus* (2–8 mm). *Platevindex burnupi* is very difficult to differentiate from *P. luteus* internally. They differ only slightly with respect to the insertion of the penial retractor muscle (near the heart in *P. luteus* and in the last posterior quarter of the visceral cavity in *P. burnupi*). DNA sequences are the most reliable way to distinguish *Platevindex burnupi* and *P. luteus*, which are more than 10.5% divergent based on COI sequences.

Distribution (Fig. 10A)

Madagascar, Mozambique and South Africa (type locality and newly-collected material).
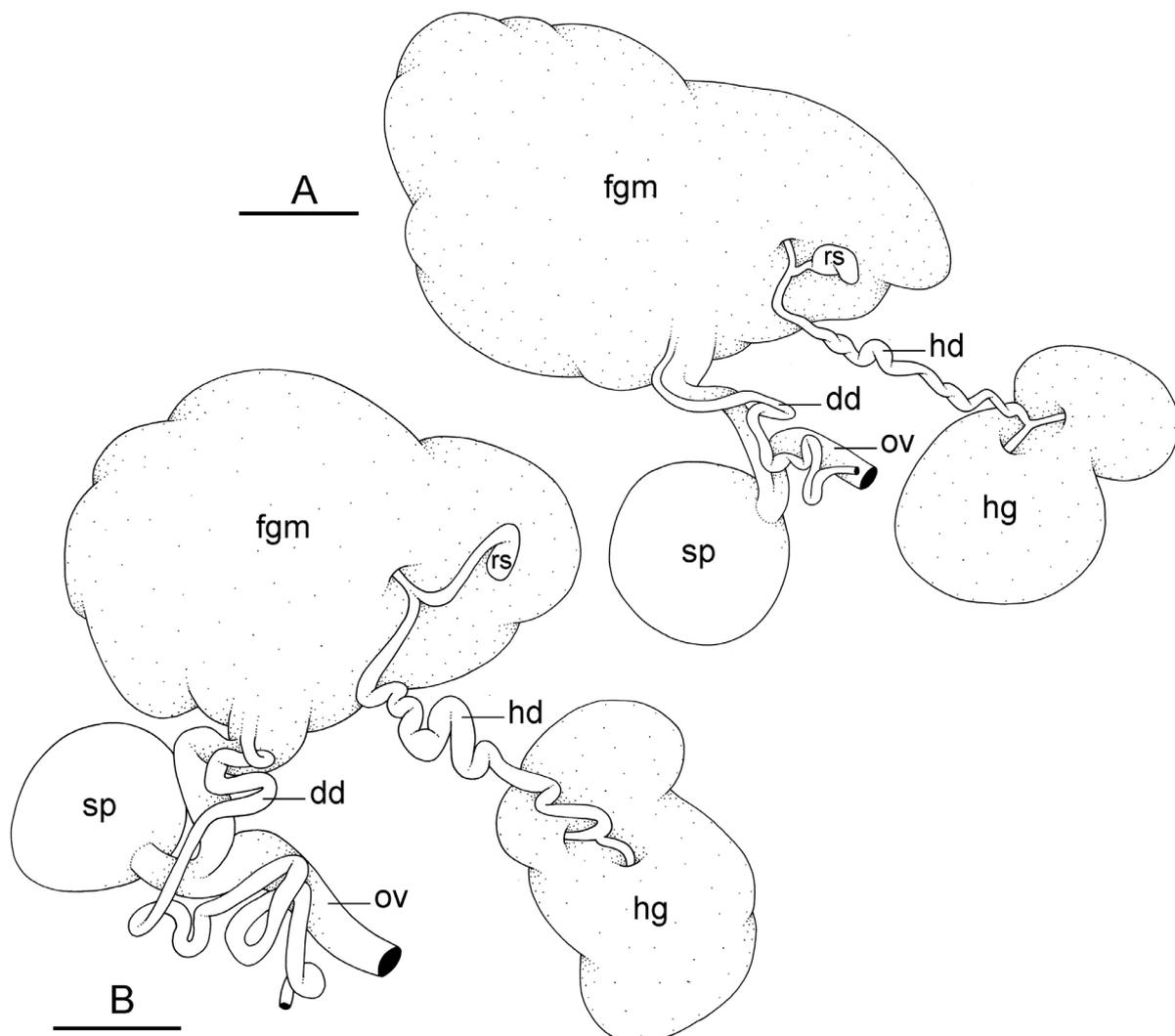
Fig. 49. *Platevindex burnupi* (Collinge, 1902) comb. nov., posterior reproductive system. **A**. South Africa, lectotype (NHMUK 1905.4.12.33). **B**. Madagascar [3603] (MNHN-IM-2019-1395). Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; rs = receptaculum seminis; sp = spermatheca. Scale bars: A = 2 mm; B = 1 mm.

Habitat (Figs 45A–B, 52C–D)

Like other species of *Platevindex*, *P. burnupi* is found on mangrove trees but, unlike other species, it may also be found on mud. Specimens in Madagascar were found high in the intertidal on moist mud not saturated in water, and one specimen was found on a piece of wood. A specimen from Mozambique was collected on the base of a *Ceriops* tree, 30 cm above ground. All specimens in South Africa were on mud, in the supra-tidal zone of a salt marsh, a few meters away from the river.

Remarks

Onchidium burnupi must be transferred to *Platevindex* because of the following combination of characters in the lectotype: flattened body, rectal gland present and no penial gland. The type locality (Umlaas Lagoon, Natal, South Africa) was visited twice by our team and several times by experts from the Natal Museum (Dai Herbert, pers. com.), but no onchidiid species were ever found. This is very likely due to the fact that the Umlaas Lagoon has been developed and natural vegetation destroyed. However, onchidiids similar to the lectotype of *O. burnupi* were recently collected by Mary Cole
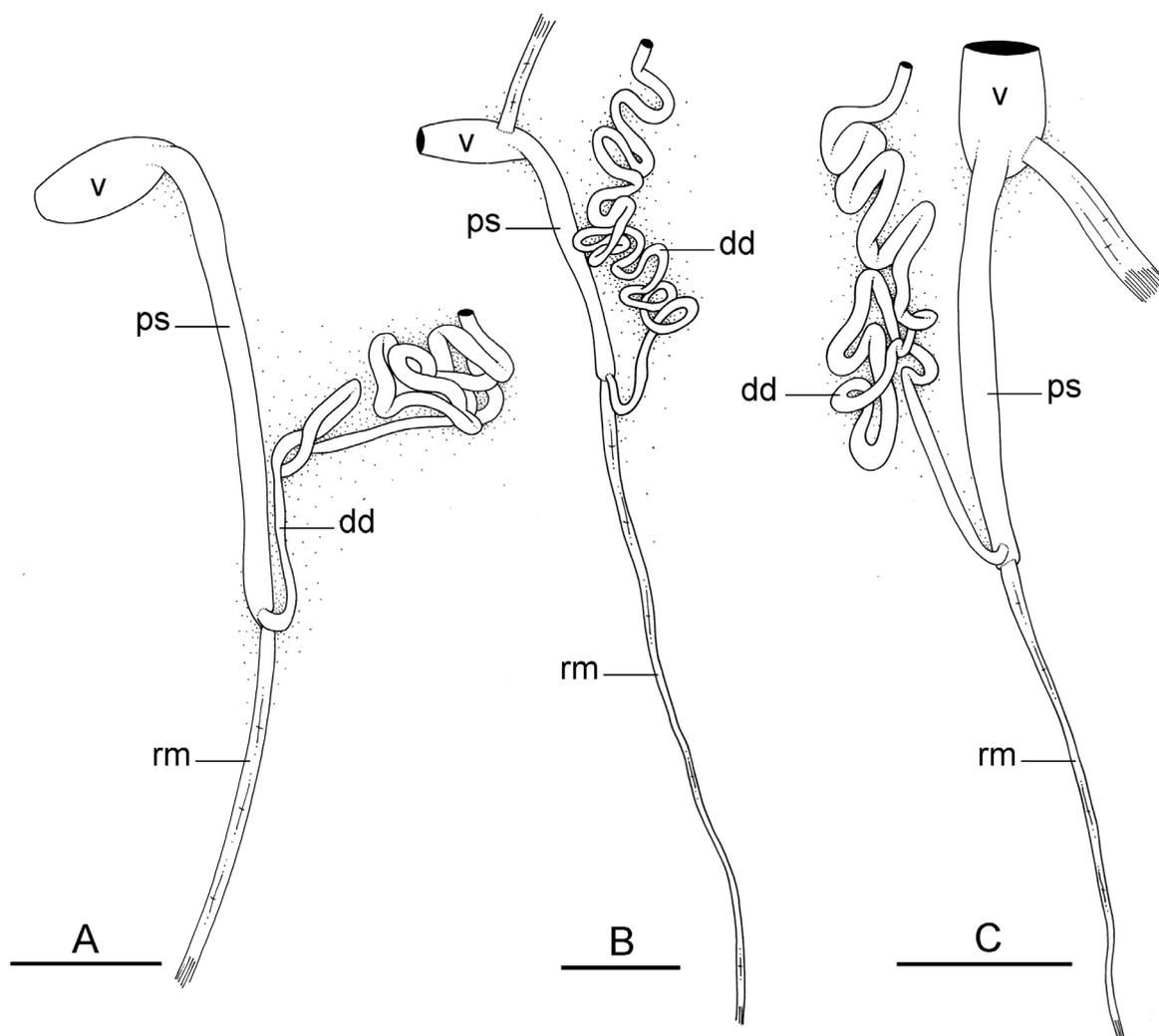
Fig. 50. *Platevindex burnupi* (Collinge, 1902) comb. nov., anterior, male copulatory apparatus. **A**. South Africa [6148] (ELM W04109). **B**. South Africa, lectotype (NHMUK 1905.4.12.33). **C**. Madagascar [3150] (MNHN-IM-2019-1398). Abbreviations: dd = deferent duct; ps = penial sheath; rm = retractor muscle; v = vestibule. Scale bars: A = 1 mm; B–C = 2 mm.
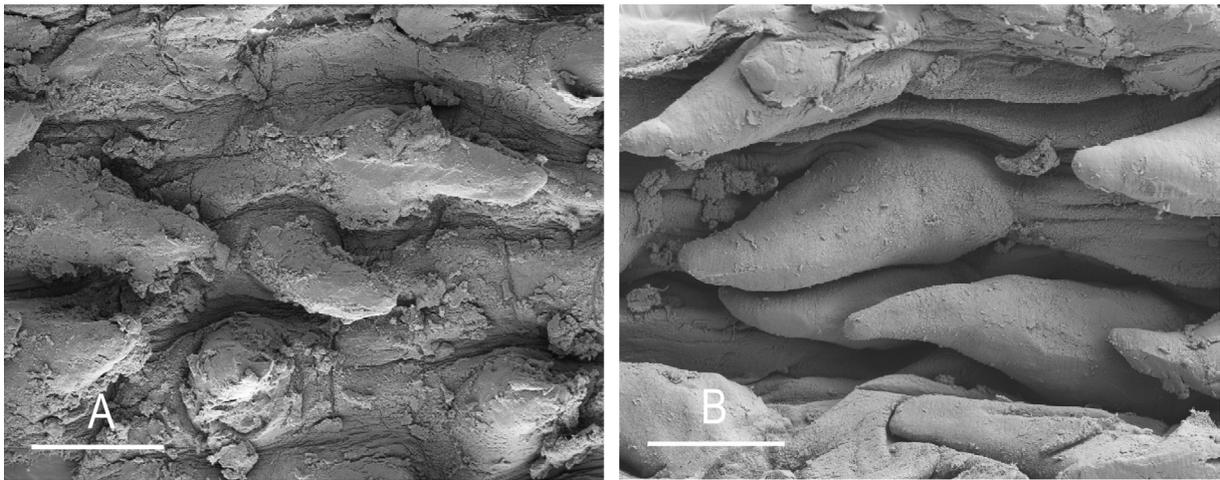
Fig. 51. *Platevindex burnupi* (Collinge, 1902) comb. nov., penial hooks **A**. South Africa [6148] (ELM W04109). **B**. Madagascar, Ambaro Bay [3603] (MNHN-IM-2019-1395). Scale bars: A = 30 μm; B = 20 μm.

and Philippe Bouchet in the estuary of the Kwelera River, East Cape, South Africa (approximately 400 km south of the type locality). As of today, no other live population of *P. burnupi* is known in South Africa (assuming that there is no live population at the type locality). Note that several authors have mentioned the existence of *Onchidium burnupi* in South Africa but exclusively based on the original
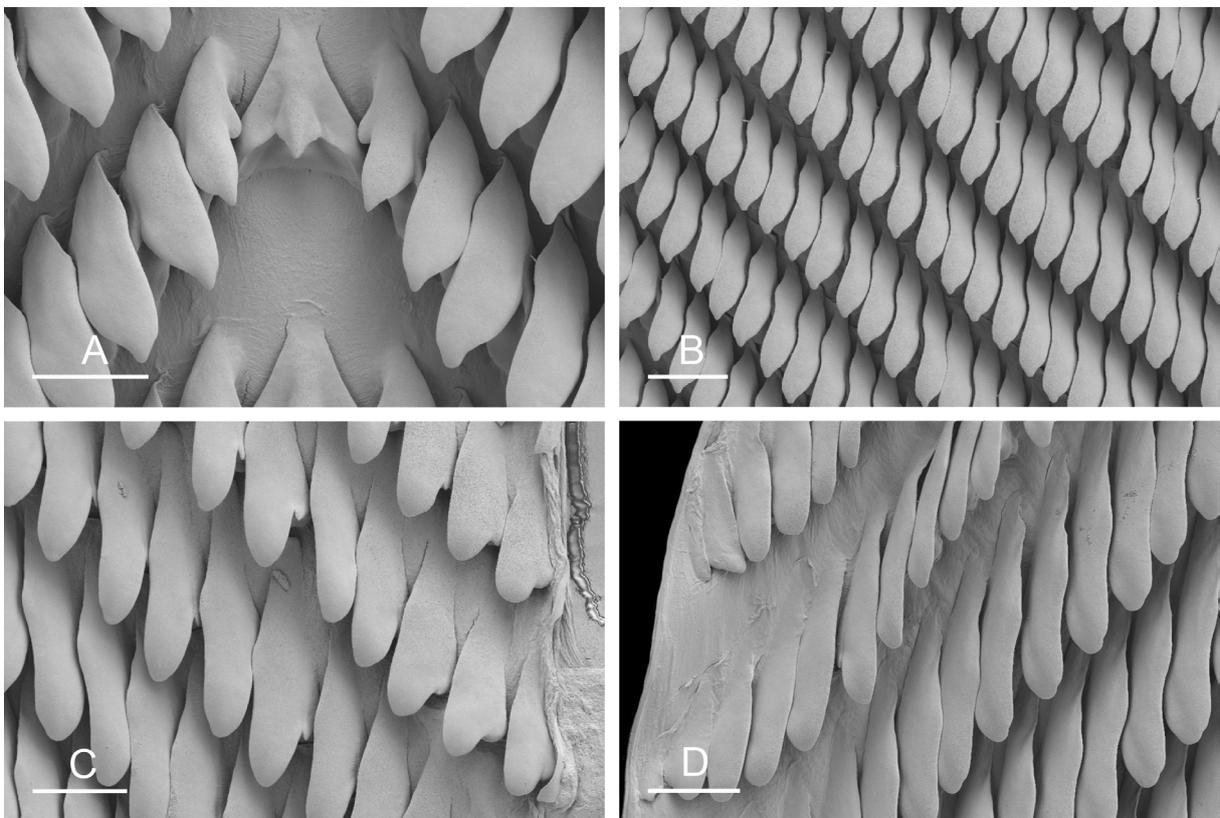
Fig. 52. *Platevindex burnupi* (Collinge, 1902) comb. nov., radula, Madagascar, Ambaro Bay [3603] (MNHN-IM-2019-1395). **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth. **C–D**. Outer lateral teeth. Scale bars: A, C–D = 20 μm; B = 30 μm.

description, i.e., without providing new specimens or records (Connolly 1912, 1939; Collinge 1910; Hoffmann 1928).

Platevindex burnupi is known from two localities in South Africa, three localities in Madagascar and one locality in Mozambique. High genetic divergences between populations from Madagascar and Mozambique versus South Africa (5.4–6.0%) as well as the fact that they are consistently recovered as
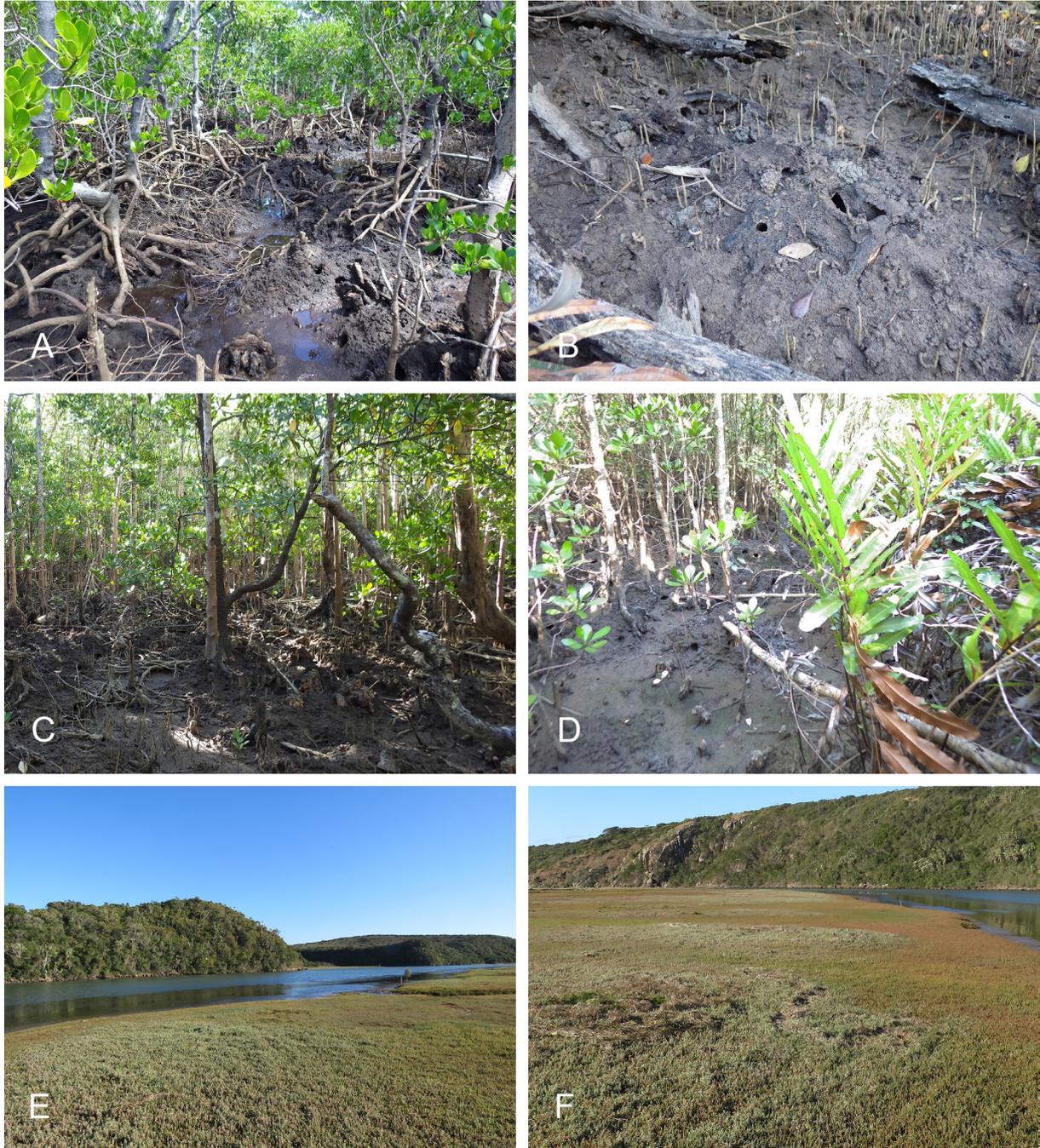
Fig. 53. Habitats of *Platevindex burnupi* (Collinge, 1902) comb. nov. **A**. Madagascar, near Mangaoka (station 160). **B–D**. Madagascar, Ambaro Bay, vegetation and close view of the high intertidal mud (station 164). **E–F**. South Africa, East Cape, Kwelera Estuary, estuarine plants in the supra-tidal fringe of salt marsh.

reciprocally-monophyletic units (Figs 4–8) suggest that there could be more than one species. However, there is not enough evidence to justify the description of a new species in Madagascar. The anatomy of populations from South Africa and Madagascar are similar, and little is known about intraspecific variation across its distribution. The genetic divergences between Madagascar and East Africa (Mozambique and South Africa) could be the result of the large geographic distance between localities. However, there are some noticeable differences between the populations in the two regions.

The most noticeable difference between regions is animal length: individuals collected from South Africa (up to 32 mm) are significantly larger than those from Madagascar (up to 16 mm) and Mozambique (13 mm). However, intermediate sizes may be found when additional populations are discovered, or this could be due to a difference in climate. The deferent duct in the posterior (female) reproductive system is slightly longer in specimens from Madagascar than in specimens from South Africa (even though animal size is larger in South Africa), but this could also be the result of population structure (this trait is known to vary between individuals). In addition, the insertion of the retractor muscle is more posterior in specimens from Madagascar than in South Africa. Finally, Madagascan individuals were found in a different habitat (mangrove) than in South Africa (salt marsh). Salt marshes in Madagascar were not visited for this study and may need to be explored in the future.

Platevindex martensi (Plate, 1893)
Figs 54–58

Oncis martensi Plate, 1893: 196–197, pl. 7, figs 7, 23a, pl. 10, fig. 50.
Oncis inspectabilis Plate, 1893: 198–199. **Syn. nov.**

Onchidium coriaceum – Semper 1880: 271–273 (in part only) [non *Onchidium coriaceum* Semper, 1880].
Oncis martensi – Stantschinsky 1907: 395. — Hoffmann 1928: 89.
Oncis inspectabilis – Stantschinsky 1907: 395.
Platevindex martensi – Dayrat 2009: 5.
Platevindex mortoni – Zhang *et al*. 2017: fig. 1e (non *Platevindex mortoni* Britton, 1984).

Material examined

Holotype
THAILAND • holotype (44/41 mm) by monotypy; Petshaburi, Gulf of Siam [Phetchaburi, Gulf of Thailand]; ZMB/Moll 8454.

Holotype of *Oncis inspectabilis*
MYANMAR • holotype (28/23 mm) by monotypy; Lampee, Birma [Lampi Island, Mergui Archipelago, southern Myanmar, Andaman Sea]; Anderson leg.; ZMB/Moll 38934.

Notes on type material
Oncis martensi. The holotype was previously dissected. Internal organs are mostly missing; only a few pieces of the female (posterior) reproductive system and digestive system remain. The penial complex and buccal mass are missing.

Oncis inspectabilis. The holotype was previously dissected. Internal organs are mostly missing. The buccal mass remains, as well as pieces of the deferent duct, oviduct and spermatheca.

Other material

AUSTRALIA – **Northern Territory** • 4 specs (39/26 [1711], 25/20 [1709], 25/20 [1710] and 13/12 [1707] 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.57611.

BRUNEI • 1 spec. (43/29 [1040] mm); near Batu Marang; 04°59.131′ N, 115°01.820′ E; 29 Jul. 2011; station 34; old mangrove with tall *Rhizophora* trees with high roots and *Thalassina* mounds; BDMNH.

INDONESIA – **Sumatra** • 1 spec. (52/19 [1767] mm); Pulau Sinaboi; 02°18.145′ N, 100°59.309′ E; 8 Oct. 2012; station 73; some small *Avicennia* and *Rhizophora* near shore; UMIZ 00107 • 1 spec. (22/13 [1776] mm); Dumai; 01°42.838′ N, 101°23.286′ E; 9 Oct. 2012; station 74; mangrove just behind abandoned buildings, high intertidal; UMIZ 00108 • 1 spec. (34/19 [1748] mm); Sungai Lubuk; 05°40.174′ S, 105°34.097′ E; 19 Oct. 2012; station 79; mounds of *Thalassina*, *Rhizophora*, dead logs in the high intertidal; UMIZ 00109. – **Sulawesi** • 2 specs (36/23 [2334] and 35/23 [2333] mm); Makassar City, Tallo; 05°06.117′ S, 119°26.777′ E; 21 Mar. 2013; station 92; small mangrove with outhouse in center; UMIZ 00111.

MALAYSIA – **Peninsular Malaysia** • 1 spec. (30/18 [964] mm); Nibong Tebal, Pulau Burung; 05°12.488′ N, 100°25.564′ E; 11 Jul. 2011; station 17; *Rhizophora* mangrove with a few *Sonneratia* and soft mud; USMMC 00029 • 1 spec. (31/30 [934] mm); Balok; 03°53.219′ N, 103°21.978′ E; 14 Jul. 2011; station 19; *Rhizophora* mangrove with some *Avicennia* and mostly hard mud; USMMC 00030 • 2 specs (37/23 [no DNA] and 36/18 [no DNA] mm); Merbok; 05°39.035′ N, 100°25.782′ E; 18 Jul. 2011; station 21; deep *Rhizophora* forest with old, tall trees, hard mud, many small creeks and dead logs; USMMC 00031 • 1 spec. (39/21 [933] mm); Merbok; 05°40.143′ N, 100°26.178′ E; 19 Jul. 2011; station 22; mangrove of mostly *Rhizophora*, some *Avicennia* with soft mud near creek; USMMC 00077 • 1 spec. (37/15 [no DNA] mm); Langkawi, Tanjung Rhu; 06°25.317′ N, 99°50.106′ E; 15 Jul. 2011; station 26; open forest of *Rhizophora*, *Sonneratia*, *Bruguiera* with high mounds of mud around some trees; USMMC 00032 • 1 spec. (32/24 [930] mm); Kuala Sepatang; 04°50.434′ N, 100°38.176′ E; 19 Jul. 2011; station 27; old *Rhizophora* and *Acrostichum* ferns very high in tidal zone, near boardwalk; USMMC 00033.

PHILIPPINES – **Bohol** • 2 specs (31/16 [3342] and 14/8 [3336] mm); Mabini; 09°51.532′ N, 124°31.685′ E; 17 Jul. 2014; station 194; narrow *Rhizophora* and *Avicennia* mangrove by the sea with fish ponds built on landward side, many dead logs; PNM 041250 • 4 specs (51/27 [3365], 34/22 [3364], 33/14 [3362] and 24/11 [3358] mm); Mabini; 09°51.402′ N, 124°30.982′ E; 18 Jul. 2014; station 195; narrow *Rhizophora* and *Avicennia* mangrove by the sea with fish ponds built on landward side, cement ditches between the mangrove patches and the ponds; PNM 041251.

SINGAPORE • 1 spec. (31/20 [988] mm); Pasir Ris Park; 01°22.840′ N, 103°57.224′ E; 30 Mar. 2010; station 5; mud and dead logs in upper tidal; ZRC.MOL.10480 • 3 specs (40/22 [no DNA], 37/20 [no DNA] and 35/21 [987] mm); Lim Chu Kang; 01°26.785′ N, 103°42.531′ E; 5 Apr. 2010; station 9; piece of wood in *Avicennia* and *Rhizophora* mangrove; ZRC.MOL.10481.

Description

Color and morphology of live animals (Figs 54–55A)

Live animals are not usually covered with mud, and their natural color is visible without washing. The dorsal notum is brown to dark brown or black, often mottled with two colors. The notum bears small elongated (longitudinal) ridges. The ventral color varies but the hyponotum is yellow, beige or yellow-orange, with distinct darker spots of variable size (small to large) and color (faintly tan to black). When those spots are large and dark enough, the hyponotum appears nearly black (which was most common in the Strait of Malacca). The hyponotum of juvenile specimens can be marked by fewer spots.

Fig. 54. *Platevindex martensi* (Plate, 1893), live animals. **A**. Dorsal view, 34 mm long [1748], Indonesia, Sumatra (UMIZ 00109). **B**. Dorsal view, 24 mm long [3358], Philippines, Bohol (PNM 041251). **C**. Dorsal view, 34 mm long [3364], Philippines, Bohol (PNM 041251). **D**. Dorsal view, 13 mm long [1707], Australia, Darwin (NTM P.57611). **E**. Dorsal view, 38 mm long [#1], Peninsular Malaysia, Langkawi (USMMC 00032). **F**. Dorsal view, 25 mm long [1709], Australia, Darwin (NTM P.57611). **G**. Ventral view, 36 mm long [2334], Indonesia, Sulawesi (UMIZ 00111). **H**. Ventral view, same as C. **I**. Ventral view, same as F. **J**. Ventral view, 31 mm long [934], Peninsular Malaysia, Balok (USMMC 00030). **K**. Ventral view, 30 mm long, [964], Peninsular Malaysia, Penang (USMMC 00029).
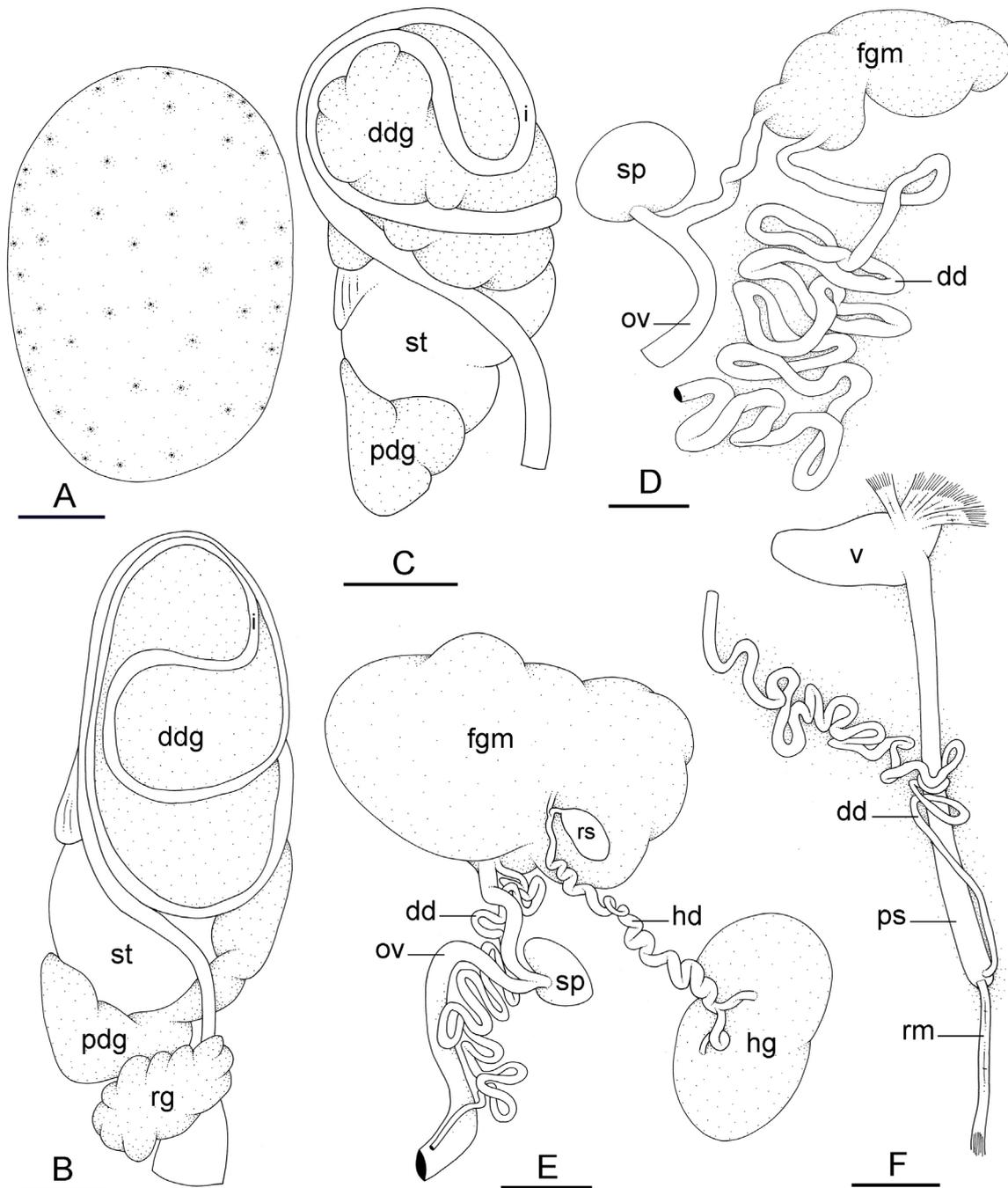
Fig. 55 *Platevindex martensi* (Plate, 1893), external morphology, digestive and reproductive systems. **A**. Dorsal notum, entire animal, Bohol, Philippines [3365] (PNM 041251). **B**. Digestive system, dorsal view, type II with a transitional loop oriented at 9 o'clock, Sulawesi, Indonesia [2333] (UMIZ 00111). **C**. Digestive system, dorsal view, type II with a transitional loop oriented at 6 o'clock, Peninsular Malaysia [964] (USMMC 00029). **D**. Posterior reproductive system (remaining parts), Phetchaburi, Gulf of Thailand, holotype (ZMB/Moll 8454). **E**. Posterior reproductive system, Darwin, Northern Territory, Australia [1711] (NTM P.57611). **F**. Anterior, male copulatory apparatus, same as E. Abbreviations: dd = deferent duct; ddg = dorsal digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior digestive gland; ps = penial sheath; rg = rectal gland; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scale bars: A = 10 mm; B–C = 3 mm; D–F = 2 mm.

In Malaysia, Singapore and Brunei, the edge of the hyponotum commonly is orange, which was also occasionally observed in other populations. The foot is distinctively orange. Papillae with dorsal eyes are present. Their exact number is variable (generally between 20 and 65). Each papilla bears one dorsal eye. Eyes are distributed across the notum and many eyes are found at the margin (i.e., eyes can be <2 mm from the notum edge).

Digestive system (Figs 2C–D, 55B–C, 56)
Radulae measure up to 5 mm in length. Examples of radular formulae are presented in Table 5. The intestinal loops are of type II, with a transitional loop oriented between 6 and 9 o'clock.

Reproductive system (Figs 55D–F, 57)
In the posterior part of the reproductive system, the oviduct is wider than the deferent duct (approximately up to twice as wide). Its distal section (distal to the spermatheca) is approximately up to twice as long as its proximal section. The deferent duct is longer than the oviduct, not attached to it, and highly coiled with tight, long, U-shaped loops. However, the deferent duct tends to be shorter in Malaysia and Northern Territory (Australia), and considerably longer in Brunei and the Philippines. The female pore is very close to the anus, between 0.5 mm and 2.5 mm apart. The distal, flexible region of the penis with hooks is approximately 2 to 2.5 mm long and approximately 170 μm wide. Penial hooks are relatively large, approximately 35 to 55 μm long (Fig. 57B), and can be seen inside the semi-transparent penis or when the penis is evaginated like the finger of a glove in the vestibule (Fig. 57A). The posterior retractor muscle of the penis inserts on the right side, within the third (posterior) quarter of the visceral cavity.
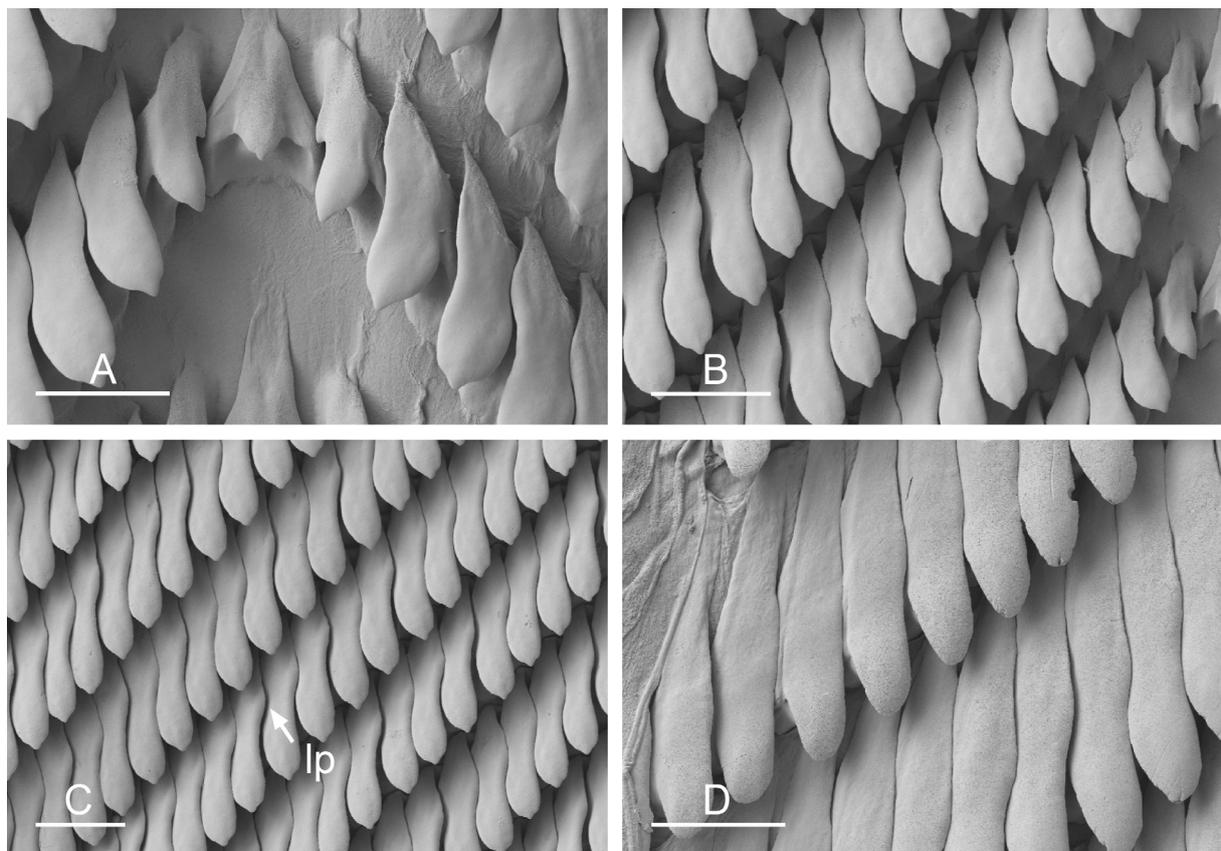
Fig. 56. *Platevindex martensi* (Plate, 1893), radula, Philippines, Bohol [3336]. **A**. Rachidian and innermost lateral teeth. **B**. Innermost lateral teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Abrreviations: lp = lateral protuberance. Scale bars: A, D = 20 μm; B–C = 30 μm.

The length of the retractor muscle varies from half the length of the penial sheath to slightly longer than the penial sheath. The deferent duct is highly convoluted (but is less convoluted in juvenile specimens).

Distinctive diagnostic features (Table 4)

Externally, the orange foot distinguishes *Platevindex martensi* from all other species of *Platevindex*. The small, elongated ridges on its dorsal notum are also present in *P. aptei* sp. nov., but the foot of *P. aptei* sp. nov. is black. The presence of many dorsal eyes right at the margin of the dorsal notum (within 2 mm from the edge) is only shared by *P. martensi* and *P. aptei* sp. nov. Internally, the long deferent duct with elongated loops in the anterior penial apparatus (which is not closely attached to the oviduct) differentiate *P. martensi* from other species of *Platevindex*. Also, the penial retractor muscle inserts between ½ to ¾ down the length of the visceral cavity in *P. martensi* while it inserts at the posterior end of the cavity in *P. aptei* sp. nov.

Distribution (Fig. 10C)

Australia: Northern Territory. Brunei. Indonesia: Sulawesi, Sumatra. Peninsular Malaysia. Myanmar: Andaman Sea (type locality of *P. inspectabilis*). Philippines: Bohol. Singapore. Thailand: Gulf of Thailand (type locality of *P. martensi*). All records are new, except for the type localities.

Habitat (Fig. 58)

Platevindex martensi is typically found in or near mangroves, on tree roots and trunks as well as dead logs. It usually lives in the high intertidal only reached by the highest tides (with *Acrostichum* ferns). It can also be found in cement ditches nearby a mangrove. One juvenile was found on coarse-grained sand in a mangrove forest in the Philippines, but *Platevindex* slugs normally are not found directly on mud or sand. *Platevindex martensi* is not found on rocky shores.

Remarks

All of the distinctive characters of *Platevindex* are present in the holotype of *Oncis martensi*, including a flattened and hard body, a narrow foot, a male opening to the right of the midline between the two eye tentacles and no accessory penial gland. In the original description of *P. martensi*, Plate (1893: 196) wrote that the holotype was collected from Singapore by professor von Martens. However, von Martens (1897: 128) later wrote that "*Oncis martensi* Plate was not found by me at Singapore, but at Petshaburi in the Gulf of Siam," which is in the north of the Gulf of Thailand. The label of the holotype at the Berlin Museum now reads "Siam, Petehabardi" (presumably a misspelling). Hoffmann (1928: 89) considered
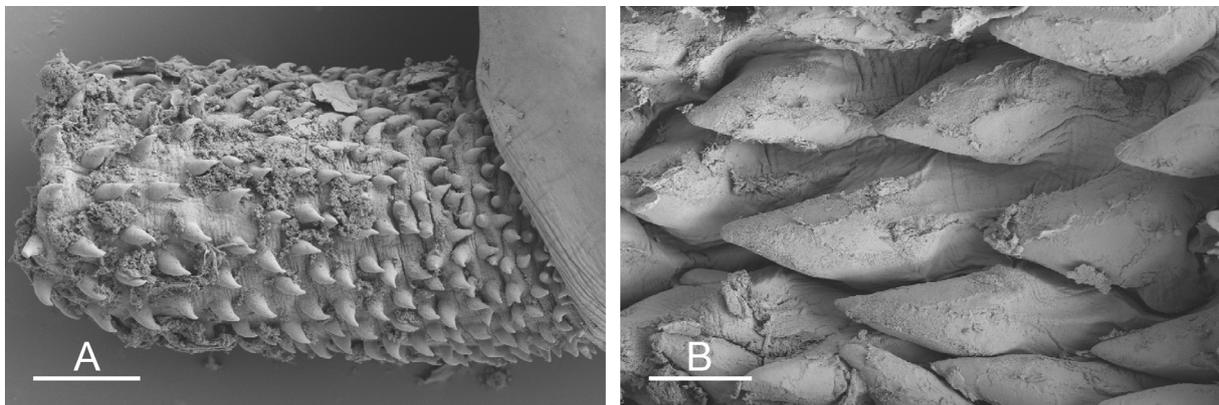
Fig. 57. *Platevindex martensi* (Plate, 1893), penial hooks. **A**. Penis everted with hooks outside, Peninsular Malaysia, Penang [964] (USMMC 00029). **B**. Australia, Darwin [1711] (NTM P.57611). Scale bars: A = 50 μm; B = 30 μm.

Petshaburi to be the type locality and even specified "Singapore, Plate, ex errore, nach Martens 1897." Also, note that the specific name appears as "*martensi*" in the text and in one figure caption (Plate 1893: 196, pl. 7, fig. 23a) but as "*martensii*" in the two other figure captions (Plate 1893: pl. 7, fig. 7, pl. 10, fig. 50).

The posterior (female) reproductive system in the holotype of *P. martensi* is largely destroyed. The hermaphroditic gland is in pieces and disconnected from the hermaphroditic duct. A large part of the female gland mass is separated from the oviduct and the deferent duct. However, the long and convoluted deferent duct is intact and is only consistent with the species described here. Plate (1893: 197) also described the color of the live animal (based on field notes from von Martens) as having an intense yellow hyponotum with black marbling as well as a light gray-brown foot. A yellow hyponotum is only found in *P. martensi* and *P. aptei* sp. nov. The color of the foot is the external trait which can distinguish these two species, and Plate's description of "light gray-brown" is a closer match to the bright orange foot of *P. martensi* than the dark black foot of *P. aptei* sp. nov. The number of dorsal eyes he described (90) is higher than what we have observed in *P. martensi*, but we could not check this as the dorsal eyes have lost their pigment. Plate's (1893: 197) description of the dorsal eyes that "sit alone on the big warts" is consistent with this species, but his comment that "this rule does not apply without exception, because on about 12 warts there are 2 eye spots, so that one can speak in these cases of a group" is surprising. We have found no evidence that dorsal eyes occur in groups of two in this species; Plate's statement that dorsal eyes occurred in pairs suggests that his count of dorsal eyes is likely an overestimate.

Plate's (1893: 198–199) original description of *Platevindex inspectabilis* from an island in southern Myanmar, in the Andaman Sea, mentioned the diagnostic characters of *Platevindex*. Plate indicated intestinal loops of type II, but this could not be verified because the intestine of the holotype was previously dissected. Plate's original description indicates a black-blue hyponotum (the color of the holotype has faded over time and could not be verified). Fresh specimens were not available from Myanmar, but many specimens were observed with a nearly solid black hyponotum (due to a high density of black spots) along the north-western coast of peninsular Malaysia. Despite a slight difference in the description of the hyponotum color, it can be determined that the holotype of *P. inspectabilis* belongs to the species described here due to the remains of its female (posterior) reproductive system. The length of the deferent duct adjacent to the oviduct is long and convoluted with elongated loops, which is indistinguishable from *P. martensi* (the deferent duct is similar in length in specimens of a similar size from Peninsular Malaysia). The length of the distal portion of the penis with hooks in *P. inspectabilis* (2 mm) also fits exactly the size range observed in *P. martensi* (2–2.5 mm). So, for all the reasons above, *P. inspectabilis* is considered here to be a junior synonym of *P. martensi*.

Semper's (1882) original description of *Onchidium coriaceum* was based on syntypes that are part of at least two species (see our remarks on *Platevindex coriaceus coriaceus*). One paralectotype of *O. coriaceum* from Penang belongs to *P. martensi*. Indeed, its posterior (female) reproductive system is not compatible with *P. coriaceus*, *P. tigrinus* or *P. luteus*, but displays the diagnostic feature of *P. martensi* (the wide, long, highly-convoluted deferent duct adjacent to the oviduct). In addition, Semper rightly noted that dorsal eyes are present across the notum including on its margin, and dorsal eyes very close to the notum edge (<2 mm) are only found in *P. martensi* and *P. aptei* sp. nov.

Zhang *et al*. (2017) recently re-described a species they identified as *Platevindex mortoni* based on specimens from Hong Kong, but *P. mortoni* is considered here a nomen dubium and their description is based on specimens that belong to at least two different species. One individual illustrated with a bright orange foot (Zhang *et al*. 2017: fig. 1e) is identified here as *P. martensi*.

Plate (1893: 196–199) did not comment on the very close similarity between *Platevindex inspectabilis* and *P. martensi* in his original descriptions, but he compared *P. inspectabilis* to *P. semperi*, from the

Philippines (Plate 1893: 199). This may be due to a similarity in their hyponotum color; the preserved hyponota of both *O. inspectabilis* and *O. semperi* were described by Plate as dark blue (though, now, decades later, the hyponotum is creamish in the type specimens of both species). However, *P. inspectabilis* and *P. semperi* are not regarded as synonyms because Plate's (1893: 193) description of the copulatory apparatus of *P. semperi* indicates that it is a junior synonym of *P. coriaceus*. *Platevindex inspectabilis* was also proposed as a synonym of *Oncis stuxbergi* by Hoffmann (1928: 88) and Labbé (1934: 235), but *Vaginulus stuxbergi* Westerlund, 1883 actually belongs to the genus *Onchidium* (Dayrat *et al.* 2016).

We collected *Platevindex martensi* in Northern Territory, Australia, but did not find it in Queensland, Australia, though it cannot be excluded that we missed it there. An online photo (viewed at https://www.inaturalist.org/observations/14094815 on 30 Jul. 2018) from Maroochy, Mooloolaba, Queensland, shows a *Platevindex* slug with elongated dorsal ridges similar to those found in *P. martensi* and *P. aptei* sp. nov. Also, its description mentions that it is an "orange footed mangrove onch slug." Because no photograph of the ventral surface is available, the identification of that slug cannot be confirmed. Until this geographic record is confirmed by the examination of actual specimens, Queensland is not considered part of the geographic distribution for *P. martensi*.

Fig. 58. Habitats of *Platevindex martensi* (Plate, 1893). **A**. Philippines, Bohol, narrow mangrove will tall trees on edge of fish ponds, cement ditches between the mangrove patches and the ponds (station 195). **B**. Philippines, Bohol, narrow mangrove on the edge of fish ponds, tall *Rhizophora* and *Avicennia*, many dead logs (station 194). **C**. Indonesia, Sulawesi, small mangrove used as outhouse by village, very impacted by trash (station 92). **D**. Australia, Darwin, *Ceriops* and old logs in *Rhizophora* forest (station 70).

Platevindex aptei Goulding & Dayrat sp. nov.
urn:lsid:zoobank.org:act:25DECF9A-226F-40A8-BC49-99815E6B2B9D
Figs 59–63

Etymology

Platevindex aptei sp. nov. is named for Deepak Apte, a great naturalist and the Executive Director of the Bombay Natural History Society, Mumbai, India. Deepak Apte provided great help in the organization of our fieldwork in India as well as with molecular lab work at the National Centre for Cell Science in Pune. We would not have been able to explore the mangroves of India without his assistance.

Material examined

Holotype

INDIA • holotype (45/20 [1112] mm); Andaman Islands, Shantipur, Kadamtala; 12°19.844′ N, 92°46.377′ E; 12 Jan. 2011; station 58, mangrove creek, open forest, lots of dead logs and trees; BNHS 3-1112.

Other material

INDIA – **Andaman Islands** • 1 spec. (35/20 [1092] mm); Shamkund, near Rangat; 12°29.448′ N, 92°50.620′ E; 11 Jan. 2011; station 57; ditches by road to the mangroves with high trees down to the mud on side of river; BNHS 8-1092 • 1 spec. (35/20 [1093] mm); same collection data as for preceding; BNHS 8-1093 • 3 specs (55/35 [#1], 50/35 [#2] and 25/18 [#3] mm); same collection data as for preceding; BNHS 8 • 1 spec. (25/20 [1111] mm); Shantipur, Kadamtala; 12°19.844′ N, 92°46.377′ E; 12 Jan. 2011; station 58; mangrove creek, open forest, lots of dead logs and trees; BNHS 3-1111 • 1 spec. (38/22 [1121] mm); Shoal Bay, by Bamboo Flat; 11°47.531′ N, 92°42.576′ E; 13 Jan. 2011; station 59; ditches and mud along the road; BNHS 14-1121.

MALAYSIA – **Peninsular Malaysia** • 1 spec. (28/17 [no DNA] mm); Penang; 05°23.782′ N, 100°11.469′ E; 8 Jul. 2011; station 12; open *Avicennia* mangrove with many dead logs; USMMC 00035 • 2 specs (50/39 [#1] and 35/23 [932] mm); Merbok; 05°39.035′ N, 100°25.782′ E; 14 Jul. 2011; station 21; deep *Rhizophora* forest with old, tall trees, hard mud, many small creeks and dead logs; USMMC 00036 • 1 spec. (31/24 [917] mm); Matang; 04°50.154′ N, 100°36.868′ E; 20 Jul. 2011; station 29; old *Rhizophora* mangrove with hard mud and open space between trees; USMMC 00037 • 3 specs (42/25 [5967], 37/21 [5968] and 35/22 [5955] mm); Matang; 04°50.217′ N, 100°36.826′ E; 26 Jul. 2016; station 256; old *Rhizophora* mangrove with hard mud and open space between trees; USMMC 00078.

Description

Color and morphology of live animals (Fig. 59)

Live animals are not usually covered with mud, and their natural color is usually visible without washing. The dorsal notum is brown, sometimes with darker markings. The notum bears low, elongated (longitudinal) ridges. The foot is black (Malaysia) or dark brown (India). The background of the hyponotum is bright yellow (Malaysia) to light yellow or beige (India) with a varying number of spots that range from light brown (India) to dark brown or black (Malaysia). Spots tend to be more concentrated around the margin of the hyponotum, but their density is highly variable (from only around the margin to the entire hyponotum). Exceptionally, the hyponotum can be homogenously dark brown with only a small yellow band around the foot. Small or juvenile specimens tend to have fewer or no spots on the hyponotum. Papillae with dorsal eyes are present. Their exact number is variable (between 35 and 50). Each papilla bears one dorsal eye. The dorsal eyes are distributed across the notum, with numerous eyes at the margin of the notum (i.e., many eyes are <2 mm from the notum edge).
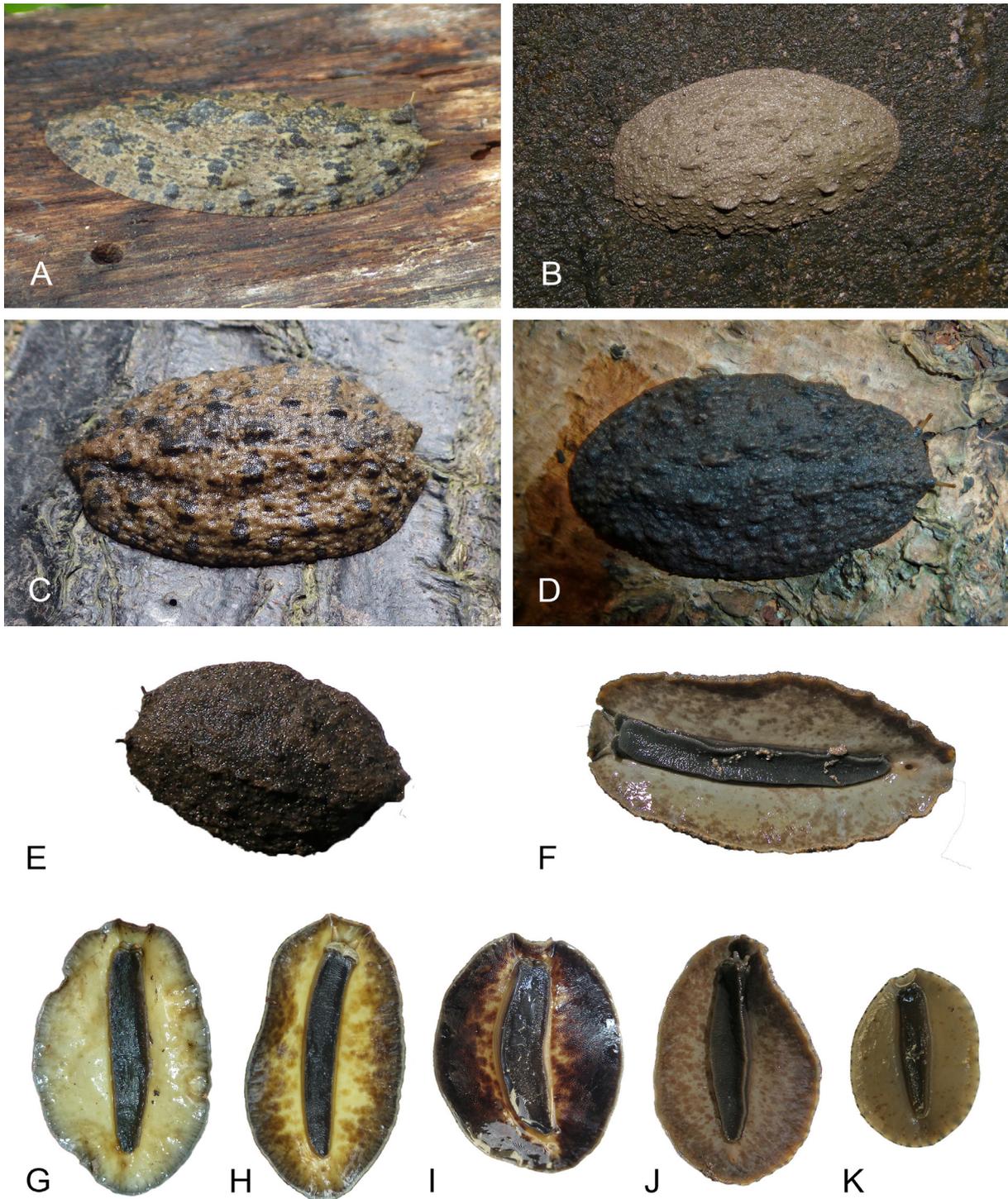
Fig. 59. *Platevindex aptei* Goulding & Dayrat sp. nov., live animals. **A**. Dorsal view, 42 mm long [5967], Malaysia, Matang (USMMC 00078). **B**. Dorsal view, ~55 mm [#1], India, Andaman Islands, Shamkund, near Rangat (BNHS 8). **C**. Dorsal view, 35 mm long [5955], Peninsular Malaysia, Matang (USMMC 00078). **D**. Dorsal view, 45 mm long [#2], Peninsular Malaysia, Merbok (USMMC 00036). **E**. Dorsal view, holotype, 45 mm long [1112], India, Andaman Islands, Shantipur (BNHS 3-1112). **F**. Ventral view, same as E. **G**. Ventral view, same as D. **H**. Ventral view, same as A. **I**. Ventral view, ~50 mm [#2] India, Andaman Islands (BNHS 8). **J**. Ventral view, 25 mm long [1111], India, Andaman Islands (BNHS 3-1111). **K**. Ventral view, ~25 mm [#3] India, Andaman Islands (BNHS 8).

Digestive system (Figs 2F, 60, 61A–B)

Radulae measure up to 6.4 mm long. Examples of radular formulae are presented in Table 5. The intestinal loops are of type II, with a transitional loop oriented between 7 and 9 o'clock (Figs 2F, 61A–B).

Reproductive system (Figs 61C, 62)

In the posterior part of the reproductive system, the oviduct is wider than the deferent duct (up to twice as wide). Its distal section (distal to the spermatheca) is slightly longer than its proximal section and is sharply bent (U-shaped). The deferent duct is slightly longer than the oviduct, not attached to it, and loosely to highly convoluted (Fig. 61C). The penial sheath is very thick but the penis inside is extremely thin. The vestibule is cylindrical and attached to the anterior, dorsal wall of the visceral cavity by many short muscle fibers. The distal, flexible region of the penis with hooks is approximately 2.5 to 5 mm long and is very narrow, approximately 80 μm wide. Penial hooks are large, approximately 30 to 40 μm long, and can be seen inside the semi-transparent penis. The retractor muscle of the penis inserts at the posterior end of the visceral cavity, near the rectum. The retractor muscle varies from much shorter than the penial sheath (one-fifth its length) to approximately as long as the penial sheath. In the penial complex, the deferent duct is convoluted in small loops (Fig. 62D).

Distinctive diagnostic features (Table 4)

Externally, *Platevindex aptei* sp. nov. can be easily distinguished from all other known species of *Platevindex* by its strikingly distinctive black or dark brown foot. The bright yellow or beige hyponotum
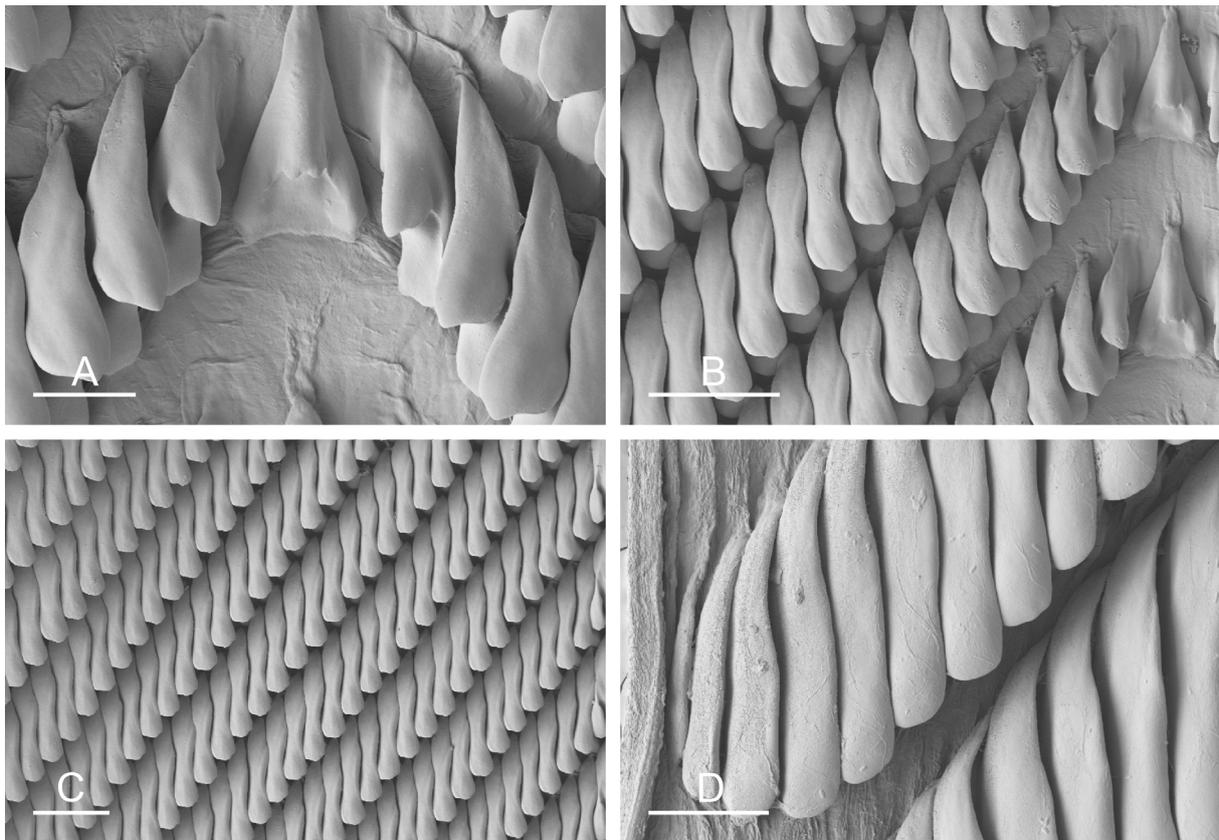
Fig. 60. *Platevindex aptei* Goulding & Dayrat sp. nov., radula, Peninsular Malaysia, Matang [5967] (USMMC 00078). **A**. Rachidian and innermost lateral teeth. **B**. Innermost lateral teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Scale bars: A, D = 20 μm; B = 50 μm; C = 60 μm.

distinguishes it from most other species of *Platevindex*, but this also occurs in *P. martensi*. Low, elongated (longitudinal) ridges on the dorsal notum are diagnostic of *P. aptei* sp. nov. as well as *P. martensi*. Internally, the thick penial sheath with a very narrow penis is a distinctive characteristic of *P. aptei* sp. nov., and the flexible region of the penis bearing spines is longer in *P. aptei* sp. nov. (2.5–5 mm) than in *P. martensi* (2–2.5 mm long).
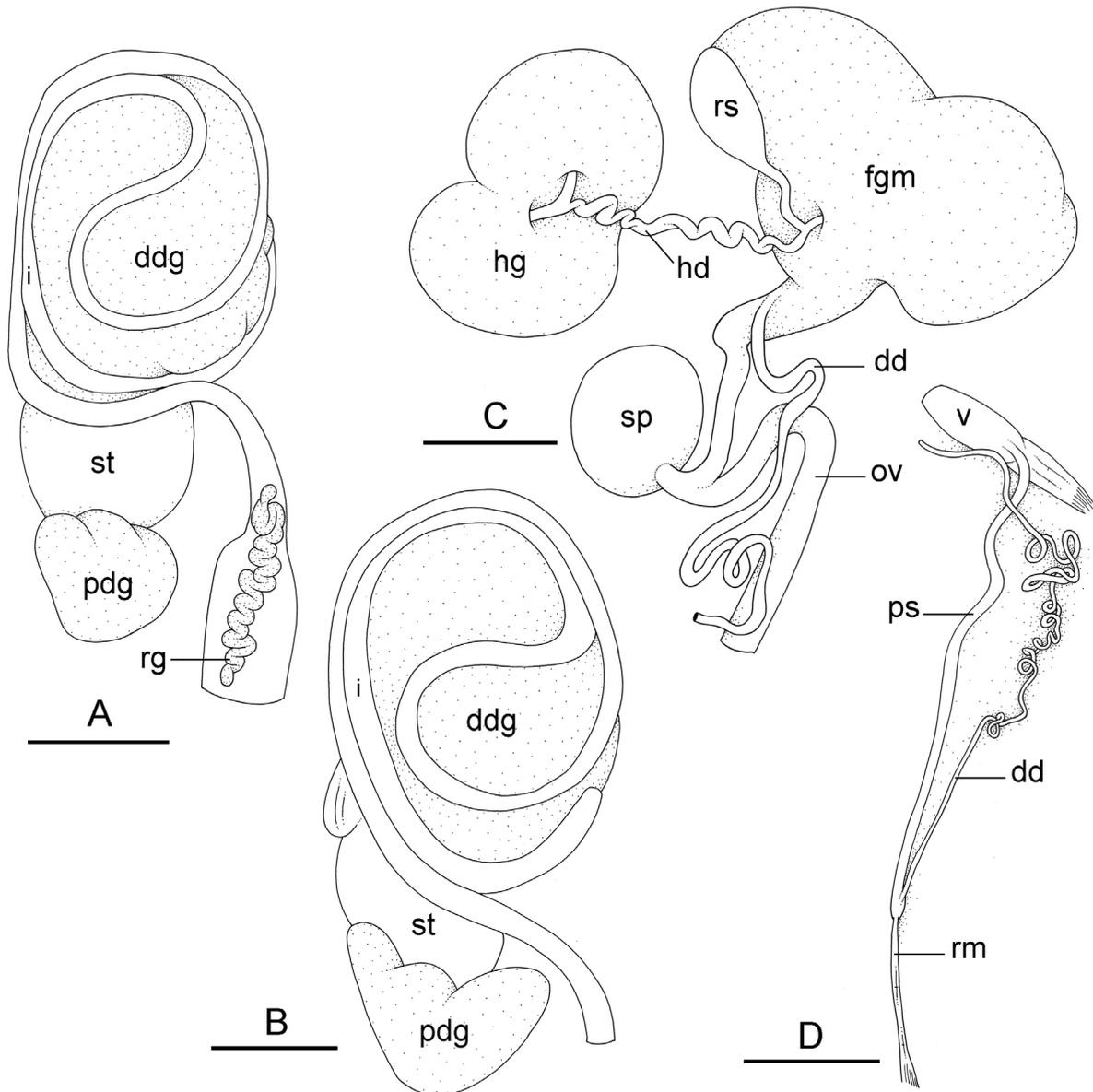
Fig. 61. *Platevindex aptei* Goulding & Dayrat sp. nov., digestive and reproductive systems, Peninsular Malaysia. **A**. Digestive system, dorsal view, type II, with a transitional loop oriented at 8 o'clock, [5955] (USMMC 00078). **B**. Digestive system, dorsal view, type II, with a transitional loop oriented at 9 o'clock, [5968] (USMMC 00078). **C**. Posterior reproductive system, same as A. **D**. Anterior, male copulatory apparatus, same as A. Abbreviations: dd = deferent duct; ddg = dorsal digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior digestive gland; ps = penial sheath; rg = rectal gland; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scale bars: A, D = 4 mm; B = 3 mm; C = 2 mm.

Distribution (Fig. 10C)

India: Andaman Islands. Malaysia: Peninsular Malaysia.

Habitat (Fig. 63)

Platevindex aptei sp. nov. is found in mangroves, typically on large, dead logs, as well as on tree trunks and roots, and cement ditches adjacent to mangroves, but is not found directly on mud. It is usually found in the high intertidal. It does not live on rocky shores.

Remarks

Platevindex aptei sp. nov. may also be present in Singapore, although it was not found there during our recent visit. Many onchidiid species present in the Bay of Bengal and Peninsular Malaysia are also present in Singapore, such as *Platevindex coriaceus, P. tigrinus*, *P. martensi*, *Peronina tenera* (Goulding *et al.* 2018c), *Onchidium typhae* (Dayrat *et al.* 2016), *Melayonchis siongkiati* and *M. eloisae* (Dayrat *et al.* 2017). However, there are other instances of onchidiid species which have not recently been found in Singapore even though they should be there based on their known geographic distribution, such as *Onchidium stuxbergi* (Dayrat *et al.* 2016) and *Melayonchis aileenae* Dayrat & Goulding, 2017 (Dayrat *et al.* 2017). A photo of a slug erroneously identified as *Onchidium griseum*, but which actually illustrates *Platevindex aptei* sp. nov., was found online, posted on the website WildSingapore.com with photos of *P. martensi*. The locality listed with the photo online is Sungei Buloh Wetland Reserve, Singapore, suggesting that *P. aptei* sp. nov. is present there. However, if *P. aptei* sp. nov. is present in Singapore, it may be at low abundance.
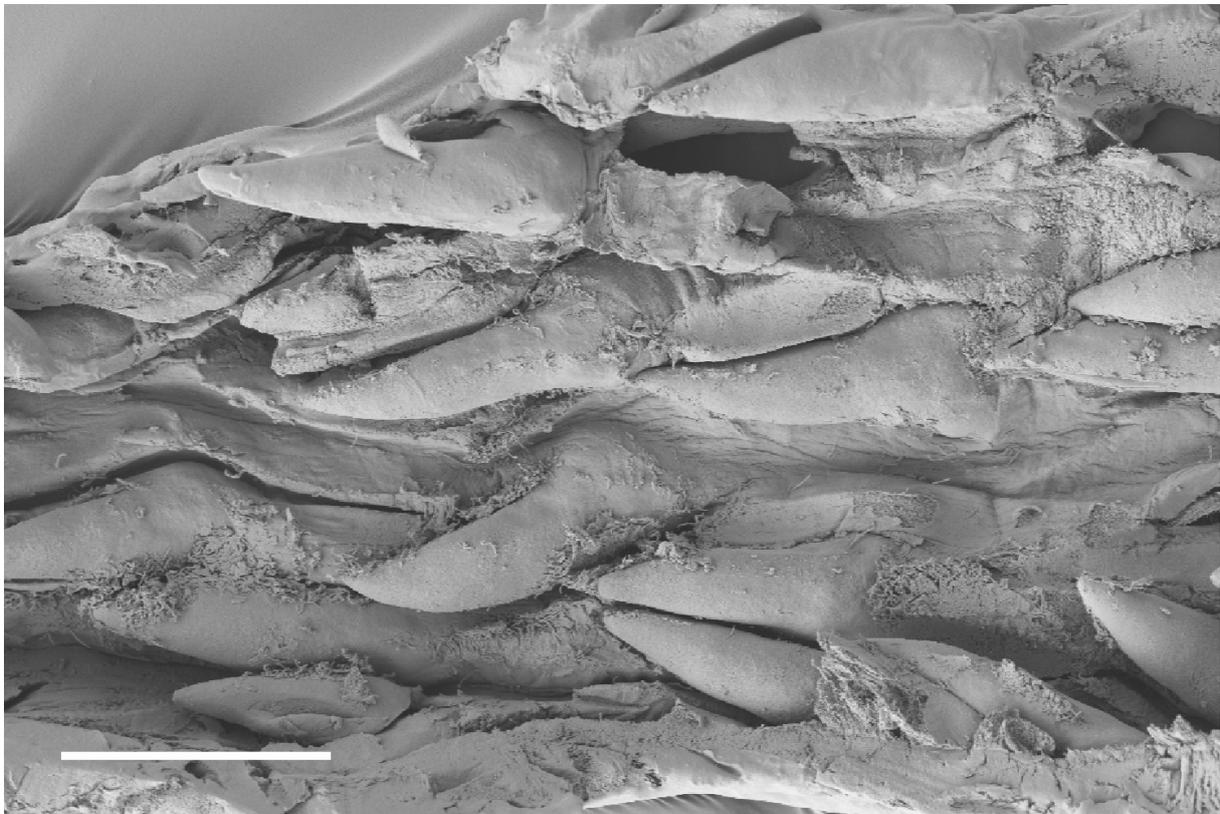
Fig. 62. *Platevindex aptei* Goulding & Dayrat sp. nov., penial hooks, Peninsular Malaysia, Matang [5967] (USMMC 00078). Scale bar = 30 μm.

Platevindex amboinae (Plate, 1893)
Figs 64–69

Onchidium amboinae Plate, 1893: 177–179, pl. 7, fig. 8, pl. 11, fig. 66.
Oncis coeca Plate, 1893: 199–200, pl. 7, fig. 9.

Oncis lata – von Martens 1897: 128 [non *Oncis lata* Plate, 1893].
Oncis coeca – Stantschinsky 1907: 395. — Hoffmann 1928: 86–87.
Oncis amboinae – Hoffmann 1928: 86–87.
Platevindex amboinae – Dayrat 2009: 5.

Material examined

Lectotype (here designated)
INDONESIA • lectotype (28/18 mm); Amboina [Ambon]; von Martens leg.; ZMB/Moll 11621a.

Paralectotypes
INDONESIA • 9 paralectotypes (29/20 to 18/12 mm); same collection data as for lectotype; ZMB/Moll 11621b.

Fig. 63. Habitats of *Platevindex aptei* Goulding & Dayrat sp. nov. **A**. India, Andaman Islands, mangrove creek, open, lots of dead logs and trees (station 58). **B**. India, Andaman Islands, ditches by road to the mangroves with high trees (station 57). **C**. Peninsular Malaysia, Matang, large, old *Rhizophora* forest, hard mud and open space (station 256). **D**. Peninsular Malaysia, Matang, large, old *Rhizophora* forest, hard mud and open space between trees (station 29).

Holotype of *Oncis coeca*

INDONESIA • holotype (27/16 mm) by monotypy; Amboina [Ambon]; expedition Gazelle leg.; ZMB/Moll 27446.

Notes on type material

Onchidium amboinae. The notum of the lectotype was cut open for the present study to examine the internal anatomy; no internal organs were removed. Three paralectotypes (29/20, 28/21 and 27/23 mm) are completely empty with no internal organs. Two paralectotypes (25/17 and 24/15 mm) were previously dissected, with their internal organs remaining except for the male parts. Four paralectotypes (24/14, 23/20, 20/15 and 18/12 mm) are still unopened.

Oncis coeca. Parts of the posterior (female) reproductive system and of the digestive system are still present in the holotype, although they were previously dissected into pieces, likely by Plate himself. Of the male reproductive parts, only the deferent duct remains.

Other material

INDONESIA – **Seram** • 1 spec. (38/28 [2883] mm); Piru; 03°04.072′ S, 128°11.362′ E; 19 Feb. 2014; station 136; beach of palms and *Acrostichum* ferns behind *Sonneratia* mangrove; UMIZ 00105. – **Halmahera** • 2 specs (32/14 [5043] and 32/22 [5843] mm); Buli; 00°55.367′ N, 128°20.647′ E; 17 Mar. 2015; station 213; tall and old *Rhizophora* forest, high intertidal; UMIZ 00106. – **Sulawesi** • 5 specs (30/25, 20/20, 20/15, 18/15 and 15/15 mm); Luwu; M. Weber leg.; ZMB/Moll 46314 • 3 specs (25/20, 22/17 [#1] and 15/12 mm); SMF 333602/3.
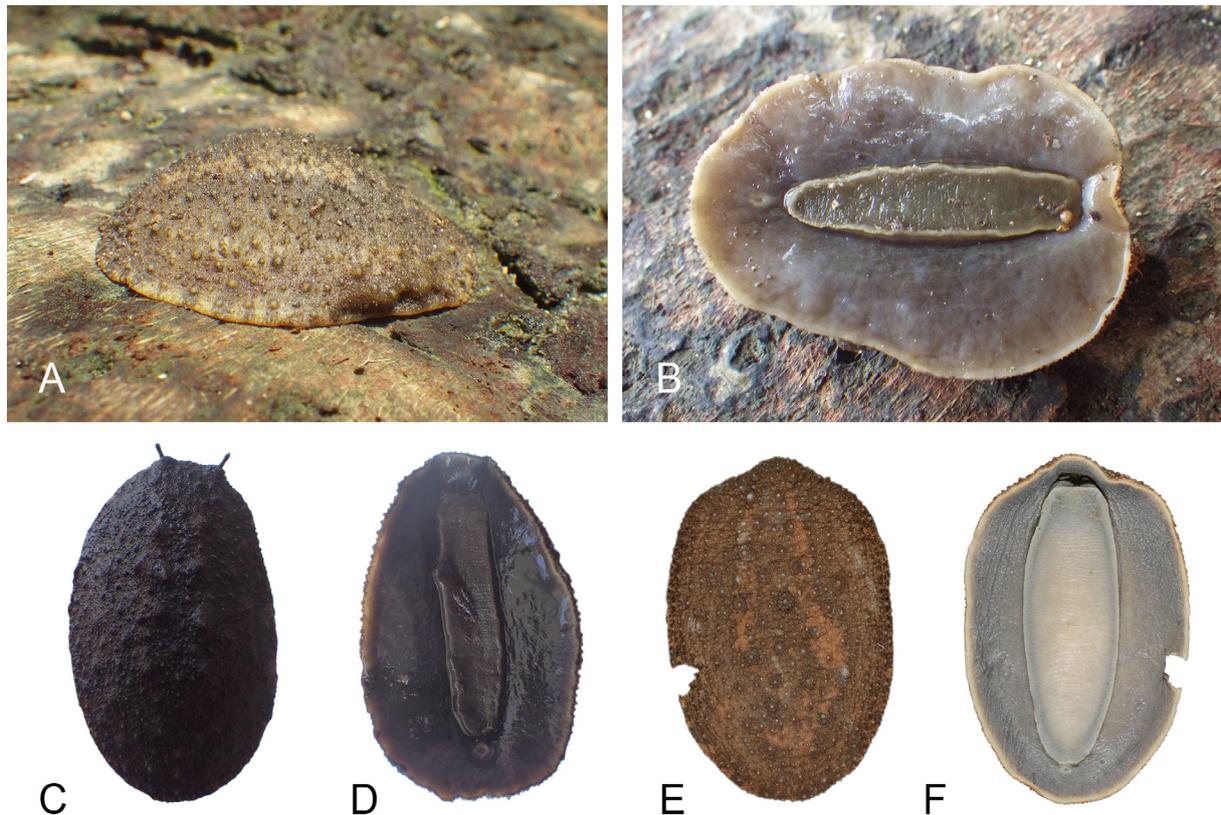
Fig. 64. *Platevindex amboinae* (Plate, 1893), live and preserved animals, Indonesia. **A**. Dorsal view, 38 mm long [2883], Seram (UMIZ 00105). **B**. Ventral view, same as A. **C**. Dorsal view, 32 mm long [5043], Halmahera (UMIZ 00106). **D**. Ventral view, same as C. **E**. Dorsal view, preserved specimen, 32 mm long [5843], Halmahera (UMIZ 00106). **F**. Ventral view, same as E.

Description

Color and morphology of live animals (Fig. 64)

Live animals are usually not covered with mud, and their natural color is usually mostly visible without washing. The dorsal notum varies from light brown to dark brown, almost black. The hyponotum varies from grey to dark blue, almost black. The foot is yellowish-grey to dark grey (almost black). Dorsal papillae are short (<1 mm) and do not bear eyes. Large, thorny papillae are absent.

Digestive system (Figs 3C–E, 65–66, 67A)

Radulae measure up to 5.2 mm long. Examples of radular formulae are presented in Table 5. The intestinal loops are of type III, with a transitional loop oriented between 1 and 6 o'clock (Figs 3C–E, 66A–B). The intestinal loops of the lectotype (Fig. 67A) are indistinguishable from those observed in a specimen from Sulawesi (Fig. 66B).

Reproductive system (Figs 67B–68)

In the posterior part of the reproductive system, the oviduct is slightly wider than the deferent duct. Its distal section (distal to the spermatheca) is slightly shorter than its proximal section (or of the same length). The deferent duct is much longer than the oviduct, not attached to it, and highly coiled with long loops. The distal, flexible region of the penis is from 1 to 2.5 mm long and bears no hooks. The posterior retractor muscle of the penis inserts within the anterior half of the visceral cavity (and near the nervous system in specimens from Halmahera). The retractor muscle varies from approximately half the length of the penial sheath to as long as the penial sheath. The deferent duct is highly convoluted, with many loops around the penis. The deferent duct is twice as wide distally as proximally.
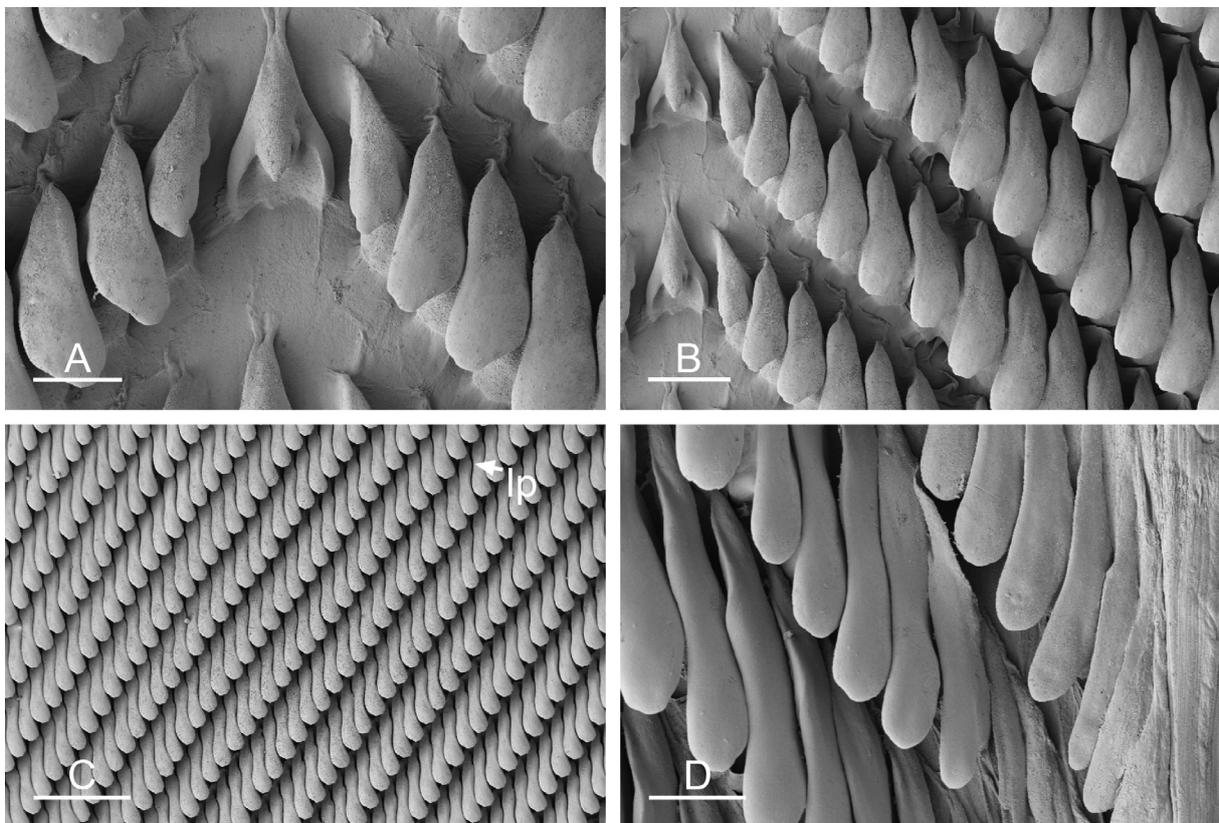
Fig. 65. *Platevindex amboinae* (Plate, 1893), radula, Indonesia, Seram [2883]. **A**. Rachidian and innermost lateral teeth. **B**. Lateral teeth with rachidian teeth. **C**. Lateral teeth. **D**. Outermost lateral teeth. Abbreviation: lp = lateral protuberance. Scale bars: A, D = 20 μm; B = 30 μm; C = 100 μm.

Distinctive diagnostic features (Table 4)

Externally, the lack of dorsal eyes is shared by both *Platevindex amboinae* and *P. latus*. However, the lack of dorsal eyes should be used with caution for identification because dorsal eyes often are retracted (and thus hard to see). *Platevindex amboinae* can be distinguished from *P. latus* by the presence of smaller dorsal papillae (the papillae of *P. latus* are larger and thorny). Internally, intestinal loops of type III are found in only two species of *Platevindex*, *P. amboinae* and *P. latus*. Both species, however, can be distinguished by the deferent duct in the anterior reproductive system, which seems to be slightly more convoluted in *P. amboinae* than in *P. latus*, although this should probably be evaluated with additional individuals. Based on the available data, however, *P. amboinae* and *P. latus* do not overlap geographically (Fig. 10).
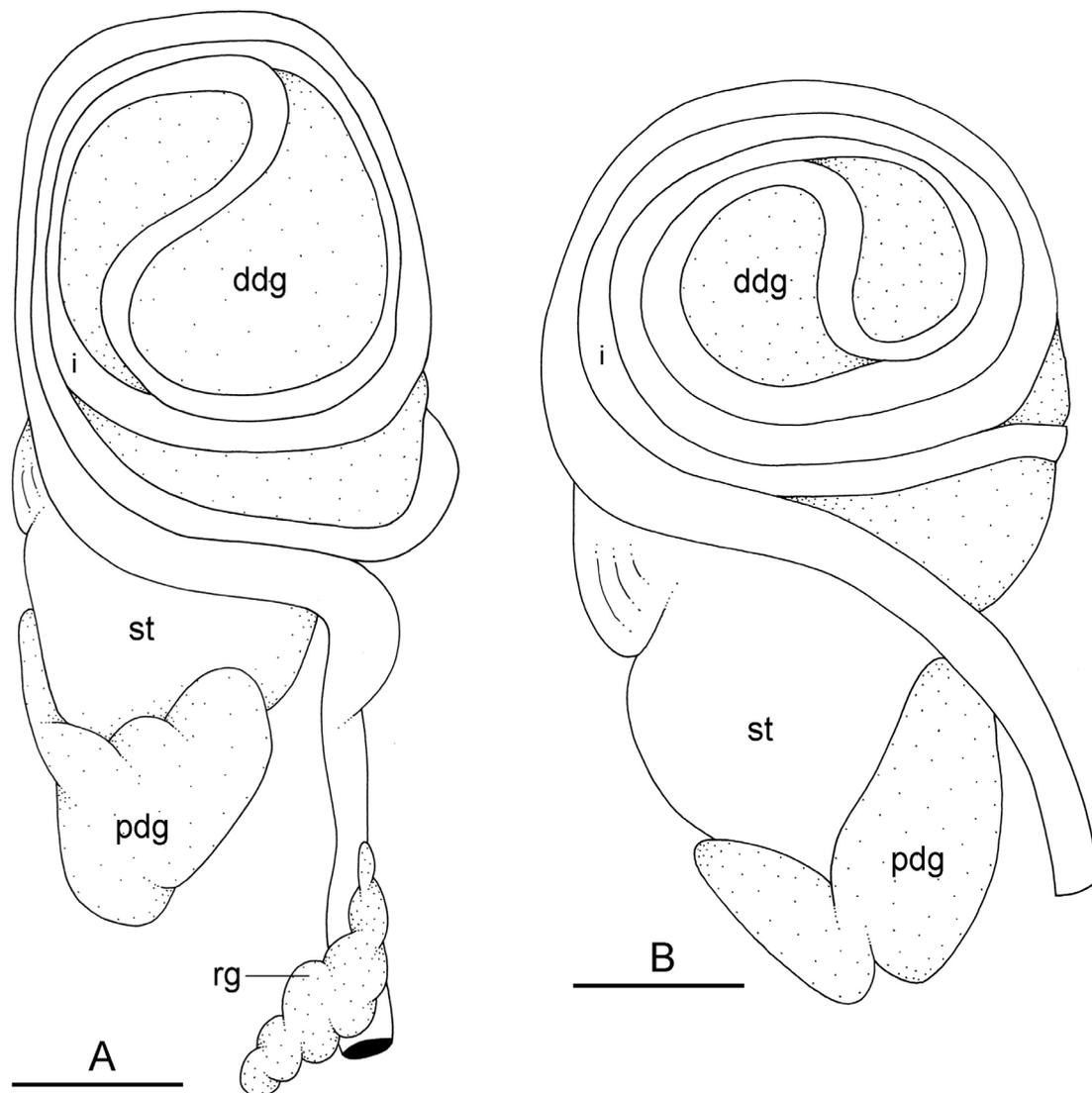
Fig. 66. *Platevindex amboinae* (Plate, 1893), digestive system, dorsal view, intestinal loops of type III. **A**. Transitional loop oriented at 2 o'clock, Seram, Indonesia [2883] (UMIZ 00105). **B**. Transitional loop oriented at 6 o'clock, Sulawesi, Indonesia [#1] (SMF 333602). Abbreviations: ddg = dorsal digestive gland; i = intestine; pdg = posterior digestive gland; rg = rectal gland; st = stomach. Scale bars: A = 4 mm; B = 3 mm.
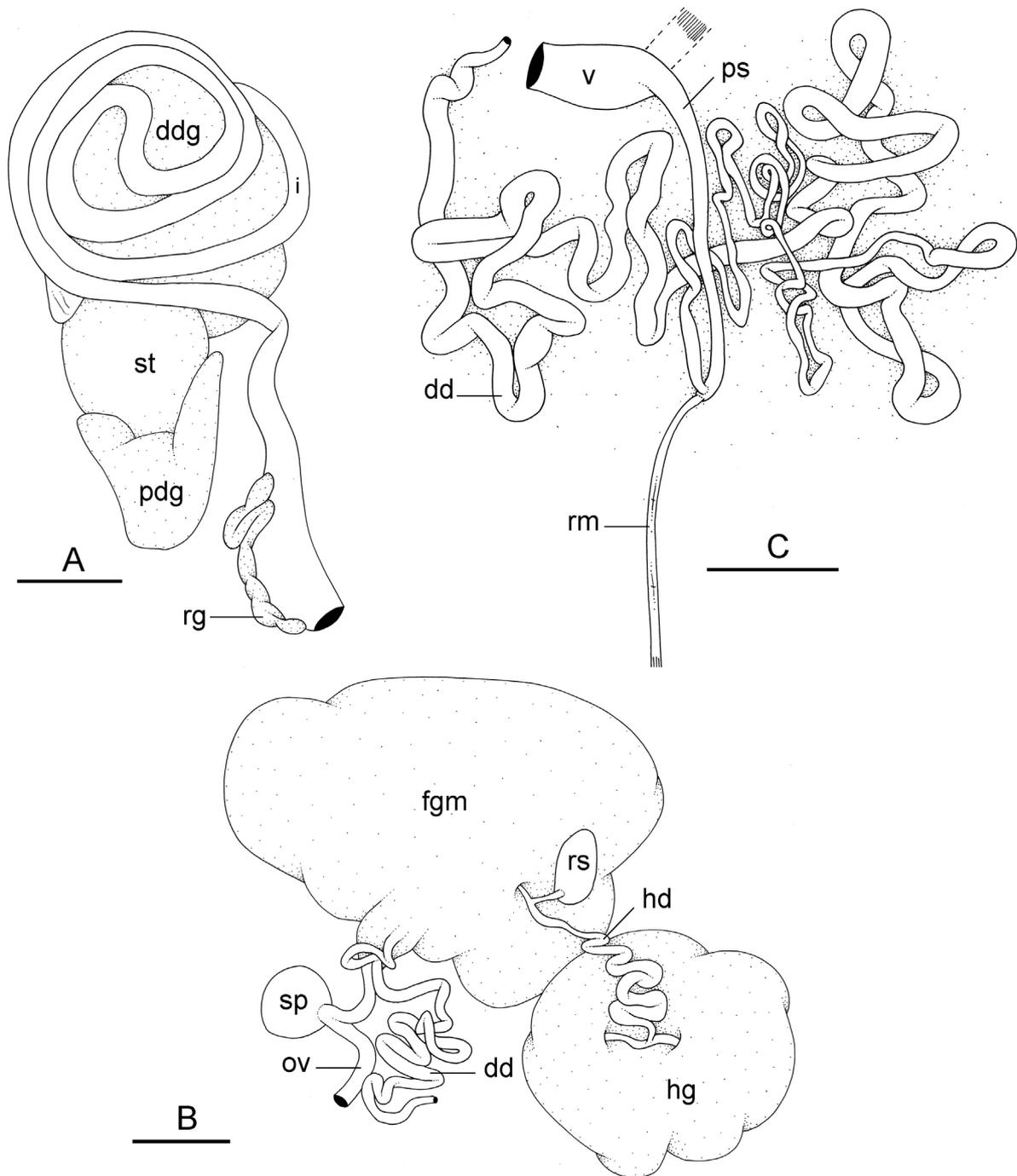
Fig. 67. *Platevindex amboinae* (Plate, 1893), digestive and reproductive systems, lectotype, Ambon, Indonesia (ZMB/Moll 11621a). **A**. Digestive system, dorsal view, type III, with a transitional loop oriented at 1 o'clock. **B**. Posterior reproductive system. **C**. Anterior, male copulatory apparatus. Abbreviations: dd = deferent duct; ddg = dorsal digestive gland; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; i = intestine; ov = oviduct; pdg = posterior digestive gland; ps = penial sheath; rg = rectal gland; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; st = stomach; v = vestibule. Scale bars: A = 4 mm; B = 3 mm; C = 2 mm.

Distribution (Fig. 10C)

Indonesia: Ambon (type locality of both *Platevindex amboinae* and *P. coecus*), Halmahera (new record) and Seram (new record).

Habitat (Fig. 69)

Platevindex amboinae is found on dead logs or tree trunks but not directly on mud, within a mangrove forest or in the higher intertidal adjacent to mangrove trees. It is not found on rocky shores.

Remarks

Onchidium amboinae needs to be transferred to the genus *Platevindex* due to the following combination of characters of the lectotype: flattened body, male pore slightly to the right of the midline between the ocular tentacles and no accessory penial gland. Plate (1893: 178) also indicated that there is a rectal gland in the original description, and it is clearly present in the lectotype (as in all *Platevindex* slugs). The absence of dorsal eyes and a short penis with no hooks mentioned by Plate (1893: 177) were confirmed by our examination of the lectotype. The hyponotum color was described as black with a white margin (1 to 1.5 mm wide), which is exactly what was observed in one of our live specimens.
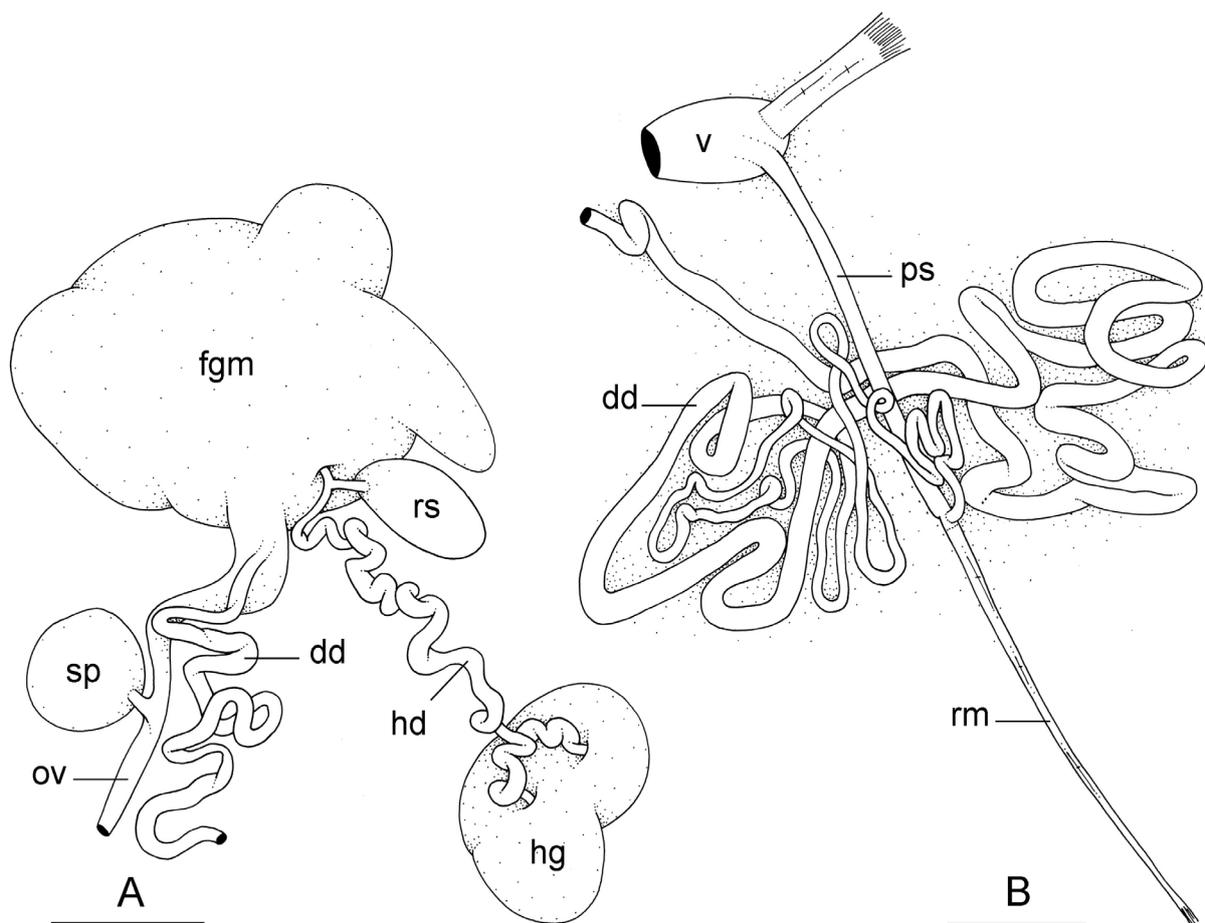
Fig. 68. *Platevindex amboinae* (Plate, 1893), reproductive system, Seram, Indonesia [2883] (UMIZ 00105). **A**. Posterior reproductive system. **B**. Anterior, male copulatory apparatus. Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; ps = penial sheath; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; v = vestibule. Scale bars: A = 4 mm; B = 2 mm.

However, Plate (1893: 178) described an intestine of type II in *Onchidium amboinae*, while the intestine of the lectotype (and of all newly-collected individuals) is clearly of type III (Fig. 67A).

The holotype of *P. coecus* (by monotypy) is characterized by a combination of traits diagnostic of species of *Platevindex*: a flattened body, a male opening slightly to the right of the midline between the ocular tentacles, a rectal gland and no accessory penial gland. In the original description, Plate (1893:199–200) indicated a grayish-yellow sole and a black-blue hyponotum with a white margin, and also the absence of dorsal eyes. The only species in Ambon which lacks dorsal eyes is *P. amboinae*. Hoffmann (1928: 86–87) transferred *Onchidium amboinae* to *Oncis* (i.e., *Platevindex*) and considered *Oncis coeca* (i.e., *Platevindex coecus*) to be a synonym of *Oncis amboinae* (i.e., *Platevindex amboinae*). Labbé (1934: 234–235) agreed with Hoffmann even though he did not examine any new material. The deferent duct in the penial apparatus and in the posterior part of the reproductive system is extremely convoluted, exactly like in *P. amboinae*. The pieces of the intestine of the holotype were put together and are of type III, although Plate (1893: 200) described a digestive system of type II. There is no anatomical difference between the name-bearing types of *Platevindex coecus* and *P. amboinae*, both of which were described from Ambon, Indonesia. We did not find *Platevindex amboinae* during our mangrove survey in Ambon but we found it on the nearby island of Seram, where it seems to be rare. *Platevindex amboinae* was also rare in Halmahera. It may still be present in Ambon, but most likely as a rare species.

Two lots previously identified as *Oncis lata* from Sulawesi are re-identified here as *P. amboinae* (ZMB/Moll 46314, SMF 333602/3). The original label for ZMB/Moll 46314 indicates that the specimens were collected in Luwu by M. Weber, which means that they are very likely the specimens which von Martens (1897: 128) identified as *Oncis lata*. Von Martens indicated that he examined 10 specimens. Five of those are in Berlin (ZMB/Moll 46314) and three of them are in Frankfurt-am-Main (SMF 333602/3), which were originally part of the Heidelberg collections. The specimens examined here all lack dorsal eyes, a character shared by both *P. lata* and *P. amboinae*, but they also lack the large, thorny papillae that are diagnostic of *P. lata*, suggesting that they belong to *P. amboinae*.

Labbé (1934: 234–235) described a specimen (14/11 mm) from New Zealand which he identified as *Oncis amboinae*. However, if Labbé's description is accurate, this specimen cannot be part of *Platevindex amboinae* or any species of *Platevindex* because Labbé (1934: 235) indicated that a group of dorsal eyes was present in the middle of the notum (in *Platevindex*, dorsal eyes are always single). It is unclear which species Labbé examined, as *Onchidella* is the only onchidiid genus documented so far in New

Fig. 69. Habitats of *Platevindex amboinae* (Plate, 1893), Indonesia. **A**. Halmahera, open, tall *Rhizophora* forest, impacted by mining (station 213). **B**. Seram, on base of palm tree surrounded by *Acrostichum* ferns behind a *Sonneratia* mangrove (station 136).

Zealand. The combination of traits mentioned in the brief description (dorsal eyes, no accessory penial gland and no penial hooks), suggests it could be a *Wallaconchis* slug, although that is incompatible with intestinal loops of type II. Besides, *Wallaconchis* is not known south of New Caledonia. Most likely, as often with Labbé's work, the locality or the description, or even both, are erroneous (Dayrat *et al.* 2020).

Platevindex latus (Plate, 1893)
Figs 70–73

Oncis lata Plate, 1893: 191–192, pl. 7, fig. 2, pl. 11, fig. 59.

Oncis lata – Stantschinsky 1907: 395.
Platevindex latus – Dayrat 2009: 5.

Material examined

Lectotype (here designated)
PAPUA NEW GUINEA • lectotype (27/27 mm); Neu-Britannien [New Britain, Papua New Guinea]; ZMB/Moll 45656a.

Paralectotypes
PAPUA NEW GUINEA • 3 paralectotypes (28/27, 27/24 and 23/26 mm); same collection data as for lectotype; ZMB/Moll 45656b.

Notes on type material
The lectotype was dissected for the present study and all its internal organs were left inside except for the penial complex, which was extracted and retained in a small vial. The three paralectotypes were previously dissected and are completely empty with no internal organs. All their male parts are missing. Pieces of dorsal notum, stomach, digestive gland, intestine and female gland mass remain in the jar, all mixed together, but they cannot be assigned to a particular paralectotype.

Other material
PAPUA NEW GUINEA • 3 specs (33/28 [#3], 32/31 [#1] and 30/25 [#2] mm); New Britain?; ZMH 27511.

Description

Color and morphology (Fig. 70)
The color of live slugs is unknown. The preserved dorsal surface is dark brown, occasionally with lighter brown, longitudinal stripes. The preserved hyponotum is blue-grey and the foot is light yellow. Dorsal papillae are large and thorny, and do not bear dorsal eyes.
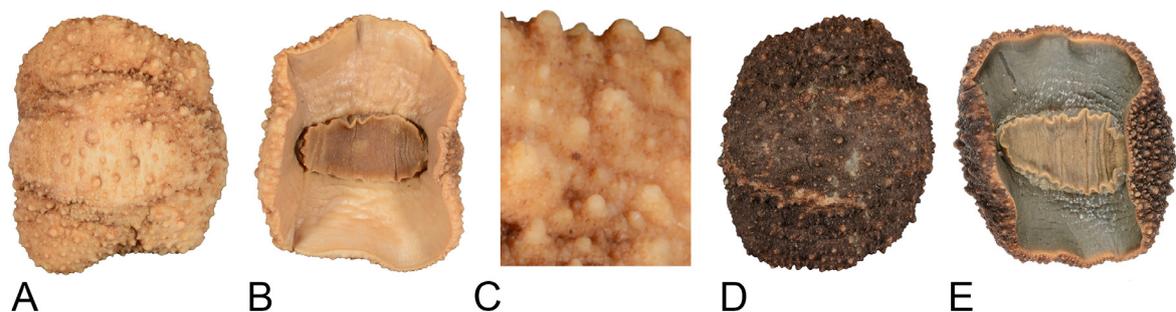
Fig. 70. *Platevindex latus* (Plate, 1893), preserved specimens. **A**. Dorsal view, 24 mm, syntype, New Britain, Papua New Guinea (ZMB/Moll 45656). **B**. Ventral view, same as A. **C**. Close-up of papillae, same as A. **D**. Dorsal view, 25 mm, Papua New Guinea (ZMH 27511). **E.** Ventral view, same as D.

Digestive system (Figs 3B, 71–72)

Radulae measure up to 7.2 mm in length. Examples of radular formulae are presented in Table 5. The intestinal loops are of type III, with a transitional loop oriented between 12 and 2 o'clock (Figs 3B, 72).

Reproductive system (Fig. 73)

In the posterior reproductive system, the oviduct is short and approximately as wide as the deferent duct. Its distal section (distal to the spermatheca) is approximately as long as its proximal section. The deferent duct is longer than the oviduct, not attached to it, and is tightly coiled with a few short U-shaped loops. There are no hooks inside the distal, flexible region of the penis. The posterior retractor muscle inserts in the anterior half of the visceral cavity. The retractor muscle of the penis varies from approximately half the length of the penial sheath to ¾ its length. The deferent duct is highly convoluted.
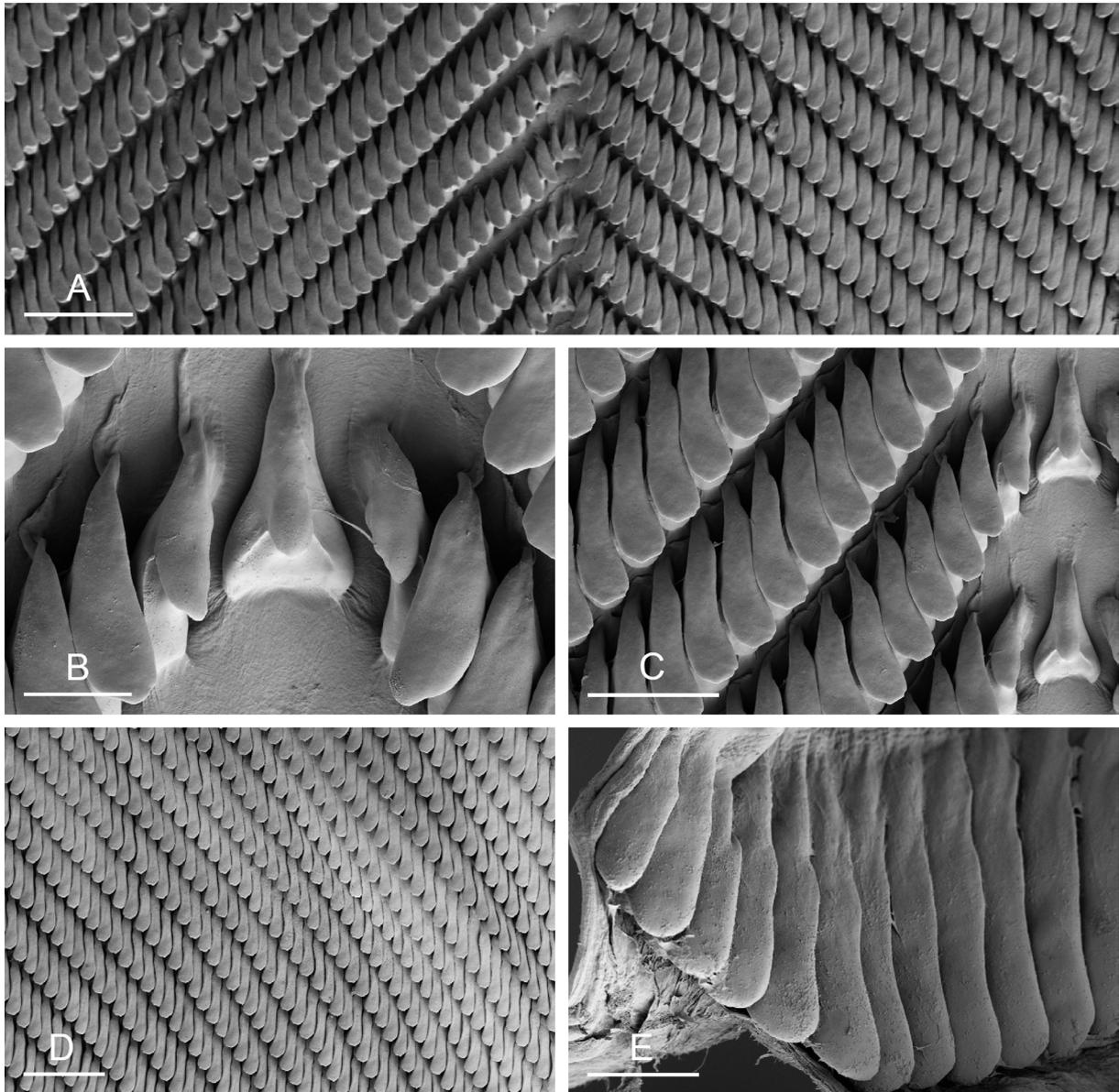
Fig. 71. *Platevindex latus* (Plate, 1893), radula, Papua New Guinea [#1] (ZMB/Moll 45656). **A–C**. Rachidian and lateral teeth. **D**. Lateral teeth. **E**. Outermost lateral teeth. Scale bars: A, D = 100 μm; B, E = 20 μm; C = 50 μm.

Distinctive diagnostic features (Table 4)

Platevindex latus and *P. amboinae* are the only known species of *Platevindex* with no dorsal eyes and no penial hooks. *Platevindex latus* can be distinguished from *P. amboinae* externally by its large and thorny dorsal papillae and internally by its anterior deferent duct, which is slightly less convoluted.

Distribution (Fig. 10C)

Papua New Guinea: New Britain (type locality and present study).
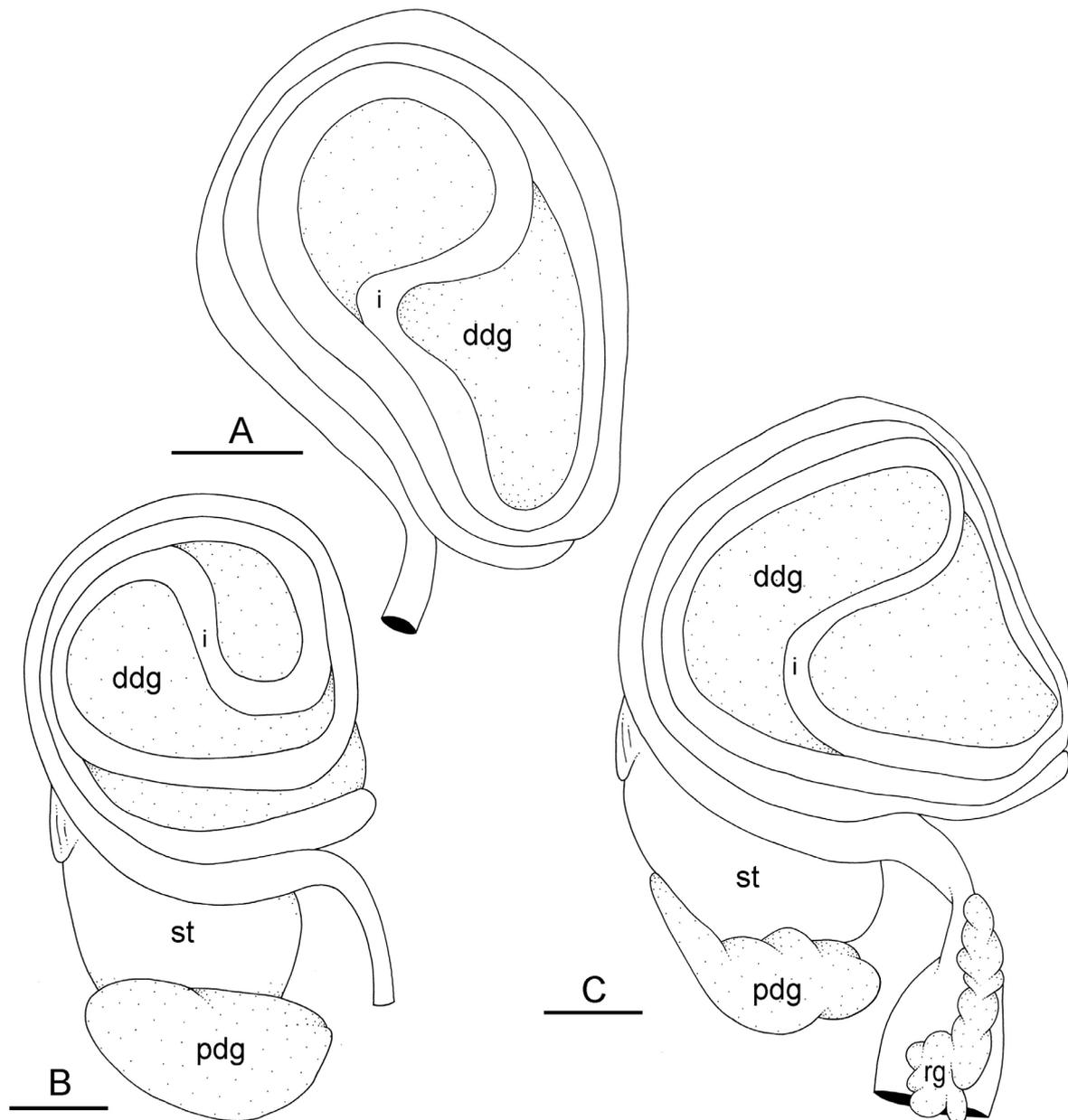
Fig. 72. *Platevindex latus* (Plate, 1893), digestive system, dorsal view, intestinal loops of type III. **A**. Transitional loop oriented at 2 o'clock, New Britain, Papua New Guinea, lectotype (ZMB/Moll 45656a). **B**. Transitional loop oriented at 12 o'clock, Papua New Guinea [#1] (ZMH 27511). **C**. Transitional loop oriented at 2 o'clock, Papua New Guinea [#2] (ZMH 27511). Abbreviations: ddg = dorsal digestive gland; i = intestine; pdg = posterior digestive gland; rg = rectal gland; st = stomach. Scale bars = 3 mm.
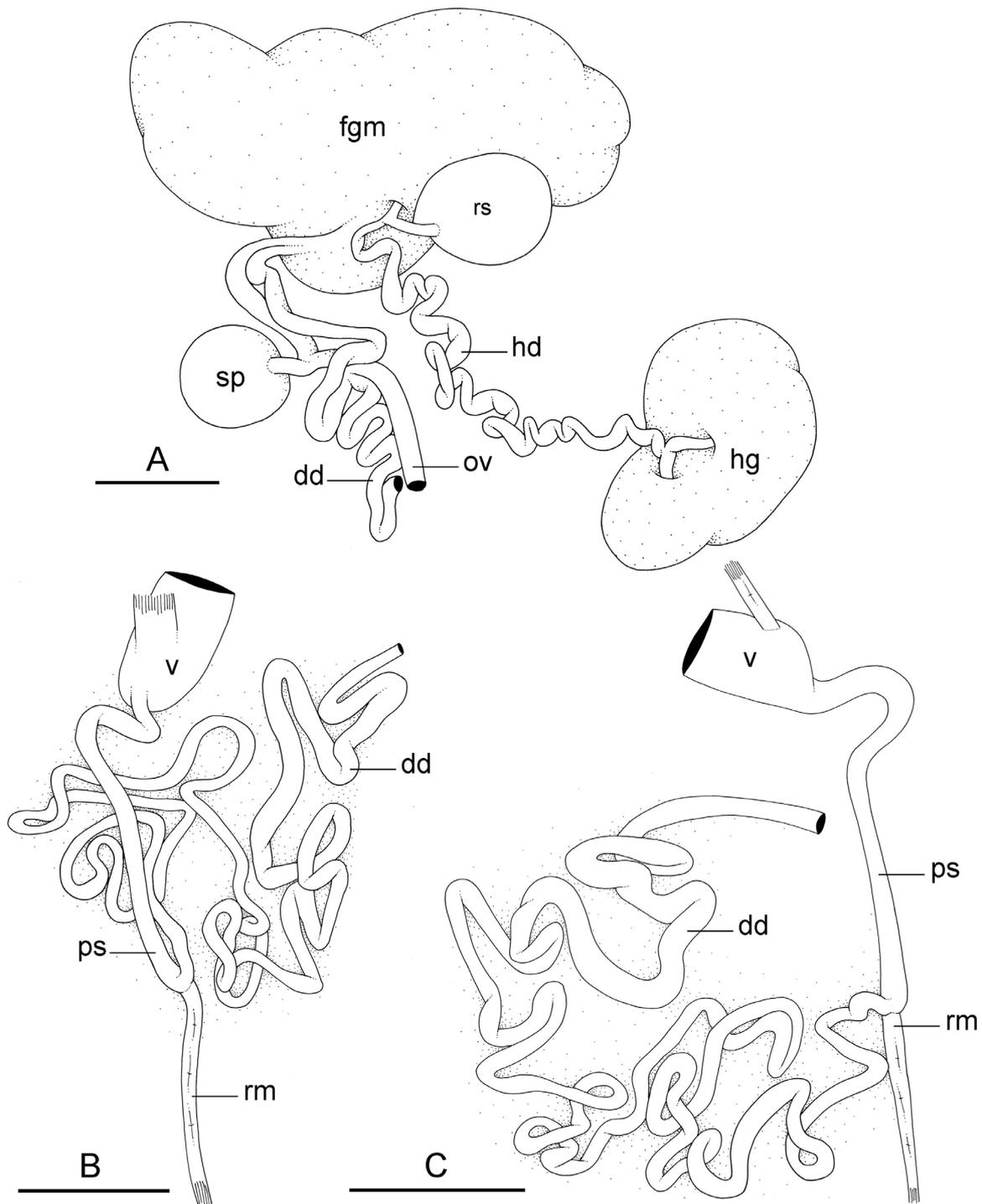
Fig. 73. *Platevindex latus* (Plate, 1893), reproductive system. **A**. Posterior reproductive system, Papua New Guinea [#2] (ZMH 27511). **B**. Anterior, male copulatory apparatus, New Britain, Papua New Guinea, lectotype (ZMB/Moll 45656a). **C**. Anterior, male copulatory apparatus, same as A. Abbreviations: dd = deferent duct; fgm = female gland mass; hd = hermaphroditic duct; hg = hermaphroditic gland; ov = oviduct; ps = penial sheath; rm = retractor muscle; rs = receptaculum seminis; sp = spermatheca; v = vestibule. Scale bars: A = 3 mm; B–C = 2 mm.

Habitat

No habitat was mentioned in the original description of *P. latus* or on the labels of the additional material. However, *P. latus* likely lives on dead logs in mangroves, like its close relative *P. amboinae*.

Remarks

The flattened body and narrow foot of the lectotype of *Platevindex latus* clearly indicate that it belongs to *Platevindex*. In the original description, Plate (1893) did not mention whether a rectal gland is present or absent, but it is present in the lectotype as well as in the non-type material (it is present in all species of *Platevindex*). An accessory penial gland is also absent in both the lectotype and the non-type material (it is absent in all species of *Platevindex*).

In the original description, Plate (1893: 191) described dorsal "conical granules" and indicated that "the mantle appears through them as if spiked with small thorns." Conical papillae are present in the lectotype and all paralectotypes of *P. latus* as well as in the additional material from Papua New Guinea. Plate (1893: 192) described the length of the penis but did not mention penial hooks, so it can be assumed that he did not see penial hooks in the types he dissected (now paralectotypes). However, because the male parts are missing from the three paralectotypes dissected by Plate, this could not be confirmed. At any rate, penial hooks are absent in the lectotype dissected for the present study. The intestinal loops of the lectotype are of type III and Plate's (1893: 192) description of a type II likely is a mistake, which would be consistent as he made the same error in the description of *P. amboinae*.

Fresh material for DNA sequencing was not available. *Platevindex latus* was not collected during the recent MNHN expeditions in Madang and New Ireland, Papua New Guinea. Some old material discovered at the Zoologisches Museum in Hamburg seems to be part of *P. latus* even though its locality is uncertain (the label in the jar states "Papua New Guinea. New Britain? Museum Godeffroy"). This material is externally identical to the lectotype (and paralectotypes) of *P. latus*. Plate (1893: 192) described a penis measuring 7 mm long (the proximal chondroid tube being 5 mm long and the distal, flexible region being 2 mm long). In one specimen from the Zoologisches Museum in Hamburg, the chondroid tube also measured 5 mm, but the distal region without hooks was 0.5 mm long rather than 2 mm. However, individual variation in this character occurs within species of *Platevindex*, and more specimens are needed to evaluate the variation for this trait within *P. latus*.

Hoffmann (1928: 86) suggested that *Platevindex latus* (as *Oncis lata*) was a synonym of *Onchidium granulosum* Lesson, 1831 (type locality New Ireland, Papua New Guinea), based on the original descriptions. Although Hoffmann acknowledged that Lesson's description was not very informative, he considered that Lesson's description of a notum being much wider than the sole indicated that *Onchidium granulosum* referred to a species of *Oncis* (*Platevindex*). Labbé (1934: 234) agreed with Hoffmann. However, Lesson's description is brief and leaves out many important details, such as whether dorsal eyes are present or not. The wide foot in Lesson's illustration of *Onchidium granulosum* (Lesson 1831: pl. 14, fig. 2) does not appear to represent a species of *Platevindex*. The description of the habitat as a rocky shore also strongly suggests that *Onchidium granulosum* does not apply to a species of *Platevindex*, but, instead, possibly to a species of *Peronia* or *Wallaconchis*. Adams & Adams (1855: 234) transferred *Onchidium granulosum* to *Onchidella* with no justification. Because its type material could not be located and its internal anatomy was not described by Lesson, *Onchidium granulosum* is regarded here as a nomen dubium which applies to an onchidiid species of an unidentifiable genus.

Von Martens (1897: 128) indicated that M. Weber found *Oncis lata* in "Celebs: Mündung des Flusses Djenemaedja in Luwu" [Sulawesi: mouth of the river Djenemaedja in Luwu]. Measurements were provided for the largest and smallest specimens, and the edge of the hyponotum was described as dirty yellow-gray. Von Martens indicated that the specimens are exactly the same as Plate's (1893)

description of *O. lata*, except for the color of edge of the hyponotum. However, when specimens from Luwu collected by M. Weber (identified as *Oncis lata*) were examined, they did not have the large thorn-like papillae characteristic of *P. lata*. Thus, Sulawesi is not considered part of the geographic range of *P. lata*, and those specimens are identified here as *P. amboinae* (see that species).

Bretnall's (1919: 323) description of *Oncis lata* is merely a translation of Plate's original description, except that Plate's (1893: 191) correct statement that "eyes are missing" was changed to "eyes are present on all of the papillae." Bretnall likely assumed that Plate made a mistake because dorsal eyes are present in most other species of *Platevindex* and because eyes can be difficult to see when dorsal papillae are retracted. However, it is confirmed here that dorsal eyes are not present in the type material of *Platevindex latus*.

Labbé (1934: 234) identified two specimens (24/17 and 19/14 mm) from the Malabar coast (southwest India) collected by M. Dussumier as *Oncis granulosa*, but also indicated that the exterior aspect of his specimens was similar to that of *Oncis lata* from New Britain. However, Labbé also reported that the notum is granular with tubers that are not prominent, and that dorsal eyes are not very visible. The intestinal loops are also described as type II by Labbé, while they are of type III in *Oncis lata*. Due to the lack of dorsal papillae in the specimens Labbé examined, and the fact that Labbé's description suggests that dorsal eyes may have simply been retracted, the specimens he examined are not considered to be *Oncis lata*. It is also worth noting that the specimens Labbé examined from western India are very distant from New Britain, Papua New Guinea, and that no observations of *Oncis lata* have been confirmed west of New Britain.

Morphological evidence suggests that *Platevindex latus* is closely related to *P. amboinae* because both species lack penial hooks and dorsal eyes, which are present in all other species of *Platevindex*. They also are the only species of *Platevindex* with intestinal loops of type III.

Discussion

Nomenclature

Historically, 18 specific names have been originally or subsequently combined with the generic name *Platevindex*, though authors in the past often used Plate's (1893) generic name *Oncis* instead of *Platevindex* (see our remarks on the genus). Five of these names are regarded as valid species names of *Platevindex*: *Onchidium amboinae*, *Onchidium coriaceum*, *Oncis lata*, *Onchidium luteum* and *Oncis martensi*. Five other names are considered junior synonyms: *Oncis coeca* Plate, 1893, *Onchidella condoriana* Rochebrune, 1882, *Oncis inspectabilis* Plate, 1893, *Oncis schneideri* Hoffmann, 1932 and *Oncis semperi* Plate, 1893. Two other names apply to species of *Platevindex* but are considered nomina dubia: *Oncis cinerea* Odhner, 1917 and *P. mortoni* Britton, 1984 (see our remarks on *P. coriaceus* and *P. tigrinus*). Another name, *Onchidium granulosum* Lesson, 1831, was previously thought to apply to a species of *Platevindex* (as *Oncis*) by Hoffmann (1928: 86), but the original description is not informative enough and the type material could not be located, so it is also considered a nomen dubium which may apply to a species of *Peronia* or *Wallaconchis* (see our remarks on *P. latus*). Four other names apply to *Semperoncis* slugs which live in high-elevation rain forests (Dayrat 2010): *Platevindex apoikistes* Tillier, 1983, *Onchidium glabrum* Semper, 1880 (type species), *Oncis montana* Plate, 1893 and *Onchidium ponsonbyi* Collinge, 1901. Finally, it was already demonstrated that *Onchidium stuxbergi* does not refer to a species of *Platevindex* but to a species of *Onchidium* instead (Dayrat *et al*. 2016, 2019d).

In addition to the five valid species names which were historically classified in *Platevindex* (or *Oncis*), three additional existing species names are newly transferred to *Platevindex* and are regarded as valid: *Onchidium applanatum* Simroth, 1920, *Onchidium burnupi* Collinge, 1902 and *Onchidium tigrinum*

Stoliczka, 1869. In addition to the eight species of *Platevindex* for which names already exist, one new species and one new sub-species are now recognized.

The genus *Platevindex*

The multi-locus molecular phylogeny strongly supports the monophyly of *Platevindex*, which is largely due to including the slower evolving nuclear loci 28S and H3 (Fig. 4). species of *Platevindex* share a close resemblance in external appearance and internal anatomy, but two species, *P. amboinae* and *P. latus*, differ from the rest in two notable traits: they have no dorsal eyes and no penial hooks. The absence of dorsal eyes and the absence of penial hooks are synapomorphies shared by *P. amboinae* and *P. latus* with respect to other species of *Platevindex*. However, dorsal eyes are also absent in *Onchidella* and *Onchidina*, which means that they have been lost several times in onchidiids. As for penial hooks, it has been shown that they were lost by a few species in other genera as well, such as *Wallaconchis* (Goulding *et al.* 2018b). So, overall, the lack of dorsal eyes and penial hooks is not exclusive to *P. amboinae* and *P. latus*. Our results suggest that the three clades of *Platevindex* likely diverged long ago (Fig. 4): clade B (*P. amboinae* and *P. latus*), clade D (*P. martensi* and *P. aptei* sp. nov.), and clade C (all other known species of *Platevindex*).

The terrestrial slugs of the genus *Semperoncis* closely resemble *Platevindex* slugs, but there are noticeable morphological differences between them (Dayrat 2010). First, the position of the male opening is to the left of the right ocular tentacle in *Platevindex*, while it is on the right side of the right ocular tentacle in *Semperoncis*. Second, the pneumostome is approximately median in *Platevindex*, but it is slightly to the right in *Semperoncis*. Third, a central dorsal papilla with multiple dorsal eyes is present in *Semperoncis* and absent in *Platevindex*. Finally, an accessory penial gland is present in *Semperoncis* and absent in *Platevindex*.

Integrating sequence data with morphology

Based on an integrative approach, we have determined that species of *Platevindex* can be identified morphologically by examining a combination of characters (Table 4). Automatic Barcode Gap Discovery analysis was successful in delimiting species of *Platevindex*, with the exception of *P. luteus* and *P. applanatus* (Fig. 9). Mitochondrial COI and nuclear ITS2 sequences were obtained from specimens of *P. luteus* or *P. applanatus* from 19 different geographic regions. The majority of *P. applanatus* mitochondrial sequences cluster together, but mitochondrial sequences of *P. applanatus* from Mauritius, Seram and Sulawesi cluster within a clade of *P. luteus* sequences. These specimens have been identified as *P. applanatus* based on nuclear DNA sequences and morphology (e.g., the intestinal loops, Fig. 40B). Thus *P. luteus* and *P. applanatus* cannot be distinguished reliably based on mitochondrial DNA sequences. The incongruence between mitochondrial DNA and nuclear DNA may be due to mitochondrial introgression, which is increasingly recognized as causing paraphyly in mitochondrial gene trees; a survey of the literature by Funk & Omland (2003) indicated that 23% of the assayed species showed evidence of species-level paraphyly or polyphyly with mitochondrial loci.

High mitochondrial intraspecific divergence is found within five of the nine species of *Platevindex* delineated here (*P. coriaceus*, *P. luteus*, *P. applanatus*, *P. burnupi* and *P. amboinae*). This high divergence is not limited to species of *Platevindex*. High mitochondrial sequence divergence has also been observed in other onchidiids, such as *Peronina zulfigari* (Goulding *et al.* 2018c), *Paromoionchis* spp. (Dayrat *et al.* 2019a) and *Peronia verruculata* (Dayrat *et al.* 2020). Unexpectedly high mitochondrial intraspecific genetic divergence is also known in other pulmonate gastropods (e.g., Thomaz *et al.* 1996; Pinceel *et al.* 2005), which emphasizes the importance of using an integrative taxonomic approach combining both nuclear and mitochondrial markers with comparative anatomy, rather than relying exclusively on mitochondrial loci.

Within *P. coriaceus*, four mitochondrial clades display substantial divergence in mitochondrial COI sequences (Fig. 9). Two subspecies are recognized here within *P. coriaceus* due to an agreement of mitochondrial data with comparative anatomy and nuclear DNA sequences. The three mitochondrial clades within *P. coriaceus coriaceus* cannot be distinguished anatomically and are allopatric. Given that their reciprocal monophyly is not recovered using nuclear markers (Fig. 6), they are considered part of a single subspecies (*P. coriaceus coriaceus*). The fourth mitochondrial clade, *Platevindex coriaceus darwinensis* subsp. nov., of which the reciprocal monophyly is recovered using nuclear markers (Fig. 6), differs anatomically from *P. coriaceus coriaceus* (with respect to the deferent duct in the posterior reproductive system and its hyponotum color).

Two mitochondrial clades are genetically divergent within *P. burnupi*: one northern clade includes all Madagascar and Mozambique sequences, and the southern clade includes all sequences from South Africa. A similar divergence is observed in nuclear ITS2 sequences (the specimen from Mozambique shares the same ITS2 haplotype as several individuals from Madagascar). Anatomically, specimens from the two units are similar, except that animals tend to be larger in South Africa than in Madagascar and Mozambique. However, only three populations were sampled, one from each country, and thus additional sampling is required to understand intraspecific variation. In the future, populations may be found in southern Mozambique or western Madagascar with unsampled haplotypes that could fall in between the two clades here from South Africa and Madagascar, which may then not be reciprocally monophyletic in phylogenetic analyses and which may no longer be separated by any barcode gap.

In *P. amboinae*, the mitochondrial genetic divergence did not correspond to any observed anatomical differences. However, additional samples are needed to evaluate intraspecific variation in this species (which was only found at two localities).

Habitats

Most onchidiid slugs are only found in a specific microhabitat. For instance, *Melayonchis* slugs are only found in mangroves, on tree roots and trunks as well as old logs (Dayrat *et al.* 2017), and *Peronina* slugs are found on mud saturated with water, in mangroves and adjacent mudflats (Goulding *et al.* 2018c). Nearly all *Platevindex* slugs live on the trunks and roots of mangrove trees and on old logs, but species are not randomly distributed across the tidal zone: *Platevindex coriaceus*, *P. tigrinus*, *P. luteus* and *P. applanatus* are all found in the mid-intertidal zone, and sometimes occur in close proximity; *Platevindex martensi*, *P. aptei* sp. nov. and *P. burnupi* are generally found in the high intertidal. Data on the habitat of *P. amboinae* is limited (only three specimens were found in recent surveys), but current data suggests that the species is also found in the high intertidal (there is no published information about the habitat of *P. latus*). *Platevindex burnupi*, *P. luteus* and *P. applanatus* are the only species of *Platevindex* that are not exclusively found in mangroves, although the presence of *P. luteus* outside mangroves is rare. *Platevindex burnupi* occurs in salt marshes, *P. luteus* has occasionally been found on coral rubble beaches, and *P. applanatus* is found on rocks and coral rubble. These three species are closely related (Fig. 4), and it is possible that these novel habitats outside mangroves were colonized by their common ancestral lineage.

The different microhabitats and areas of the tidal zone where species occur may contribute to the fairly high number of sympatric species of *Platevindex* in the South China Sea and Coral Triangle. The highest number of sympatric species of the same onchidiid genus found at one site so far is six species of *Wallaconchis* found at one site in Loay, Bohol, Philippines (Goulding *et al.* 2018b: 25). Sympatry in *Melayonchis* can also be high, as five species of *Melayonchis* live in the same mangrove forest in Matang, Peninsular Malaysia (Dayrat *et al.* 2019c). Five species of *Platevindex* (*P. amboinae*, *P. applanatus*, *P. coriaceus*, *P. luteus* and *P. martensi*) are recorded from Sulawesi, although they have not all been

found in the same region of the island. The highest number of species of *Platevindex* in close proximity was found in Singapore (*P. coriaceus*, *P. luteus*, *P. tigrinus* and *P. martensi*).

Biogeography and endemism

With nine species recognized here, *Platevindex* is among the most diverse genera of onchidiids, being only slightly less diverse than *Wallaconchis* (10 species). Most species of *Platevindex* are broadly distributed, particularly *P. applanatus* and *P. luteus*. *Platevindex latus* is the only species with a narrow geographic range (it is only known from New Britain, Papua New Guinea). Although DNA sequences could not be obtained for *P. latus*, it appears to be externally distinct from *P. amboinae* (known from Ambon, Halmahera and Seram, in Indonesia). Fresh samples are needed from New Britain to examine the genetic divergence between *P. amboinae* and *P. latus*, as well as the natural history of *P. latus*. *Platevindex amboinae* could not be found during a recent survey in Ambon (type locality) despite considerable time spent exploring mangroves on the island. The habitat of *P. amboinae* was not indicated by Plate (1893) in the original description, but the individuals we found in Seram (which is very close to Ambon) and Halmahera were closely associated with mangroves, in the high intertidal. It is possible that *P. amboinae* was formerly more common in supra-tidal mangrove habitats in Ambon, where most have been lost due to urban development.

There may still be undiscovered species of *Platevindex*. As new populations are found in the future, because anatomical differences between species are generally subtle, it will remain critical to study them using molecular data, particularly nuclear DNA sequences, to determine whether they are distinct species or divergent populations of known species.

Although names already existed for all but one species of *Platevindex* described here, no species could be properly identified prior to this revision. Only one species, *P. aptei* sp. nov. (Strait of Malacca and the southern Bay of Bengal), had not previously been named, despite its slugs being some of the largest onchidiids (up to 6 cm long). It is worth noting that *P. aptei* sp. nov. has not been found in any museum collection either. Although its geographic distribution is narrower than for most other species of *Platevindex*, it is remarkable that it remained undiscovered until now. Given that *P. aptei* sp. nov. is one of the few onchidiid species which can easily be identified both externally and internally, its discovery is illustrative of our limited knowledge of the invertebrate fauna of mangroves in the Indo-West Pacific in general and in South-East Asia in particular.

Identification key

A key is provided to help identify the nine species of *Platevindex*. Because species cannot always be distinguished externally, the key also includes internal characters.

1. Dorsal eyes absent, penial hooks absent, intestinal loops of type III 2
   – Dorsal eyes present, penial hooks present (in mature specimens), intestinal loops of type I or II, but never of type III 3

2. Dorsal surface bears large, thorny papillae ....***P. latus*** (Plate, 1893)
   – Dorsal surface bears only small papillae ....***P. amboinae*** (Plate, 1893)

3. Hyponotum yellow with dark spots, foot orange or black, dorsal surface bears low longi-
   tudinal ridges, dorsal eyes can be very close (<2 mm) to the notum edge 4
   – Hyponotum variable (white, light to dark grey, light blue to dark blue) but not marked by distinct dark spots, foot light to bright yellow (exceptionally dark blue-grey), dorsal surface without small longitudinal ridges, dorsal eyes are not very close (<2 mm) to the notum edge 5

4. Foot bright or dark orange ....*P. martensi* (Plate, 1893)
– Foot black ....*P. aptei* Goulding & Dayrat sp. nov.

5. Notum bears distinctly-raised papillae (with or without eyes), slug frequently semi-hemispherical (especially when disturbed) 6
– Notum granular, with papillae with dorsal eyes but no distinctly-raised, prominent papillae, slugs normally remain flattened (even when disturbed) 7

6. No bright yellow longitudinal areas on dorsal notum, intestinal loops of types I or II with a transitional loop oriented between 3 and 8 o'clock, retractor muscle of penis inserts near heart ....
....*P. luteus* (Semper, 1880)
– Bright yellow longitudinal areas present on dorsal notum, intestinal loops of type I with a transitional loop oriented between 1 and 2 o'clock, retractor muscle of penis inserts near heart or at posterior end of visceral cavity ....*P. applanatus* (Simroth, 1920)

7. Distal portion of oviduct (distal to spermatheca) shorter than proximal portion (from female gland mass to spermatheca) ....*P. burnupi* (Collinge, 1902)
– Distal portion of oviduct (distal to spermatheca) much longer than proximal portion (from female gland mass to spermatheca) 8

8. Retractor muscle of penis inserts near heart, distal region of penis (with hooks) less than 1.5 mm long, deferent duct attached to oviduct (in posterior part of reproductive system) and almost straight ....*P. tigrinus* (Stoliczka, 1869)
– Retractor muscle of penis inserts near posterior end of visceral cavity, distal region of penis (with hooks) more than 2 mm long, deferent duct attached to oviduct (in posterior part of reproductive system) and highly coiled ....*P. coriaceus* (Semper, 1880)

Acknowledgments

References

Adams H. & Adams A. 1853–1858. *The Genera of Recent Mollusca; Arranged According to their Organization*. London, J. van Voorst. Volume 1: xl + 484 pp; Volume 2: 661 pp; Volume 3: 138 pls. [Published in parts: Vol. 1: i–xl (1858), 1–256 (1853), 257–484 (1854). Vol. 2: 1–92 (1854), 93–284 (1855), 285–412 (1856), 413–540 (1857), 541–661 (1858). Vol. 3: pl. 1–32 (1853), 33–96 (1855), 97–112 (1856), 113–128 (1857), 129–138 (1858).] https://doi.org/10.5962/bhl.title.4772

Ashkenazy H., Cohen O., Pupko T. & Huchon D. 2014. Indel reliability in indel-based phylogenetic inference. *Genome Biology and Evolution* 6 (12): 3199–3209. https://doi.org/10.1093/gbe/evu252

Audouin V. & Milne-Edwards H. 1832–1834. *Recherches pour servir à l'histoire naturelle du littoral de la France*. Crochard, Paris. 2 volumes [Vol. 1: 406 pp.; Vol. 2: 290 pp., 8 pls.]. https://doi.org/10.5962/bhl.title.43796

Baker H.B. 1938. Nomenclature of Onchidiidae. *The Nautilus* 51: 85–88. https://doi.org/10.5962/bhl.part.10914

Bourke A.J. 2016. Field identification of the *Platevindex* mangrove slugs (Mollusca: Gastropoda: Onchidiidae) of Darwin Harbour. *Northern Territory Naturalist* 27: 102–105.

Bretnall W. 1919. Onchidiidae from Australia and the south-western Pacific Islands. *Records of the Australian Museum* 12: 303–328. https://doi.org/10.3853/j.0067-1975.12.1919.888

Britton K.M. 1984. The Onchidiacea (Gastropoda, Pulmonata) of Hong Kong with a worldwide review of the genera. *Journal of Molluscan Studies* 50: 179–191. https://doi.org/10.1093/oxfordjournals.mollus.a065863

Buchannan F. 1800. An account of the *Onchidium*, a new genus of the class of Vermes, found in Bengal. *Transactions of the Linnean Society of London* 5: 132–134. https://doi.org/10.1111/j.1096-3642.1800.tb00584.x

Cannicci S., Ruwa R.K., Giuggioli M. & Vannini M. 1998. Predatory activity and spatial strategies of *Epixanthus dentatus* (Decapoda: Oziidae), an ambush predator among the mangroves. *Journal of Crustacean Biology* 18 (1): 57–63. https://doi.org/10.1163/193724098X00061

Colgan D.J., Ponder W.F. & Eggler P.E. 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and histone H3 sequences. *Zoologica Scripta* 29: 29–63. https://doi.org/10.1046/j.1463-6409.2000.00021.x

Collinge W.E. 1901. On the anatomy of a collection of slugs from N.W. Borneo. *Transactions of the Royal Society of Edinburgh* 40: 295–312. Available from https://biodiversitylibrary.org/page/41678716 [accessed 20 Jan. 2020].

Collinge W.E. 1902. Description of a new species of *Onchidium* from South Africa. *The Journal of Malacology* 9: 17. Available from https://biodiversitylibrary.org/page/28220831 [accessed 20 Jan. 2020].

Collinge W.E. 1910. The slugs of Natal. *Annals of the Natal Museum* 2 (2): 159–174. Available from https://biodiversitylibrary.org/page/6322951 [accessed 20 Jan. 2020].

Connolly M. 1912. A revised reference list of South African non-marine Mollusca; with descriptions of new species in the South African Museum. *Annals of the South African Museum* 11: 59–306. Available from https://biodiversitylibrary.org/page/1521968 [accessed 20 Jan. 2020].

Connolly M. 1939. A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum* 33: 1–660. Available from https://biodiversitylibrary.org/page/40865351 [accessed 20 Jan. 2020].

Cretella M. 2010. The complete collation and dating of the section *Zoologie* of the *Coquille* voyage. *Bollettino Malacologico* 46: 83–103. Available from https://biodiversitylibrary.org/page/51117488 [accessed 20 Jan. 2020].

Dall W.H. 1885. Notes on some Floridian land and fresh-water shells with a revision of the Auriculacea of the eastern United States. *Proceedings of the U.S. National Museum* 8: 255–289. Available from https://biodiversitylibrary.org/page/15383195 [accessed 20 Jan. 2020].

Dayrat B. 2009. Review of the current knowledge of the systematics of Onchidiidae (Mollusca: Gastropoda: Pulmonata) with a checklist of nominal species. *Zootaxa* 2068: 1–26. https://doi.org/10.11646/zootaxa.2068.1.1

Dayrat B. 2010. Anatomical re-description of the terrestrial onchidiid slug *Semperoncis montana* (Plate, 1893). *Malacologia* 52 (1):1–20. https://doi.org/10.4002/040.052.0101

Dayrat B. & Goulding T.C. 2017. Systematics of the onchidiid slug *Onchidina australis* (Mollusca: Gastropoda: Pulmonata). *Archiv für Molluskenkunde* 146: 121–133. https://doi.org/10.1127/arch.moll/146/121-133

Dayrat B., Conrad M., Balayan S., White T.R., Albrecht C., Golding R., Gomes S.R., Harasewych M.G. & de Frias Martins A.M. 2011. Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): New insights from increased taxon sampling. *Molecular Phylogenetics and Evolution* 59: 425–437. https://doi.org/10.1016/j.ympev.2011.02.014

Dayrat B., Goulding T.C., Apte D., Bhave V., Comendador J., Ngô X.Q., Tan S.K. & Tan S.H. 2016. Integrative taxonomy of the genus *Onchidium* Buchannan, 1800 (Mollusca: Gastropoda: Pulmonata: Onchidiidae). *ZooKeys* 636: 1–40. https://doi.org/10.3897/zookeys.636.8879

Dayrat B., Goulding T.C., Apte D., Bhave V. & Ngô X.Q. 2017. A new genus and four new species of onchidiid slugs from South-East Asia (Mollusca: Gastropoda: Pulmonata: Onchidiidae). *Journal of Natural History* 51: 1851–1897. https://doi.org/10.1080/00222933.2017.1347297

Dayrat B., Goulding T.C., Khalil M., Lozouet P. & Tan S.H. 2018. Systematic revision one clade at a time: A new genus of onchidiid slugs from the Indo-West Pacific (Gastropoda: Euthyneura: Pulmonata). *Raffles Bulletin of Zoology* 66: 814–837. Available from https://lkcnhm.nus.edu.sg/app/uploads/2018/01/66rbz814-837.pdf [accessed 20 Jan. 2020].

Dayrat B., Goulding T.C., Khalil M., Apte D., Bourke B., Comendador J. & Tan S.H. 2019a. A new genus and three new species of mangrove slugs from the Indo-West Pacific (Mollusca: Gastropoda: Pulmonata: Onchidiidae). *European Journal of Taxonomy* 500: 1–77. https://doi.org/10.5852/ejt.2019.500

Dayrat B., Goulding T.C., Khalil M., Comendador J., Ngô X.Q., Tan S.K. & Tan S.H. 2019b. A new genus of air-breathing marine slugs from South-East Asia (Gastropoda: Pulmonata: Onchidiidae). *ZooKeys* 877: 31–80. https://doi.org/10.3897/zookeys.877.36698

Dayrat B., Goulding T.C., Bourke B., Khalil M. & Tan S.H. 2019c. New species and new records of *Melayonchis* slugs (Gastropoda: Euthyneura: Pulmonata: Onchidiidae). *Raffles Bulletin of Zoology* 67: 557–585. Available from https://lkcnhm.nus.edu.sg/app/uploads/2019/01/RBZ-2019-0043.pdf [accessed 20 Jan. 2020].

Dayrat B., Goulding T.C., Khalil M., Apte D. & Tan S.H. 2019d. A new species and new records of *Onchidium* slugs (Gastropoda, Euthyneura, Pulmonata, Onchidiidae). *ZooKeys* 892: 27–57. https://doi.org/10.3897/zookeys.892.39524

Dayrat B., Goulding T.C., Apte D., Aslam S., Bourke A.J., Comendador J., Khalil M., Ngô X.Q., Tan S.K. & Tan S.H. 2020. Systematic revision of *Peronia* Fleming, 1822 (Gastropoda, Euthyneura, Pulmonata, Onchidiidae). *ZooKeys* 972: 1–224. https://doi.org/10.3897/zookeys.972.52853

Dorenbosch M., Grol M.G.G., Christianen J.A., Nagelkerken I. & van der Velde G. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. *Marine Ecology Progress Series* 302: 63–76. https://doi.org/10.3354/meps302063

Ellison A.M., Farnswoth E.J. & Merkt R.W. 1999. Origin of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography* 8: 95–115. https://doi.org/10.1046/j.1466-822X.1999.00126.x

Fleming J. 1822. Mollusca. *In*: Napier M. (ed.) *Supplement to the Fourth, Fifth and Sixth Editions of the Encyclopædia Britannica*. Volume 5: 567–584. Edinburgh.

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

Funk D.J. & Omland K.E. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34 (1): 397–423. https://doi.org/10.1146/annurev.ecolsys.34.011802.132421

Geller J., Meyer C., Parker M. & Hawk H. 2013. Redesign of PCR primers for mitochondrial cytochrome *c* oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* 13: 851–861. https://doi.org/10.1111/1755-0998.12138

Goulding T.C., Khalil M., Tan S.H. & Dayrat B. 2018a. A new genus and a new species of onchidiid slugs from eastern Indonesia (Gastropoda: Euthyneura: Onchidiidae). *Raffles Bulletin of Zoology* 66: 337–349. Available from https://lkcnhm.nus.edu.sg/app/uploads/2018/01/66rbz814-837.pdf [accessed 20 Jan. 2020].

Goulding T.C., Khalil M., Tan S.H. & Dayrat B. 2018b. Integrative taxonomy of a new and highly-diverse genus of onchidiid slugs from the Coral Triangle (Gastropoda: Pulmonata: Onchidiidae). *ZooKeys* 763: 1–111. https://doi.org/10.3897/zookeys.763.21252

Goulding T.C., Tan S.H., Tan S.K., Apte D., Bhave V., Narayana S., Salunkhe R. & Dayrat B. 2018c. A revision of *Peronina* Plate, 1893 (Gastropoda: Euthyneura: Onchidiidae) based on mitochondrial and nuclear DNA sequences, morphology, and natural history (Gastropoda: Pulmonata: Onchidiidae). *Invertebrate Systematics* 32 (4): 803–826. https://doi.org/10.1071/is17094

Gray J.E. 1850. *Figures of Molluscous Animals Selected from Various Authors. Etched for the Use of Students by M.E. Gray. Volume IV*. Longman, Brown, Green and Longmans, London. https://doi.org/10.5962/bhl.title.4772

Guindon S. & Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. https://doi.org/10.1080/10635150390235520

Hassouna N., Mithot B. & Bachellerie J.P. 1984. The complete nucleotide sequence of mouse 28S rRNA gene. Implications for the process of size increase of the large subunit rRNA in higher eukaryotes. *Nucleic Acids Research* 12: 3563–3583. https://doi.org/10.1093/nar/12.8.3563

Herrmannsen A.N. 1846–1852. *Index Generum Malacozoorum Primordia*. T. Fischer, Cassell [Kassel, Germany]. Volume 1: 1–232 [1846], 233–637 [1847]; Volume 2: 1–352 [1847], 353–492 [1848], 493–717 [1849]; Supplement: v + 1–140 [1852].
Available from https://www.biodiversitylibrary.org/page/10695423 [accessed 20 Jan. 2020].

Hoeksema B.W. 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. *In*: Renema W. (ed.) *Biogeography, Time, and Place: Distributions, Barriers, and Islands*: 117–178. Springer, Dordrecht, the Netherlands. https://doi.org/10.1007/978-1-4020-6374-9_5

Hill B.J. 1976. Natural food, foregut clearance-rate and activity of the crab *Scylla serrata*. *Marine Biology* 34 (2): 109–116. https://doi.org/10.1007/BF00390752

Hoffmann H. 1928. Zur Kenntnis der Oncidiiden. *Zoologische Jahrbücher (Jena)* 55: 29–118.

Hoffmann H. 1932. Nacktschnecken aus dem Bismarck-Archipel. *Zoologischer Anzeiger, Leipzig* 100: 133–149.

Hughes J.M. 1984. A note on predation by toadfish *Spheroides* spp. on the snail *Littorina scabra*. *In*: Coleman R.J., Covacevich J. & Davie P. (eds) *Focus on Stradbroke*: 312–314. Boolarong, Brisbane.

Johnson R.I. 1969. Semper's Reisen im Archipel der Philippenen [sic], wissenshaftliche [sic] Resultate, 1867–1916. A complete collation. *Journal of the Society for the Bibliography of Natural History* 5: 144–147. https://doi.org/10.3366/jsbnh.1969.5.2.144

Katoh K., Misawa K., Kuma K. & Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066. https://doi.org/10.1093/nar/gkf436

Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Mentjies P. & Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28 (12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kristensen E., Bouillon S., Dittmar T. & Marchand C. 2008. Organic carbon dynamics in mangrove ecosystems: a review. *Aquatic Botany* 89 (2): 201–219. https://doi.org/10.1016/j.aquabot.2007.12.005

Kumar S., Stecher G. & Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Labbé A. 1934. Les Silicodermés (Labbé) du Muséum d'Histoire naturelle de Paris. Première partie: Classification, formes nouvelles ou peu connues. *Annales de l'Institut océanographique* 14: 173–246.

Lanfear R., Calcott B., Ho S.Y. & Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29 (6): 1695–1701. https://doi.org/10.1093/molbev/mss020

Lee S.Y. 2008. Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research* 59: 16–29. https://doi.org/10.1016/j.seares.2007.05.002

Lesson R.P. 1830–1831. Voyage autour du monde, Exécuté par Ordre du Roi, sur La Corvette de Sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825, sous le ministère et conformément aux Instructions de S.E.M. le Marquis de Clermont-Tonnerre, Ministre de la Marine; Et publié sous les auspices de son Excellence Mgr le Cte de Chabrol, Ministre de la Marine et des Colonies, par M.L.I. Duperrey, Capitaine de Frégate, Chevalier de Saint-Louis et Membre de la Légion d'Honneur, Commandant de l'Expédition. Zoologie, par M. Lesson. Volume 2, Part 1: 1–471, pls 1–16. Arthus Bertrand, Libraire-Editeur, Paris. [pp 241–471 published on 15 Nov. 1831; plates on mollusks published between 9 Jan. 1830 and 22 Dec. 1831; plate 14 published on 15 Nov. 1831; see Cretella 2010]. https://doi.org/10.5962/bhl.title.57936

Lloyd D.G. & Calder V.L. 1991. Multiresidue gaps, a class of molecular characters with exceptional reliability for phylogenetic analyses. *Journal of Evolutionary Biology* 4 (1): 9–21. https://doi.org/10.1046/j.1420-9101.1991.4010009.x

Long J., Napton D., Giri C. & Graesser J. 2014. A mapping and monitoring assessment of the Philippines mangrove forests from 1990 to 2010. *Journal of Coastal Research* 30 (2): 260–271. https://doi.org/10.2112/JCOASTRES-D-13-00057.1

Lovelock C.E., Cahoon D.R., Friess D.A., Guntenspergen G.R., Krauss K.W., Reef R., Rogers K., Saunders M., Sidik F., Swales A., Saintilan N., Thuyen L.X. & Triet T. 2015. The vulnerability of Indo-Pacific mangrove forests to sea level rise. *Nature* 526: 559–563. https://doi.org/10.1038/nature15538

Luther D.A. & Greenberg R. 2009. Mangroves: A global perspective on the evolution and conservation of the terrestrial vertebrates. *BioScience* 59 (7): 602–612. https://doi.org/10.1525/bio.2009.59.7.11

Martens E. von. 1897. Süss- und Brackwasser-Mollusken des Indischen Archipels. *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* 4: 1–332. https://doi.org/10.5962/bhl.title.46994

Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In*: *Proceedings of the Gateway Computing Environments Workshop (GCE 2010)*: 1–8. https://doi.org/10.1109/GCE.2010.5676129

Milne I., Wright F., Rowe G., Marshal D.F., Husmeier D. & McGuire G. 2004. TOPALi: Software for automatic identification of recombinant sequences within DNA multiple alignments. *Bioinformatics* 20: 1806–1807. https://doi.org/10.1093/bioinformatics/bth155

Nagy L.G., Kocsubé S., Csanádi Z., Kovács G.M., Petkovits T., Vágvölgyi C. & Papp T. 2012. Re-mind the gap! Insertion–deletion data reveal neglected phylogenetic potential of the nuclear ribosomal internal transcribed spacer (ITS) of fungi. *PloS One* 7 (11): e49794. https://doi.org/10.1371/journal.pone.0049794

Odhner N.H.J. 1917. Results of Dr. E. Mjöbergs Swedish scientific expeditions to Australia 1910–1913, XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar Stockholm* 52: 1–115. https://doi.org/10.5962/bhl.title.12985

Palumbi S.R. 1996. Nucleic acid II: The polymerase chain reaction. *In*: Hillis D.M., Moritz C., Mable B.K. (eds) *Molecular Systematics*. Second edition: 205–247. Sinauer Press, Sunderland, MA.

Pinceel J., Jordaens K. & Backeljau T. 2005. Extreme mtDNA divergences in a terrestrial slug (Gastropoda, Pulmonata, Arionidae): accelerated evolution, allopatric divergence and secondary contact. *Journal of Evolutionary Biology* 18: 1264–1280. https://doi.org/10.1111/j.1420-9101.2005.00932.x

Plate L.H. 1893. Studien über opisthopneumone Lungenschnecken, II, Die Oncidiiden. *Zoologische Jahrbücher, Abtheilung für Anatomie und Ontogenie der Thiere* 7: 93–234. Available from https://biodiversitylibrary.org/page/11175213 [accessed 27 Sep. 2016].

Puillandre N., Lambert A., Brouillet S. & Achaz G. 2011. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Quoy J.R.C. & Gaimard J.P. 1824–1826. *Zoologie. Voyage autour du Monde entrepris par ordre du Roi, sous le ministère et conformément aux instructions de S. Exc. M. Le Vicomte du Bouchage, secrétaire d'État au Département de la Marine, exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820; publié par M. Louis de Freycinet*. Pillet Aîné, Paris. 2 volumes [Volume 1: vii + 712 pp; Volume 2: 96 pls (atlas)]. https://doi.org/10.5962/bhl.title.15862

Quoy J.R.C. & Gaimard J.P. 1832–1833. *Zoologie, Tome Second. Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville*. J. Tastu, Paris. https://doi.org/10.5962/bhl.title.2132

Rafinesque C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Self-published by the author, Palermo. https://doi.org/10.5962/bhl.title.106607

Rambaut A., Drummond A.J., Xie D., Baele G. & Suchard M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67 (5): 901–904. https://doi.org/10.1093/sysbio/syy032

Richards D.R. & Friess D.A. 2016. Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. *Proceedings of the National Academy of Sciences* 113 (2): 344–349. https://doi.org/10.1073/pnas.1510272113

Rochebrune A.T. de. 1882. Documents sur la faune malacologique de la Cochinchine et du Cambodge. *Bulletin de la Société philomathique de Paris* 6: 35–74. Available from https://www.biodiversitylibrary.org/page/31660821 [accessed 7 Aug. 2020].

Ronquist F. & Huelsenbeck J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Sabri N.A. & Singh H.R. 2018. Distribution and abundance of the Onchidiidae of the coastal mangroves of Selangor, Peninsular Malaysia. *International Journal of Engineering & Technology* 7 (4.14): 67–71.

Semper C. 1880–1885. Dritte Familie, Onchidiidae. *In*: Semper C. (ed.) *Reisen im Archipel der Philippinen. Zweiter Theil. Wissenschaftliche Resultate. Dritter Band. Landmollusken*: 251–264 [1880], 265–290 [1882], pls 19–20, 22–23 [1880], pl. 21 [1882], pls 24–27 [1885]. C.W. Kreidel, Wiesbaden, Germany. Available from https://biodiversitylibrary.org/page/32630046 [accessed 22 Dec. 2018].

Simmons M.P., Ochoterena H. & Carr T.G. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analyses. *Systematic Biology* 50 (3): 454–462. https://doi.org/10.1080/106351501300318049

Simroth H. 1920. Über einige Nacktschnecken vom Malayischen Archipel von Lombok an ostwärts bis zu den Gesellschafts-Inseln. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 35: 259–306. Available from https://biodiversitylibrary.org/page/48256899 [accessed 22 Dec. 2018].

Smith G.R. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. *Systematic Biology* 41 (1): 41–57. https://doi.org/10.1093/sysbio/41.1.41

Soltis P.S. & Soltis D.E. 2003. Applying the bootstrap in phylogeny reconstruction. *Statistical Science* 18 (2): 256–267. https://doi.org/10.1214/ss/1063994980

Spalding M.D., Blasco F. & Field C.D. 1997. *World Mangrove Atlas.* International Society for Mangrove Ecosystems, Okinawa, Japan. Available from http://www.environmentalunit.com/Documentation/04%20 Resources%20at%20Risk/World%20mangrove%20atlas.pdf [accessed 23 Feb. 2021].

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30 (9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stantschinsky W. 1907. Zur Anatomie und Systematik der Gattung *Onchidium*. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 25: 353–402. https://doi.org/10.5962/bhl.part.11959

Starobogatov Y.I. 1976. Composition and taxonomic position of marine pulmonate mollusks. *Soviet Journal of Marine Biology* 4: 206–212.

Stoliczka F. 1869. The malacology of lower Bengal and the adjoining provinces. *Journal of the Asiatic Society of Bengal* 38: 86–111. Available from https://www.biodiversitylibrary.org/item/128669#page/366/mode/1up [accessed 27 Sep. 2016]

Sun B., Chen C., Shen H., Zhang K., Zhou N. & Qian J. 2014. Species diversity of Onchidiidae (Eupulmonata: Heterobranchia) on the mainland of China based on molecular data. *Molluscan Research* 34: 62–70. https://doi.org/10.1080/13235818.2013.868860

Swofford D.L. 2002. PAUP: Phylogenetic Analysis Using Parsimony, version 4.0b10. Sinauer, Sunderland, MA.

Takagi M., Takao Y., Mizuno K. & Ieyama H. 2019. Genetic diversity of Onchidiidae in Japan. *Fauna Ryukyuana* 49: 23–37.

Tan K.S. & Oh T.M. 2002. Feeding habits of *Chicoreus capucinu*s (Neogastropoda: Muricidae) in a Singapore mangrove. *Bollettino Malacologico* 38: 43–50. Available from http://www.societaitalianadimalacologia.it/Bollettino/Supplemento%204/Boll.%20Mal.%202002%20 43-50.pdf [accessed 20 Jan. 2020].

Tapparone-Canefri C. 1883. Fauna malacologica delle Nuova Guinea e delle Isole adiacenti. *Annali del Museo Civico di Storia Naturale, Genova* 19: 1–313. Available from https://biodiversitylibrary.org/page/10812600 [accessed 22 Dec. 2018].

Thomaz D., Guiller A. & Clarke B. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails. *Proceedings of the Royal Society B* 263: 363–368. https://doi.org/10.1098/rspb.1996.0056

Tillier S. 1983. A new mountain *Platevindex* from Philippine Islands (Pulmonata: Onchidiidae). *Journal of Molluscan Studies* Suppl. 12A: 198–202. https://doi.org/10.1093/oxfordjournals.mollus.a065743

Valiela I., Bowen J.L. & York J.K. 2001. Mangrove forests: one of the World's threatened major tropical environments. *BioScience* 51 (10): 807–815. https://doi.org/10.1641/0006-3568(2001)051%5B0807:MFOOTW%5D2.0.CO;2

Vo Q.T., Kuenzer C., Vo Q.M., Moder F. & Oppelt N. 2012. Review of valuation methods for mangrove ecosystem services. *Ecological Indicators* 23: 431–446. https://doi.org/10.1016/j.ecolind.2012.04.022

Vonnemann V., Schrödl M., Klussmann-Kolb A. & Wägele H. 2005. Reconstruction of the phylogeny of the Opisthobranchia (Mollusca: Gastropoda) by means of 18S and 28S rRNA gene sequences. *Journal of Molluscan Studies* 71: 113–125. https://doi.org/10.1093/mollus/eyi014

Wade C.M. & Mordan P.B. 2000. Evolution within the gastropod molluscs; using the ribosomal RNA gene-cluster as an indicator of phylogenetic relationships. *Journal of Molluscan Studies* 66: 565–570. https://doi.org/10.1093/mollus/66.4.565

Westerlund C.A. 1883. Noch einige von der Vega-Expedition gesammelte Mollusken. *Nachrichtsblatt der deutschen malakozoologischen Gesellschaft* 15: 164–166.

Woodward B.B. 1894. Mollusca. *Zoological Record* 30: 57.

Yuri T., Kimball R.T., Harshman J., Bowie R.C., Braun M.J., Chojnowski J.L., Han K.L., Hackett S.J., Huddleston C.J., Moore W.S., Reddy S., Sheldon F.H., Steadman D.W., Witt C.C. & Braun E.L. 2013. Parsimony and model-based analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology* 2 (1): 419–444. https://doi.org/10.3390/biology2010419

Zhang K., Wang D., Shen H., Qian J., Guan H., Wu H. & Gao Y. 2017. Redescription of *Platevindex mortoni* (Gastropoda: Eupulmonata: Onchidiidae) from China. *Molluscan Research* 37: 72–78. https://doi.org/10.1080/13235818.2016.1223535