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Systematic revision one clade at a time: A new genus of onchidiid slugs from the Indo-West Pacific (Gastropoda: Euthyneura: Pulmonata)

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Abstract. In the context of a complete revision of the Onchidiidae, it is shown here that *Onchidium vaigiense* Quoy & Gaimard, 1825 and *Onchidium marmoratum* Lesson, 1831 belong to a clade that is separate from all other onchidiid genera and so a new genus is described: *Marmaronchis* Dayrat & Goulding, new genus. *Marmaronchis* slugs are characterised by a unique combination of anatomical traits: intestinal loops of type I, rectal gland present, accessory penial gland present. *Marmaronchis vaigiensis* and *M. marmoratus* are cryptic externally and internally but are delineated as distinct species with both mitochondrial (COI, 16S, 12S) and nuclear (ITS2, 28S, H3) DNA sequences. *Onchidium ambiguum* Semper, 1880 and *O. steenstrupii* Semper, 1882 are proposed as new junior synonyms of *M. vaigiensis*. *Marmaronchis* slugs primarily live in the rocky intertidal and, unlike many onchidiids from Southeast Asia, they are not found inside mangroves. Both *Marmaronchis* species are geographically sympatric and can even be found at the same stations, but *Marmaronchis vaigiensis* is widely distributed, from the Nicobar Islands (Bay of Bengal) all the way to Vanuatu and the Philippines, while *M. marmoratus* is only known from New Ireland and Madang (Papua New Guinea). Several new geographical records are provided: Bali and Sulawesi (Indonesia) and Vanuatu for *M. vaigiensis*; Madang (Papua New Guinea) for *M. marmoratus*. The diversity of *Marmaronchis* slugs is compared to other onchidiid genera.

Key words. biodiversity, Coral Triangle, cryptic species, integrative taxonomy, Southeast Asia

INTRODUCTION

Ten years ago, our knowledge of the onchidiid biodiversity was still very poor, to say the least (Dayrat, 2009): the application of existing species- and genus-group names was largely unknown; most species were only known from the type material (often lost); and almost no fresh material was available in museum collections. For the past ten years, however, special efforts have been made to revise the taxonomy of the Onchidiidae (Dayrat et al., 2016, 2017; Dayrat & Goulding, 2017; Goulding et al., 2018a, b, c): thousands of fresh specimens have been collected worldwide, especially in Southeast Asia where onchidiids are abundant and diverse; the application of existing names is being clarified; new species and new genera are described; the colour of live animals is documented in detail for each species; species boundaries are evaluated using an integrative approach to taxonomy (Dayrat, 2005).

The genus *Onchidium* Buchannan, 1800, which was traditionally used for dozens of onchidiid species from the Indo-West Pacific, includes only three species (Dayrat et al., 2016). As a result, many species originally classified in *Onchidium* must be transferred to different genera (e.g., Goulding et al., 2018b). Here we show that *Onchidium vaigiense* Quoy & Gaimard, 1825 and *Onchidium marmoratum* Lesson, 1831 belong to a clade that is distinct from other onchidiid genera. Because no existing generic name applies to that clade, a new genus is described here: *Marmaronchis* Dayrat & Goulding, new genus. The new genus described in this paper is the responsibility of Benoît Dayrat and Tricia C. Goulding. The authorship of the new genus should be cited as Dayrat & Goulding in Dayrat, Goulding, Khalil, Lozouet & Tan, 2018.

Both *Marmaronchis vaigiensis* and *M. marmoratus* are well delineated thanks to both mitochondrial (COI, 16S, 12S) and nuclear (ITS2, 28S, H3) DNA sequences and it is shown that they are cryptic morphologically. In particular, the male copulatory apparatus—which can sometimes be used to separate closely-related species that are cryptic externally (e.g., Goulding et al., 2018b, c)—is similar in both species. The anatomy of *O. vaigiense* was already described in detail (Dayrat, 2010), but with no access to molecular data because specimens were too old to be sequenced (except for one specimen from Singapore). At the time, based on anatomy only, *O. marmoratum* (type locality: New Ireland) was

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thought to be a synonym of *O. vaigiense* (type locality: West Papua), and *O. vaigiense* was thought to be distributed from Singapore to Papua New Guinea. Here it is shown that *M. vaigiensis* is even more widely distributed, from the Nicobar Islands (Bay of Bengal) to Vanuatu (West Pacific), and that the geographical distribution of *M. marmoratus* is contained within that of *M. vaigiensis* but restricted to Madang (Papua New Guinea) and New Ireland.

Two new synonymies are proposed based on the re-examination of type materials: *Onchidium ambiguum* Semper, 1880 and *Onchidium steenstrupii* Semper, 1882 are regarded as synonyms of *Marmaronchis vaigiensis*. Several new geographical records are provided: Bali and Sulawesi (Indonesia) and Vanuatu, for *M. vaigiensis*; Madang (Papua New Guinea) for *M. marmoratus*. Prior to the present study, the colour of live animals was only known from the type material of *Onchidium marmoratum* originally illustrated by Lesson (1831: pl. 14, Fig. 3; Dayrat, 2010: Fig. 1R) and from live pictures of one individual from Singapore (Dayrat, 2010: Fig. 1S, T). The colour variation of live animals is illustrated here based on material newly collected from many localities.

The anatomical description of *O. vaigiense* by Dayrat (2010) was partly based on specimens from localities in Papua New Guinea and New Ireland which could potentially be part of either *M. vaigiensis* or *M. marmoratus* (because the two species are sympatric there). Here, the anatomy is not described in detail again, but some organs important for taxonomy (radula, intestinal loops, posterior reproductive system, anterior copulatory apparatus) are illustrated for individuals identified as *M. vaigiensis* and *M. marmoratus* with DNA sequences in order to show that both species are cryptic anatomically.

In the general discussion, the diversity and anatomy of *Marmaronchis* are placed within the broader context of the Onchidiidae. The anatomy of *Marmaronchis* is compared with other onchidiid genera and its relationships are discussed. The existence of two closely-related, cryptic species in *Marmaronchis* is compared with the known species diversity in other onchidiid genera.

MATERIAL & METHODS

Collecting. All specimens (except one) examined here were newly collected, which provided fresh material for DNA sequencing and natural history field observations. Specimens from Singapore were collected by Benoît Dayrat and Siong Kiat Tan. Specimens from Indonesia were collected by Munawar Khalil and party. Specimens from Papua New Guinea and Vanuatu were collected during field expeditions organised by Philippe Bouchet (Muséum national d'Histoire naturelle, Paris, France). One specimen from the Philippines was found in the collections of the University of Florida at Gainesville. Specimens were collected by hand at low tide. GPS coordinates are available for all stations and each site is labeled with a unique station number. In Singapore and Indonesia, a piece of tissue was cut from specimens for DNA extraction, the rest of the specimen being relaxed in magnesium chloride and preserved in 70% ethanol for comparative anatomy. In Papua New Guinea and Vanuatu, specimens were all directly preserved in 95% ethanol.

Specimens. Mitochondrial COI sequences are provided here for 42 individuals. Nuclear ITS2 sequences are provided for 26 of those 42 individuals, and mitochondrial 16S and 12S sequences and nuclear 28S and H3 sequences are provided here for 9 of those 42 individuals. For ITS2, 28S, H3, 16S and 12S sequences, individuals were subsampled to represent the highest COI genetic divergence within each species, as well as a broad range of geographic localities. DNA extraction numbers used in phylogenetic analyses are indicated in the list of material examined as well as in the figure captions (numbers are between brackets). Sizes (length/width) are indicated in millimetres for each specimen. Many additional specimens were examined in the context of our worldwide revision of the family, including all available types and hundreds of onchidiids representing all the known genera and nearly all species. Specimens freshly collected in Indonesia were deposited as vouchers at the Universitas Malikussaleh, North Aceh, Sumatra, Indonesia. Specimens from Singapore were deposited at the Lee Kong Chian Natural History Museum, Singapore, and specimens from Papua New Guinea and Vanuatu were deposited at the Muséum national d'Histoire naturelle, France.

Museum abbreviations. Muséum national d'Histoire naturelle, Paris, France (MNHN); Natural History Museum, London, United Kingdom (NHMUK); Royal Belgian Institute of Natural Sciences (RBINS); University of Florida, Gainesville, USA (UF); Universitas Malikussaleh, North Aceh, Sumatra, Indonesia (UMIZ); Museum für Naturkunde, Berlin, Germany (ZMB); Zoologisches Museum, Hamburg, Germany (ZMH); Zoological Museum of the University of Copenhagen, Denmark (ZMUC); and Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

DNA extraction and PCR amplification. DNA was extracted using a phenol-chloroform extraction protocol with cetyltrimethyl-ammonium bromide (CTAB). The mitochondrial cytochrome *c* oxidase I region (COI), and the 16S and 12S regions were amplified using the following primers (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), 16Sar-L CGC CTG TTT ATC AAA AAC AT (Palumbi, 1996), 16S 972R CCG GTC TGA ACT CAG ATC ATG T (Dayrat et al., 2011), 12sai-L AAA CTA GGA TTA GAT ACC CTA TTA T, and 12SB-H GAG GGTGAC GGG CGG TGT GT (Palumbi, 1996). The nuclear ITS2, 28S, and H3 regions were amplified using the following primers (all 5′–3′): 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). The PCRs for COI and 16S were 25 µl reactions containing 15.8 µl of water, 2.5 µl of 10X 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 100X BSA (Bovine Serum Albumin). The PCRs for 12S differed by reducing the water to 14.3 µl, and replacing the $MgCl_2$ and BSA with 4 µl of Q solution (QIAGEN, ID: 201203). The PCRs for 28S was the same as for 12S, except that the dNTP mixture was reduced to 1 µl, the Q solution increased to 5 µl, and the amount of template DNA reduced to 0.5 µl. The 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 100X BSA was increased to 2 µl, and the amount of template DNA reduced to 0.5 µl. The PCRs for H3 were 25 µl reactions containing 14.8 µl of water, 2.5 µl of 10X 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), 2 µl of 100X BSA and 1 µl of 20 ng/µl template DNA. The COI and 16S thermoprofile was: 5 minutes at 94°C; 35 cycles of 40 seconds at 94°C, 1 minute at 46°C, and 1 minute at 72°C; and 10 minutes at 72°C. The 12S thermoprofile was the same as for COI, except that it was run for 40 cycles. The 28S thermoprofile was: 4 minutes at 94°C; 38 cycles of 30 seconds at 94°C, 50 seconds at 52°C, and 2 and a half minutes at 72°C; and 10 minutes at 72°C. The ITS2 thermoprofile was: 1 minute at 96°C; 35 cycles of 30 seconds at 94°C, 30 seconds at 50°C, and 1 minute at 72°C; and a final extension of 10 minutes at 72°C. The H3 thermoprofile was: 5 minutes at 93°C; 30 cycles of 1 minute at 93°C, 2 minutes at 55°C, and 1 minute at 73°C; and a final extension of 10 minutes at 73°C. The PCR products were cleaned with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) prior to sequencing. Sequenced fragments represented approximately 680 bp of COI, 530 bp of 16S, 350 bp of 12S, 1000 bp of 28S, 580 bp of ITS2 and 340 bp of H3. Finally, COI sequences were also translated into amino acid sequences in MEGA using the invertebrate mitochondrial genetic code to check for the presence of stop codons (no stop codon was found).

Phylogenetic analyses. Chromatograms were consulted to resolve rare ambiguous base calls. DNA sequences were aligned using Clustal W in MEGA 7 (Kumar et al., 2016). Alignments included 42 COI sequences, 26 ITS2 sequences, and 9 16S, 12S, 28S, and H3 sequences of *Marmaronchis* individuals. Seventeen other onchidiid species were selected as outgroups from previous studies from our lab (Dayrat et al., 2011, 2016, 2017; Dayrat & Goulding, 2017; Goulding et al., 2018a, b, c) to represent other onchidiid genera: *Alionchis jailoloensis* Goulding & Dayrat in Goulding et al., 2018a, *Melayonchis aileenae* Dayrat & Goulding in Dayrat et al., 2017, *Melayonchis annae* Dayrat in Dayrat et al., 2017, *Melayonchis eloisae* Dayrat in Dayrat et al., 2017, *Melayonchis siongkiati* Dayrat & Goulding in Dayrat et al., 2017, *Onchidella celtica* (Cuvier in Audouin & Milne-Edwards, 1832), *Onchidella floridana* (Dall, 1885), *Onchidella patelloidis* (Quoy & Gaimard, 1832), *Onchidina australis* (Semper, 1880), *Onchidium typhae* Buchannan, 1800, *Onchidium stuxbergi* (Westerlund, 1883), *Platevindex luteus* (Semper, 1880), *Peronia* sp. (Okinawa), *Peronia* sp. (Hawaii), *Peronina tenera* (Stoliczka, 1869), *Wallaconchis melanesiensis* Goulding & Dayrat in Goulding et al., 2018b, and *Wallaconchis sinanui* Goulding & Dayrat in Goulding et al., 2018b.

DNA sequences were all deposited in GenBank and vouchers deposited in museum collections (Table 1). The ends of each alignment were trimmed and sequences were concatenated. The COI alignment included 614 nucleotide positions. The concatenated mitochondrial alignment included 1,267 nucleotide positions: 576 (COI), 366 (16S), and 325 (12S). The ITS2 alignment included 718 positions, including gaps (but with insertions in one sequence removed). The concatenated nuclear alignment included 1895 nucleotide positions: 718 (ITS2), 883 (28S), and 294 (H3).

Pairwise genetic distances between COI sequences were calculated in MEGA 7. Mitochondrial and nuclear sequences were not concatenated all together in a single data set of 6 markers to demonstrate that the mitochondrial and nuclear data sets independently support the same phylogenetic relationships. Prior to phylogenetic analyses, the best-fitting evolutionary model was selected for each locus separately using the Model Selection option from Topali v2.5 (Milne et al., 2004). A GTR + G model was independently selected for COI, 16S, and 12S, and a HKY + G model was independently selected for ITS2, 28S, and H3. Maximum Likelihood analyses were performed using PhyML (Guindon & Gascuel, 2003) as implemented in Topali v2.5. Node support was evaluated using bootstrapping with 100 replicates. Bayesian analyses were performed using MrBayes v3.1.2 (Ronquist & Huelsenbeck, 2003) as implemented in Topali v2.5, with five simultaneous runs of 1.5×10^6 generations each, sample frequency of 100, and burn in of 25% (and posterior probabilities were also calculated). Topali did not detect any issue with respect to convergence. Other (unpublished) analyses were performed using different combinations of outgroups, which all yielded identical results.

Comparative anatomy. The anatomical description of *M. vaigiensis* published by Dayrat (2010, as *Onchidium vaigiense*) was partly based on specimens from Madang, Papua New Guinea, as well as New Britain, New Ireland, and New Hannover. All these specimens could potentially be part of either *M. vaigiensis* or *M. marmoratus* given the proximity of New Britain and New Hannover with New Ireland, and given that *M. vaigiensis* and *M. marmoratus* are sympatric in Madang (Papua New Guinea) and Kavieng (New Ireland, Papua New Guinea). So, it is for instance unknown whether the illustrations of the digestive system of a specimen from Madang (Dayrat, 2010: Figs. 2C–E) refer to *M. vaigiensis* or *M. marmoratus*. Here, in order to avoid any misidentification, anatomical data and illustrations are provided for each species separately, i.e., for specimens identified as *M. vaigiensis* or *M. marmoratus* thanks to DNA sequences. However, because there is no need to repeat the detailed anatomical description published earlier (Dayrat, 2010), the anatomy of *M. vaigiensis* and *M. marmoratus*

Table 1. DNA extraction numbers and Genbank accession numbers for all the specimens included in the present study (for details and Museum voucher catalog numbers, see the lists of Material examined and Figs. 1–4). All *Marmaronchis* sequences are new. Outgroup sequences marked with an asterisk are from our former publications (Dayrat et al., 2011, 2016, 2017; Dayrat & Goulding, 2017; Goulding et al., 2018a, b, c). Other outgroup sequences are new. Abbreviations: Australian Museum, Sydney (AM); Institute of Tropical Biology, Zoology Collection, Vietnam Academy of Science and Technology (ITBZC); Muséum national d'Histoire naturelle, Paris, France (MNHN); University of Florida, Gainesville (UF); Universitas Malikussaleh, North Aceh, Sumatra, Indonesia (UMIZ); Universiti Sains Malaysia Mollusc Collection (USMMC); Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

Species	**DNA #**	**Locality**	**COI**	**16S**	**12S**	**ITS2**	**28S**	**H3**
M. vaigiensis	715	Philippines	MK122811	MK122853	MK122862	MK122876	MK122909	MK122924
	1183	Singapore	MK122812	MK122854	MK122863	MK122877	MK122910	MK122925
	2224	Sulawesi	MK122813					
	2243	Sulawesi	MK122814					
	2244	Sulawesi	MK122815					
	2294	Sulawesi	MK122816			MK122878		
	2309	Sulawesi	MK122817			MK122879		
	2908	Kei	MK122818					
	3081	Bali	MK122819			MK122880		
	3083	Bali	MK122820	MK122855	MK122864	MK122881	MK122911	MK122926
	3590	Bali	MK122821			MK122882		
	5046	Halmahera	MK122822					
	5153	Halmahera	MK122823	MK122856	MK122865	MK122883	MK122912	MK122927
	5154	Halmahera	MK122824			MK122884		
	5403	PNG, Madang	MK122825			MK122885		
	5406	PNG, Madang	MK122826			MK122886		
	5434	PNG, Madang	MK122827	MK122857	MK122866	MK122887	MK122913	MK122928
	5435	PNG, Madang	MK122828			MK122888		
	5463	PNG, Madang	MK122829			MK122889		
	6091	New Ireland, Kavieng	MK122830			MK122890		
	6099	New Ireland, Kavieng	MK122831					
	6100	New Ireland, Kavieng	MK122832					
	5486	Vanuatu	MK122833					
	5487	Vanuatu	MK122834	MK122858	MK122867	MK122891	MK122914	MK122929
	5489	Vanuatu	MK122835					
	5490	Vanuatu	MK122836			MK122892		
M. marmoratus	5404	PNG, Madang	MK122837					
	5409	PNG, Madang	MK122838	MK122859	MK122868	MK122893	MK122915	MK122930
	5413	PNG, Madang	MK122839			MK122894		
	5414	PNG, Madang	MK122840			MK122895		
	5416	PNG, Madang	MK122841			MK122896		
	5425	PNG, Madang	MK122842			MK122897		
	5441	PNG, Madang	MK122843					
	5442	PNG, Madang	MK122844					

Species	DNA #	Locality	COI	16S	12S	ITS2	28S	H3
	5443	PNG, Madang	MK122845	MK122860	MK122869	MK122898	MK122916	MK122931
	5452	PNG, Madang	MK122846					
	5458	PNG, Madang	MK122847					
	5459	PNG, Madang	MK122848					
	5466	PNG, Madang	MK122849	MK122861	MK122870	MK122899	MK122917	MK122932
	5475	PNG, Madang	MK122850			MK122900		
	6092	New Ireland, Kavieng	MK122851			MK122901		
	6093	New Ireland, Kavieng	MK122852					
Alionchis jailoloensis	5137	Indonesia, Halmahera	MG953528*	MG953538*	MK122871	MG953548*	MK122918	MK122933
Melayonchis aileenae	970	Peninsular Malaysia	KX240033*	KX240057*	MK122872	MK122902	MK125514	MK122934
Melayonchis annae	1010	Singapore	KX240015*	KX240039*	MK122873	MK122903	MK122919	MK122935
Melayonchis eloisae	1011	Singapore	KX240026*	KX240050*	MK122874	MK122904	MK125515	MK122936
Melayonchis siongkiati	1002	Singapore	KX240020*	KX240044*	MK122875	MK122905	MK122920	MK122937
Onchidella celtica	5013	France	MG958715*	MG958717*	MG971018*	MK122906	MK122921	MK122938
Onchidella floridana	713	Tobago	HQ660035*	HQ659903*	MG971017*	MK122907	MK122922	MK122939
Onchidella patelloidis	1524	Australia, NSW	MG970878*	MG970944*	MG971019*	MK122908	MK122923	MK122940
Onchidina australis	1523	Australia, NSW	KX179548*	KX179561*	MG971012*	MG958719*	MG971209*	MK122941
Onchidium stuxbergi	5605	Vietnam	KX179520*	KX179537*	MG971014*	MG958721*	MG971211*	MK122942
Onchidium typhae	965	Peninsular Malaysia	KX179509*	KX179525*	MG971013*	MG958720*	MG971210*	MK122943
Peronia sp.	706	USA, Hawaii	HQ660038*	HQ659906*	MG971016*	MG958722*	MG971212*	MK122944
Peronia sp.	696	Japan, Okinawa	HQ660043*	HQ659911*	MG971015*	MG958871*	MG958883*	MK122945
Peronina tenera	960	Peninsular Malaysia	MG958740*	MG958796*	MG971011*	MG958840*	MG958874*	MK122946
Platevindex luteus	1001	Singapore	MG958714*	MG958716*	MG971010*	MG958718*	MG958888*	MK122947
Wallaconchis melanesiensis	5417	PNG, Madang	MG970870*	MG970939*	MG971005*	MG971154*	MG971204*	MK122948
Wallaconchis sinanui	2740	Indonesia, Ambon	MG970713*	MG970881*	MG970947*	MG971093*	MG971161*	MK122949

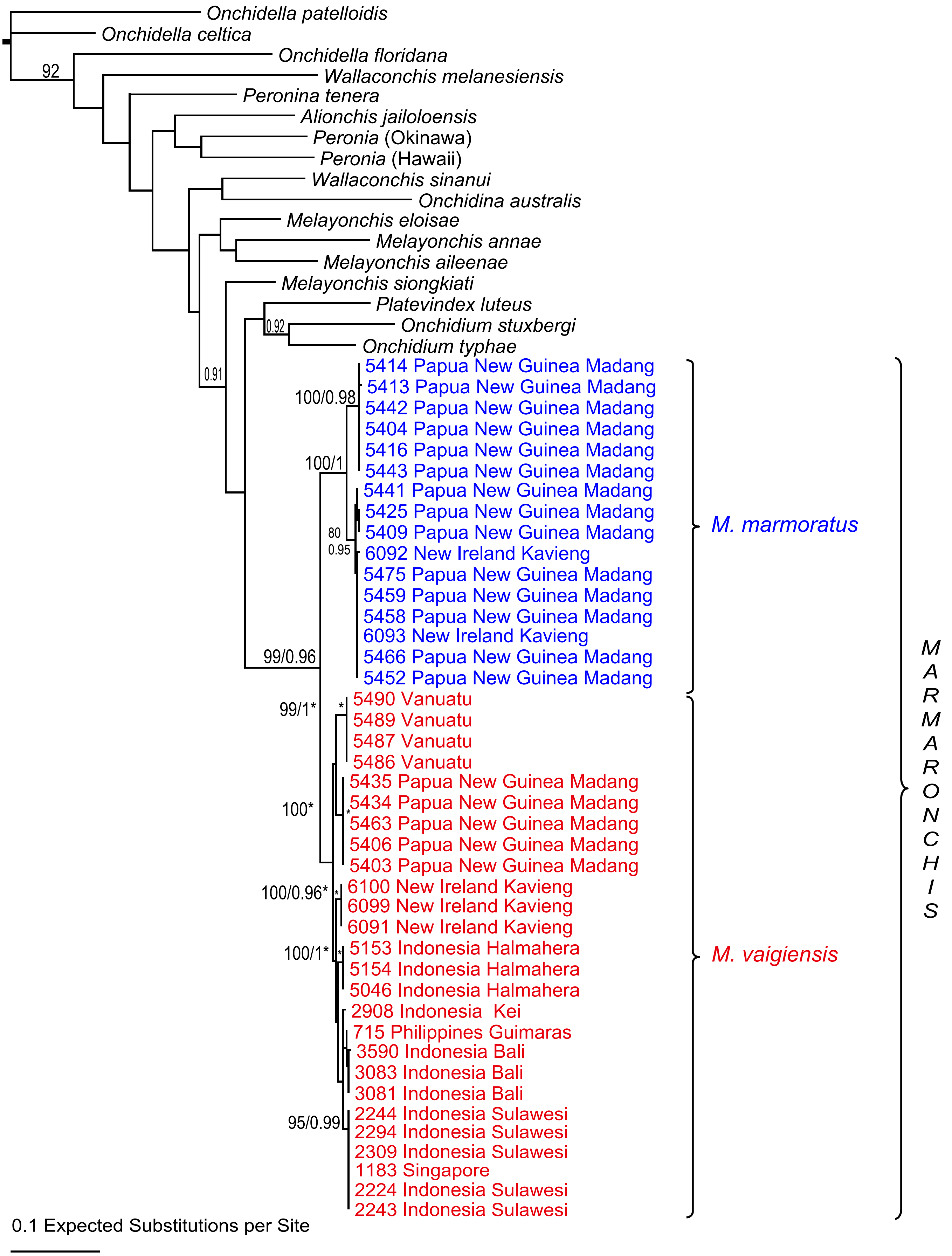

Fig. 1. Phylogenetic tree showing relationships between *Marmaronchis* individuals based on mitochondrial COI sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (>75% and >0.9) are indicated. All other sequences serve as outgroups. Information on individually-identified *Marmaronchis* specimens can be found in the list of material examined.

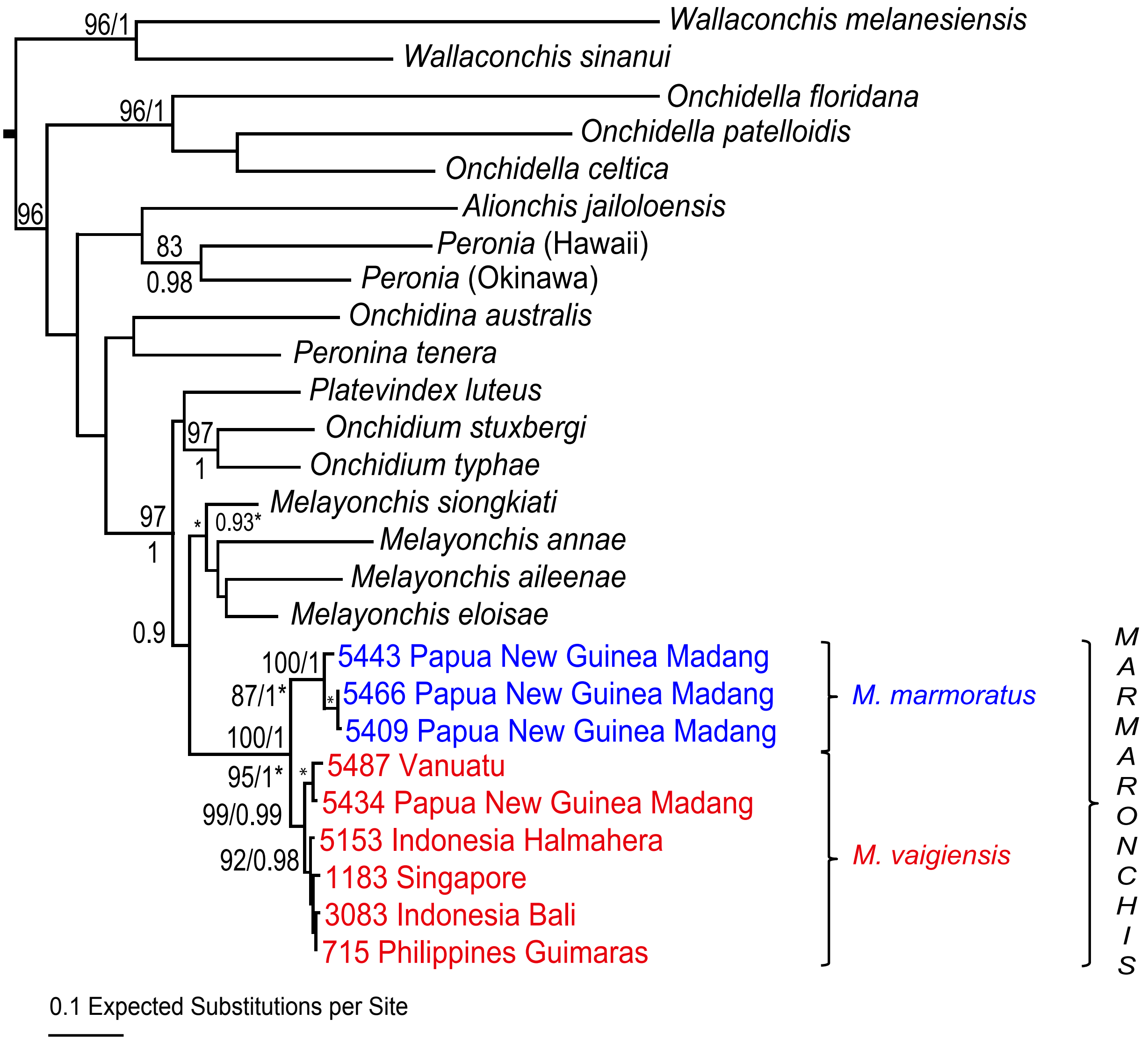

Fig. 2. Phylogenetic tree showing relationships between *Marmaronchis* individuals based on concatenated mitochondrial COI, 16S, and 12S sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (>75% and >0.9) are indicated. All other sequences serve as outgroups. Information on individually-identified *Marmaronchis* specimens can be found in the list of material examined.

simply is compared in a section before the systematic accounts.

PHYLOGENETIC RESULTS

Molecular phylogenetic analyses (Figs. 1–4). DNA sequences are used here to test (1) whether *Marmaronchis* is a distinct clade or nested within an existing genus and (2) how many species there are within *Marmaronchis*. All phylogenetic analyses yielded two species within one clade distinct from other onchidiid taxa. The monophyly of *Marmaronchis* is strongly supported in all analyses, including analyses with only one marker (COI or ITS2), with bootstrap values from 98 to 100 and posterior probabilities from 0.96 to 1.0. Also, *Marmaronchis* is not included within any of the existing onchidiid genera but concatenated data sets suggest that it is most closely related to *Melayonchis* Dayrat & Goulding in Dayrat et al., 2017, *Platevindex* Baker, 1938 and *Onchidium* — the clade including these three genera and *Marmaronchis* is supported with a bootstrap value of 96 and a posterior probability of 0.96 (Figs. 2, 4). As for species, two reciprocally-monophyletic, highly-supported molecular units are consistently recovered in all analyses, and are regarded as two distinct species of *Marmaronchis*: *M. vaigiensis*, and *M. marmoratus*.

Pairwise genetic divergences. Pairwise genetic distances also support the existence of two *Marmaronchis* species (Table 2). Pairwise genetic divergences are all lower than 2.9% within *M. vaigiensis* and all lower than 4.1% within *M. marmoratus*. Pairwise divergences between these two units are between 7.5% to 10.5%. Thus, a large barcode gap (from 4.1% to 7.5%) separates the two *Marmaronchis* species. The highest intra-specific divergences observed within *M. vaigiensis* are between individuals from Vanuatu and individuals from Singapore or Indonesia (Sulawesi and Kei Islands), which is easily explained by the fact that the two individuals most distant geographically in our sampling are precisely from Singapore and Vanuatu. Interestingly, however, the highest intra-specific genetic divergences

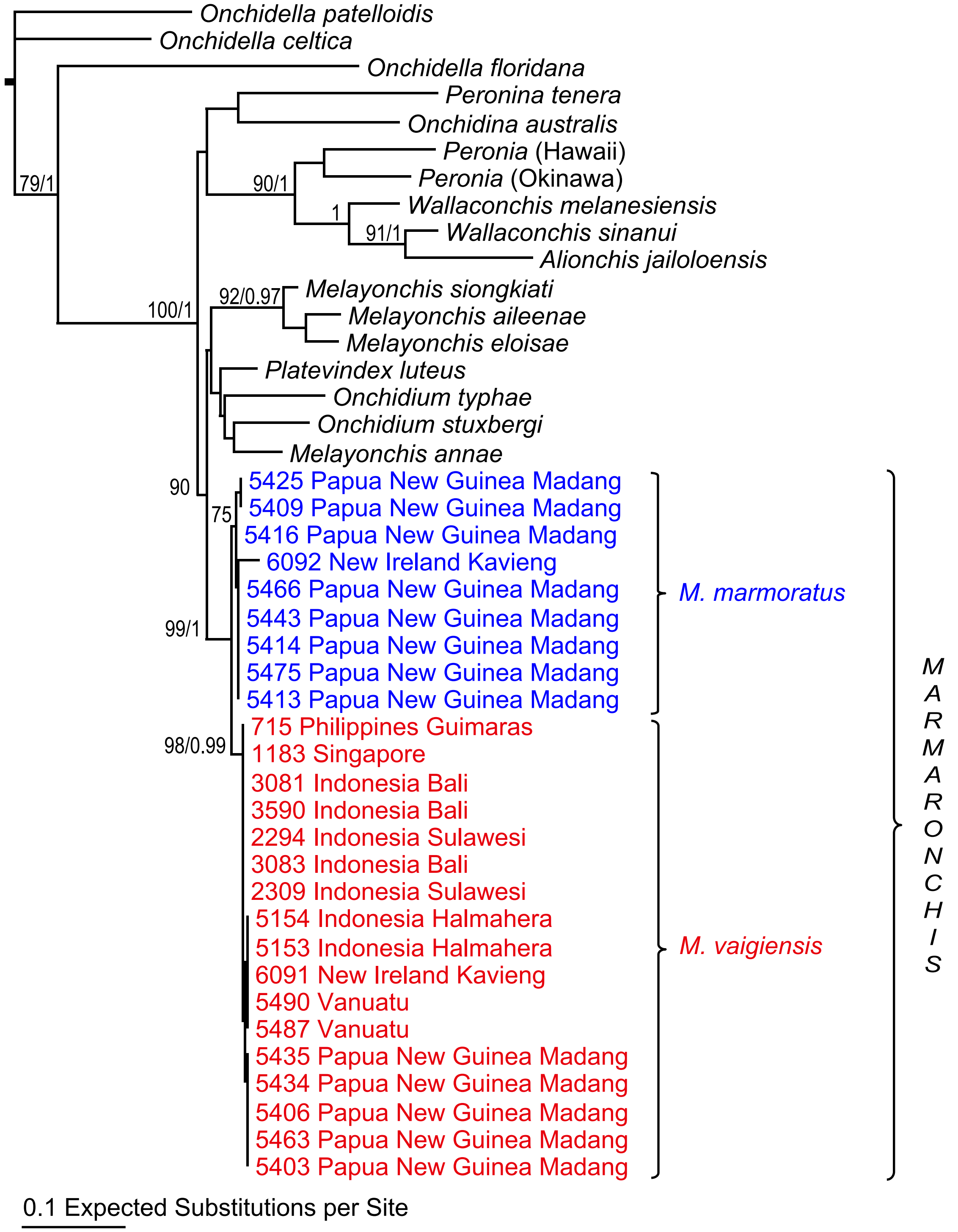

Fig. 3. Phylogenetic tree showing relationships between *Marmaronchis* individuals based on nuclear ITS2 sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (>75% and >0.9) are indicated. All other sequences serve as outgroups. Information on individually-identified *Marmaronchis* specimens can be found in the list of material examined.

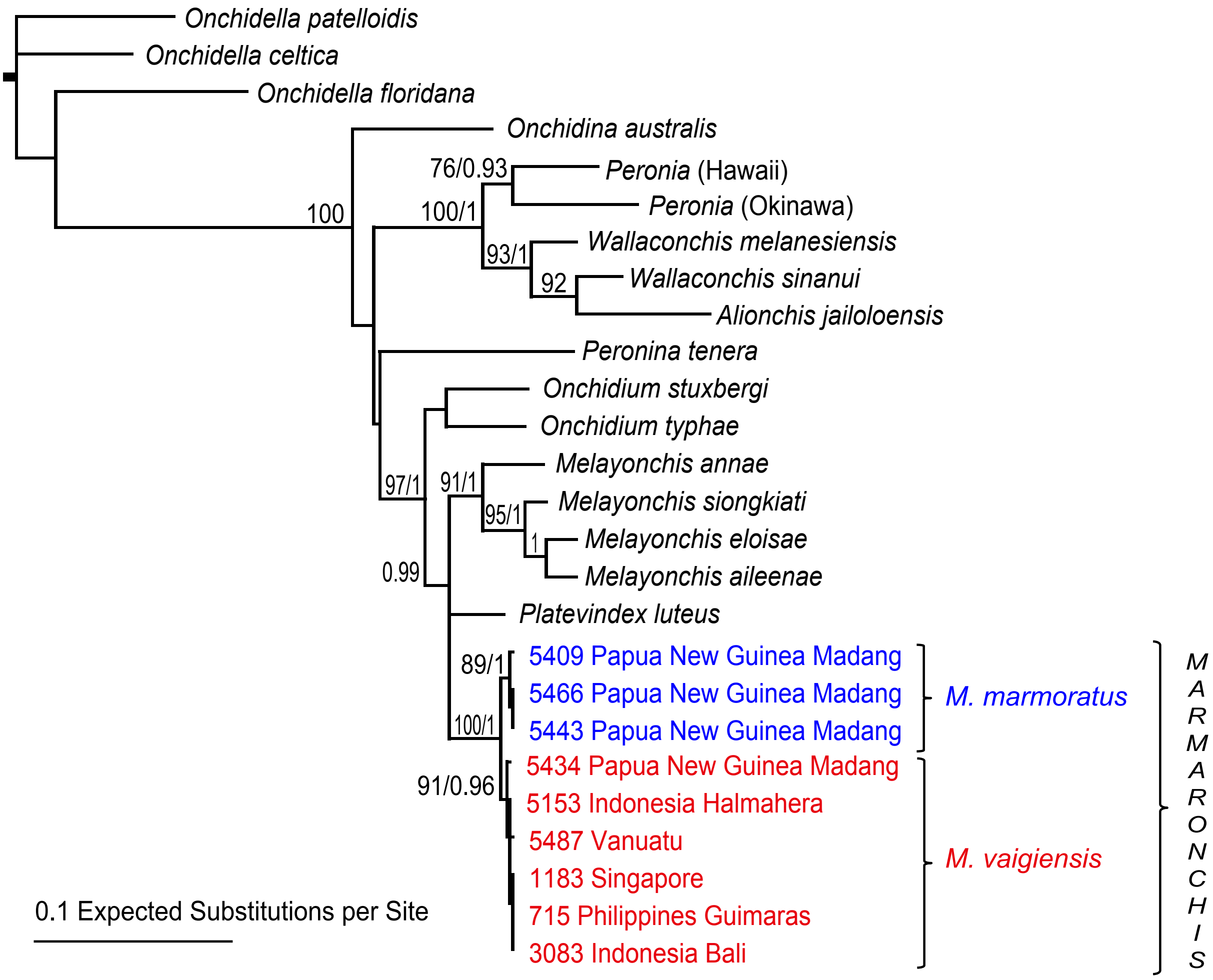

Fig. 4. Phylogenetic tree showing relationships between *Marmaronchis* individuals based on concatenated nuclear ITS2, 28S, and H3 sequences. Numbers above branches are the bootstrap values (Maximum Likelihood analysis) and below are the posterior probabilities (Bayesian analysis); only significant numbers (>75% and >0.9) are indicated. All other sequences serve as outgroups. Information on individually-identified *Marmaronchis* specimens can be found in the list of material examined.

Table 2. Pairwise genetic distances between mitochondrial *COI* DNA sequences in *Marmaronchis*. Ranges of minimum to maximum distances are indicated (in percentage).

Species	***M. vaigiensis***	***M. marmoratus***
M. vaigiensis	0.0–2.9	
M. marmoratus	7.5–10.5	0.0–4.1

within *M. marmoratus* are between individuals from Madang (4.1%), suggesting that, for some reason, there is a much higher population structure within *M. marmoratus* (even between individuals from localities that are very close geographically), than within *M. vaigiensis*. In fact, the pairwise genetic distances between individuals of *M. vaigiensis* from Singapore and Kavieng, New Ireland, are only 1.4%, and those between individuals from Singapore and Madang are only 1.7%.

COMPARATIVE ANATOMY

Colour and morphology of live animals (Fig. 5). The colour of live animals is illustrated here only for *M. vaigiensis* because no live pictures were available for specimens collected in Madang and Kavieng. Slugs are not covered with mud but are occasionally oily. The colour of live animals is highly variable, both dorsally and ventrally. The dorsal notum is randomly mottled with dark (brown or black) and light (whitish-beige) areas, but varies from completely dark to completely light (and even transparent). The foot is usually light yellowish, but it can also be orange or dark grey. The colour of the hyponotum (the ventral part of the notum, around the foot) varies from light to dark grey, and can even be black. The shape of live slugs varies greatly, from flattened to hemispherical. The notum of live animals is evenly covered with small, rounded, papillae, which give it a finely granular appearance (the notum of preserved animals tend to be smooth). Dorsal eyes are present. A central group of three to five dorsal eyes is always present. It is accompanied by a variable number of additional eyes (isolated or in groups) which can be difficult to observe because of the dark background of the notum.

External morphology. Externally, preserved specimens of *M. vaigiensis* and *M. marmoratus* are impossible to distinguish. They typically are hemispherical, with a narrow, wavy notum margin (Dayrat, 2010: fig. 1), which is distinctive

Table 3. Radular formulae for the two *Marmaronchis* species following the same format: number of rows × number of lateral teeth per left half row - 1 (rachidian tooth) - number of lateral teeth per right half row. Each DNA extraction number corresponds to one individual. The voucher catalog numbers can be shared by several individuals when collected at exactly the same locality (each individual is preserved in its own separate vial with its corresponding DNA number).

Species	Radular formula	Spm length (mm)	Voucher	DNA extraction number
M. vaigiensis	55 × 75-1-75	14	UMIZ 00183	2244
	65 × 70-1-70	23	UMIZ 00186	3081
	65 × 80-1-80	17	MNHN IM-2013-54460	6091
M. marmoratus	65 × 100-1-100	18	MNHN IM-2013-55527	6092
	80 × 105-1-105	13	MNHN IM-2013-13352	5413
	70 × 105-1-105	15	MNHN IM-2013-15866	5475

Table 4. Individual variation of the spine of the accessory penial gland and of the penis hooks in *Marmaronchis vaigiensis* and *Marmaronchis marmoratum* (Fig. 8), as well as a comparison with past observations (Dayrat, 2010).

	M. vaigiensis	*M. marmoratus*	Dayrat, 2010
Shape of the spine of accessory penial gland	Straight, slightly bent, strongly bent	Slightly bent	Straight
Size of the spine of accessory penial gland	0.4 to 0.7 mm	0.7 to 0.8 mm	0.4 to 1 mm
Penis solid stalk	0.9 to 1.1 mm	0.9 to 1.2 mm	< 1 mm
Penis soft tube with conical hooks	0.3 mm	0.3 to 0.4 mm	< 0. 5 mm
Conical hooks	70 to 100 µm	20 to 80 µm	60 to 100 µm

(not found in any other preserved onchidiids) and helps to identify specimens in museum collections as *Marmaronchis*.

Internal anatomy (Figs. 6–8). Specimens identified as *M. vaigiensis* and *M. marmoratus* with DNA sequences cannot be distinguished internally and the detailed anatomical description of *O. vaigiense* by Dayrat (2010), which applies to both species, is not repeated here. However, a few characters important for taxonomy are mentioned: the intestinal loops are of type I (Fig. 6A, B); radular teeth are illustrated on Fig. 7 and examples of radular formulae are found in Table 3; the receptaculum seminis in the posterior (hermaphroditic) reproductive parts is of a small size (Fig. 6C, D); the retractor muscle of the anterior (male) copulatory parts inserts on the floor of the anterior half of the visceral cavity, most often behind the central nervous system (Fig. 6E, F); there is an accessory penial gland but with no muscular sac (Fig. 6E, F); the shape and length of the spine of the accessory penial gland vary between individuals (Fig. 8A–F; Table 4); the penis is composed of a proximal, elongated, straight or slightly curved, solid but flexible, cylindrical stalk, and a shorter, distal, soft tube with approximately 30 conical hooks internally (Fig. 8G, H).

SYSTEMATICS

Onchidiidae Rafinesque, 1815

Marmaronchis Dayrat & Goulding, new genus

Type species. *Marmaronchis vaigiensis*, designated here.

Etymology. The name *Marmaronchis* is a combination of *mármaros* (ὁ μάρμαρος), which means 'marble' in Greek (because the dorsal notum of *Marmaronchis* slugs is marbled with dark and light areas), and *onchis*, a word derived from the Greek ὁ ὄγκος and one of the early names used to refer to onchidiid slugs.

Gender. Gender. Masculine, gender of *onchis* (ICZN Art. 30.1.1; ICZN, 1999), a word derived from the masculine Greek word ὁ ὄγκος, which means 'mass' or 'tumour'. As a result (ICZN Art. 31.2; ICZN, 1999), the endings of the specific names *vaigiense* (an adjective from the Latinisation of a geographical name — Vaigiou) and *marmoratum* (a Latin adjective) must be changed from neuter gender (because *Onchidium* is a name of neuter gender) to masculine gender (i.e., *vaigiensis* and *marmoratus*).

Diagnosis. Body not flattened. No dorsal gills. Dorsal eyes present on notum. Retractable, central papilla absent. Foot wide, approximately half of total width. Eye tentacles short and narrow. Eyes at tip of ocular tentacles. Pneumostome median, closer to anus and pedal sole than to hyponotum margin. Female opening close to anus. Male opening below and on left of right ocular tentacle (in dorsal view). Intestinal loops of type I. Rectal gland present. Penial hooks present. Accessory penial gland present, with spine but no muscular sac.

Diagnostic features. Externally, *Marmaronchis* is not easily distinguished from other onchidiid genera. It could be confused with *Melayonchis* and *Wallaconchis* Goulding

& Dayrat in Goulding et al., 2018b. Internally, however, *Marmaronchis* is characterised by a unique combination of anatomical traits which is not found in any other onchidiid genus: intestinal loops of type I, rectal gland present, and accessory penial gland present.

Remarks. *Onchidium vaigiense* and *Onchidium marmoratum* belong to a clade that is separate from all other onchidiid genera (Figs. 1–4). A new generic name is needed for that clade because no existing generic name applies to it (for a recent review of the application of all onchidiid genus-group names, see Dayrat et al., 2017). More specifically, molecular phylogenetic analyses here clearly show that *O. vaigiense* and *O. marmoratum* do not belong to *Onchidium* (type species: *Onchidium typhae* Buchannan, 1800) which agrees with anatomical data because both *O. vaigiense* and *O. marmoratum* lack the distinct synapomorphy of *Onchidium* (large, conical, pointed papillae on the dorsum of live animals).

Marmaronchis vaigiensis (Quoy & Gaimard, 1825) new combination

(Figs. 5, 6A, C, F, 7A, C, E, 8A–C, G, 10)

Onchidium vaigiense Quoy & Gaimard, 1825: 429; Tapparone-Canefri, 1883: 213; Plate, 1893: 175–176, figs. 10, 79; Bretnall, 1919: 314–315; Hoffmann, 1928: 76; Dayrat, 2010: 88–101, figs. 1–7.

Paraoncidium vaigiense (Quoy & Gaimard, 1825). Labbé, 1934a: 229–230, figs. 68–70.

Onchidium ambiguum Semper, 1880: 264, pl. 19, figs. 4–5, 10, pl. 22, figs. 16–19; Semper, 1882: 265, 289. **New synonym**.

Onchidium steenstrupii Semper, 1882: 265–266, pl. 20, fig. 5, pl. 21, figs. 22, 24; Plate, 1893: 176; Bretnall, 1919: 315; Hoffmann, 1928: 45; Labbé, 1934a: 222 [as *O. streenstrupii*, spelling mistake]. **New synonym**.

Onchidella steenstrupii (Semper, 1882). Tapparone-Canefri, 1883: 213 [as *Oncidiella steenstrupii*].

Onchidium leopoldi Labbé, 1934b: 70–73, figs. 10A, 11B, 13, 15, 23, 26, 33–35, pl. I, fig. 4 [as *Oncidium leopoldi*].

Onchidella maculata — Labbé, 1934b: 78–80, figs. 10, 13, 39, pl. I, fig. 7 [not of Plate, 1893; as *Oncidiella maculata*].

Type localities. *Onchidium ambiguum*: ‘Aibukit, Palaos’ [i.e., Palau], which is the locality of the lectotype designated here (see Type Materials below). Other localities mentioned by Semper for other former syntypes (now paralectotypes) are Singapore and Nicobar Islands. Palau is selected here as the type locality because Semper regarded the specimens from Singapore and Nicobar Islands to be part of a distinct variety (which he did not name).

Onchidium leopoldi: ‘Pisang Eiland (Nouvelle-Guinée)’ [i.e., Pisang Island, Banda Islands, Maluku, Indonesia]. Pisang Island is not on the northwest coast of New Guinea (Dayrat, 2010) but in the Banda Sea, west of Irian Jaya and south of Seram and Ambon.

Onchidium steenstrupii: ‘Sambelang’ [i.e., Little Nicobar Island, Nicobar Islands], which is the locality of the lectotype designated here (see Type Materials below). Other localities mentioned by Semper for other former syntypes (now paralectotypes) are Pohnpei (Caroline Islands, Micronesia) and New Guinea. In the original description, Semper (1882: 266) mentions the Nicobar locality as “Sambelang am Gangeshafen (4 Exemplare), an und in verfaulten Baumstämmen (Kopenhagener Museum, Expedition der Galathea),” [translation: 4 specimens, preserved at the Copenhagen Museum, collected on rotten logs, Ganges harbor, Sambelang, Galathea expedition]. There are four labels in the jar of the lectotype and one paralectotype (ZMUC). Three labels can hardly be read. One label, however, says ‘*Oncidium steenstrupii* Semper 1885 / *Loc*. Sambelang, Ganges Havn., Nicobarerne. Paa en raaden Træstamme / *Legit*. Rhrdt. Galathea. *Datum*. Januar-Febr. 1846’, [translation: collected on rotten logs, Ganges harbor, Sambelang, Nicobar Islands, by J. T. Reinhardt, Galathea expedition, January-February 1846], which perfectly matches the locality mentioned in Semper’s original description (Sambelang is an old name for Little Nicobar Island). The label of the jar with the two other paralectotypes from Nicobar (ZMB 39041) says “Sambelong, Nikobas’, which refers to Sambelang, Little Nicobar Island. Ponape (Pohnpei, Caroline Islands, Micronesia) is not a type locality but there is no doubt that the paralectotypes from Pohnpei are the specimens examined by Semper because both the label and the original description refer to specimens from the Museum Godeffroy collected by Kubary from Ponape. Finally, it is not possible to know where exactly in New Guinea the other paralectotypes were collected from. In the original description, Semper (1882: 266) only mentions that Tapparone-Canefri sent him one specimen from New Guinea. One label for two paralectotypes from New Guinea says ‘Neu-Guinea / Tapp’. (ZMB 39046b) while the label for the other two paralectotypes simply says ‘Neu-Guinea’ (ZMB 39046a). Note that Tapparone-Canefri (1883: 213) briefly mentions three localities for *O. steenstrupii*: Ponape; Sambelang, India; and Sorong, New Guinea. It is therefore possible that the specimen(s) examined by Semper came from Sorong, which is in West Papua, Indonesia (near the type locality of *M. vaigiensis*). At any rate, it is considered here that these paralectotypes could have been collected anywhere in New Guinea (West Papua and Papua New Guinea), which is vague but falls within the known distribution of *M. vaigiensis*. Even though it is unclear whether or not Semper examined all four New Guinea paralectotypes for the purpose of the original description—he may have mentioned only one specimen instead of four by mistake, or he may have identified some specimens from New Guinea as *O. steenstrupii* after the publication came out—they are all part of *Marmaronchis* and they are all regarded as paralectotypes here.

Onchidium vaigiense: ‘Îles Vaigiou et Rawak’ [i.e., Waigeo and Rawak islands, northwest of Irian Jaya, West Papua, Indonesia].

Type materials. *Onchidium ambiguum*: The material examined by Semper for the original description of *Onchidium ambiguum* included 15 specimens: six specimens from Palau, eight from Singapore, and one from Nicobar. Semper (1882: 265) regarded the specimens from Singapore and Nicobar as a distinct variety (unnamed) of the species. A total of

Fig. 5. Live specimens, dorsal (A–H) and ventral (I–K) views, *Marmaronchis vaigiensis*, Indonesia. A, Bali, 23 mm long [3081] (UMIZ 00186); B, Bali, 17 mm long [3083] (UMIZ 00186); C, Halmahera, 18 mm long [5046] (UMIZ 00187); D, Halmahera, 19 mm long [5153] (UMIZ 00187); E, Kei, 10 mm long [2908] (UMIZ 00185); F, Sulawesi, 8 mm long [2224] (UMIZ 00182); G, Sulawesi, 8 mm long [2243] (UMIZ 00183); H, Sulawesi, 14 mm long [2244] (UMIZ 00183); I, same as A; J, same as C; K, same as H.

10 syntypes were found in various collections, six from Singapore and four from Palau, all of which were examined for the present study and all of which look externally like *M. vaigiensis*. One of the specimens from Palau is designated here as a lectotype: 12/10 mm (ZMB 39024a). The three other specimens from Palau are paralectotypes: 14/10, 12/8, and 12/10 mm (ZMB 39024b). All specimens from Singapore are paralectotypes: four specimens 16/10, 11/8, 10/9, and 10/7 mm (ZMB 39044), one specimen 10/8 mm (ZMUC), and one specimen 12/10 mm (NHMUK 80.10.8.7). The lectotype was left entire by Semper and was opened for the present study to check the characters diagnostic of *Marmaronchis*: intestinal loops of type I, rectal gland present, and accessory penial gland present. The three paralectotypes from Palau were dissected (likely by Semper) prior to the present study. Internal parts are partly or completely missing. The ZMUC paralectotype from Singapore was opened (by Semper or Hoffmann) prior to the present study and internal organs are mostly destroyed. Two ZMB paralectotypes (16/10 and 10/9 mm) from Singapore were opened (likely by Semper) prior to the present study and some internal organs are missing. Two ZMB paralectotypes (11/8 and 10/7 mm) from Singapore were opened for the present study to check the characters diagnostic of *Marmaronchis*. Finally, the

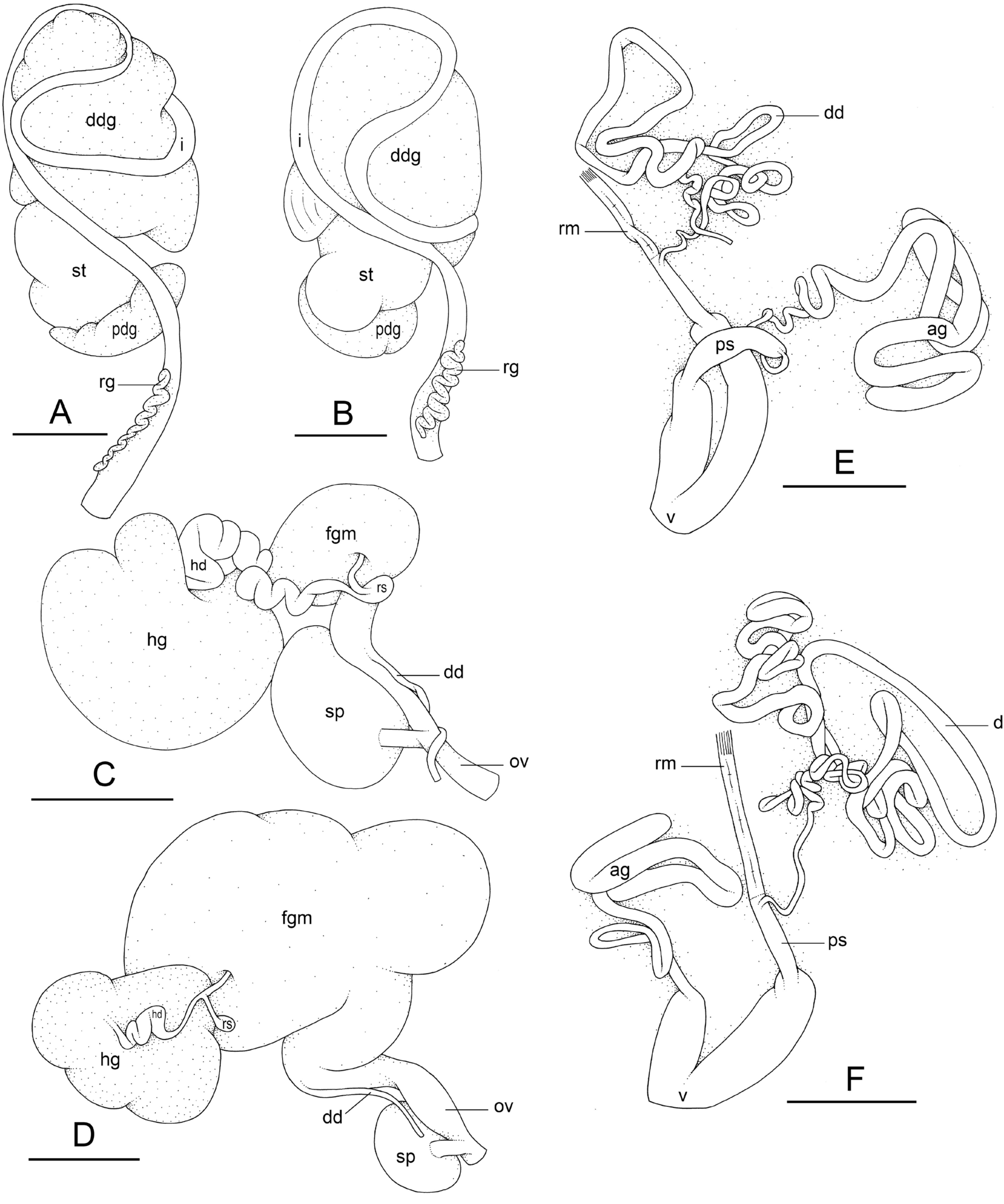

Fig. 6. Digestive system and reproductive system, *Marmaronchis vaigiensis* (A, C, F) and *Marmaronchis marmoratus* (B, D, E). A, Digestive system (type I), dorsal view, scale bar = 3 mm, Indonesia, Sulawesi [2244] (UMIZ 00183); B, Digestive system (type I), dorsal view, scale bar = 3 mm, Papua New Guinea, New Ireland, Kavieng [6092] (MNHN IM-2013-55527); C, Posterior reproductive parts, scale bar = 2 mm, same as A; D, Posterior reproductive parts, scale bar = 2 mm, same as B; E, Anterior male copulatory parts, scale bar = 2 mm, same as B; F, Anterior male copulatory parts, scale bar = 2 mm, Papua New Guinea, Madang [5435] (MNHN IM-2013-11718). Abbreviations: dd, deferent duct; ddg, dorsal lobe of digestive gland; fgm, female gland mass; hd, hermaphroditic duct; hg, hermaphroditic gland; i, intestine; ov, oviduct; pdg, posterior lobe of the digestive gland; ps, penial sheath; rg, rectal gland; rm, penial retractor muscle; rs, receptaculum seminis; sp, spermatheca; st, stomach; v, vestibule.

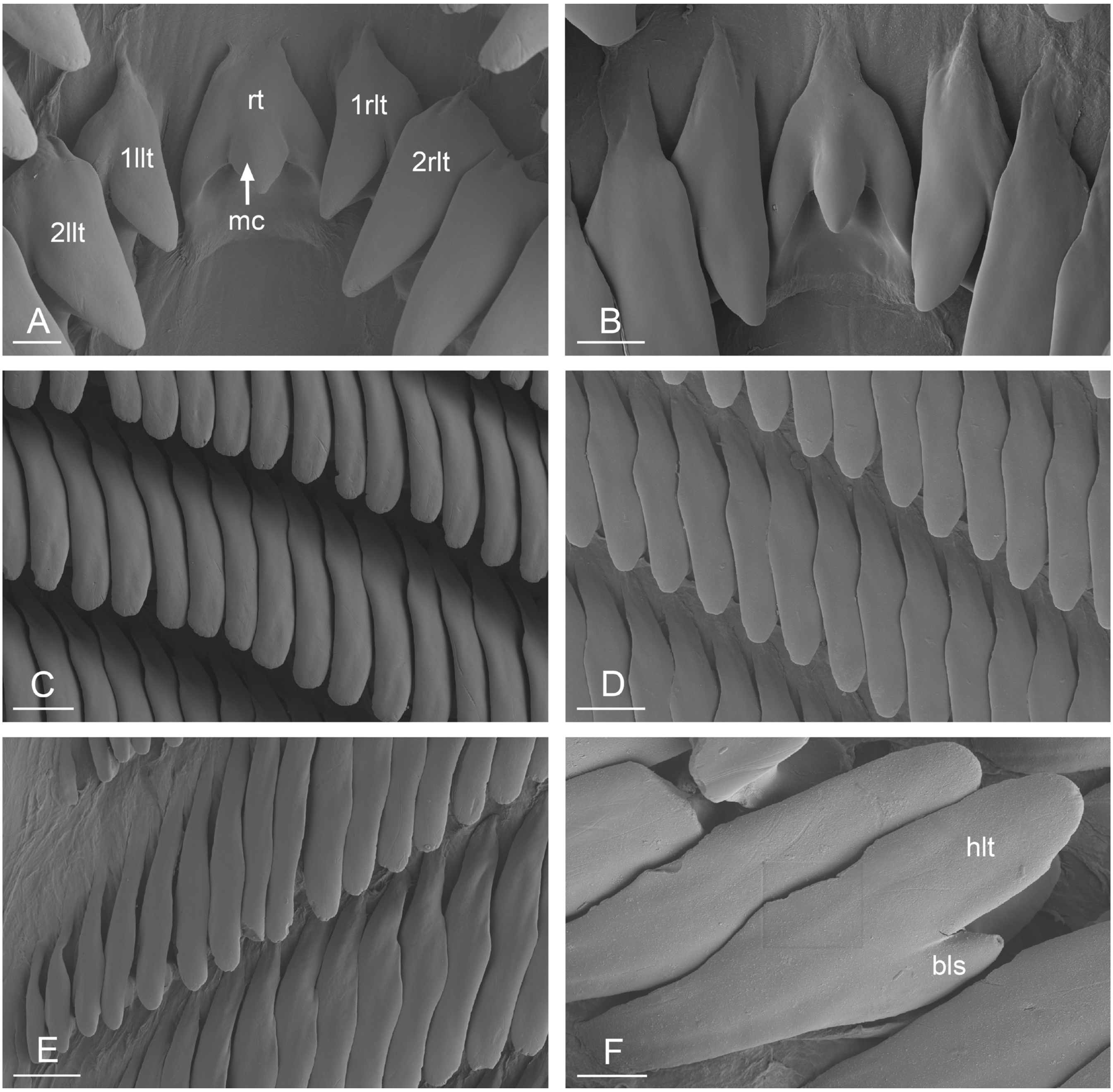

Fig. 7. Radula, *Marmaronchis vaigiensis* (A, C, E) *and Marmaronchis marmoratus* (B, D, F). A, Rachidian and innermost lateral teeth, scale bar = 10 µm, Indonesia, Bali [3081] (UMIZ 00186); B, Rachidian and innermost lateral teeth, scale bar = 10 µm, Papua New Guinea, New Ireland, Kavieng [6092] (MNHN IM-2013-55527); C, Right lateral teeth, scale bar = 20 µm, same as A; D, Right lateral teeth, scale bar = 20 µm, Papua New Guinea, Madang [5475] (MNHN IM-2013-15866); E, Outermost, left lateral teeth, scale bar = 20 µm, same as A; F, Left lateral tooth with basal lateral spine, outer lateral view, scale bar = 10 µm, same as D. Abbreviations: 1llt, first, left, lateral tooth; 1rlt, first, right, lateral tooth; 2llt, second, left, lateral tooth; 2rlt, second, right, lateral tooth; bls, basal lateral spine; hlt, hook of lateral tooth; mc, median cusp of rachidian tooth; rt, rachidian tooth.

NHMUK paralectotype from Singapore still is entire and was not dissected for the present study.

Onchidium leopoldi: Remarks on the type material of *O. leopoldi*, composed of three syntypes (20/17, 13/11, and 11/9 mm) in the collections of the Royal Belgian Institute of Natural Sciences (RBINS, no catalog number), can be found in Dayrat (2010).

Onchidium steenstrupii: According to the original description, the material examined by Semper (1882: 266) for *Onchidium steenstrupii* included eight specimens: four specimens from Nicobar Islands, three from Ponape (Pohnpei, Caroline Islands, Micronesia), and one from New Guinea. A total of 10 syntypes were found in various collections (four from Nicobar, two from Pohnpei, and four from New Guinea), all of which were examined for the present study and all of which look externally like *M. vaigiensis*. One specimen 18/16 mm from Nicobar is designated here as a lectotype (ZMUC). The three other specimens from Nicobar are paralectotypes: two specimens 16/14 and 20/17 mm (ZMB 39041) and one specimen 18/15 mm (ZMUC). The two specimens (20/16 and

17/12 mm) from Pohnpei are paralectotypes (ZMH 27481/3). The vial with the two Pohnpei paralectotypes includes a third specimen which actually is a nudibranch. Finally, the four specimens from New Guinea are paralectotypes: 18/15 and 18/15 mm (ZMB 39046a) and 15/12 and 11/10 mm (ZMB 39046b). The ZMUC lectotype was dissected (likely by Semper) prior to the present study but we could still check all the characters diagnostic of *Marmaronchis*: intestinal loops of type I, rectal gland present, and accessory penial gland present. The ZMUC paralectotype from Nicobar is entire and was not dissected for the present study. One ZMB paralectotype (16/14 mm) from Nicobar was completely destroyed (likely by Semper) prior to the present study and all internal parts are missing. The second ZMB paralectotype (20/17 mm) from Nicobar was dissected (likely by Semper) prior to the present study but we could still check all the characters diagnostic of *Marmaronchis*. One ZMUC paralectotype from Nicobar was dissected (likely by Semper) prior to the present study but internal organs remain in the vial. One ZMH paralectotype (20/16 mm) from Pohnpei was dissected for the present study; the second ZMH paralectotype (17/12 mm) is still entire and was not dissected here. The 18/15 mm ZMB New Guinea paralectotype was dissected (likely by Semper) prior to the present study, but all organs remain inside the animal; the ZMB New Guinea paralectotype (15/12 mm) was dissected (likely by Semper) prior to the present study, and only pieces of the digestive gland and of the female reproductive system remain inside the specimen; two ZMB paralectotypes (18/15 and 11/10 mm) from New Guinea are still entire and were not dissected for the present study.

Onchidium vaigiense: The type material of *O. vaigiense* could not be located earlier (Dayrat, 2009, 2010). At that time, the specimen that Labbé (1934a: 229–230, figs. 68–70) examined and thought was the type material of *O. vaigiense* could not be found either, and Labbé's re-description of that specimen as *Paraoncidium vaigiense* was originally regarded as a misidentification because Labbé mentioned no accessory penial gland (Dayrat, 2010: 88). In 2017, however, a specimen was located at the MNHN (MNHN-IM-33703) which likely is the specimen that Labbé described as *Paraoncidium vaigiense*, even though it is not a syntype of *O. vaigiense* (it is unclear how many type specimens were deposited at the MNHN for Quoy and Gaimard's *O. vaigiense*). The specimen MNHN-IM-33703 (14/12 mm) is extremely poorly preserved but its notum is smooth, as usual in *M. vaigiensis*. There is a recent label with the number '55' (unknown meaning) and, as mentioned by Labbé, another label indicating '*Peronia* Quoy et Gaimard, 1829'. However, and more importantly, there is a much older label, not mentioned by Labbé, on which one can read — though with some difficulty: 'Vaigiou' 'Gaimard' and 'Astrolabe'. Those words strongly suggest that the specimen is part of the collection made during the voyage of the *Astrolabe* (1826–1829), which means that it cannot be the type material of *O. vaigiense* because the later was described based on collections made during the voyage of the *Uranie* and of the *Physicienne* (1817–1820). Most likely, that old label indicates that the specimen was identified as the '*Onchidium* de Vaigiou' and that it was collected by Quoy and Gaimard during the voyage of the Astrolabe (1826–1829) which visited places like New Ireland, Ambon, and Sulawesi, but not Waigeo Island. The specimen MNHN-IM-33703 could be part of *M. vaigiensis* but that is not certain. That being said, it probably does not matter whether MNHN-IM-33703 is part of *M. vaigiensis* or not given that no locality is known and that it cannot be considered to be part of the type material of *O. vaigiense*. Its digestive system is largely destroyed and the type of intestinal loops cannot be checked (Labbé says that it is of type I but he often made mistakes regarding the intestinal type). Its anterior male parts are missing and so the presence or absence of an accessory penial gland cannot be checked. Finally, a thin rectal gland seems to be present. If we trust that the intestinal type was of type I and that the rectal gland is present, then the specimen MNHN-IM-33703 likely is part of *M. vaigiensis*, assuming that Labbé—as often—made a mistake when he reported no penial accessory gland. Indeed, the only onchidiids with an intestinal type I, a rectal gland, and no penial accessory gland are a few *Platevindex* species and that specimen is not a *Platevindex* (its body is not flattened). There are two other jars with old *Marmaronchis* specimens in the MNHN collections, both labeled as '*Onchidium* / Nouvelle-Irlande [New Ireland] 1829 / M^{rs} Quoy et Gaimard'. One jar labeled with the number '45' contains two specimens (20/15 and 15/15 mm). The other jar labeled with the number '47' contains two specimens (20/15 and 16/15 mm). These four specimens clearly are part of *Marmaronchis*, even though it cannot be determined whether they are part of *M. vaigiensis* or *M. marmoratus*. They apparently have not been used either by Quoy & Gaimard (1832–1833) or by Labbé (1934a). It is possible that the specimen MNHN-IM-33703 came from the same series of specimens from New Ireland and was identified by Quoy and Gaimard as what they called earlier the '*Onchidium* de Vaigiou'.

Additional material examined. Singapore, North Coast, Admiralty Road West, 01°27.071′N, 103°46.633′E, 1 specimen 15/8 [1183] mm, station 10, cemented wall under jetty (ZRC.MOL.3007). Philippines, Guimaras Island, Iloilo Province, Buenavista City, Santa Rosario, [no coordinates], 1 specimen 12/10 [715] mm, shore below Bavani Resort (UF 245715). Indonesia, Sulawesi, Bahoi, 01°43.355′N, 125°01.232′E, 1 specimen (8/6 [2224] mm), station 88, sand, small rocks, pieces of wood outside narrow coastal mangrove (UMIZ 00182). Indonesia, Sulawesi, Wori, 01°36.06′N, 124°51.73′E, 3 specimens (8/7 mm [2243], 14/8 [2244], and 5/4 [2294] mm), station 90, old *Avicennia*, *Sonneratia*, *Rhizophora* mangrove forest with, rocks and dead logs (UMIZ 00183). Indonesia, Sulawesi, Mantehage Island, 01°41.880′N, 124°46.741′E, 1 specimen (7/6 [2309] mm), station 91, *Sonneratia* at low intertidal and *Rhizophora* at high intertidal (UMIZ 00184). Indonesia, Kei Islands, Un, 05°38.273′S, 132°45.738′E, 1 specimen (10/8 [2908] mm), station 140, back of mangrove, on rocks, on mud, inside logs, and under leaf litter (UMIZ 00185). Indonesia, Bali, Gilimanuk, 08°10.259′S, 114°26.606′E, 4 specimens (23/17 [3081], 17/12 [3083], and 12/10 [3590] mm), station 155, from high intertidal with water pools and many mounds up

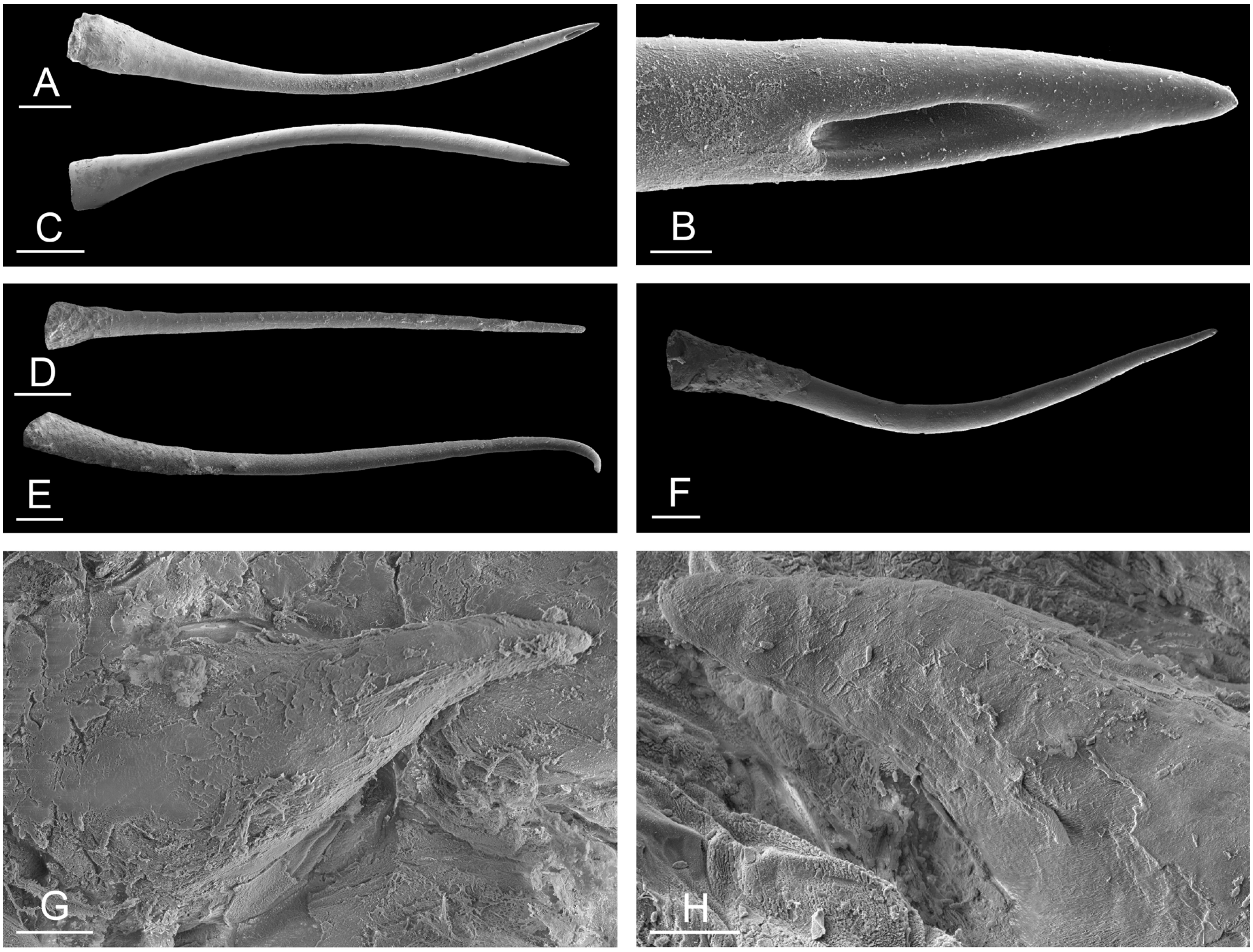

Fig. 8. Spine of the accessory penial gland (A–F) and hooks of the penis (G, H), *Marmaronchis marmoratus* (A–C, G) *and Marmaronchis vaigiensis* (D–F, H). A, Scale bar = 100 µm, Papua New Guinea, New Ireland, Kavieng [6092] (MNHN IM-2013-55527); B, Spine tip, scale bar = 10 µm, same as A; C, Scale = 100 µm, Papua New Guinea, Madang [5413] (MNHN IM-2013-13352); D. Scale bar = 40 µm, Indonesia, Sulawesi [2244] (UMIZ 00183); E, Scale bar = 40 µm, Indonesia, Bali [3081] (UMIZ 00186); F, Scale bar = 40 µm, Papua New Guinea, New Ireland, Kavieng [6091] (MNHN IM-2013-54460); G, Scale bar = 10 µm, same as C; H, Scale bar = 10 µm, same as E.

to shore with sand and rocks (UMIZ 00186). Indonesia, Halmahera, Foli, 01°14.66′N, 128°10.61′E, 3 specimens (18/15 [5046], 19/12 [5153], and 24/15 [5154] mm), station 217, rocky shore near a beach (UMIZ 00187). Papua New Guinea, Madang, Rempi Area, S Dumduman Island, 05°00.2′S, 145°47.6′E, 1 specimen (11/9 [5434] mm), leg. MNHN expedition Papua Niugini, station PM11, brackish stream mouth near ocean (MNHN IM-2013-11717). Papua New Guinea, Madang, Rempi Area, S Dumduman Island, 05°00.2′S, 145°47.6′E, 1 specimen (16/11 [5435] mm), leg. MNHN expedition Papua Niugini, station PM11, brackish stream mouth near ocean (MNHN IM-2013-11718). Papua New Guinea, Madang, Rempi Area, S Dumduman Island, 05°00.2′S, 145°47.6′E, 1 specimen (17/13 [5403] mm), leg. MNHN expedition Papua Niugini, station PM12, limestone rocky intertidal (MNHN IM-2013-12491). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.6′S, 145°47.9′E, 1 specimen (21/18 [5406] mm), leg. MNHN expedition Papua Niugini, station PM24, limestone rocky intertidal (MNHN IM-2013-14040). Papua New Guinea, Madang, Riwo waters, 05°08.9′S, 145°48.2′E, 1 specimen (8/7 [5463] mm), leg. MNHN expedition Papua Niugini, station PM40, sandy beach and intertidal rocks (MNHN IM-2013-15566). Papua New Guinea, New Ireland, Nusalomon Island, 02°37.3′S, 150°40.4′E, 1 specimen (17/15 [6091] mm), leg. MNHN expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54460). Papua New Guinea, New Ireland, Nusalomon Island, 02°37.3′S, 150°40.4′E, 1 specimen (5/3 [6100] mm), leg. MNHN expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54467). Papua New Guinea, New Ireland, Nusalomon Island, 02°37.3′S, 150°40.4′E, 1 specimen (7/5 [6099] mm), leg. MNHN expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54463). Vanuatu, Santo Rose Point, 15°34.9′S, 167°02.4′E, 1 specimen (15/13 [5486] mm), leg. MNHN expedition Santo 2006, station VM02, intertidal, coral sand (MNHN IM-2013-62408). Vanuatu, Santo Rose Point, 15°34.9′S, 167°02.4′E, 1 specimen (14/11 [5487] mm), leg. MNHN expedition Santo 2006, station VM02, intertidal, coral sand (MNHN IM-2013-62409). Vanuatu, Santo Rose Point, 15°34.9′S, 167°02.4′E, 1 specimen (15/14 [5490] mm), leg. MNHN expedition Santo 2006, station VM02, intertidal, coral sand (MNHN IM-2013-

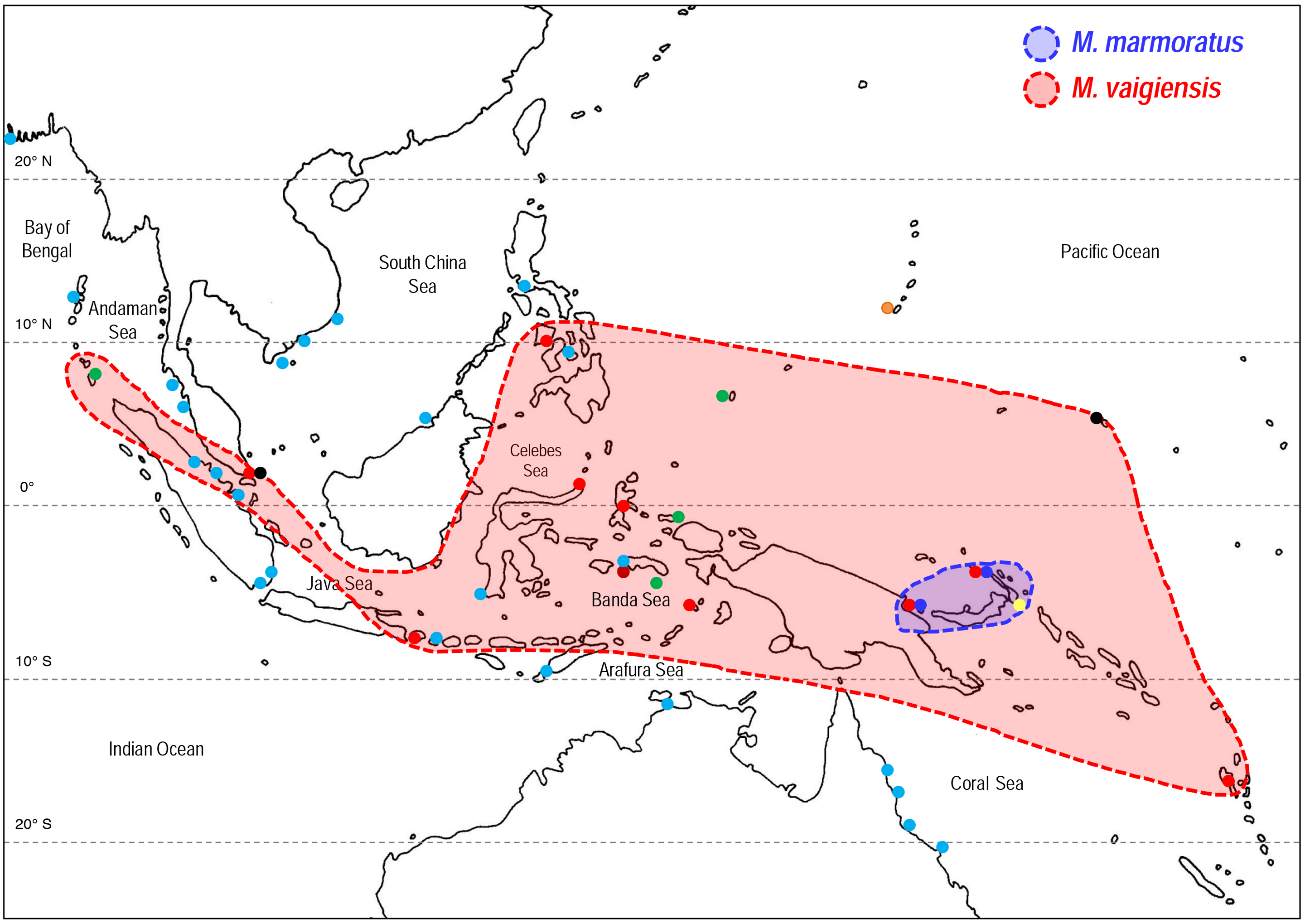

Fig. 9. Geographic distribution of the two known species of the genus *Marmaronchis*. The red and dark blue dots correspond to the records for each species from the material included in the present study (the same colour are used on the phylogenetic trees represented in Figs. 1–4). The dark red dot (Ambon, Indonesia) corresponds to a record of *Marmaronchis vaigiensis* for an old specimen for which no DNA sequences was available (Dayrat, 2010). The four green dots corresponds to type localities of *M. vaigiensis* and its synonyms. The black dots correspond to paralectotypes of synonyms of *M. vaigiensis*. The yellow dot corresponds to the type locality of *M. marmoratus*. The many light blue dots correspond to regions where we collected gastropods in the past few years and where *Marmaronchis* was not found (acknowledging that it may have been missed in some of them). The orange dot (Guam) corresponds to a record of a *Marmaronchis* species (likely *M. viagiensis*) based on a picture and so it is not included within the species distribution area (see Discussion). Finally, the coloured areas correspond to hypothetical ranges based on known records.

62401). Vanuatu, W Mavéa Island, 15°22.4′S, 167°13.0′E, 1 specimen (15/14 [5489] mm), leg. MNHN expedition Santo 2006, station FM36, intertidal (MNHN IM-2013-62418).

Distribution (Fig. 9). Nicobar Islands (type locality of *Onchidium steenstrupii*, new synonym; Semper, 1880, as *O. ambiguum*, new synonym). Singapore (Semper, 1880, as *O. ambiguum*, new synonym; Dayrat, 2010; present study). Indonesia: Ambon (Dayrat, 2010); Bali (present study, new record); Banda Islands (type locality of *O. leopoldi*); Halmahera (Dayrat, 2010; present study); Kei Islands (Dayrat, 2010; present study); Sulawesi (present study, new record); West Papua (type locality of *O. vaigiense*; Dayrat, 2010). Philippines (Hoffmann, 1928; Dayrat, 2010; present study). Palau (type locality of *O. ambiguum*, new synonym). Micronesia: Pohnpei (Semper, 1882, as *O. steenstrupii*, new synonym). Papua New Guinea: Madang (Dayrat, 2010; present study); New Ireland (present study). Vanuatu (present study, new record). Note that the records of *O. vaigiense* in Madang, New Britain, and New Ireland (Dayrat, 2010) as well as New Hanover (Plate, 1893, Dayrat, 2010) could refer to *M. vaigiensis* or *M. marmoratus*, given the close proximity of New Hanover and New Britain to New Ireland and Madang (and given that *M. vaigiensis* and *M. marmoratus* are sympatric in New Ireland and Madang).

Habitat (Fig. 10). *Marmaronchis vaigiensis* lives in the rocky intertidal, on rocks near a beach or not, mixed with sand or not. It can also be found on cemented, human-made structures, such as bridges, ditches, and retaining walls. It is not specifically associated with mangroves, but it can be found on rocks near mangroves. Occasionally, it can be found on tree trunks on the shore (e.g., station PM24, Madang, Papua New Guinea; Fig. 10H). Rocks usually are covered by a thin algal mat. *Marmaronchis vaigiensis* can be locally abundant but its presence is less predictable than other onchidiids. It may not always be found even though a habitat may seem perfect for it, and weather conditions seem to matter as well (Dayrat, 2010).

Fig. 10. Habitats, *Marmaronchis vaigiensis* (A–H) and *Marmaronchis marmoratus* (H), Indonesia (A–E), Singapore (F), and Papua New Guinea (G, H). A, Halmahera, station 217 (UMIZ 00187); B, Same as A; C, Sulawesi, station 91 (UMIZ 00184); D, Kei, station 140 (UMIZ 00185); E, Bali, station 155 (UMIZ 00186); F, Singapore, station 10 (ZRC.MOL.3007); G, New Ireland, Kavieng, station KM20 (MNHN IM-2013-54460, -54467, -54463); H, Madang, station PM24 (MNHN IM-2013-13760, -15566).

Remarks. The year 1824 adopted as the publication date for *Onchidium vaigiense* by all authors so far (Bretnall, 1919; Hoffmann, 1928; Labbé, 1934a; Dayrat, 2009, 2010) is erroneous. According to collations of Quoy and Gaimard's *Zoology* of the *Uranie* and *Physicienne* voyage (1817–1820), page 429 was part of a section published in 1825 (Sherborn & Woodward, 1901: 392). 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 combination *Onchidium ambiguum* was first published by Semper in 1880, with a part of the written description (p. 264) and all illustrations (plates 19 and 22). The end of the written description (p. 265) was printed only in 1882. The combination *Onchidium steenstrupii* was first published by Semper in 1882, with the complete written description and the illustrations on plate 21. The illustration of *O. steenstrupii* on plate 20 (figure 5) was published in 1880. However, the species name used by Semper in 1880 in the caption for figure 5 (plate 20) was '*Onchidium ambiguum*', and he later indicated in his written description in 1882 that figure 5 (plate 20) actually referred to *O. steenstrupii* instead of *O. ambiguum*.

It cannot be determined whether the lectotype—designated in the present study—of *Onchidium ambiguum* from Palau (ZMB 39024a) is part of *Marmaronchis vaigiensis* or *M. marmoratus* because both species are cryptic anatomically. However, given that *M. vaigiensis* is geographically distributed from Singapore all the way to Vanuatu and the Philippines while *M. marmoratus* is restricted to a much smaller geographical area (New Ireland and Madang), it is decided here that the lectotype of *O. ambiguum* from Palau is part of *M. vaigiensis*, and that, as a result, *O. ambiguum* is a junior synonym of *M. vaigiensis*. Unfortunately, this cannot be confirmed here because we did not have access to freshly-collected specimens of *Marmaronchis* from Palau. It naturally cannot be completely excluded that it is *M. marmoratus* that is found in Palau (instead of *M. vaigiensis*), in which case *O. ambiguum* would just become a junior synonym of *M. marmoratus*. Semper (1882: 289) briefly commented that Quoy & Gaimard's *Onchidium vaigiense* may be identical to his *O. ambiguum*. Semper's original description of the anatomy of *O. ambiguum* perfectly matches the anatomy of *M. vaigiensis* (e.g., penis with a cartilaginous tube and a distal portion bearing hooks approximately 70 µm in length, retractor muscle in front of the pericardium). Semper (1882: 265) thought that the specimens from Singapore and Nicobar were a variety with a higher number of dorsal eyes of the species while the typical species from Palau displayed a lower number of dorsal eyes. A higher number of dorsal eyes was also found in one Singapore individual by Dayrat (2010: 91) but the number of clusters of dorsal eyes varies from one to ten within the species. Bretnall (1919: 314) briefly mentioned *O. ambiguum*, which he regarded as valid even though he pointed out that Semper thought that *O. ambiguum* may be the same as Quoy & Gaimard's *O. vaigiense*. Bretnall summarised Semper's description and recorded *O. ambiguum* from Dunk Island, Queensland (17°56′S). Given that Bretnall did not describe the internal anatomy of the specimen from Queensland, it is unclear whether his record can be taken for granted. In fact, our team has spent four weeks exploring mangroves on the coast of Queensland, collecting gastropods from 29 stations from 16° to 21° S, and we did not find any *M. vaigiensis* there. That being said, we may have missed it and *M. vaigiensis* may be present in Queensland, even though it is questionable at this stage. Hoffmann (1928: 46) briefly described and commented on *O. ambiguum*, based on one specimen from Singapore (which he found in the ZMUC collections) and four specimens from Mindanao, Philippines (which he found in the Stockholm collections). The specimen he examined from the ZMUC collection (16 mm long) likely was not the ZMUC paralectotype (10/8 mm). Regardless, the fact that he mentions that a rectal gland is missing suggests that he misidentified *O. ambiguum*, which is surprising given that he supposedly had access to the ZMUC paralectotype of *O. ambiguum*. Finally, Labbé (1934a: 224) regarded *O. ambiguum* as valid, which he recorded from Palau, Singapore, Mindanao, Nicobar, and Samar (Philippines). Samar was not mentioned by earlier authors and there is no way to determine whether Labbé's record was correct or not (he did not comment on the anatomy or morphology of any specimens). At any rate, based on what we know about the distribution of *M. vaigiensis* (Fig. 9), it is very likely present in Samar.

It cannot be determined whether the lectotype—designated in the present study—of *Onchidium steenstrupii* from Nicobar Islands (ZMUC) is part of *Marmaronchis vaigiensis* or *M. marmoratus* because both species are cryptic anatomically. However, given that *M. vaigiensis* is geographically distributed from Singapore all the way to Vanuatu and the Philippines while *M. marmoratus* is restricted to a much smaller geographical area (New Ireland and Madang), it is decided here that the lectotype of *O. steenstrupii* from Nicobar Islands is part of *M. vaigiensis*, and that, as a result, *O. steenstrupii* is a junior synonym of *M. vaigiensis*. Unfortunately, this cannot be confirmed here because we did not have access to freshly-collected specimens of *Marmaronchis* from Nicobar Islands. It naturally cannot be entirely excluded that the populations of *Marmaronchis* in Nicobar Islands are part of a third species restricted to the Bay of Bengal, in which case *O. steenstrupii* would just become a valid name. However, given the broad distribution of *M. vaigiensis* and given that many onchidiid species are shared between Singapore and the Bay of Bengal (e.g., Dayrat et al., 2017; Goulding et al., 2018b, c), it is assumed here that *M. vaigiensis* is present in Nicobar Islands (our team did not find it in the Andaman Island in 2011, but we may have missed it there). Semper (1882: 266) acknowledges that *O. steenstrupii* is externally very similar to *O. ambiguum*, but claims that their reproductive anatomy differs. However, the descriptions that he gives are similar and, most importantly, fit perfectly the anatomy of *M. vaigiensis*: Semper mentions that penial hooks (which he calls cartilaginous teeth) measure 70 µm in both *O. steenstrupii* and *O. ambiguum*, and the penial hooks of *M. vaigiensis* measure from 70 to 100 µm (Table 4). Tapparone-Canefri (1883: 213) transferred *O. steenstrupii* to *Onchidella* with no justification and with no new material. Plate (1893: 176) agreed that *Onchidium steenstrupii* was very close to *O. vaigiense* but still regarded them as two different species, mostly based on differences in the dorsal colour and the foot width, which are traits that greatly vary between individuals. Bretnall (1919) regarded *O. steenstrupii* as valid without adding any new material. Hoffmann (1928: 45) examined the two specimens of *O. steenstrupii* preserved at the ZMUC (now the lectotype and a paralectotype) and mentioned *O. steenstrupii* as a valid species. Finally, Labbé (1934a: 222) described some specimens from the Philippines as *O. steentrupii* which seem to match the characteristics of *M. vaigiensis* (intestinal loops of type I, rectal gland present, accessory penial gland present) even though Labbé's descriptions are always questionable. At any rate, *M. vaigiensis* is known to be present in the Philippines, regardless of Labbé's records. Labbé suggested—with a question mark—that Mörch's (1872: 325) '*Peronia mauritiana* Blainville, 1824' might be a misidentification of *O. steenstrupii*, but that seems unlikely because Mörch clearly refers to Gray's (1850) illustrations of *Peronia* Fleming, 1822.

The detailed comments on the type material of *Onchidium leopoldi* are not repeated here (see Dayrat, 2010). There is no doubt that *O. leopoldi* refers to a *Marmaronchis* species. Strictly speaking, however, it cannot be determined whether *O. leopoldi* refers to *Marmaronchis vaigiensis* or *M. marmoratus* because both species are cryptic anatomically. However, given that *M. vaigiensis* is known to be present (based on identification with DNA sequences provided here) in Sulawesi, Kei Islands, Bali, and Halmahera (Fig. 9) and that the type locality of *O. leopoldi* (Banda Islands, in the Banda Sea, just south of Ambon) is surrounded by all those known localities of *M. vaigiensis*, it is confirmed here that *O. leopoldi* is a junior synonym of *M. vaigiensis*.

Dayrat (2010) examined the voucher specimen used by Labbé (1934b) to re-describe *Onchidella maculata* and there is no doubt that Labbé's re-description was based on a misidentification. Dayrat (2010) assumed that Labbé examined a specimen that was part of *O. vaigiense* but it is not possible to know unequivocally whether that specimen is part of *M. vaigiensis* or *M. marmoratus* because both species are anatomically cryptic. However, that voucher specimen was collected in Manokwari, Irian Jaya, West Papua, very close to the type locality of *M. vaigiensis* (Waigeo and Rawak islands, Irian Jaya, West Papua) and it can reasonably be assumed that Labbé's (1934b) specimen misidentified as *O. maculata* is part of *M. vaigiensis*.

Marmaronchis marmoratus **(Lesson, 1831) new combination**

(Figs. 6B, D, E, 7B, D, F, 8D–F, H, 10H)

Onchidium marmoratum Lesson, 1831: 297–299, pl. 14, fig. 3.
Onchidella marmorata (Lesson, 1831). Gray, 1850: 117, pl. 181, fig. 6; Adams & Adams, 1855: 234.

Type locality. *Onchidium marmoratum*: 'Nelle Irlande' [i.e., New Ireland, Papua New Guinea] according to the label, and 'port Praslin, à la Nouvelle Irlande' [i.e., New Ireland, Papua New Guinea] according to Lesson's (1831: 297) written original description. Port Praslin is now called Gower's Harbour and is located near the village of Lambon, at the southernmost end of New Ireland Island.

Type material. For a detailed description of the type material of *O. marmoratum* see Dayrat (2010).

Additional material examined. Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.6′S, 145°47.9′E, 1 specimen (10/10 [5416] mm), leg. MNHN expedition Papua Niugini, station PM24, limestone rocky intertidal (MNHN IM-2013-13760). Papua New Guinea, Madang, Rempi Area, Barag Island, 05°01.1′S, 145°47.9′E, 1 specimen (13/13 [5404] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13353). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.1′S, 145°47.9′E, 1 specimen (13/12 [5413] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13352). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.1′S, 145°47.9′E, 1 specimen (11/11 [5414] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13354). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.1′S, 145°47.9′E, 1 specimen (8/8 [5441] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13356). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.1′S, 145°47.9′E, 1 specimen (10/10 [5442] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13357). Papua New Guinea, Madang, Rempi Area, SW Hargun Island, 05°01.1′S, 145°47.9′E, 1 specimen (6/5 [5443] mm), leg. MNHN expedition Papua Niugini, station PM25, fringing reef on narrow barrier island (MNHN IM-2013-13358). Papua New Guinea, Madang, Riwo waters, 05°08.9′S, 145°48.2′E, 1 specimen (10/8 [5409] mm), leg. MNHN expedition Papua Niugini, station PM40, sandy beach and intertidal rocks (MNHN IM-2013-15764). Papua New Guinea, Madang, Riwo waters, 05°08.9′S, 145°48.2′E, 1 specimen (12/12 [5425] mm), leg. MNHN expedition Papua Niugini, station PM40, sandy beach and intertidal rocks (MNHN IM-2013-15763). Papua New Guinea, Madang, Wonad Island, 05°08.1′S, 145°49.3′E, 1 specimen (10/5 [5452] mm), leg. MNHN expedition Papua Niugini, station PM41, sandy beach and intertidal rocks (MNHN IM-2013-15276). Papua New Guinea, Madang, Wonad Island, 05°08.1′S, 145°49.3′E, 1 specimen (10/10 [5458] mm), leg. MNHN expedition Papua Niugini, station PM41, sandy beach and intertidal rocks (MNHN IM-2013-15868). Papua New Guinea, Madang, Wonad Island, 05°08.1′S, 145°49.3′E, 1 specimen (10/10 [5459] mm), leg. MNHN expedition Papua Niugini, station PM41, sandy beach and intertidal rocks (MNHN IM-2013-15869). Papua New Guinea, Madang, Wonad Island, 05°08.1′S, 145°49.3′E, 1 specimen (8/7 [5466] mm), leg. MNHN expedition Papua Niugini, station PM41, sandy beach and intertidal rocks (MNHN IM-2013-18263). Papua New Guinea, Madang, Wonad Island, 05°08.1′S, 145°49.3′E, 1 specimen (15/15 [5475] mm), leg. MNHN expedition Papua Niugini, station

PM41, sandy beach and intertidal rocks (MNHN IM-2013-15866). Papua New Guinea, New Ireland, Lokono, south coast of New Ireland mainland, 02°46.9′S, 150°48.2′E, 1 specimen (18/12 [6092] mm), leg. MNHN expedition Kavieng 2014, station KM70, platform and freshwater (MNHN IM-2013-55527). Papua New Guinea, New Ireland, Lokono, S coast of New Ireland mainland, 02°46.9′S, 150°48.2′E, 1 specimen (13/11 [6093] mm), leg. MNHN expedition Kavieng 2014, station KM70, platform and freshwater (MNHN IM-2013-55528).

Distribution (Fig. 9). Papua New Guinea: Madang (present study, new record); New Ireland Island (type locality of *Onchidium marmoratum*; present study). Note that the records of *Onchidium vaigiense* in Madang, New Britain, and New Ireland (Dayrat, 2010) as well as New Hanover Island (Plate, 1893; Dayrat, 2010) could refer to *M. vaigiensis* or *M. marmoratus*, given the close proximity of New Hanover and New Britain to New Ireland and Madang.

Habitat (Fig. 10H). *Marmaronchis marmoratus* seems to live in the same kind of habitats as *M. vaigiensis*: primarily the rocky intertidal and occasionally tree trunks on the shore.

Remarks. The publication date for *Onchidium marmoratum* in Dayrat (2009, 2010) is erroneous. Based on the complete collation of the voyage of the *Coquille* by Cretella (2010), the date of the original publication for both the text (pp. 297–299) and the plate (pl. 14, fig. 3) with the name *Onchidium marmoratum* is November 15, 1831, even though the dates on the title pages are 1826 (atlas) and 1830 (text).

Because the type material of *O. marmoratum* is anatomically similar to *O. vaigiense*, Dayrat (2010) considered *O. marmoratum* to be a junior synonym of *O. vaigiense*. However, the DNA sequences provided here show that *Marmaronchis* includes two species (Figs. 1–4). One species, widespread geographically, is called *M. vaigiensis* because its distribution includes the type locality of *O. vaigiense* (Fig. 9). The second species is much more restricted geographically because it is known only from Kavieng (northwestern end of New Ireland Island) and Madang (Papua New Guinea). The type locality of *O. marmoratum* being at the southernmost end of New Ireland Island, it is decided that *O. marmoratum* should apply to that second species. However, the type material of *O. marmoratum* cannot be distinguished anatomically from *M. vaigiensis* and *O. marmoratum* could still be regarded as a junior synonym of *M. vaigiensis* if new data later warrants it. The transfer of *O. marmoratum* into *Onchidella* by Gray (1850) and Adams & Adams (1855) was unjustified.

DISCUSSION

In the Onchidiidae, there are genera in which species can be identified both externally and internally, such as *Onchidium* (Dayrat et al., 2016) and *Melayonchis* (Dayrat et al., 2017). *Onchidium* and *Melayonchis* slugs can be identified directly in the field at the species level by the colour of live animals, and they can also be identified by their internal anatomy and DNA sequences if necessary. Also, there are genera in which species are cryptic externally but distinct internally, such as *Wallaconchis* (Goulding et al., 2018b) and *Peronina* Plate, 1893 (Goulding et al., 2018c). *Wallaconchis* and *Peronina* slugs cannot be identified in the field at the species level (the colour of live animals is too variable between individuals and too similar between species), but they can be easily identified by their internal anatomy and DNA sequences. Finally, there are genera in which species are cryptic externally and internally, such as *Peronia* (monograph in progress). Indeed, most *Peronia* slugs can be identified at the species level only by their DNA sequences. Thus, *Marmaronchis* is similar to *Peronia* in the sense that *M. vaigiensis* and *M. marmoratus* can only be identified by their DNA sequences. Cryptic diversity (both external and internal) is also found in a few species of *Platevindex* (monograph in progress).

Given that *Marmaronchis vaigiensis* and *M. marmoratus* are cryptic, both externally and internally, one could question whether it is appropriate to consider them to be two separate species or not. Several arguments suggest that they are real, distinct species. First, cryptic diversity does exist in at least two other onchidiid genera (see above), and *M. vaigiensis* and *M. marmoratus* are by no mean an exception. Second, they are consistently recovered as two reciprocally-monophyletic, highly-supported molecular units in all mitochondrial and nuclear analyses (Figs. 1–4). Third, a large barcode gap (from 4.1% to 7.5%) in COI genetic divergences separates them. Fourth, individuals of both species live all together at exactly the same places (both species can be found at the same stations) but do not seem to exchange any genes, strongly suggesting the existence of a reproductive barrier of some sort. Finally, one should note that the species name *M. marmoratus* already exists in the literature. We are not participating in inflating the number of names available. Applying that available species name to a units that is distinct from *M. vaigiensis* seems to be an appropriate taxonomic decision given the available data.

A comparison of radular formulae seem to suggest that the radulae of individuals of *M. marmoratus* tend to be characterised by a higher number of rows and teeth per half row (Table 3). However, additional radular formulae for specimens of *M. vaigiensis* from Halmahera (70 × 120-1-120), Singapore (65 × 85-1-85), and Kei Islands (65 × 90-1-90), suggest that radular formulae should not be used for distinguishing *M. marmoratus* and *M. vaigiensis* (Dayrat, 2010: 91).

Geographically, *Marmaronchis vaigiensis* and *M. marmoratus* are truly sympatric (Fig. 9). Not only the narrow distribution of *M. marmoratus* is contained within the wide distribution of *M. vaigiensis*, but they can be found in the exact same stations: for instance, both species were found at stations PM 24 (Fig. 10H) and PM 40 in Madang, Papua New Guinea. Surprisingly, intra-specific divergences between COI sequences are significantly lower within *M. vaigiensis* than within *M. marmoratus*, even though *M. vaigiensis* is much more widely distributed geographically. A possible explanation is that today's individuals of *M. marmoratus* are the descendants of few small populations that were isolated. Also, somehow, it seems that there has been (and still is) significantly more gene flow within *M. vaigiensis* than within *M. marmoratus*. Possibly, the larvae of *M. vaigiensis* are capable of spending more time in the water than those of *M. marmoratus*. Interestingly, the geographic distribution of two species of *Marmaronchis* resemble to a certain extent the geographical distribution observed in *Peronia* with one species broadly distributed and a few endemic species at the periphery, as if species were formed by peripatry.

Unlike most onchidiid genera from Southeast Asia (e.g., *Melayonchis*, *Onchidium*, *Peronina*, *Platevindex*), *Marmaronchis* and *Peronia* are not found in mangroves. They are essentially found in the rocky intertidal (even though the rocky intertidal can be near mangroves or scattered mangrove trees). Most *Wallaconchis* species are also not found in mangroves (only three of the ten *Wallaconchis* species are found on mud near or inside mangroves). Interestingly, the geographic distribution of *Marmaronchis* is very similar to that of *Wallaconchis* in the sense that both genera are absent from the South China Sea (Goulding et al., 2018b: fig. 6). In fact, we did not find *Wallaconchis* and *Marmaronchis* on the eastern coast of Peninsular Malaysia, Vietnam, or Brunei). Naturally, we may have missed both genera there and additional field work should be done to confirm that *Wallaconchis* and *Marmaronchis* are not in the South China Sea. Interesting places to explore could be Palawan (Philippines), Sarawak (Borneo, Malaysia), or the Riau Islands (Indonesia). At any rate, that we did not find *Wallaconchis* and *Marmaronchis* in the South China Sea and that they may actually not live there could be explained by the fact that the coastline of that region is especially rich in deep mangroves around large rivers, while the core of the Coral Triangle (Philippines, Sulawesi, West Papua) is much richer in rocky areas favored by *Wallaconchis* and *Marmaronchis* species.

We did not find *Marmaronchis* in Australia (Northern Territory, Queensland, New South Wales) where it likely does not live. We did not find *Marmaronchis* in the Strait of Malacca but it likely lives there given that it lives in Singapore (eastern end of the Strait of Malacca) and the Nicobar Islands (western end of the Strait of Malacca). We did not find it in Lombok but it likely lives there given that it is in Bali. It is important to keep in mind that the presence of *Marmaronchis* slugs is less predictable than that of other onchidiids, even in a perfect habitat. In a sense, they resemble slugs of the genus *Onchidella* J. E. Gray, 1850, which can occasionally be extremely abundant but remain uncommon the rest of the time. Finally, a picture of an onchidiid slug from Guam was sent to the first author (Clay Carlson, personal communication) which seemed to be a *Marmaronchis* (Fig. 9).

Molecular phylogenetic trees show that *Marmaronchis* is distinct from other onchidiid genera (Figs. 1–4). It is more closely related to *Melayonchis*, *Onchidium*, and *Platevindex*, but exact relationships are unclear. Anatomically, *Marmaronchis* is characterised by a unique combination of characters: intestinal loops of type I, rectal gland present, accessory penial gland present. Among the other onchidiids with a rectal gland (e.g., *Onchidium*, *Peronina*, *Platevindex*, and *Melayonchis*), intestinal loops of type I are only found in *Marmaronchis* and some species of *Platevindex*, but there is no *Platevindex* with an accessory penial gland. Therefore, at present, any slug with the unique combination of characters above belongs to *Marmaronchis*. Also, importantly, *Marmaronchis* species lack the synapomorphies that characterise *Platevindex* (narrow foot and flattened body), *Melayonchis* (protuberance on the inner lateral margin of lateral radular teeth; see, Dayrat et al., 2017: figs. 6, 13, 18, 24), and *Onchidium* (large, conical, pointed papillae on the dorsum of live animals; see, Dayrat et al., 2016: figs. 4, 10).

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