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814 Systematic revision one clade at a time: A new genus of onchidiid slugs from Indo-West (Gastropoda: Pulmonata) Benoît Dayrat 1*, Tricia C. Goulding 1,2, Munawar Khalil 3, Pierre Lozouet 4 & Shau Hwai Tan 5,6 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 RAFFLES BULLETIN OF ZOOLOGY 66: 814–837 Date of publication: 13 December 2018 http://zoobank.org/urn:lsid:zoobank.org:pub:4CB778AA-79D5-4C17-8222-57DB9AC39E

2E © Nationa l University of Singapore ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print) 1Pennsylvania State University, Department of Biology, Mueller Laboratory 514, University Park, PA 16802, USA; Email: bad25@psu.edu (*corresponding author) 2Current address: Bernice Pauahi Bishop Museum, 1525 Bernice St, Honolulu, HI 96817, USA 3Department of Marine Science, Universitas Malikussaleh, Reuleut Main Campus, Kecamatan Muara Batu, North Aceh, Aceh, 24355, Indonesia 4Malacologie, Muséum national d'Histoire naturelle, 55 rue Buffon, 75005 Paris, France 5Marine Science Laboratory, School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia 6Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Minden Penang, Malaysia 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 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 Taxonomy & Systematics 815 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 of to (West and 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 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 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 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 – 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 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 816 GGC ATR ATR GTG AC (Colgan et al., 2000). The PCRs for and were µl containing µl water, µl 10X Buffer, µl 25 MgCl 2, 0.5 of 10 primer, µl dNTP 0.2 (1 of Taq Cat R001A), µl of ng/µl DNA, 1 of BSA Serum Albumin). The PCRs for 12S differed by reducing the water 14.3 and the 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 1 the solution to µl, the amount template reduced 0.5 The for ITS2 used the reagents in the same amounts as for COI and 16S, that was to µl, amount 25 reactions 14.8

of 2.5 of PCR 1.5 of mM 2 , µl each µM primer, µl dNTP 0.2 (1 of Taq (Clontech, Cat No. R001A), 2 µl of 100X BSA and 1 µl of ng/µl DNA. COI 16S 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 The thermoprofile the as COI, except it run 40 The 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 at The thermoprofile 1 at 96°C; 35 cycles of 30 seconds at 94°C, 30 seconds at minutes 72°C. H3 was: minutes 93°C; 30 cycles of 1 minute at 93°C, 2 minutes at 55°C, and minute 73°C; a extension 10 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), (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 simultaneous of × 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. 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 817 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 818 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 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 819 Onchidella patelloidis Onchidella celtica 92 Onchidella floridana Wallaconchis melanesiensis Peronina tenera Alionchis jailoloensis Peronia (Okinawa) Peronia (Hawaii) Wallaconchis sinanui Onchidina australis Melayonchis eloisae Melayonchis annae Melayonchis aileenae Melayonchis siongkiati Platevindex luteus Onchidium stuxbergi Onchidium typhae 99/0.96 100/1 100/0.98 5414 Papua New Guinea Madang 5413 Papua New Guinea Madang 5442 Papua New Guinea Madang 5404 Papua New Guinea Madang 5416 Papua New Guinea Madang 5443 Papua New Guinea Madang 80 0.95 5441 Papua New Guinea Madang 5425 Papua New Guinea Madang 5409 Papua New Guinea Madang 6092 New Ireland Kavieng 5475 Papua New Guinea Madang 5459 Papua New Guinea Madang 5458 Papua New Guinea Madang 6093 New Ireland Kavieng 5466 Papua New Guinea Madang 5452 Papua New Guinea Madang 99/1* 5490

Vanuatu 5489 Vanuatu 5487 Vanuatu 5486 Vanuatu 100* 5435 Papua New Guinea Madang 5434 Papua New Guinea Madang 5463 Papua New Guinea Madang 5406 Papua New Guinea Madang 5403 Papua New Guinea Madang 100/0.96* 6100 New Ireland Kavieng 6099 New Ireland Kavieng 6091 New Ireland Kavieng 100/1* 5153 Indonesia Halmahera 5154 Indonesia Halmahera 5046 Indonesia Halmahera 2908 Indonesia Kei 715 Philippines Guimaras 3590 Indonesia Bali 3083 Indonesia Bali 3081 Indonesia Bali 95/0.99 2294 Indonesia Sulawesi 2309 Indonesia Sulawesi 1183 Singapore 2224 Indonesia Sulawesi 2243 Indonesia Sulawesi 0.1 Expected Substitutions per Site 2244 Indonesia Sulawesi 0.91 0.92 * * * * M. marmoratus M.

vaigiensis M A R M A R O N C H I S 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 numbers and are All sequences as Information individually-identified Marmaronchis specimens can be found in the list of material examined. 820 96/1 Wallaconchis melanesiensis Wallaconchis sinanui 96 96/1 Onchidella floridana Onchidella patelloidis Onchidella celtica Alionchis jailoloensis 83 0.98 Peronia (Hawaii) Peronia (Okinawa) Onchidina australis Peronina tenera Platevindex luteus 97 1 Onchidium stuxbergi Onchidium typhae Melayonchis siongkiati Melayonchis annae Melayonchis aileenae Melayonchis eloisae 100/1 5443 Papua New Guinea Madang 87/1* 5466 Papua New Guinea Madang 5409 Papua New Guinea Madang 95/1* 5487 Vanuatu 5434 Papua New Guinea Madang 92/0.98 5153 Indonesia Halmahera 1183 Singapore 3083 Indonesia Bali 715 Philippines Guimaras 0.1 Expected Substitutions per Site M. marmoratus M.

vaigiensis M A R M A R O N C H I S 97 1 0.93* * 0.9 100/1 99/0.99 * * 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 individually-identified Marmaronchis specimens can be found in the list of material examined. simply is compared in a section before the systematic accounts. PHYLOGENETIC 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 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 821 Onchidella patelloidis Onchidella celtica 79/1 Onchidella floridana 100/1 Peronina tenera Onchidina australis 90/1 Peronia (Hawaii) Peronia (Okinawa) 1 Wallaconchis melanesiensis 91/1 Wallaconchis sinanui Alionchis jailoloensis 92/0.97 Melayonchis siongkiati Melayonchis aileenae Melayonchis eloisae Platevindex luteus Onchidium typhae Onchidium stuxbergi Melayonchis annae 99/1 90 5425 Papua New Guinea Madang 5409 Papua New Guinea Madang 5416 Papua New Guinea Madang 6092 New Ireland Kavieng 5466 Papua New Guinea Madang 5443 Papua New Guinea Madang 5414 Papua New Guinea Madang 5475 Papua New Guinea Madang 5413 Papua New Guinea Madang 98/0.99 715 Philippines Guimaras 1183 Singapore 3081 Indonesia Bali 3590 Indonesia Bali 2294 Indonesia Sulawesi 3083 Indonesia Bali 2309 Indonesia Sulawesi 5154 Indonesia Halmahera 5153 Indonesia Halmahera 6091 New Ireland Kavieng 5490 Vanuatu 5487 Vanuatu 5435 Papua New Guinea Madang 5434 Papua New Guinea Madang 5406 Papua New Guinea Madang 5463 Papua New Guinea Madang 5403 Papua New Guinea Madang 0.1 Expected Substitutions per Site 75 M. marmoratus M. vaigiensis M A R M A R O N C H I S Fig. 3.

Phylogenetic tree showing relationships between Marmaronchis individuals based on nuclear ITS2 sequences. Numbers above branches are bootstrap (Maximum analysis) below the probabilities analysis); significant numbers and are All sequences as Information individually-identified Marmaronchis specimens can be found in the list of material examined. 822 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 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 to The of animals is evenly covered with small, rounded, papillae, which give animals tend to be smooth). Dorsal eyes are present. A central of to dorsal is present.

It is accompanied by a variable number of additional eyes because of the dark background of the notum. 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 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

Onchidella patelloidis Onchidella celtica Onchidella floridana 100 Onchidina australis 100/1 76/0.93 Peronia (Hawaii) Peronia (Okinawa) 93/1 Wallaconchis melanesiensis 92 Wallaconchis sinanui Alionchis jailoloensis Peronina tenera 97/1 Onchidium stuxbergi Onchidium typhae 0.99 91/1 Melayonchis annae 95/1 Melayonchis siongkiati 1 Melayonchis eloisae Melayonchis aileenae Platevindex luteus 100/1 89/1 5409 Papua New Guinea Madang 5466 Papua New Guinea Madang 5443 Papua New Guinea Madang 91/0.96 5434 Papua New Guinea Madang 5153 Indonesia Halmahera 5487 Vanuatu 1183 Singapore 715 Philippines Guimaras 3083 Indonesia Bali 0.1 Expected Substitutions per Site M. marmoratus M. vaigiensis M A R M A R O N C H I S 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 individually-identified Marmaronchis specimens can be found in the list of material examined. 823 (not found in any other preserved onchidiids) and helps to identify specimens in museum collections as Marmaronchis. Internal (Figs. identified 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 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 curved, but cylindrical and a shorter, distal, soft tube with approximately 30 conical hooks internally (Fig. 8G, H).

SYSTEMATICS Onchidiidae 1815 Marmaronchis & new Type Marmaronchis vaigiensis, designated here. Etymology. The name Marmaronchis is a combination of mármaros (Đ), 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 Đ Ôgkoj 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 Đ Ôgkoj, 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. not No gills. 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 Table 3. Radular formulae for the two Marmaronchis following same number rows number lateral 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 (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, 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 70 100 20 80 60 100 824 & 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- 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, new combination (Figs. 5, 6A, C, F, 7A, C, E, 8A–C, G, 10) Onchidium vaigiense Quoy & Gaimard, 1825: 429; Tapparone- Canefri, 1883: 213; Pgs 1919: 314–315; Hoffmann, 1928: 76; Dayrat, 2010: 88–101, figs. Paraoncidium vaigiense (Quoy & Gaimard, 1825).

Labbé, 1934a: 229–230, 68–70. Onchidium ambiguum pl. figs. Semper, 265, New synonym. Onchidium steenstrupii 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, 70–73, 10A, 13, 23, 33–35, I, 4 Oncidium leopoldi]. Onchidella maculata — Labbé, 78–80, 10, 39, I, 7 of 1893; Oncidiella maculata]. 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 three 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]. 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 825 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 826 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. 827 Fig. 7. Radula, Marmaronchis vaigiensis (A, C, E) and Marmaronchis marmoratus (B, D, F). A, Rachidian and innermost lateral teeth, scale = μm, Bali (UMIZ B, and lateral scale = μm, New New Kavieng (MNHN C, lateral scale = μm, as D, lateral scale bar 20 Papua Guinea, [5475] IM-2013-15866); Outermost, lateral scale = μm, as A; Left tooth basal spine, lateral scale = μm, as Abbreviations: first, lateral tooth; first, lateral 2llt, left, tooth; second, lateral bls, lateral hlt, 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 828 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 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 difficulty: ‘Gaimard’ ‘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 body not There two other jars with old Marmaronchis specimens in the MNHN collections, both labeled as ‘ Onchidium / Nouvelle-Irlande [New Ireland] 1829 / Mrs 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 Quoy Gaimard what called the ‘Onchidium de Vaigiou’. Additional material examined.

Singapore, North Coast, 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 125°01.232'E, 1 specimen (8/6 [2224] mm), station 88, sand, small rocks, pieces of wood outside narrow coastal mangrove 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, 1 (7/6 mm), station 91, Sonneratia at low intertidal and Rhizophora at high intertidal (UMIZ 00184). Indonesia, Kei Islands, Un, 05°38.273'S, 1 (10/8 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 829 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 H). Scale = µm, New New Kavieng (MNHN B, tip, scale = µm, as C, = µm, New Madang (MNHN D. bar 40 Indonesia, [2244] 00183); Scale = µm, Bali (UMIZ F, bar 40 Papua New New Kavieng (MNHN G, bar 10 same C; Scale = µm, as to shore with sand and rocks (UMIZ 00186). Indonesia, (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, 1 (11/9 mm), 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, 1 (16/11 mm), 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, 1 (17/13 mm), 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, expedition Papua Niugini, station PM24, limestone rocky intertidal (MNHN IM-2013-14040).

Papua New Guinea, Madang, waters, 145°48.2'E, 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 mm), leg. MNHN expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54460). Papua New Guinea, New Ireland, Nusalomon Island, MNHN expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54467). Papua expedition Kavieng 2014, station KM20, intertidal platform, sand and blocks (MNHN IM-2013-54463). Vanuatu, Santo Rosoint, 15°34.9'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). specimen (15/14 [5490] mm), leg. MNHN expedition Santo 2006, station VM02, intertidal, coral sand (MNHN IM-2013- 830 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). 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). 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 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. 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 th at it may hav e 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. 831 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). 832 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 Onchidium ambiguum 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 20 5) was published in 1880. However, the species name used by Semper 1880 the for 5 20) 'Onchidium ambiguum', and he later indicated in his written description 1882 figure (plate actually 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 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 stations 16° 21° and did find 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) 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 that 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 it the Island 2011, we 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 O. steenstrupii and O. ambiguum , and the penial hooks of M. vaigiensis from to µm (Table 4). Tapparone-Canefri (1883: 213) transferred O. steenstrupii to Onchidella no new material. Plate (1893: 176) agreed that Onchidium steenstrupii was very close to O. vaigiense but still regarded 833 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 , is here 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 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 Labbé's specimen as O. maculata is part of M. vaigiensis. Marmaronchis marmoratus (Lesson, new combination (Figs. 6B, D, E, 7B, D, F, 8D–F, H, 10H) Onchidium marmoratum Lesson, 297–299, 14, 3. Onchidella marmorata (Lesson, 1831). Gray, 1850: 117, pl. 181, fig.

Adams Adams, 234. 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). Madang expedition Papua Niugini, station PM24, limestone rocky intertidal (MNHN IM-2013-13760). Papua New Guinea, M 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 SW Island, 145°47.9'E, 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 SW Island, 145°47.9'E, 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 SW Island, 145°47.9'E, 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 SW Island, 145°47.9'E, 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 SW Island, 145°47.9'E, 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, waters, 145°48.2'E, 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, 1 (12/12 mm), MNHN expedition Papua Niugini, station PM40, sandy beach and intertidal rocks (MNHN IM-2013-15763).

Papua New 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, [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, 1 (10/10 mm), MNHN expedition Papua Niugini, station PM41, sandy beach and intertidal rocks (MNHN IM-2013-15869). Papua New 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, [5475] mm), leg.

MNHN expedition Papua Niugini, station 834 PM41, sandy beach and intertidal rocks (MNHN IM-2013- 15866). Papua New Guinea, New Ireland, Lokono, south coast of New (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 (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. 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 & (1855) unjustified. DISCUSSION In the Onchidiidae, there are genera in which species can be identified externally internally, 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 can identified the 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 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 Halmahera × 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 COI are lower 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 835 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., fig.

In we not Wallaconchis and Marmaronchis on the eastern coast of Peninsular Malaysia, Vietnam, or Brunei). Naturally, we may have missed both Wallaconchis and Marmaronchis are not in the South China Sea. Interesting places to explore could be Palawan (Philippines), Sarawak (Borneo, Malaysia), or the Riau (Indonesia). any that did 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 live. did 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 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 onchidiid from was to first (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 teeth; Dayrat al., figs.

13, 24), and Onchidium (large, conical, pointed papillae on the dorsum of live animals; see, Dayrat et al., 2016: figs. 4, 10). ACKNOWLEDGEMENTS We thank Fred Wells (associate editor), Isabel Hyman (reviewer), and an anonymous reviewer for their constructive comments which helped improve the manuscript. We also thank editorial of

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