Mapping the missing branch on the neogastropod tree of life: molecular phylogeny of marginelliform gastropods

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Abstract :

Marginelliform gastropods are a heterogeneous and diverse group of molluscs encompassing over 1,600 living species, among which are the smallest known neogastropods. The relationships of marginelliform gastropods within the order Neogastropoda are controversial, and the monophyly of the two marginelliform families the Marginellidae (J. Fleming, 1828) and the Cystiscidae (Stimpson, 1865), remains unconfirmed. DNA sequence data have never been used to assess the relationships of the marginelliform gastropods, making this group the only major branch missing in our current understanding of the neogastropod tree of life. Here we report results of the first multilocus phylogenetic analysis of marginelliform gastropods, which is based on a dataset comprising 63 species (20 genera) of Marginellidae and Cystiscidae, and a wide range of neogastropod lineages. The Marginellidae and Cystiscidae form a moderately supported Glade that is sister to the family Volutidae. *Marginellona gigas* appears to be sister to all other marginelliforms. The subfamily Marginellinae was recovered as a well-supported Glade, and good resolution of this part of the tree makes it possible to propose amendments to the family-level classification of the group. The relationship between Granulina and other marginelliforms could not be resolved and requires further study. Due to poor resolution of basal relationships within the Marginellidae Cystiscidae Glade, the monophyly of the Cystiscidae was neither confirmed nor convincingly rejected. The shell morphology of most marginellid and cystiscid genera is taxonomically not very informative but, nevertheless, of the traditionally recognized genera only *Gibberula* and *Dentimargo* were shown to be polyphyletic. Although a comprehensive systematic revision of the group requires more extensive taxonomic sampling (e.g. with better representation of the type species of nominal genus-group names), our results support the superfamily Volutioidea, comprising four families (Volutidae, Cystiscidae, Marginellidae and Marginellonidae), with the placement of the Granulinidae uncertain for the time being.

INTRODUCTION

The so-called marginelliform gastropods of the families Marginellidae and Cystiscidae harbour an impressive diversity of over 1,600 described living species (MolluscaBase, 2019; for taxonomic authorities, see revised classification below). This includes the smallest known neogastropod, *Ticofurcilla mariolysae* Ortea, 2016 (Fig. 1A), the adults of which attain a length of just 1.35 mm (Ortea, 2016). The shell morphology of marginelliform gastropods is taxonomically uninformative. These molluscs generally possess ovate or elongate shells, which are either involute or low-spired and have a distinctly thickened margin of the outer lip (Covert & Covert, 1995). The shell surface usually lacks sculpture and is glossy and translucent —with some remarkable exceptions, e.g. the shell of *Extra extra* Jousseaume, 1894 is rough and strongly ribbed. The origin of marginelliforms dates back to at least the Eocene (Wenz, 1938) or late Cretaceous (Ponder, 1973: the genus *Myobarbium* Sohl, 1963). Recent marginellids and cystiscids occur predominantly in tropics, being about equally diverse in the Indo-Pacific and Atlantic (West Africa and Caribbean); the most iconic species, such as those in the genera *Marginella* and *Persicula*, occur mainly outside the Indo-Pacific.

Detailed anatomical studies of the marginelliforms (Ponder, 1970; Fretter, 1976; Covert & Covert, 1995) have revealed an extraordinary diversity of alimentary canal arrangements and this has been reflected in the revised classification proposed by Covert & Covert (1995). This classification, which was based on a broad taxonomic sampling and a substantial number of characters, presented a generally plausible scheme for relationships within major marginelliform lineages. Relationships among these lineages, however, remain uncertain and differing interpretations of character evolution have led to conflicting phylogenetic hypotheses (Harasewych & Kantor, 1991; Covert & Covert, 1995; de Souza, 2007; de Souza & Simone, 2019). The relationships between the Marginellidae, Cystiscidae and other neogastropod taxa also remain poorly understood. Some marginelliforms have a uniseriate radula and a set of anatomical features that are shared with the Volutidae. This suggests common ancestry with the Volutidae and thus that the marginelliforms belong to a lineage that originates from a split deep in the neogastropod tree (Ponder, 1973; Harasewych & Kantor, 1991). However, evidence for this hypothesis is poor; it is supported by only few characters, which are either plesiomorphic or likely to be the result of convergent evolution (Ponder, 1973; Kantor, 2002).

The extensive molecular phylogenetic studies of the last decade have profoundly changed our understanding of the systematics of Neogastropoda. Marginelliforms, however, have not been included in these studies. DNA sequence-based analyses of species limits and phylogenetic relationships are lacking for marginelliform gastropods and, remarkably, not a single DNA sequence of a marginellid or cystiscid has to date been deposited in GenBank. Therefore, the monophyly of the main lineages of marginelliform gastropods remains unconfirmed, as well as their affinities to other neogastropod taxa.

Until the recognition of the Cystiscidae Stimpson, 1865, based on the peculiar morphology of head and radula of *Cystiscus*, marginelliform gastropods were classified in the single family Marginellidae. Coan (1965) ranked Cystiscinae (with *Cystiscus*, *Cypraeolina* Cerulli-Irelli, 1911 and *Kogomea* Habe, 1951 as constituent genera) as a subfamily of Marginellidae, and established a third subfamily Marginelloninae for the genera *Marginellona* and *Afrivoluta*. The classification proposed by Covert & Covert (1995) considered the Marginellidae and Cystiscidae to be separate families. In this classification the Marginellidae consisted of the subfamilies Marginellinae (with tribes Marginellini, Austroginellini and Prunini), Marginelloninae and a new subfamily, Granulininae. The Cystiscidae also comprised three subfamilies, the Cystiscinae, Persiculinae and Plesiocystiscinae, and included the genera *Gibberula* and *Persicula*, which had formerly been placed in the Marginellidae. Furthermore, on the basis of substantial differences in radular apparatus and the morphology of the head, Covert & Covert (1995) argued that the Cystiscidae and Marginellidae were not closely related. The current classification of Bouchet *et al.* (2017) essentially follows that of Covert & Covert (1995).

The genus-level taxonomy of the Marginellidae and Cystiscidae is also problematic. Early attempts to establish genus-level classifications of marginelliform gastropods (reviewed by Coan, 1965) suffered notably from inconsistent use of names; phases when genus-level taxa were proliferating have alternated with periods of extensive lumping. There have been three major recent bursts in the description of supraspecific taxa. The first was associated with the work of Laseron (1957), who reassigned Australian species of marginellids to some 30 genera. The work of G.A. Covert and H.K. Covert followed on from this and culminated in a comprehensive revision of marginelliform gastropods (Covert & Covert, 1995). The more recent studies by J. Espinosa, J. Ortea and co-workers have been largely focused on Caribbean taxa (Ortea, 2014; 2016; Ortea, et al. 2019).

109 Notwithstanding, the concept of widespread and speciose marginelliform genera, such as
110 *Gibberula*, *Cystiscus*, *Volvarina* Hinds, 1844 and *Marginella*, each comprising species from the
111 Indo-West Pacific, eastern Atlantic, and Caribbean, remains mainly based on shell features, and
112 calls for a critical reassessment.

113 Using molecular phylogenetic analyses, based on a total of five mitochondrial and nuclear loci,
114 the present study seeks to clarify the relationships between the marginelliforms and other
115 neogastropods, to assess the validity of currently recognized marginelliform families and
116 subfamilies and to provide a revised family-level classification for this group.

MATERIAL AND METHODS

Taxon sampling

The present study is based largely on material collected during expeditions conducted by Muséum National d'Histoire Naturelle (MNHN) to New Caledonia (KANACONO, EXBODI), Western Australia, Tasmania and Papua New Guinea (PAPUA NIUGINI, KAVIENG 2014, MADEEP), the South China Sea (DongSha), Mozambique (INHACA 2011, MAINBAZA), South Madagascar (ATIMO VATAE), Congo (Mission ZANAGA), Senegal (DAKAR), French Guiana (ILES DU SALUT, ACUPA), Guadeloupe (KARUBENTHOS 2) and Martinique (MADIBENTHOS). Additional specimens were contributed by AF (the Philippines, collected in cooperation with the University of the Philippines, 2016) and FB (Oman), or were received on loan from the University of Vienna (Table 1). The accessed specimens represent three tropical biogeographical regions (as defined by Briggs & Bowen, 2012): the Indo-West Pacific, West Indian Ocean and Atlantic (including West Africa and Caribbean), as well as the warm temperate waters of the Mediterranean, Tasmania and southwestern Australia.

Marginelliform gastropods are often very small and possess a narrow, slit-shaped aperture, so that if living animals are preserved by immersion in ethanol, proper tissue fixation is hampered and the extraction of DNA of appropriate quality is often problematic. In this study, therefore, we used only recently collected specimens (starting in 2013), with most having been tissue-clipped in the field. Most of these specimens were processed using a microwave oven (Galindo *et al.*, 2014), followed by subsequent preservation of tissue samples in 96% ethanol. Whenever possible, live animals were imaged prior to tissue sampling, in order to record details of the morphology and colouration of the body in its living state (Fig. 1). Vouchers of shells have been deposited in MNHN, Natural History Museum Vienna or in the Laboratory of Ecology and Morphology of Marine Invertebrates at the A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (IEE), Moscow.

Specimens were initially sorted into morphospecies based on shell morphology. Then the barcode fragment of the cytochrome c oxidase subunit I (COI) gene was sequenced for up to four specimens of each morphospecies (results not shown). Phylogenetic relationships between marginelliform taxa were investigated by reconstructing a phylogeny based on five genes: three mitochondrial genes (COI, 16S rRNA and 12S rRNA) and two nuclear genes (histone 3 (H3) and 28S rRNA). Marginelliform species for this phylogeny were selected by assessing the status of

the morphospecies using molecular systematic data for the COI gene. We analysed pairwise Kimura 2-parameter distances for COI (following Puillandre *et al.*, 2012, the threshold between intraspecific and interspecific variation was taken as 3%) and assessed the monophyly of individual morphospecies in a phylogeny based on COI data. The generally low number of specimens sequenced for each morphospecies precluded the use of automatic species delimitation tools, such as that of Puillandre *et al.* (2012). Morphospecies selected for the multilocus phylogeny were each represented by a single specimen.

Applying species names to the morphospecies identified by us was often problematic because of the generally uninformative shell morphology of marginelliforms and the scarcity of data on the colouration of living animals. Uncertain species-level identifications were indicated by the use of 'cf.' (e.g. *Eratoidea* cf. *hematita*) and 'aff.' (e.g. *Gibberula* aff. *moscatellii*). In total, 27 of the 63 marginelliform species included in our phylogenetic analysis were identified only to genus level.

A total of 86 specimens from 20 nominal genera (47% of the 43 extant and currently recognized genera) were included in the multilocus dataset; these represent the three currently recognized subfamilies of Marginellidae, the three proposed tribes of Marginellinae, as well as the three subfamilies of Cystiscidae. Whenever possible, nominal genera were represented by multiple species that were collected from widely separate geographical localities; the aim was to confirm the monophyly of genera that are currently considered to have circumtropical distribution and to assess whether phylogenetic structuring in such genera reflects the distance between sampling locations. Only about 43% of the marginelliform species in our dataset could be confidently identified and this included just three type species of nominal genera (*Marginellona gigas* (Martens, 1904), *Gibberula oryza* (Lamarck, 1822) and *Prunum prunum* (Gmelin, 1791)). Thus, the results of our phylogenetic analyses are of limited value for taxonomic revisions below the subfamily level.

The monophyly of marginelliform gastropods has never been investigated using DNA sequence data and in an effort to do so we included 58 non-marginelliform species, belonging to 40 caenogastropod families. These non-marginelliforms represented a wide range of neogastropod lineages; sequence data were either from published studies (Zou *et al.*, 2011; Claremont *et al.*, 2012; Fedosov *et al.*, 2015, 2017, 2018; Galindo *et al.*, 2016; Kantor *et al.*, 2017) and retrieved from GenBank, or were generated specifically for this study.

180 *DNA extraction, PCR, and phylogenetic analysis*

181 DNA extraction and PCR were carried out as described by Fedosov *et al.* (2017, 2018). The
 182 amplification of the 28S rRNA fragment was carried out as detailed by Kantor *et al.* (2018). In
 183 total, six molecular datasets were analysed, five single-gene datasets and one concatenated
 184 dataset containing all five mitochondrial and nuclear genes. The single-gene phylogenetic
 185 reconstructions were congruent (see below), so a five-gene concatenated dataset (3018 bp;
 186 referred to hereafter as the MaCys-5G dataset) was assembled. Sequences were aligned using
 187 Muscle v. 3.8.425 (Edgar, 2004) and the alignments edited manually where necessary. COI and
 188 H3 alignments were translated using BioEdit v. 7.2.0.0 (Hall, 1999) to ensure that the
 189 corresponding amino-acid sequences were not interrupted by stop codons.

190 The best-fit substitution models were identified for each gene separately using Partition
 191 Finder2 (Lanfear *et al.*, 2016). The single-gene datasets of 12S rRNA, 16S rRNA, H3 and 28S
 192 rRNA were analysed as a single partition each, whereas the 1st, 2nd and 3rd codon positions of
 193 COI were treated as three distinct partitions. The MaCys-5G dataset thus comprised seven
 194 unlinked partitions.

195 Best-scoring maximum likelihood (ML) trees were estimated using RaxML v. 8.2.12
 196 (Stamatakis, 2006) and IQtree v. 1.6.10 (Nguyen *et al.*, 2014). RaxML analyses were based on
 197 1000 iterations of the thorough bootstrapping algorithm (Felsenstein, 1985). IQtree analyses
 198 were run with the best nucleotide substitution model selected by Model Finder Plus
 199 (Kalyaanamoorthy *et al.*, 2017) and using 1000 iterations of the ultra-fast bootstrap strategy
 200 (Nguyen *et al.*, 2014). Bayesian analyses were performed in two parallel runs in MrBayes v.
 201 3.2.6 (Huelsenbeck *et al.*, 2001). For the COI, 16S rRNA, 12S rRNA, 28S rRNA and H3 single-gene
 202 analyses, each Bayesian run consisted of six Markov chains and 10,000,000 generations, with
 203 default number of chain swaps and a sampling frequency of one tree every 1,000 generations.
 204 For the MaCys-5G dataset, Bayesian analyses were performed with the following parameter
 205 settings: number of chains = 8, number of generations = 30,000,000, number of chain swaps = 5
 206 and sampling frequency = 1 tree every 1,500 generations. A chain temperature of 0.02 was
 207 used in all analyses. Convergence was assessed using Tracer v. 1.4.1 (Rambaut *et al.*, 2014); the
 208 runs were considered to have converged if all ESS values exceeded 200. Consensus trees were
 209 calculated after discarding the first 25% of trees as burn-in. RaxML and Bayesian analyses were

performed on the Cipres Science Gateway (<http://www.phylo.org/portal2> - Miller *et al.*, 2010). The IQ tree analysis was run locally on a 32-CPU working station. All trees were rooted on the outgroup taxon *Xenophora* sp. (Xenophoridae).

A branch/clade was considered to be strongly/well supported if bootstrap support (BS1 for RaxML, BS2 for IQtree) values were $\geq 70\%$ and posterior probability (PP) values were ≥ 0.95 , respectively.

Morphological studies

In many cases all the tissue retrieved from a specimen was used for DNA extraction. In other cases, use of a microwave for tissue extraction prevented subsequent study of fine morphology. Fortunately, a comprehensive analysis of marginelliform anatomy was provided by Coover & Coover (1995), so their data were re-examined in the light of the molecular phylogeny. One aspect of internal anatomy that we were able to investigate in detail and compare with descriptions by Coover & Coover (1995) was the radula. We studied the radula of all the marginelliform taxa included in our phylogeny. For each morphospecies included in the phylogeny, we tried as far as possible to examine the radula of the sequenced specimen; when this was not possible a specimen collected from the same exact locality as the sequenced specimen was used. For larger specimens the radulae were extracted by dissecting out the foregut complex and dissolving the tissue in a 5% solution of commercial bleach; in the case of smaller specimens all tissue was simply dissolved in 5% bleach solution. Following the removal of associated soft tissue, the radulae were rinsed in several changes of distilled water and mounted on 12-mm coverslips for investigation by scanning electron microscopy (SEM). The air-dried radulae were then gold-coated. Examination and imaging by SEM was performed using a Hitachi Jeol SEM and a TeScan TS5130MM SEM, at MNHN and IEE, respectively.

RESULTS

Multilocus molecular phylogeny: deep relationships

While the single gene trees were generally congruent with each other, neither the placement of marginelliform lineages within the Neogastropoda, nor relationships between marginelliform taxa were strongly supported. In the analyses of the multilocus dataset, the topology and levels of branch support were strikingly different between analyses including and excluding the two species of *Granulina*. Although *Granulina* was always shown to fall within the main Marginellidae + main Cystidae clade (see Supplementary Material Fig. S1), its position was unstable and its inclusion tended to reduce support values across the tree. Therefore, the final analyses (i.e. those discussed below) were carried out without *Granulina*.

Our ML (IQtree and RaxML) and Bayesian trees were largely congruent for relationships among neogastropod families and superfamilies, but deeper relationships were generally poorly resolved and the branching order varied depending on the method of phylogenetic reconstruction. Our analyses consistently recovered two major clades (Fig. 2): a clade comprising the marginelliforms and the Volutidae, which was strongly supported in two of the three main analyses (PP = 0.97, BS2 = 88%), and a consistently strongly supported clade (PP = 1, BS1 = 76%, BS2 = 97%) consisting of the remaining neogastropod taxa, the Ficoidea and the Tonnoidea. The monophyly of the marginelliforms, although recovered in all analyses, was strongly supported only in the IQ tree (BS2 = 95).

The first split within the marginelliforms separates *Marginellona gigas* from a consistently well-supported clade containing all the remaining species (PP = 1, BS1 = 73%, BS2 = 100%; Fig. 2). The latter cluster consists of four major clades: (1) the 'Main Cystiscidae' clade (strongly supported in the IQtree: BS2 = 100%), (2) *Canalispira* (strongly supported in all three analyses: PP = 1, BS1 = 100%, BS2 = 100%), (3) *Plesiocystiscus* (strongly supported in the IQ tree: BS2 = 91%) and (4) the 'Main Marginellidae' clade (always strongly supported: PP = 1, BS1 = 100%, BS2 = 100%).

The 'Main Cystiscidae' clade

The Main Cystiscidae clade consists of five subclades (MC1–5) and includes species that, on the basis of shell characters, belong to five nominal genera in the subfamilies Cystiscinae and

Persiculinae: *Cystiscus*, *Crithe*, *Gibberula*, *Persicula* and *Pachy bathron*. Together, *Cystiscus* and *Crithe* always formed a maximally supported clade (MC1 subclade) that contains species from both the Indo West Pacific (IWP) and the Caribbean. The MC2 subclade (also maximally supported) comprises two Caribbean species with similar shells ornamented with a pattern of lines: *Gibberula* aff. *moscatellii* Boyer, 2004 and *Persicula pulcherrima* (Gaskoin, 1849). The well supported MC3 subclade (PP = 1, BS2 = 99%) consists of six small unidentified species, mostly from the Indo-Pacific; despite substantial variability in shells morphology, these were tentatively attributed to *Gibberula* (4 species) and *Persicula* (one species, from Oman). The MC4 subclade is a strongly supported clade comprising two West African species of *Gibberula* and *G. nebulosa* Boyer, 2002, from deep water off New Caledonia (note the deep divergence between the West African taxa and *G. nebulosa*). Finally, the strongly supported MC5 subclade (PP = 1, BS1 = 99%, BS2 = 100%) comprises three Caribbean taxa: two species of *Pachy bathron* and '*Gibberula*' *colombiana* Boyer, 2003. The relationships among the five subclades of the Main Cystiscidae clade were unresolved. The monophyly of each of the genera *Cystiscus* and *Pachy bathron* was consistently maximally supported. The relationships observed between and within the MC2, MC3 and MC4 subclades suggest that *Persicula* and *Gibberula*, as currently perceived, are not monophyletic.

'Main Marginellidae' clade

The Main Marginellidae clade includes 40 sequenced species, grouped into two strongly supported subclades, MM1 (PP = 1, BS1 = 99%, BS2 = 100%) and the MM2+MM3+MM4 subclade (PP = 1, BS1 = 99%, BS2 = 100%). The MM1 subclade comprises 13 sequenced species (all from the west Pacific, and only 3 confidently identified) in the genera *Serrata*, *Protoginella*, *Mesoginella*, *Hydroginella*, and *Dentimargo*. Three of the four well supported groups that constitute MM1 consist of species that occur exclusively in deep water; on the basis of shell morphology these have been placed in the genera *Dentimargo*, *Serrata*, *Mesoginella* and *Protoginella*. The fourth well supported group in MM1 consists of four shallow-water species; on the basis of shell characters these have been assigned to the genus *Hydroginella*.

The MM2 subclade is maximally supported and comprises ten species in two strongly supported clusters. The first cluster consists of two shallow-water species from Papua New Guinea, which have been tentatively assigned to *Dentimargo*. The second cluster is composed

of eight deep-water species of *Dentimargo*, *Marginella* and *Eratoidea* from New Caledonia and the Caribbean. The MM3 subclade is maximally supported and consists of five described species of *Marginella* and *Glabella* Swainson, 1840, all exclusively from shallow water localities off the coast of South and West Africa. The MM2 and MM3 subclades were shown to be sister groups in two of the three main analyses (BA, IQ). The strongly supported MM4 subclade (PP = 1, BS1 = 81%, BS2 = 100%) consists of a pair of *Closia* species (from off Madagascar) and a large *Volvarina*–*Prunum*–*Hyalina* cluster uniting species from both shallow and deep-water localities in the Caribbean, South and West Africa and the IWP. Although deeper relationships within this group are generally well supported, no clear pattern can be observed with regard to geographic or bathymetric distribution.

Our results confirm the monophyly of the genera *Hydroginella*, *Mesoginella*, *Protojinella* and *Closia*, indicate that *Dentimargo* and *Marginella* are clearly polyphyletic, and demonstrate that *Volvarina* is paraphyletic in relation to *Prunum* and *Hyalina*.

Morphology of the radula

Radula morphology was studied in 26 sequenced species of marginelliiform gastropods (including two species of *Granulina*); five other species were dissected, but no radula was found (Fig. 3). We also studied published SEM images of the radulae of *Volvarina avena* and *V. lactea* (Bandel, 1984; these are similar in shell morphology to the sequenced specimens MNHN-IM-2013-60828 and MNHN-IM-2013-60956, respectively). The radulae examined correspond to the following radula types delineated by Covert & Covert (1995): types 1–7, type 9 and the ‘modified type 6’ radula (Fig. 4). Only in type 1 radulae were transverse rows observed to have three teeth (Fig. 4A, B); the radulae of the remaining seven types are uniseriate and composed of rachidian teeth only. The distribution of radula types (Fig. 3) across our trees shows clear phylogenetic structuring. Cystiscid lineages are characterized by three types of radulae: type 1 (*Plesiocystiscus* Covert & Covert, 1995; Fig. 4A, B), type 2 (*Cystiscus*; Fig. 4C, D) and a variable type 3 (all other lineages, including *Canalispira* Fig. 4E–L). All cystiscids have well-developed odontophoral hoods—wide, symmetrical chitinous lobes that are attached to the anterior part of the radula where it bends over the odontophore. According to Covert & Covert (1995), these odontophoral hoods are supported by separate odontophore cartilages. The radula teeth of *Plesiocystiscus* sp. (Fig. 4B), ‘*Gibberula*’ *nebulosa* from New Caledonia (MNHN-IM-2013-

68353, Fig. 4G), *Canalispira* sp. (Fig. 4I) and ‘*Persicula*’ sp. from Oman (Fig. 4K) showed pronounced wear.

Among marginellids included in our phylogeny, a ‘modified type 6’ radula is found in *Serrata tuii* (Cossignani, 2001) (MNHN-IM-2013-69537), an undescribed ‘*Dentimargo*’ species (MNHN-IM-2013-45628; Fig. 4O) and in the two species of *Closia*. This radula type is characterized by wide, multicuspidate rachidians with a somewhat wavy anterior edge and subequal cusps. In contrast, ‘true type 6’ radulae have teeth that are distinctly rectangular, with a straight anterior edge and cusps of often unequal length; the surface of the tooth is marked by prominent pits, the function of which is to receive the cusps of the succeeding tooth (Fig. 4P). This type of radula, which is characteristic of the type species of *Volvarina*, *V. mitrella* (Ortea *et al.*, 2014), was found in most members of the *Volvarina*–*Prunum*–*Hyalina* cluster of the MM4 subclade; the exceptions were *Hyalina buskei* Espinosa & Ortea, 2013 (not shown on Fig. 4), *Volvarina avena* and *V. lactea* (Bandel, 1984). The very wide radula of *Marginellona gigas* (Fig. 4Q), in which each rachidian bears over 100 cusps, essentially does not differ from type 6 radulae, although we note that it was classified by Coover & Coover (1995) in a separate category, type 7. Type 4 (Figs 4M, N), type 5 (Fig. 4R) and type 9 radulae (Fig. 4S) appear to be more phylogenetically restricted, occurring, respectively, in the two *Granulina* species, the *Protoginella*–*Mesoginella* cluster in the MM1 subclade and the *Hydroginella* cluster in the MM1 subclade. None of the marginellids examined had radula with odontophoral hoods or with signs of wear. None of the dissected members of the MM2 and MM3 subclades possessed a radula.

DISCUSSION

Implications of the phylogenetic analysis for genus-level taxonomy of marginelliform gastropods

Within the ‘Main Cystiscidae’ clade, the generic names *Cystiscus* and *Crithe* can provisionally be used for the lineages that constitute the MC1 subclade. Similarly, the generic name *Pachybatron* can be used for the MC5 subclade. In addition, a specimen of the type species of *Gibberula*, *Gibberula zonata* Swainson, 1840 (= *Volvaria oryza* Lamarck, 1822), was successfully sequenced for five genes and, based on its placement, we can unequivocally assign the name *Gibberula* to the MC4 subclade of our Main Cystiscidae clade. The remaining species in the Main Cystiscidae clade, which are all from the IWP and the Caribbean, were initially assigned to *Gibberula*. Our phylogenetic data indicate that these should be assigned elsewhere. Of these taxa, ‘*G.*’ *colombiana* can confidently be reclassified in *Pachybatron*. Neither of the two sequenced species provisionally identified as *Persicula* (but shown not to be related to one another) provides grounds for a confident attribution of the name *Persicula* to either the MC2 or MC3 subclades of the Main Cystiscidae clade. So, to ascertain the proper application of names to these clusters, the type species of *Persicula* should be sequenced, as well as species of the Caribbean genus *Osvaldoginella*.

Based on the inclusion of its type species in our molecular analyses, the name *Prunum* can be applied unequivocally to the MM4 subclade of the ‘Main Marginellidae’ clade. Nevertheless, until the type species of *Volvarina* and *Hyalina* are sequenced and their relationships to *Prunum* established, the scope and status of all three of these names remains uncertain. Our analyses showed *Volvarina* to be paraphyletic. We note the substantial morphological variation that has been reported for this genus, eight subgenera having been proposed, largely on the basis of radula morphology (Ortea, 2014; Ortea *et al.*, 2019). Clearly, the relationships between the nominal taxa *Volvarina*, *Prunum* and *Hyalina* require further investigation. Particular efforts are needed to assess the validity and rank of the divisions proposed for *Volvarina*.

Our analyses recovered the West and South African species of *Marginella* and *Glabella* in the MM3 subclade, and the Caribbean *Marginella cloveri* – in the MM2 subclade. Neither the type species of *Marginella* (*M. glabella* Linnaeus, 1758) nor of *Glabella* (*G. faba* (Linnaeus, 1758)) were included in the present analysis; both of these genera are from relatively shallow water in the East Atlantic, as are some of the species in the MM3 subclade (Fig. 2). The distinction between *Marginella* and *Glabella* is based on the presence of axial ribs and a

denticulate outer lip in *Glabella* and lack of these characters in *Marginella* (Coover & Coover, 1995). Our analyses, however, show that species belonging to these genera are intermixed in the MM3 subclade and so we apply the older name *Marginella* to the MM3 subclade as a whole. The recent subdivision by Veldsman (2017) of *Marginella* into numerous 'subgenera' also needs to be further investigated using DNA sequence data.

The genus *Dentimargo* appears to be one of the most problematic taxa among marginelliforms. Species that were assigned to this genus are split between the MM1 and MM2 subclades, with more in the latter. These results show that the shell characters treated by Coover & Coover (1995) as being diagnostic for *Dentimargo* (type species *Marginella dentifera* Lamarck, 1803 from the French Eocene) are inadequate. Coover & Coover (1995: 76) stated that the posterior denticle was "distinctly stronger than the others", but this character is highly variable and applies equally to species in both the MM1 and MM2 subclades. The "spire medium to tall, shell usually narrowly biconic" seems better to suit species in the MM1 subclade, such as those represented by specimens MNHN-IM-2013-45652 and MNHN-IM-2013-45628 (Fig. 2). Although Coover & Coover (1995) treated *Dentimargo* as a genus with radulaless species, this character can of course not be examined in the type species, which is a fossil. In fact in our study the species that possess more elongate shells and are included in the clade MM1 actually do have a radula. Therefore, the name *Dentimargo* cannot be applied to either the MM1 or MM2 subclades.

The Caribbean *Eratoidea* cf. *hematita* (Kiener, 1834), which is a member of the MM2 subclade, appears to be morphologically similar to the type species of the genus *Eratoidea*, *E. margarita* (Kiener, 1834), also from the Caribbean region. Thus, the name *Eratoidea* Weinkauff, 1879 can be more or less confidently applied to this clade and, in this case, would have a priority over the later name *Dentimargo* Cossmann, 1899. Likewise, *Serrata tuii* is conchologically similar to the type species of *Serrata*, *S. serrata* and, thus, if applied to the MM1 subclade, the name *Serrata* Jousseaume, 1875 would have priority over *Dentimargo*. However, as the type species of *Eratoidea* and *Serrata* have not been sequenced in the present study, we refrain from applying these names to the clades in question. Our analysis strongly suggests that if the name *Dentimargo* is to be used in the context of extant species, the scope of its application should be greatly modified and the genus reviewed in depth.

The application of the names *Mesoginella*, *Protoginella* and *Hydroginella* to the relevant clusters within the MM1 subclade is straightforward, as is the use of *Closia* for the pair of species that constitute the sister group of the *Volvarina*–*Hyalina*–*Prunum* cluster.

Family-level classification of marginelliform gastropods

Our phylogenetic analyses suggest that the three subfamilies currently recognized for the Marginellidae (Marginellinae, Marginelloninae and Granulininae) do not together constitute an exclusive clade (i.e. one containing only these three groups). We obtained strong support for the sister-group relationship between *Marginellona gigas* (Marginelloninae) and *all* other marginelliforms. We also found the position of *Granulina* in the marginelliform part of the tree to be unstable (likely due to long branch attraction); a discussion of the relationships of *Granulina* to other marginelliforms would be premature at this point, but the distinctiveness of this lineage is nevertheless obvious. On the basis of these results, we elevate Marginelloninae to family rank and follow Boyer (2017) in elevating Granulininae to family rank also. We thereby restrict the family Marginellidae to the the Main Marginellidae clade of our phylogenetic trees.

Following on from the elevation of the former subfamilies of Marginellidae to family rank, we elevate the three tribes currently recognized for the Marginellinae (Marginellini, Prunini and Austroginellini) to subfamily rank. We propose that the the name Marginellinae be applied to the clade uniting the MM2 and MM3 subclades, which comprises radula-less species of *Marginella*, *Dentimargo* and *Eratoidea*. The name Pruninae is applied to the MM4 subclade, which consists of the *Closia* lineage and species of *Prunum*, *Volvarina* and *Hyalina*. Finally, on the basis of similar radula morphology, we use the name Austroginellinae for the MM1 subclade, which includes the genera *Mesoginella* and *Protoginella*. These two genera are characterized by Covert & Covert's (1995) type 5 radula; a strikingly similar radula has been illustrated by Ponder & Taylor (1992) for *Austroginella* (not included in our study).

Deep-level relationships within the Cystiscidae (traditionally comprising the subfamilies Cystiscinae, Persiculinae and Plesiocystiscinae) were not resolved. Since we cannot unequivocally rule out the monophyly of the Cystiscidae, we retain the use of this family-level name in its traditional sense. With the exception of *Canalispira* (all species of this genus constituted a maximally supported clade), the members of the genera formerly included in Cystiscinae and Persiculinae formed part of the MC1 subclade. The lack of resolution of

relationships within this subclade makes delineating the limits of the Cystiscinae and Persiculinae a difficult task. Therefore, we favour designating the MC1 subclade, in its entirety, a single subfamily, the Cystiscinae. The subfamily-level systematics of the Cystiscidae should be revised to account for the divergent positions of *Plesiocystiscus* (treated by Covert & Covert, 1995, as a distinct subfamily, the Plesiocystiscinae) and *Canalispira* (see below). We therefore propose three subfamilies for the Cystiscidae—Cystiscinae, Plesiocystiscinae and Canalispirinae new subfamily.

On the basis of the molecular and morphological data presented above, we revise the Bouchet *et al.*'s (2017) classification of the marginelliforms as follows:

Superfamily VOLUTOIDEA Rafinesque, 1815

Family MARGINELLONIDAE Coan, 1965

Genera *Marginellona* Martens, 1904; *Afrivoluta* Tomlin, 1947; *Tateshia* Kosuge, 1986

Family CYSTISCIDAE Stimpson, 1865

Subfamily CYSTISCINAE Stimpson, 1865

Genera *Cystiscus* Stimpson, 1865; *Crithe* Gould, 1860; *Extra* Jousseaume, 1894; *Gibberula* Swainson, 1840; *Inbiocystiscus* Ortea & Espinosa, 2001; *Intelcystiscus* Ortea & Espinosa, 2001; *Pachy bathron* Gaskoin, 1853; *Persicula* Schumacher, 1817; *Ticocystiscus* Espinosa & Ortea, 2002; *Ticofurcilla* Espinosa & Ortea, 2002; ? †*Marginocystiscus* Landau, C. M. Silva & Heitz, 2016.

Subfamily PLESIOCYSTISCINAE G. A. Covert & H. K. Covert, 1995

Genus *Plesiocystiscus* G. A. Covert & H. K. Covert, 1995.

Subfamily CANALISPIRINAE new subfamily Fedosov, Caballer, Boyer & Bouchet

Genera *Canalispira* Jousseaume, 1875; ?*Osvaldoginella* Espinosa & Ortea, 1997.

Zoobank registration: urn:lsid:zoobank.org:act:D2C62BDC-753F-4537-8464-F4D5CD20C963

Diagnosis (adapted from Covert & Covert, 1995): Shell minute to medium sized, white, unsculptured, rarely with faint pattern, cylindrical-biconic to obovate or obconic. Sutures impressed to deeply channeled. Aperture with deeply channeled posterior notch; siphonal notch absent. Outer apertural lip thickened, smooth or lirate; external varix absent. Columella bearing 3–6 plications and weaker parietal lirae. Tentacles absent; siphon not visible; foot split anteromedially, covering external shell surface anterolaterally. Radula uniseriate, composed of horseshoe-shaped rachidians, bearing 7 strong triangular cusps.

Family GRANULINIDAE G. A. Covert & H. K. Covert, 1995

Genera *Granulina* Jousseaume, 1888; *Granulinella* Boyer, 2017; *Granulinopsis* Boyer, 2017; *Marginellopsis* Bavay, 1911; *Paolaura* Smriglio & Mariottini, 2001; *Pugnus* Hedley, 1896; †*Hiwia* Marwick, 1931.

Family MARGINELLIDAE J. Fleming, 1828

Subfamily MARGINELLINAE J. Fleming, 1828

Genera *Marginella* Lamarck, 1799; *Eratoidea* Weinkauff, 1879; ?*Gibbacousteau* Espinosa & Ortea, 2013; ?*Dentimargo* Cossmann, 1899; ? †*Stazzania* Sacco, 1890.

Subfamily AUSTROGINELLINAE G. A. Covert & H. K. Covert, 1995

Genera *Austroginella* Laseron, 1957; *Alaginella* Laseron, 1957; *Hydroginella* Laseron, 1957; *Mesoginella* Laseron, 1957; *Ovaginella* Laseron, 1957; *Protoginella* Laseron, 1957; *Serrata* Jousseaume, 1875; ?*Caribeginella* Espinosa & Ortea, 1998; ?*Marigordiella* Espinosa & Ortea, 2010.

Subfamily PRUNINAE G. A. Covert & H. K. Covert, 1995

Genera *Prunum* Herrmannsen, 1852; *Balanetta* Jousseaume, 1875; *Bullata* Jousseaume, 1875; *Closia* Gray, 1857; *Cryptospira* Hinds, 1844; *Hyalina* Schumacher, 1817; *Mirpurina* Ortea, Moro & Espinosa, 2019; *Rivomarginella* Brandt, 1968; *Volvarina* Hinds, 1844.

Marginelliform branch in the neogastropod tree of life

Our results provide the first molecular phylogenetic data for marginelliform neogastropods. Neither the Marginellidae nor the Cystiscidae, as currently conceived, were found to be monophyletic. Deep-level marginilliform relationships were not resolved, but this does not completely rule out the potential monophyly of Cystiscidae. The Marginellidae, in contrast, were clearly shown to be paraphyletic: *Marginellona gigas* shows no sister-group relationship to the Main Marginellidae clade and the placement of Granulininae remains unresolved. Our analyses demonstrated that the marginelliform gastropods as a whole are monophyletic and that, as hypothesized on the basis of morphological similarities (Ponder, 1970, 1973), they are sister to the family Volutidae. The basal split between *Marginellona* and the other marginelliform taxa is reflected in the morphology of *Marginellona gigas*; this taxon has some typical marginellid characters, as well as others that are regarded as plesiomorphic for the Neogastropoda as a whole and are not recorded in other marginelliforms (Harasewych & Kantor, 1991). The anatomy of the marginelliform foregut is known in detail and the characters shared by *Marginellona* and other marginellids include the uniseriate comb-like radula within a buccal pouch (Fretter, 1976; Ponder, 1970; Harasewych & Kantor, 1991; Covert & Covert, 1995).

The pattern of branching of the marginelliform lineages in our trees contradicts the hypothesis of Covert (1989) and Covert & Covert (1995) that the Cystiscidae are the sister lineage of all other marginelliforms. The strongest evidence for this hypothesis is the fundamentally different radula morphology of the Marginellidae and *Marginellona*, on the one hand, and of the Cystiscidae, on the other. Our examinations showed that the Marginellidae and *Marginellona* possess a buccal pouch, while cystiscid radulae have large, firm, paired odontophoral hoods, and retain plesiomorphic morphology with three teeth in each row in *Plesiocystiscus*. Although the distinction drawn by Covert & Covert (1995) does hold overall, the difference in radula morphology does not correspond to the two reciprocally monophyletic marginellid and cystiscid lineages. Both marginellid and cystiscid radulae have apomorphic

features, and so any attempt to trace the history of morphological change from one type of radula to the other (e.g. from the radulae of cystiscids to the radula of *Marginellona*) would be problematic. However, if we look for the homology of cystiscid odontophoral hoods, we find that they could be derived from the marginal cuticular flanges of an ancestral marginellid-type radulae (the membranaceous folds persist, for example, in type 6 radulae). Coover & Coover (1995) considered that these hoods and flanges were fundamentally different, but we argue that the quantitative differences that they emphasized do not preclude the possibility that these structures are, in fact, homologous. The profound transformation of the radula in the ancestor of modern cystiscids could have been driven by selective pressures associated with the evolution of a novel feeding strategy, such as feeding on hard-shelled prey. The presence of a common set of radula features across cystiscids supports a single origin of the Cystiscidae and, given that our trees were only partly resolved, this is the scenario we have reflected in our classification. The disappearance of the buccal pouch can most plausibly be explained by paedomorphosis, that is a shortened postembryonic development leading to the conservation of ancestral features in adult morphology. The same mechanism can be evoked to explain the presence of a triseriate radula in *Plesiocystiscus* vs uniseriate radulae in all other marginelliforms except *Tateshia* (see below). The evolution of cystiscids has clearly involved a progressive reduction in adult size, consistent with a paedomorphic origin of this taxon.

The uniseriate radulae of marginelliforms are similar to those in the Volutidae and uniseriate radulae (although of different morphology) are also typical for the Cancellariidae and Volutomitridae. Furthermore, members of these families possess distinct columellar plaits (a character also found in other neogastropod lineages). Relationships among the marginelliforms, Volutidae, Volutomitridae and Cancellariidae are controversial and poorly understood, and these taxa are inadequately represented in published phylogenies. Cunha *et al.* (2009) and Oliverio & Modica (2010) showed the Cancellariidae as the sister group of other neogastropods and the former study suggested paraphyly of the Neogastropoda. A more recent topology (Fedosov *et al.*, 2015) conflicts with this, showing the Cancellariidae and Volutidae as sister taxa, and the Volutomitridae branch clustering with the costellariid and ptychatractid lineages. A recent phylogenomic analysis of the Conoidea (Abdelkrim *et al.*, 2018) provided additional insights into the early radiation of the Neogastropoda, placing the Cancellariidae, Volutidae and Volutomitridae as three early and independent lineages.

Our morphological data are fragmentary and so a formal analysis of radula evolution in the marginelliforms was not possible. Nonetheless, observations made in the course of this study contradict those of Covert & Covert (1995). These authors described two separate radula types, ‘type 6’ (characteristic of the Pruninae) and ‘modified type 6’ (found in the genus *Serrata*), interpreting the latter as the derived state (Fig. 4O). However, in our trees this ‘modified type 6’ radula appears to be present in several distantly related lineages originating from splits deep within the Marginellidae radiation. This suggests that this character state is the ancestral morphology of the Marginellidae, as circumscribed in our study. Our phylogenetic data suggest that the true ‘type 6’ radula of Covert & Covert (1995) (Fig. 4P), which is found only in the *Volvarina*–*Prunum*–*Hyalina* clade (MM4 subclade), is the derived state. The available data on the feeding of the Pruninae *sensu stricto* (all of the MM4 subclade except *Closia*) suggests that they pry open small bivalves (Winner, 1989); the pits present on the radula teeth of most species of *Prunum* and *Volvarina* (Covert, 1989; Fig. 4P), apparently enhance the capacity of the teeth to interlock and likely prevent radula distortions in the lateral plane. More detailed observations of feeding are needed, however, to understand the links between radula morphology and function.

Whereas the ancestral type 6 radula gave rise to the radulae of *Prunum* and *Volvarina* in the MM4 subclade, in the MM1 subclade (i.e. in *Mesoginella* and *Protoginella*; Fig. 4R) it has been transformed into the type 5 radula. Ponder & Taylor (1992) demonstrated the ability of *Austroginella johnstoni* (Petterd, 1884) and *A. muscaria* (Lamarck, 1822) to drill bivalve shells. Both of these species possess a type 5 radula (Ponder & Taylor, 1992), as well as a convoluted tubular midgut gland, which is similar to the venom gland of the Conoidea and is equipped with a ventral duct bypassing the valve of Leiblein. Based on this morphology of the midgut gland, Ponder & Taylor (1992) suggested that shell drilling in these species is complemented by the use of a toxic secretion of this gland to subdue prey. The fact that a type 5 radula is present in both the *Mesoginella* and *Protoginella* groups in the MM1 subclade suggests that it was also present in their common ancestor, and so have also been present in the ancestor of *Hydroginella*. It follows from this that a duct of Leiblein, similar in morphology to the one described in *A. johnstoni* (Ponder & Taylor, 1992), may also have been present in the ancestor of *Hydroginella*. Species of *Hydroginella* are peculiar not only because of their unusual type 9 radula (composed of a few, very thin teeth; Fig. 4S), but also because they parasitize sleeping

fish, by sucking the blood of their prey (Bouchet, 1989; Bouchet & Perrine, 1996). Sucking blood of large and usually highly mobile prey requires certain biochemical adaptations to both narcotize the prey and prevent blood coagulation. The adaptations for feeding by blood sucking have been described in detail for another neogastropod, the ‘vampire snail’ *Cumia reticulata* (Blainville, 1829), which belongs to the Colubrariidae (Modica *et al.*, 2015; Gerdol *et al.*, 2018). *Hydroginella* species are characterized by a highly modified tubular gland of Leiblein, the legacy of their shell-boring ancestors; this adaptation may have been a key prerequisite for the evolution of blood sucking in this group. Interestingly, *Hydroginella* is not the only marginellid parasitizing fish. A similar feeding biology was described by Kosuge (1986) for *Tateshia yadai* Kosuge, 1986, multiple specimens of which were found attached to the pectoral fins of the scorpaenid fish *Helicolenus hilgendorfi* at depths of about 300 m. Kosuge (1986) originally placed *Tateshia* in Olividae on the basis of its triseriate radula. However, the genus was reassigned to the Marginellidae by Bouchet (1989), who regarded the type of radula (comprising rachidian as well as laterals) found in *Tateshia* to be an underived ancestral feature, and the evidence that *Tateshia* originated from rachiglossate predecessors. The phylogenetic relationships of this enigmatic gastropod require further investigation, but this is hampered at present by the exceptional rarity of *Tateshia*.

The type 3 radula (Figs 4E–M) is most widespread in the cystiscid lineages, including the *Gibberula*–*Persicula*–*Pachy bathron* subclade and *Canalispira*. This type of radula usually has bow- or horseshoe-shaped multicuspidate teeth, each bearing a strong central cusp. The uniseriate radulae of the nematoglossan type is often considered as an adaptation to suctorial feeding; the extremely elongated central cusps pierce the integument of prey, while the lateral cusps facilitate interlocking of successive teeth, rendering the radula more rigid and possibly more resistant to lateral deformation (Petit & Harasewych, 1986; Modica *et al.*, 2011). Published observations on *Cystiscus* species feeding on bryozoans (Coleman, 1975) suggest that the radulae of marginelliforms may function in a similar manner. However, of particular interest is the clear signs of wear that were observed in nearly all the examined cystiscid radulae (Figs 4B, G, I, L). This wear is most likely the result of mechanical abrasion, which suggests that cystiscid radulae come into contact with tough substrata, such as the frontal membrane or the cryptocyst of colonial bryozoans. The specialization for feeding on sedentary prey with thick integument may explain the origin of the cystiscid type of radula. The firm odontophoral hoods presumably provide additional mechanical support for the radula by leveraging the pressure on

631 the odontophore cartilage. The rapid wearing-down of the radula implies a need for prompt
632 replacement of teeth and an accelerated turnover. In this context, the very long cystiscid
633 radulae, consisting of over 100 teeth, and the occurrence of nascent teeth in groups of five or
634 six (Covert & Covert, 1995), can be seen as adaptations to counterbalance the rapid abrasion
635 of the teeth.

636

ACKNOWLEDGEMENTS

The material used in this study originates from numerous shore-based expeditions and deep sea cruises, conducted respectively by MNHN and Pro-Natura International as part of the *Our Planet Reviewed* programme, and by MNHN and Institut de Recherche pour le Développement as part of the *Tropical Deep-sea Benthos* programme. All expeditions operated under the regulations then in force in the countries in question and satisfy the conditions set by the Nagoya Protocol for access to genetic resources. Funders and sponsors include the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, Richard Lounsbery Foundation and the French Ministry of Foreign Affairs. Sampling in Western Australia was arranged by Hugh Morrison, with the support of the Western Australian Museum. We thank Noel Saguil for help with sample collection in the Philippines. The specimens used in this study were obtained in conjunction with a collecting trip of the University of the Philippines, which was supported in part by International Cooperative Biodiversity Group (ICBG grant no. 1U01TW008163). We thank, among others, Virginie Héros, Philippe Maestrati, Pierre Lozouet, Ellen Strong, Laurent Charles and Julien Brisset for their role in the processing of specimens during the expeditions and curation. The photos of live marginelliforms were taken by Laurent Charles (MNHN), Philippe Maestrati (MNHN), and Gustav Paulay (Florida Museum of Natural History). We thank Catherine Rausch (MNHN) and Anna Neretina (IPEE) for access to SEM facilities at MNHN and IEE RAS. We are grateful to Marco Oliverio and Yuri Kantor for their critical comments on the manuscript and to David Reid for his careful and thorough editing of the final version of the manuscript. This study was largely accomplished during curatorial visits made by the first author to MNHN in 2016–2019. The molecular phylogenetic studies were supported by the Service de Systématique Moléculaire (UMS 2700 CNRS-MNHN), ATM Barcode (PIs Sarah Samadi and Jean-Noël Labat, MNHN), ANR project CONOTAX (grant no. ANR-13-JSV7-0013-01, PI Nicolas Puillandre) and by a grant from the Russian Science Foundation (RSF 16-14-10118, PI Y. Kantor).

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FIGURE CAPTIONS

Figure 1. Live marginelliform gastropods (not shown to scale). **A.** *Ticofurcilla mariolysae* (MNHN, MADIBENTHOS St. AB360, 14°46'73"N, 61°00'26"W, 12 m depth). **B.** *Crithe* aff. *mariano*i (MNHN-IM-2013-2989, PAPUA NIUGINI St. PB18, 05°06.3'S, 145°49.1'E, 26 m depth). **C.** *Cystiscus* sp. (MNHN-IM-2013-3692, PAPUA NIUGINI St. PB21 5°1'26.89"S, 145°48'2"E, 5 m depth). **D.** '*Gibberula*' sp. (MNHN-IM-2013-4208, PAPUA NIUGINI St. PB26, 04°59.1'S, 145°47.7'E, 22 m depth). **E.** '*Gibberula*' aff. *moscatellii* (MNHN-IM-2013-56965, ILES DU SALUT St. SS01, 05°16.9'N, 52°35.1'W, 8 m depth). **F.** *Canalispira* sp. (MNHN-IM-2013-1838, PAPUA NIUGINI St. PS09, 05°12.3'S, 145°48.8'E, 8–10 m depth). **G.** *Marginella festiva* (MNHN-IM-2013-43709, Dakar'09 St. 09, 14°39.9'N, 17°24.0'W, 7 m depth). **H.** *Eratoidea* cf. *hematita* (MNHN-IM-2013-60596, KARUBENTHOS 2 St. DW4559, 16°24.5'N, 60°51.8'W, 72–111 m depth). **I.** '*Dentimargo*' sp. (MNHN-IM-2013-3409, PAPUA NIUGINI St. PS15, 5°5'47.4"S, 145°48'11.7"E, 12 m depth). **J.** '*Marginella*' *cloveri* (MNHN-IM-2013-56775, GUYANE 2014 St. CP4402, 6°18'N, 52°13.3'W, 95–97 m depth). **K.** *Volvarina* aff. *avena* (MNHN-IM-2013-60828, KARUBENTHOS 2

St. DW4579, 16°21'N, 60°54'W, 228–264 m depth). **L.** *Granulina* sp. (MNHN-IM-2013-1289, PAPUA NIUGINI St. PB06, 05°09.9'S, 145°50.4'E, 20 m depth).

Figure 2. ML phylogeny of the Neogastropoda showing cystiscid (blue shading) and marginellid (red shading) lineages (tree reconstructed by RaxML). Dark and light shading in the marginelliform part of the tree (*Marginellona* + 'Main Cysticidae' + *Canalispira* + *Plesiocystiscus* + 'Main Marginellidae') indicate provisional boundaries of genus-level taxa. Branch support values are shown in the following sequence: Bayesian posterior probability/% bootstrap from the RaxML analysis/% bootstrap from the IQtree analysis. Locality codes: CO, Congo; GA, French Guiana; GU, Guadeloupe; MA, Madagascar; MO, Mozambique; MQ, Martinique; NC, New Caledonia; PH, Philippines; PNG, Papua New Guinea; SE, Senegal; TA, Tasmania; TW, Taiwan; WA, South-Western Australia. Lineages identified to genus level, on the basis that they are represented by or include the type species of that genus, are shown in bold font.

Figure 3. Close up of the marginelliform part of the tree depicted in Figure 1, with images of the shells of most of the sequenced specimens. Generic names in bold and non-bold font correspond, respectively, to genera supported by molecular evidence and those in need of revision. Locality codes as in Figure 2 Colour-coding indicates the major biogeographical regions: IWP, blue; Western Indian Ocean, green; West Africa, yellow; Caribbean, red. Depth is shown by Light (shallow) or dark (deep) shadeing. Boxed numbers indicate the radula type of individuals examined by us, with '!' denoting somewhat deviating radula morphology and '6*' indicating the modified type 6 of Covert & Covert (1995).

Figure 4. Radulae of studied marginelliform specimens. Numbers under the scale bars below the radula images indicate scale units. **A, B.** Type 1, *Plesiocystiscus* sp. (MNHN-IM-2013-43724, GUYANE St. CP4380, 6°31'N, 52°27'W, 102–104m depth), showing intact (**A**) and older, worn (**B**) areas of radula. **C, D.** Type 2, *Cystiscus* sp. (MNHN-IM-2013-43726, TASMANIA St. TA44, 41°18.2'S, 148°18.8'E, 3–6 m depth), showing frontal (**C**) and lateral (**D**) views. **E.** Type 3, *Gibberula oryza* (MNHN-IM-2013-43729, DAKAR St. 20, 14°40.2'N, 17°23.8'W, 12 m depth). **F, G.** Type 3, *Gibberula nebulosa* (MNHN-IM-2013-68353, KANACONO St. DW4661, 22°48'S, 167°07'E, 405–410 m depth), showing intact (–) and worn, older (**G**) areas of radula. **H, I.** Type 3, *Canalispira* sp. (Oman, Masirah, leg. F. Boyer, 2013), showing intact (**H**) and worn, older (**I**) areas of radula. **J, K.** Type 3, '*Persicula*' sp. (Oman, Masirah, leg. Franck Boyer, 2013), showing intact (**J**) and worn, older (**K**) areas of radula. **L.** Type 3, *Pachy bathron* cf. *cassidiforme* (MNHN-IM-2013-61020, KARUBENTHOS2 St. DW4593, 15°56'N, 61°26'W, 133–152m depth). **M.** Type 4,

845 *Granulina liliputana* (MNHN-IM-2013-43723 Dakar'09 St. 10, 14°39.8'N, 17°23.9'W, 31 m
 846 depth). **N.** Type 4, *Granulina* sp. (MNHN-IM-2013-43732, MADEEP St. DW4287, 9°12'S,
 847 153°56'E, 340–375m depth). **O.** 'Modified type 6', '*Dentimargo*' sp. (MNHN-IM-2013-45652,
 848 MADEEP St. DW4292, 9°14'S, 153°52'E, 530 m depth). **P.** Type 6, *Prunum prunum* (MNHN-IM-
 849 2013-57005, GUYANE St. SN08, 5°17'N, 52°35.1'W, 6m depth). **Q.** Type 7, *Marginellona gigas*
 850 (MNHN-IM-2013-50159, DongSha St. CP4127, 20°46'N, 116°08'E, 392–408 m depth). **R.** Type 5,
 851 *Mesoginella* sp. (MNHN-IM-2013-43731, EXBODI St. DW3785, 22°15'S; 167°10'E, 386–387 m). **S.**
 852 Type 9, *Hydroginella* cf. *tridentata* (MNHN-IM-2013-43735, WESTERN AUSTRALIA St. WE03,
 853 33°59.6'S; 122°13.3'E, 11 m depth).

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1 **Table 1.** List of specimens included in molecular phylogenetic analyses, with relevant museum registration numbers, collection data, Barcode of Life
2 Datasystems (BOLD) IDs and details of DNA sequence data available for the five gene regions COI, 16s rRNA, 12S rRNA, H3 and 28S rRNA.

Family	Species	Specimen ID	Expedition	Station	Locality	BOLD	COI	16S rRNA	12S rRNA	H3	28S rRNA
INGROUP											
Cystiscidae	<i>Canalispira</i> sp.	MNHN-IM-2013-1838	PAPUA NIUGINI	PS09	5°12'20"S, 145°48'47"E (8–10 m depth)	NEOGA1335-19	1	0	1	1	1
Cystiscidae	<i>Canalispira</i> sp. 2	FBoyer_C1	-	-	Oman, Masirah	-	1	1	1	1	1
Cystiscidae	<i>Canalispira</i> sp. 3	FBoyer_C2	-	-	Oman, Masirah	-	1	1	1	1	1
Cystiscidae	<i>Persicula</i> sp.	FBoyer_P1	-	-	Oman, Masirah	-	0	1	1	1	1
Cystiscidae	<i>Crithe</i> sp.	MNHN-IM-2019-1414 /Cc-PH-301	-	-	Philippines, Mactan Is., off Punta-Engana (lumun-lumun net)	NEOGA1336-19	1	0	1	1	1
Cystiscidae	<i>Cystiscus</i> sp.	MNHN-IM-2013-3692	PAPUA NIUGINI	PB21	5°1'26.9"S, 145°48'2"E (5 m depth)	NEOGA1337-19	1	0	1	1	1
Cystiscidae	<i>Cystiscus</i> cf. <i>spiri plana</i>	MNHN-IM-2013-40705	KARUBENTHOS 2	DW4722	22°54'S, 167°17'E (496–505m depth)	NEOGA1338-19	0	1	1	1	1
Cystiscidae	<i>Cystiscus</i> aff. <i>spiri plana</i>	MNHN-IM-2013-69503	KARUBENTHOS 2	DW4722	22°54'S, 167°17'E (496–505m depth)	NEOGA1339-19	1	0	1	1	1
Cystiscidae	<i>Cystiscus</i> sp.	MNHN-IM-2013-43728	MORRISON AUSTRALIA	TA44	41°18.2'S, 148°18.8'E (3–6 m depth)	NEOGA1340-19	0	1	1	1	1
Cystiscidae	<i>Pachy bathron</i> n. sp.	MNHN-IM-2013-60765	KARUBENTHOS 2	DW4574	16°21'48"N, 60°53'51"W (140–340m depth)	NEOGA1341-19	1	1	1	1	1
Cystiscidae	<i>Gibberula</i> sp.	MNHN-IM-2013-70240	MADIBENTHOS	CP4129	14°38'35"N, 61°8'30"W (8 m depth)	NEOGA1342-19	1	0	1	0	1
Cystiscidae	<i>Gibberula lucia</i>	MNHN-IM-2013-43730	Dakar'09	Stn. 6	14°39'48"N, 17°29'0"W (14–19 m depth)	NEOGA1343-19	1	0	1	1	1
Cystiscidae	<i>Gibberula oryza</i>	MNHN-IM-2013-43729	Dakar'09	Stn. 4	14°40'12"N, 17°23'48"W (12 m depth)	NEOGA1344-19	1	1	1	1	1
Cystiscidae	<i>Gibberula</i> sp. 1	MNHN-IM-2013-68879	KANACONO	DW4686	22°29'S, 167°31'E (249–255m depth)	NEOGA1345-19	1	1	0	1	1
Cystiscidae	<i>Persicula columbiana</i>	MNHN-IM-2013-74065	MADIBENTHOS	AB152	14°30'28"N, 61°6'5"W (20–23 m depth)	NEOGA1346-19	1	1	0	1	1
Cystiscidae	<i>Pachy bathron</i> aff. <i>cassidiforme</i>	MNHN-IM-2013-60401	KARUBENTHOS 2	DW4545	16°29'42"N, 61°31'25"W (60–82 m depth)	NEOGA1347-19	1	1	1	1	1
Cystiscidae	<i>Gibberula nebulosa</i>	MNHN-IM-2013-68353	KANACONO	DW4661	22°48'S, 167°07'E (405–410 m depth)	NEOGA1348-19	1	1	0	1	1
Cystiscidae	<i>Gibberula</i> aff. <i>moscatellii</i>	MNHN-IM-2013-57223	ILES DU SALUT	SCO1	5°17'27"N, 52°35'15"W (6–9 m depth)	NEOGA1349-19	1	1	1	1	1
Cystiscidae	<i>Persicula pulcherrima</i>	MNHN-IM-2013-74064	MADIBENTHOS	AB152	14°30'28"N, 61°6'5"W (20–23 m depth)	NEOGA1350-19	1	0	0	1	1
Cystiscidae	<i>Gibberula</i> n. sp. (group <i>asellina</i>)	MNHN-IM-2013-50497	KAVIENG 2014	KS21	2°34'34"S, 150°46'21"E (4 m depth)	NEOGA1351-19	1	1	0	1	1
Cystiscidae	<i>Gibberula</i> sp. 3	MNHN-IM-2013-6195	PAPUA NIUGINI	PB47	5°11'16"S, 145°49'33"E (5 m depth)	NEOGA1352-19	1	1	0	1	1
Cystiscidae	<i>Gibberula</i> sp. 4	MNHN-IM-2013-2296	PAPUA NIUGINI	PS11	5°4'45"S, 145°48'51"E (5 m depth)	NEOGA1353-19	1	1	1	1	1

Cystiscidae	<i>Gibberula</i> sp. 2	MNHN-IM-2013-4208	PAPUA NIUGINI	PB26	4°59'6"S, 145°47'42"E (22 m depth)	NEOGA1354-19	1	1	1	0	1
Cystiscidae	<i>Plesiocystiscus</i> sp. 1	MNHN-IM-2013-40708	MADIBENTHOS	AB167	14°26.6'N, 60°53.9'W (11 m depth)	NEOGA1355-19	1	1	1	1	1
Cystiscidae	<i>Plesiocystiscus</i> sp. 2	MNHN-IM-2013-43725	GUYANE 2014	CP4353	5°12'24"N, 51°40'12"W (60 m depth)	NEOGA1356-19	1	1	1	1	0
Marginellidae	<i>Dentimargo</i> n. sp.	MNHN-IM-2013-45652	MADEEP	DW4292	9°13'49"S, 153°51'44"E (530 m depth)	NEOGA1357-19	1	1	1	1	1
Marginellidae	<i>Dentimargo</i> sp. 3	MNHN-IM-2013-45628	MADEEP	DW4290	9°13'6"S, 153°53'45"E (593 m depth)	NEOGA1358-19	0	1	1	1	1
Marginellidae	<i>Serrata tuii</i>	MNHN-IM-2013-69537	KANACONO	DW4721	22°54'S, 167°15'E (473–490 m depth)	NEOGA1359-19	1	1	1	1	1
Marginellidae	<i>Eratoidea</i> cf. <i>hematita</i>	MNHN-IM-2013-60596	KARUBENTHOS 2	DW4559	16°24'31"N, 60°51'51"W (72–111 m depth)	NEOGA1360-19	1	1	1	1	1
Marginellidae	<i>Dentimargo</i> sp.	MNHN-IM-2013-60848	KARUBENTHOS 2	DW4580	16°18'54"N, 60°49'32"W (412–500m depth)	NEOGA1361-19	1	1	1	1	1
Marginellidae	<i>Dentimargo biocal</i>	MNHN-IM-2013-69570	KANACONO	DW4720	22°50'S, 167°11'E (374–400 m depth)	NEOGA1362-19	1	1	1	1	1
Marginellidae	<i>Dentimargo cingulatus</i>	MNHN-IM-2013-69532	KANACONO	DW4731	22°31'S, 167°35'E (457–460m depth)	NEOGA1363-19	1	1	1	0	1
Marginellidae	<i>Dentimargo caledonicus</i>	MNHN-IM-2013-69064	KANACONO	DW4696	22°49'S, 167°15'E (445 m depth)	NEOGA1364-19	1	1	1	1	1
Marginellidae	<i>Dentimargo</i> n. sp.	MNHN-IM-2013-69502	KANACONO	DW4722	22°54'S, 167°17'E (496–505m depth)	NEOGA1365-19	1	1	0	1	1
Marginellidae	<i>Dentimargo</i> sp. 1	MNHN-IM-2013-68580	KANACONO	DW4666	22°53'S, 167°17'E (530–545 m depth)	NEOGA1366-19	1	1	1	1	1
Marginellidae	<i>Marginella cloveri</i>	MNHN-IM-2013-56775	GUYANE 2014	CP4402	6°17'58"N, 52°13'19"W (95–97 m depth)	NEOGA1367-19	1	1	1	1	1
Marginellidae	<i>Dentimargo</i> sp.	MNHN-IM-2013-47685	KAVIENG 2014	KS11	2°33'10"S, 150°48'9"E (7 m depth)	NEOGA1368-19	1	1	1	1	1
Marginellidae	<i>Hydroginella</i> n. sp. (group <i>scintilla</i>)	MNHN-IM-2013-51961	KAVIENG 2014	KS35	2°38'47"S, 150°40'44"E (4–5 m depth)	NEOGA1369-19	1	0	1	1	1
Marginellidae	<i>Hydroginella</i> cf. <i>tridentata</i>	MNHN-IM-2013-43736	WESTERN AUSTRALIA 2011	WE03	33°59'36"S, 122°13'13"E (11 m depth)	NEOGA1370-19	1	1	1	1	1
Marginellidae	<i>Hydroginella</i> sp.	MNHN-IM-2013-5506	PAPUA NIUGINI	PB37	5°15'55"S, 145°47'9"E (10 m depth)	NEOGA1371-19	1	1	1	1	1
Marginellidae	<i>Hydroginella</i> sp.	MNHN-IM-2013-50680	KAVIENG 2014	KB16	2°34'34"S, 150°46'21"E (13–14 m depth)	NEOGA1372-19	0	1	1	1	1
Marginellidae	<i>Mesoginella</i> n. sp.	MNHN-IM-2013-43731	EXBODI	DW3785	22°15'24"S, 167°10'24"E (386–387 m depth)	NEOGA1373-19	1	1	1	1	1
Marginellidae	<i>Mesoginella</i> sp.	MNHN-IM-2013-68895	KANACONO	DW4677	22°53'S, 167°35'E (376–390 m depth)	NEOGA1374-19	1	0	1	1	1
Marginellidae	<i>Protojinella laseroni</i>	MNHN-IM-2013-69467	KANACONO	DW4711	22°47'S, 167°24'E (325–338 m depth)	NEOGA1375-19	1	1	1	1	1
Marginellidae	<i>Protojinella maestratii</i>	MNHN-IM-2013-69554	KANACONO	DW4719	22°47'S, 167°05'E (335–350 m depth)	NEOGA1376-19	1	1	1	1	1
Marginellidae	<i>Dentimargo</i> sp.	MNHN-IM-2013-68687	KANACONO	DW4666	22°53'S 167°17'E (530–545 m) depth	NEOGA1377-19	1	0	1	1	1
Marginellidae	<i>Mesoginella</i> n. sp.	MNHN-IM-2013-68948	KANACONO	DW4690	22°59'S, 167°29'E (800 m depth)	NEOGA1378-19	1	1	0	1	1
Marginellidae	<i>Dentimargo</i> sp.	MNHN-IM-2013-47082	KAVIENG 2014	KS19	2°34'1"S, 150°47'5"E (10 m depth)	NEOGA1379-19	1	1	1	1	1

Marginellidae	<i>Marginella festiva</i>	MNHN-IM-2013-43709	Dakar'09	Stn. 9	14°39'54"N, 17°24'0"W (7 m depth)	NEOGA1380-19	1	1	1	1	1
Marginellidae	<i>Glabella denticulata</i>	MNHN-IM-2013-43710	Dakar'09	Stn. 17	14°12'4"N, 17°17'48"W (43 m depth)	NEOGA1381-19	1	1	1	1	1
Marginellidae	<i>Marginella lucani</i>	MNHN-IM-2013-43711	Port ZANAGA	553DW	4°43'19"S, 11°48'6"E (13–14 m depth)	NEOGA1382-19	1	1	1	1	1
Marginellidae	<i>Marginella sergioi</i>	MNHN-IM-2013-43713	MAINBAZA	CP3133	25°10'50"S, 35°10'11" (200–201 m depth)	NEOGA1383-19	1	1	1	1	1
Marginellidae	<i>Glabella rosadoi</i>	MNHN-IM-2013-43717	INHACA 2011	MR25	25°54'6"S, 33°3'6"E (11–13 m depth)	NEOGA1384-19	1	1	1	1	1
Marginellidae	<i>Volvarina cf. micans</i>	MNHN-IM-2013-43743	INHACA 2011	MS06	26°5'24"S, 33°0'30"E (17–28 m depth)	NEOGA1385-19	1	1	1	1	1
Marginellidae	<i>Volvarina janneefsi</i>	MNHN-IM-2019-1415 /Mr-PH-296	-	-	Philippines, Mactan Is., off Punta-Engana (lunun-lunun)	NEOGA1386-19	1	1	1	0	1
Marginellidae	<i>Hyalina buskei</i>	MNHN-IM-2013-72397	MADIBENTHOS	AR76	14°27'54"N, 61°1'10"W (16–26 m depth)	NEOGA1387-19	1	1	1	1	1
Marginellidae	<i>Volvarina cf. hennequini</i>	MNHN-IM-2013-56837	GUYANE 2014	CP4407	6°53'6"N, 52°33'28"W (495–502 m depth)	NEOGA1388-19	1	1	0	1	1
Marginellidae	<i>Volvarina constricta</i>	MNHN-IM-2013-43741	Dakar'09	Stn. 5	14°34'12"N, 17°25'6"W (31 m depth)	NEOGA1389-19	1	1	1	1	1
Marginellidae	<i>Volvarina aff. avena</i>	MNHN-IM-2013-60828	KARUBENTHOS 2	DW4579	16°21'20"N, 60°53'39"W (228–264 m depth)	NEOGA1390-19	1	1	1	1	1
Marginellidae	<i>Volvarina aff. lactea</i>	MNHN-IM-2013-60956	KARUBENTHOS 2	DW4590	15°57'28"N, 61°27'28"W (83–135 m depth)	NEOGA1391-19	1	1	1	1	0
Marginellidae	<i>Prunum prunum</i>	MNHN-IM-2013-56949	ILES DU SALUT	SR1	5°17'9"N, 52°35'14"W (0–6 m depth)	NEOGA1392-19	1	1	1	1	1
Marginellidae	<i>Prunum marginatum</i>	MNHN-IM-2013-56142	GUYANE 2014	CP4344	5°8'40"N, 51°58'40"W (47 m depth)	NEOGA1393-19	1	1	0	1	1
Marginellidae	<i>Volvarina armonica</i>	MNHN-IM-2013-68535	KANACONO	DW4661	22°48'S, 167°07'E (405–410 m depth)	NEOGA1394-19	1	1	0	1	1
Marginellidae	<i>Closia</i> sp.	MNHN-IM-2009-14753	ATIMO VATAE	DW3607	24°39'26"S, 47°31'43"E (86–87 m depth)	NEOGA1395-19	1	1	1	1	1
Marginellidae	<i>Closia giadae</i>	MNHN-IM-2009-14754	ATIMO VATAE	DW3607	25°45'44"S, 44°51'59"E (40–41 m depth)	NEOGA1396-19	1	1	0	1	1
Marginellidae	<i>Granulina liliputana</i>	MNHN-IM-2013-43723	Dakar'09	Stn. 10	14°39'48"N, 17°23'54"W (31 m depth)	NEOGA1397-19	1	1	1	1	0
Marginellidae	<i>Granulina marginata</i>	PAIbano_G2	-	-	Greece, Crete	-	1	0	1	0	1
Marginellidae	<i>Marginellona gigas</i>	MNHN-IM-2013-50159	DongSha 2014	CP4127	20°46'14"N, 116°7'59"E (392–408 m depth)	NEOGA1398-19	1	1	1	1	1
OUTGROUP											
Volutidae	<i>Lyria</i>	MNHN-IM-2009-7377	MAINBAZA	CP3144	23°33'S, 35°41'E (171–180 m depth)	NEOGA1399-19	1	0	1	1	1
Volutidae	<i>Fulgoraria</i>	MNHN-IM-2013-44037	NanHai 2014	CP4099	22°13'N, 120°24'E (310–346 m depth)	NEOGA1400-19	1	1	1	1	1
Volutidae	<i>Calliotectum</i>	MNHN-IM-2013-50202	DongSha 2014	CP4129	20°29'N, 116°08'E (590–633 m depth)	NEOGA1401-19	1	1	1	1	1
Volutidae	<i>Volutocorbis</i> sp.	MNHN-IM-2009-9486	MAINBAZA	CP3146	21°38'S, 36°07'E (1161–1185 m depth)	NEOGA1402-19	1	1	0	1	1
Cancellariidae	<i>Scalptia textilis</i>	MNHN-IM-2009-10506			Philippines, off Olango Is. (10 m depth)	CANC093-10	FR717505	FR718353	FR718426	0	1

Cancellariidae	<i>Cancellaria cancellata</i>	BAU00224	-	-	off Malaga (Spain) (40-50 m depth)	-	FM999157	FM999105	FM999074	0	FM999136
Cancellariidae	<i>Plesiotriton silinoensis</i>	MNHN-IM-2007-32123	PANGLAO 2005 Deep	CP2359	08°50'N, 123°35'E (437–476 m depth)	CANC028-10	FM999158	FM999106	FM999075	0	FM999137
CharitodoronidaeE	<i>Charitodoron bathybius</i>	MNHN-IM-2007-38306	MAINBAZA	CC3157	21°46'S, 36°25'E (1410–1416 m depth)	MITRI057-15	KR087240	KR087994	KR087335	KR088081	1
Mitridae	<i>Mitra glabra</i>	MNHN-IM-2013-40640	WESTERN AUSTRALIA 2011	WE01	15°16.94'S, 124°06.3'E (11 m depth)	MITRI042-15	KR087272	KR088022	KR087365	KR088105	1
Mitridae	<i>Neocancilla papilio</i>	MNHN-IM-2013-12560	PAPUA NIUGINI	PR24	05°12.3'S, 145°48.8'E	MITRI034-15	KR087287	KR088037	KR087376	KR088116	1
Pyrammitridae	<i>Teremitra efatensis</i>	MNHN-IM-2013-52074	PAPUA NIUGINI	CP4058	02°55'S, 142°11'E (535–540 m) depth	MITRI078-15	KR087298	KR088047	KR087383	KR088125	0
Harpidae	<i>Harpa harpa</i>	MNHN-IM-2013-51800	KAVIENG 2014	KR62	02°41.6'S, 150°38.9'E (10–11 m depth)	NEOGA1403-19	1	1	1	1	1
Muricidae	<i>Murex trapa</i>	LSGB23004	-	-	21°26'S, 109°02'E	-	GU188199	GU188090	GU188086	HQ834146	HM583721
Muricidae	<i>Vasula speciosa</i>	CNMO3105	-	-	Claremont <i>et al.</i> (2012)	-	HE584393	HE584316	HE584149	KT754141	HE584223
Muricidae	<i>Rapana venosa</i>	NHMUK20100317	-	-	Claremont <i>et al.</i> (2012)	-	HE584367	HE584279	HE584116	HQ834144	HE584197
Muricidae	<i>Leptotrophon surprisensis</i>	MNHN-IM-2009-8589	EBISCO	DW2610	19°34'S, 158°41'E (486–494 m depth)	MPOM179-10	GU575381	FN651925	FN651880	0	FN651991
Muricidae	<i>Pteryarmachia martinetana</i>	MNHN-IM-2009-5011	SANTO 2006	FR45	15°27"S, 167°13.5'E (0–7 m depth)	MPOM135-10	GU575384	FN651905	FN651863	0	FN651971
Muricidae	<i>Vitularia miliaris</i>	MNHN-IM-2009-5030	SANTO 2006	DR84	15°43.4'S, 167°15'E (6 m depth)	MPOM150-10	GU575391	FN651922	FN651877	0	FN651988
Belloliviidae	<i>Olivellopsis simplex</i>	MNHN-IM-2013-47678	KAVIENG 2014	KS11	02°33.2'S, 150°48.2'E (7 m depth)	OLIV070-16	KX233351	KX233413	KX233450	KX233476	1
Benthobiidae	<i>Benthobia</i> sp. 2	MNHN-IM-2013-18534	PAPUA NIUGINI	CP4038	04°27'S, 145°34'E (800–840 m depth)	OLIV068-16	KX233315	KX233405	KX233442	KX233473	1
Ancillariidae	<i>Amalda optima</i>	MNHN-IM-2009-22263	INHACA 2011	MR4	26°06.3'S, 32°58.0'E (17–19 m depth)	MITRI063-15	KR087230	KR087986	KR087327	KR088073	1
Olividae	<i>Olivella</i> sp.	MNHN-IM-2009-24367	KARUBENTHOS 2012	GD41	16°20,91'N, 61°32.23'W (2 m depth)	MITRI062-15	KR087290	KR088040	KR087378	KR088119	1
Olividae	<i>Oliva amethystina</i>	MNHN-IM-2007-31988	SANTO 2006	DR09	15°34.6'S, 167°13.8'E (12 m depth)	NEOGA476-10	KR087289	KR088039	KR087377	KR088118	1
Pseudolividae	<i>Fulmentum sepimentum</i>	MNHN-IM-2013-52003	Port ZANAGA	D502	04°42,25'S, 11°47'E (16 m depth)	MITRI066-15	KR087261	KR088012	KR087354	KR088098	1
Columbariidae	<i>Coluzea juliae</i>	MNHN-IM-2007-38972	MAINBAZA	CP3139	23°35'S, 36°06'E (1092–1195 m depth)	MITRI082-15	KR087242	KR087995	KR087336	KR088083	1
Costellariidae	<i>Ceratoxancus</i> sp.	MNHN-IM-2007-38552	TARASOC	DW3401	15°51'S, 148°18'W (789–831 m depth)	MITRI081-15	KR087238	KR087993	KR087334	KR088079	1
Costellariidae	<i>Vexillum exasperatum</i>	MNHN-IM-2013-11680	PAPUA NIUGINI	PR14	05°12'S, 145°48,1'E (2–3 m depth)	MITRI015-15	KR087305	KR088055	KR087393	KR088133	1
Ptychatractidae	<i>Exilia krigei</i>	MNHN-IM-2007-38331	MAINBAZA	CC3171	25°59'S, 34°42'E (771–776 m depth)	MITRI072-15	KR087257	KR088009	KR087352	KR088096	1
Vasidae	<i>Vasum globulus</i>	MNHN-IM-2013-8329	KARUBENTHOS 2012	GM02	16°20,45'N, 61°31,55'W (1 m depth)	MITRI149-16	KU986430	KU873939	KU876544	KU876559	1
Vasidae	<i>Vasum muricatum</i>	MNHN-IM-2013-20017	KARUBENTHOS 2012	GM02	16°20,45'N, 61°31,55'W (1 m depth)	MITRI148-16	KU986431	KU873940	KU876545	KU876560	0
Vasidae	<i>Vasum turbinellus</i>	LSGB23801	-	-	18°28'S, 110°04'E	-	HQ834084	JN052960	HQ833909	HQ834180	0
Volutomitridae	<i>Exilioidea</i> sp.	MNHN-IM-2013-40625	PAPUA NIUGINI	CP3963	05°06'S, 145°53'E (960–980 m depth)	MITRI067-15	KR087260	KR088011	KR087353	0	1
Volutomitridae	<i>Volutomitra glabella</i>	MNHN-IM-2007-35070	CONCALIS	DW3003	18°34'S, 163°08'E (450–454 m depth)	NEOGA824-10	KR087319	KR088064	KR087406	KR088145	1

Babyloniidae	<i>Babylonia areolata</i>	LSGB23411	-		Zou <i>et al.</i> (2011)	-	JN053013	JN052948	HQ833886	HQ834157	0
Belomitridae	<i>Belomitra paschalis</i>	MNHN-IM-2009-18853	-	CP3138	25°13'S, 35°21'E (700–707 m depth)	NEOGA1145-11	JQ950229	JQ950147	0	1	JQ950188
Buccinidae	<i>Metula</i> sp.	MNHN-IM-2007-30079	-	CP2348	09°30'N, 123°53'E (196–216 m depth)	NEOGA239-10	KC756067	1	KC756031	1	KC756010
Buccinidae	<i>Volutharpa perryi</i>	LSGB23204	-	-	Zou <i>et al.</i> (2011)	-	JN053002	JN052939	HQ833869	HQ834141	FJ710108
Buccinidae	<i>Turritatus turritus</i>	MNHN-IM-2013-17100	-	PR162	05°10.1'S, 145°50.2'E (1–4 m depth)	FASCI028-17	KT753981	KT753869	1	KT754111	KT753748
Melongenidae	<i>Melongena melongena</i>	MNHN-IM-2013-71405	-	AM032	14°42.9'N, 60°56.1'W (0 m)	NEOGA1404-19	1	1	1	1	1
Nassariidae	<i>Buccinanops cochlidium</i>	MZUSP108269	-	-	Galindo <i>et al.</i> (2016): 14°42.9'N, 60°56.1'W (0 m)	-	KY451221	KY488731	KY488928	KY489295	KY489126
Borsoniidae	<i>Bathytoma neocaledonica</i>	MNHN-IM-2007-17857	EBISCO	CP2551	21°06'S, 158°35'E (637–650 m depth)	CONO187-08	EU015653	HQ401661	HQ401591	EU015761	EU015537
Clathurellidae	<i>Etrema polydesma</i>	MNHN-IM-2007-17869	PANGLAO 2004	S21	09°41.7'N, 123°50.9'E (4–12 m depth)	CONO249-08	EU015691	HQ401675	HQ401608	EU015800	EU015576
Cochlespiridae	<i>Sibogasyrinx</i> sp.	MNHN-IM-2007-17703	BOA1	CP2432	15°00'S, 166°55'E (630–705 m depth)	CONO155-08	1	1	1	EU015756	EU015531
Conidae	<i>Conasprella pagoda</i>	MNHN-IM-2007-17914	PANGLAO 2005	CP2380	08°41'N, 123°18'E (150–163 m depth)	CONO313-08	EU015729	FJ868151	FJ868136	EU015836	EU015614
Conidae	<i>Conus consors</i>	MNHN-IM-2007-17939	SANTO 2006	AT87	15°31'S, 167°17'E (235–271 m depth)	CONO513-08	EU015751	HQ401672	HQ401605	EU015858	EU015636
Drilliidae	<i>Clavus canalicularis</i>	MNHN-IM-2007-17858	PANGLAO 2004	S12	09°29.4'N, 123°56'E (6–8 m depth)	CONO229-08	EU015680	HQ401668	HQ401601	EU015789	EU015565
Mangeliidae	<i>Citharomangelia planilabroides</i>	MNHN-IM-2007-17896	PANGLAO 2004	D5	09°33.6'N, 123°43.5'E (0–3 m depth)	CONO219-08	EU015670	1	1	EU015779	EU015555
Mitromorphidae	<i>Mitromorpha metula</i>	MNHN-IM-2007-17898	PANGLAO 2004	B8	09°37.1'N, 123°46.1'E (3 m depth)	CONO221-08	EU015672	HQ401697	HQ401633	EU015781	EU015557
Pseudomelatomidae	<i>Funa hadra</i>	MNHN-IM-2007-17843	EBISCO	DW2522	22°46'S, 159°21'E (310–318 m depth)	CONO182-08	EU015648	1	1	EU015757	EU015532
Raphitomidae	<i>Thatcheria mirabilis</i>	MNHN-IM-2007-17924	SALOMON 2	CP2184	08°17'S, 160°00'E (464–523 m depth)	CONO349-08	EU015736	FJ868138	FJ868124	EU015843	EU015621
Terebridae	<i>Terebra fujitai</i>	MNHN-IM-2007-15724	PANGLAO 2005	CP2343	09°27'N, 123°49'E (273–356 m depth)	CONO306-08	EU015725	EU685668	EU685377	EU015832	EU015610
Turridae	<i>Turris babylonia</i>	MNHN-IM-2007-17754	PANGLAO 2004	R42	09°37.1'N, 123°52.6'E (8–22 m depth)	CONO226-08	EU015677	HQ401715	HQ401652	EU015786	EU015562
Bursidae	<i>Bursa lamarckii</i>	MNHN-IM-2007-43066	-	R24	09°37.5'N, 123°46.8'E (0–2 m depth)	TONO113-12	JX241371	JX241125	1	1	JX241164
Cassidae	<i>Galeodea bituminata</i>	MNHN-IM-2007-33627	-	AT102	15°03'S, 166°53'E (517–547 m depth)	TONO236-18	MH581335	MH571354	MH571268	1	MH571198
Ficidae	<i>Ficus filosa</i>	MNHN-IM-2007-33633	-	T31	09°33'N, 123°42'E (100–140 m depth)	LITOR137-10	MH581334	MH571353	MH571267	1	MH571197
Personidae	<i>Distorsio reticularis</i>	MNHN-IM-2007-34733	-	CP2665	15°54'N, 121°42'E (123–125 m depth)	TONO194-18	MH581323	MH571342	MH571259	1	MH571190
Tonnidae	<i>Tonna perdix</i>	MNHN-IM-2007-33629	-	R34	09°35.9'N, 123°44.7'E (1–12 m depth)	TONO200-18	MH581379	MH571401	MH571309	1	MH571231
Xenophoridae	<i>Xenophora</i> sp.	MNHN-IM-2019-1413	NT		Vietnam, Nha Trang Bay, S. Mot Is. (15–18 m depth)	NEOGA1405-19	1	1	1	0	1
		/Xe-NT-76