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1 **Mapping the missing branch on the Neogastropoda tree of life: molecular phylogeny of**
2 **marginelliform gastropods**

3

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ABSTRACT

23 Marginelliform gastropods are a heterogeneous and diverse group of molluscs encompassing
24 over 1,600 living species, among which are the smallest known neogastropods. The
25 relationships of marginelliform gastropods within the order Neogastropoda are controversial
26 and the monophyly of the two marginelliform families, Marginellidae J. Fleming, 1828 and

27 Cystiscidae Stimpson, 1865 remains unconfirmed. DNA sequence data have never been used to
28 assess the relationships of the marginelliform gastropods, making this group the only major
29 branch missing in our current understanding of the neogastropod tree of life. Here we report
30 results of the first multilocus phylogenetic analysis of marginelliform gastropods, which is based
31 on a dataset comprising 63 species (20 genera) of Marginellidae and Cystiscidae, and a wide
32 range of neogastropod lineages. The Marginellidae and Cystiscidae form a moderately-
33 supported clade, sister to the family Volutidae. *Marginellona gigas* appears to be sister to all
34 other marginelliforms. The subfamily Marginellinae was recovered as a well-supported clade,
35 and good resolution of this part of the tree makes it possible to propose amendments to the
36 family-level classification of the group. The relationship between *Granulina* and other
37 marginelliforms could not be resolved and requires further study. Due to poor resolution of
38 basal relationships within the Marginellidae–Cystiscidae clade, the monophyly of the
39 Cystiscidae was neither confirmed nor convincingly rejected. The shell morphology of most
40 marginellid and cystiscid genera is taxonomically not very informative but, nevertheless, of the
41 traditionally recognized genera only *Gibberula* and *Dentimargo* were shown to be polyphyletic.
42 Although a comprehensive systematic revision of the group requires more extensive taxonomic
43 sampling (e.g. with better representation of the type species of nominal genus-group names),
44 our results support the superfamily Volutoidea, comprising four families (Volutidae, Cystiscidae,
45 Marginellidae and Marginellonidae), with the placement of the Granulinidae uncertain for the
46 time being.

47 INTRODUCTION

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

62 Detailed anatomical studies of the marginelliforms (Ponder, 1970; Fretter, 1976; Covert
63 & Covert, 1995) have revealed an extraordinary diversity of alimentary canal arrangements
64 and this has been reflected in the revised classification proposed by Covert & Covert (1995).
65 This classification, which was based on a broad taxonomic sampling and a substantial number
66 of characters, presented a generally plausible scheme for relationships within major
67 marginelliform lineages. Relationships among these lineages, however, remain uncertain and
68 differing interpretations of character evolution have led to conflicting phylogenetic hypotheses
69 (Harasewych & Kantor, 1991; Covert & Covert, 1995; de Souza, 2007; de Souza & Simone,
70 2019). The relationships between the Marginellidae, Cystiscidae and other neogastropod taxa
71 also remain poorly understood. Some marginelliforms have a uniseriate radula and a set of
72 anatomical features that are shared with the Volutidae. This suggests common ancestry with
73 the Volutidae and thus that the marginelliforms belong to a lineage that originates from a split
74 deep in the neogastropod tree (Ponder, 1973; Harasewych & Kantor, 1991). However, evidence
75 for this hypothesis is poor; it is supported by only few characters, which are either
76 plesiomorphic or likely to be the result of convergent evolution (Ponder, 1973; Kantor, 2002).

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

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

99 The genus-level taxonomy of the Marginellidae and Cystiscidae is also problematic. Early
100 attempts to establish genus-level classifications of marginelliform gastropods (reviewed by
101 Coan, 1965) suffered notably from inconsistent use of names; phases when genus-level taxa
102 were proliferating have alternated with periods of extensive lumping. There have been three
103 major recent bursts in the description of supraspecific taxa. The first was associated with the
104 work of Laseron (1957), who reassigned Australian species of marginellids to some 30 genera.
105 The work of G.A. Covert and H.K. Covert followed on from this and culminated in a
106 comprehensive revision of marginelliform gastropods (Covert & Covert, 1995). The more
107 recent studies by J. Espinosa, J. Ortea and co-workers have been largely focused on Caribbean
108 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

117

118 *Taxon sampling*

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

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

142 Specimens were initially sorted into morphospecies based on shell morphology. Then the
143 barcode fragment of the cytochrome *c* oxidase subunit I (COI) gene was sequenced for up to
144 four specimens of each morphospecies (results not shown). Phylogenetic relationships between
145 marginelliform taxa were investigated by reconstructing a phylogeny based on five genes: three
146 mitochondrial genes (COI, 16S rRNA and 12S rRNA) and two nuclear genes (histone 3 (H3) and
147 28S rRNA). Marginelliform species for this phylogeny were selected by assessing the status of

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

155 Applying species names to the morphospecies identified by us was often problematic
156 because of the generally uninformative shell morphology of marginelliforms and the scarcity of
157 data on the colouration of living animals. Uncertain species-level identifications were indicated
158 by the use of 'cf.' (e.g. *Eratoidea cf. hematita*) and 'aff.' (e.g. *Gibberula aff. moscatellii*). In total,
159 27 of the 63 marginelliform species included in our phylogenetic analysis were identified only to
160 genus level.

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

173 The monophyly of marginelliform gastropods has never been investigated using DNA
174 sequence data and in an effort to do so we included 58 non-marginelliform species, belonging
175 to 40 caenogastropod families. These non-marginelliforms represented a wide range of
176 neogastropod lineages; sequence data were either from published studies (Zou *et al.*, 2011;
177 Claremont *et al.*, 2012; Fedosov *et al.*, 2015, 2017, 2018; Galindo *et al.*, 2016; Kantor *et al.*,
178 2017) and retrieved from GenBank, or were generated specifically for this study.

179

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

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

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

216 *Morphological studies*

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

RESULTS

233

234 *Multilocus molecular phylogeny: deep relationships*

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

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

252 The first split within the marginelliforms separates *Marginellona gigas* from a consistently
253 well-supported clade containing all the remaining species (PP = 1, BS1 = 73%, BS2 = 100%; Fig.
254 2). The latter cluster consists of four major clades: (1) the 'Main Cystiscidae' clade (strongly
255 supported in the IQtree: BS2 = 100%), (2) *Canalispira* (strongly supported in all three analyses:
256 PP = 1, BS1 = 100%, BS2 = 100%), (3) *Plesiocystiscus* (strongly supported in the IQ tree: BS2 =
257 91%) and (4) the 'Main Marginellidae' clade (always strongly supported: PP = 1, BS1 = 100%,
258 BS2 = 100%).

259

260 *The 'Main Cystiscidae' clade*

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

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

280

281 '*Main Marginellidae*' clade

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

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

294 of eight deep-water species of *Dentimargo*, *Marginella* and *Eratoidea* from New Caledonia and
295 the Caribbean. The MM3 subclade is maximally supported and consists of five described species
296 of *Marginella* and *Glabella* Swainson, 1840, all exclusively from shallow water localities off the
297 coast of South and West Africa. The MM2 and MM3 subclades were shown to be sister groups
298 in two of the three main analyses (BA, IQ). The strongly supported MM4 subclade (PP = 1, BS1 =
299 81%, BS2 = 100%) consists of a pair of *Closia* species (from off Madagascar) and a large
300 *Volvarina–Prunum–Hyalina* cluster uniting species from both shallow and deep-water localities
301 in the Caribbean, South and West Africa and the IWP. Although deeper relationships within this
302 group are generally well supported, no clear pattern can be observed with regard to geographic
303 or bathymetric distribution.

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

307

308 *Morphology of the radula*

309 Radula morphology was studied in 26 sequenced species of marginelliform gastropods
310 (including two species of *Granulina*); five other species were dissected, but no radula was found
311 (Fig. 3). We also studied published SEM images of the radulae of *Volvarina avena* and *V. lactea*
312 (Bandel, 1984; these are similar in shell morphology to the sequenced specimens MNHN-IM-
313 2013-60828 and MNHN-IM-2013-60956, respectively). The radulae examined correspond to the
314 following radula types delineated by Covert & Covert (1995): types 1–7, type 9 and the
315 ‘modified type 6’ radula (Fig. 4). Only in type 1 radulae were transverse rows observed to have
316 three teeth (Fig. 4A, B); the radulae of the remaining seven types are uniseriate and composed
317 of rachidian teeth only. The distribution of radula types (Fig. 3) across our trees shows clear
318 phylogenetic structuring. Cystiscid lineages are characterized by three types of radulae: type 1
319 (*Plesiocystiscus* Covert & Covert, 1995; Fig. 4A, B), type 2 (*Cystiscus*; Fig. 4C, D) and a variable
320 type 3 (all other lineages, including *Canalispira* Fig. 4E–L). All cystiscids have well-developed
321 odontophoral hoods—wide, symmetrical chitinous lobes that are attached to the anterior part
322 of the radula where it bends over the odontophore. According to Covert & Covert (1995),
323 these odontophoral hoods are supported by separate odontophore cartilages. The radula teeth
324 of *Plesiocystiscus* sp. (Fig. 4B), ‘*Gibberula*’ *nebulosa* from New Caledonia (MNHN-IM-2013-

325 68353, Fig. 4G), *Canalispira* sp. (Fig. 4I) and ‘*Persicula*’ sp. from Oman (Fig. 4K) showed
326 pronounced wear.

327 Among marginellids included in our phylogeny, a ‘modified type 6’ radula is found in
328 *Serrata tuii* (Cossignani, 2001) (MNHN-IM-2013-69537), an undescribed ‘*Dentimargo*’ species
329 (MNHN-IM-2013-45628; Fig. 4O) and in the two species of *Closia*. This radula type is
330 characterized by wide, multicuspidate rachidians with a somewhat wavy anterior edge and
331 subequal cusps. In contrast, ‘true type 6’ radulae have teeth that are distinctly rectangular, with
332 a straight anterior edge and cusps of often unequal length; the surface of the tooth is marked
333 by prominent pits, the function of which is to receive the cusps of the succeeding tooth (Fig.
334 4P). This type of radula, which is characteristic of the type species of *Volvarina*, *V. mitrella*
335 (Ortea *et al.*, 2014), was found in most members of the *Volvarina–Prunum–Hyalina* cluster of
336 the MM4 subclade; the exceptions were *Hyalina buskei* Espinosa & Ortea, 2013 (not shown on
337 Fig. 4), *Volvarina avena* and *V. lactea* (Bandel, 1984). The very wide radula of *Marginellona*
338 *gigas* (Fig. 4Q), in which each rachidian bears over 100 cusps, essentially does not differ from
339 type 6 radulae, although we note that it was classified by Coover & Coover (1995) in a
340 separate category, type 7. Type 4 (Figs 4M, N), type 5 (Fig. 4R) and type 9 radulae (Fig. 4S)
341 appear to be more phylogenetically restricted, occurring, respectively, in the two *Granulina*
342 species, the *Protoginella–Mesoginella* cluster in the MM1 subclade and the *Hydroginella* cluster
343 in the MM1 subclade. None of the marginellids examined had radula with odontophoral hoods
344 or with signs of wear. None of the dissected members of the MM2 and MM3 subclades
345 possessed a radula.

346 **DISCUSSION**

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

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

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

371 Our analyses recovered the West and South African species of *Marginella* and *Glabella* in
372 the MM3 subclade, and the Caribbean *Marginella cloveri* – in the MM2 subclade. Neither the
373 type species of *Marginella* (*M. glabella* Linnaeus, 1758) nor of *Glabella* (*G. faba* (Linnaeus,
374 1758)) were included in the present analysis; both of these genera are from relatively shallow
375 water in the East Atlantic, as are some of the species in the MM3 subclade (Fig. 2). The
376 distinction between *Marginella* and *Glabella* is based on the presence of axial ribs and a

377 denticulate outer lip in *Glabella* and lack of these characters in *Marginella* (Covert & Covert,
378 1995). Our analyses, however, show that species belonging to these genera are intermixed in
379 the MM3 subclade and so we apply the older name *Marginella* to the MM3 subclade as a
380 whole. The recent subdivision by Veldsman (2017) of *Marginella* into numerous 'subgenera'
381 also needs to be further investigated using DNA sequence data.

382 The genus *Dentimargo* appears to be one of the most problematic taxa among
383 marginelliforms. Species that were assigned to this genus are split between the MM1 and MM2
384 subclades, with more in the latter. These results show that the shell characters treated by
385 Covert & Covert (1995) as being diagnostic for *Dentimargo* (type species *Marginella dentifera*
386 Lamarck, 1803 from the French Eocene) are inadequate. Covert & Covert (1995: 76) stated
387 that the posterior denticle was "distinctly stronger than the others", but this character is highly
388 variable and applies equally to species in both the MM1 and MM2 subclades. The "spire
389 medium to tall, shell usually narrowly biconic" seems better to suit species in the MM1
390 subclade, such as those represented by specimens MNHN-IM-2013-45652 and MNHN-IM-2013-
391 45628 (Fig. 2). Although Covert & Covert (1995) treated *Dentimargo* as a genus with radula-
392 less species, this character can of course not be examined in the type species, which is a fossil.
393 In fact in our study the species that possess more elongate shells and are included in the clade
394 MM1 actually do have a radula. Therefore, the name *Dentimargo* cannot be applied to either
395 the MM1 or MM2 subclades.

396 The Caribbean *Eratoidea* cf. *hematita* (Kiener, 1834), which is a member of the MM2
397 subclade, appears to be morphologically similar to the type species of the genus *Eratoidea*, *E.*
398 *margarita* (Kiener, 1834), also from the Caribbean region. Thus, the name *Eratoidea* Weinkauff,
399 1879 can be more or less confidently applied to this clade and, in this case, would have a
400 priority over the later name *Dentimargo* Cossmann, 1899. Likewise, *Serrata tuii* is
401 conchologically similar to the type species of *Serrata*, *S. serrata* and, thus, if applied to the
402 MM1 subclade, the name *Serrata* Jousseume, 1875 would have priority over *Dentimargo*.
403 However, as the type species of *Eratoidea* and *Serrata* have not been sequenced in the present
404 study, we refrain from applying these names to the clades in question. Our analysis strongly
405 suggests that if the name *Dentimargo* is to be used in the context of extant species, the scope
406 of its application should be greatly modified and the genus reviewed in depth.

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

410

411 *Family-level classification of marginelliform gastropods*

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

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

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

438 relationships within this subclade makes delineating the limits of the Cystiscinae and
439 Persiculinae a difficult task. Therefore, we favour designating the MC1 subclade, in its entirety,
440 a single subfamily, the Cystiscinae. The subfamily-level systematics of the Cystiscidae should be
441 revised to account for the divergent positions of *Plesiocystiscus* (treated by Covert & Covert,
442 1995, as a distinct subfamily, the Plesiocystiscinae) and *Canalispira* (see below). We therefore
443 propose three subfamilies for the Cystiscidae—Cystiscinae, Plesiocystiscinae and Canalispirinae
444 new subfamily.

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

447

448 **Superfamily VOLUTOIDEA Rafinesque, 1815**

449

450 **Family MARGINELLONIDAE Coan, 1965**

451

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

453

454 **Family CYSTISCIDAE Stimpson, 1865**

455

456 **Subfamily CYSTISCINAE Stimpson, 1865**

457

458 Genera *Cystiscus* Stimpson, 1865; *Crithe* Gould, 1860; *Extra* Jousseume, 1894; *Gibberula*
459 Swainson, 1840; *Inbiocystiscus* Ortea & Espinosa, 2001; *Intelcystiscus* Ortea & Espinosa, 2001;
460 *Pachybatron* Gaskoin, 1853; *Persicula* Schumacher, 1817; *Ticocystiscus* Espinosa & Ortea,
461 2002; *Ticofurcilla* Espinosa & Ortea, 2002; ? †*Marginocystiscus* Landau, C. M. Silva & Heitz,
462 2016.

463

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

465

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

467

468 **Subfamily CANALISPIRINAE new subfamily Fedosov, Caballer, Boyer & Bouchet**

469

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

471

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

473

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

481

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

483

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

487

488 **Family MARGINELLIDAE** J. Fleming, 1828

489

490 **Subfamily MARGINELLINAE** J. Fleming, 1828

491

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

494

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

496

497 Genera *Austroginella* Laseron, 1957; *Alaginella* Laseron, 1957; *Hydroginella* Laseron, 1957;
498 *Mesoginella* Laseron, 1957; *Ovaginella* Laseron, 1957; *Protoginella* Laseron, 1957; *Serrata*
499 Jousseaume, 1875; ?*Caribeginella* Espinosa & Ortea, 1998; ?*Marigordiella* Espinosa & Ortea,
500 2010.

501

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

503

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

507

508 *Marginelliform branch in the neogastropod tree of life*

509 Our results provide the first molecular phylogenetic data for marginelliform neogastropods.
510 Neither the Marginellidae nor the Cystiscidae, as currently conceived, were found to be
511 monophyletic. Deep-level marginilliform relationships were not resolved, but this does not
512 completely rule out the potential monophyly of Cystiscidae. The Marginellidae, in contrast,
513 were clearly shown to be paraphyletic: *Marginellona gigas* shows no sister-group relationship
514 to the Main Marginellidae clade and the placement of Granulininae remains unresolved. Our
515 analyses demonstrated that the marginelliform gastropods as a whole are monophyletic and
516 that, as hypothesized on the basis of morphological similarities (Ponder, 1970, 1973), they are
517 sister to the family Volutidae. The basal split between *Marginellona* and the other
518 marginelliform taxa is reflected in the morphology of *Marginellona gigas*; this taxon has some
519 typical marginellid characters, as well as others that are regarded as plesiomorphic for the
520 Neogastropoda as a whole and are not recorded in other marginelliforms (Harasewych &
521 Kantor, 1991). The anatomy of the marginelliform foregut is known in detail and the characters
522 shared by *Marginellona* and other marginellids include the uniseriate comb-like radula within a
523 buccal pouch (Fretter, 1976; Ponder, 1970; Harasewych & Kantor, 1991; Covert & Covert,
524 1995).

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

535 features, and so any attempt to trace the history of morphological change from one type of
536 radula to the other (e.g. from the radulae of cystiscids to the radula of *Marginellona*) would be
537 problematic. However, if we look for the homology of cystiscid odontophoral hoods, we find
538 that they could be derived from the marginal cuticular flanges of an ancestral marginellid-type
539 radulae (the membranaceous folds persist, for example, in type 6 radulae). Coover & Coover
540 (1995) considered that these hoods and flanges were fundamentally different, but we argue
541 that the quantitative differences that they emphasized do not preclude the possibility that
542 these structures are, in fact, homologous. The profound transformation of the radula in the
543 ancestor of modern cystiscids could have been driven by selective pressures associated with
544 the evolution of a novel feeding strategy, such as feeding on hard-shelled prey. The presence of
545 a common set of radula features across cystiscids supports a single origin of the Cystiscidae
546 and, given that our trees were only partly resolved, this is the scenario we have reflected in our
547 classification. The disappearance of the buccal pouch can most plausibly be explained by
548 paedomorphosis, that is a shortened postembryonic development leading to the conservation
549 of ancestral features in adult morphology. The same mechanism can be evoked to explain the
550 presence of a triseriate radula in *Plesiocystiscus* vs uniseriate radulae in all other marginelliforms
551 except *Tateshia* (see below). The evolution of cystiscids has clearly involved a progressive
552 reduction in adult size, consistent with a paedomorphic origin of this taxon.

553 The uniseriate radulae of marginelliforms are similar to those in the Volutidae and
554 uniseriate radulae (although of different morphology) are also typical for the Cancellariidae and
555 Volutomitridae. Furthermore, members of these families possess distinct columellar plaits (a
556 character also found in other neogastropod lineages). Relationships among the marginelliforms,
557 Volutidae, Volutomitridae and Cancellariidae are controversial and poorly understood, and these
558 taxa are inadequately represented in published phylogenies. Cunha *et al.* (2009) and Oliverio &
559 Modica (2010) showed the Cancellariidae as the sister group of other neogastropods and the
560 former study suggested paraphyly of the Neogastropoda. A more recent topology (Fedosov *et al.*,
561 2015) conflicts with this, showing the Cancellariidae and Volutidae as sister taxa, and the
562 Volutomitridae branch clustering with the costellariid and ptychactrid lineages. A recent
563 phylogenomic analysis of the Conoidea (Abdelkrim *et al.*, 2018) provided additional insights into
564 the early radiation of the Neogastropoda, placing the Cancellariidae, Volutidae and
565 Volutomitridae as three early and independent lineages.

566

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

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

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

616 The type 3 radula (Figs 4E–M) is most widespread in the cystiscid lineages, including the
617 *Gibberula–Persicula–Pachyathron* subclade and *Canalispira*. This type of radula usually has
618 bow- or horseshoe-shaped multicuspidate teeth, each bearing a strong central cusp. The
619 uniseriate radulae of the nematoglossan type is often considered as an adaptation to suctorial
620 feeding; the extremely elongated central cusps pierce the integument of prey, while the lateral
621 cusps facilitate interlocking of successive teeth, rendering the radula more rigid and possibly
622 more resistant to lateral deformation (Petit & Harasewych, 1986; Modica *et al.*, 2011).
623 Published observations on *Cystiscus* species feeding on bryozoans (Coleman, 1975) suggest that
624 the radulae of marginelliforms may function in a similar manner. However, of particular interest
625 is the clear signs of wear that were observed in nearly all the examined cystiscid radulae (Figs
626 4B, G, I, L). This wear is most likely the result of mechanical abrasion, which suggests that
627 cystiscid radulae come into contact with tough substrata, such as the frontal membrane or the
628 cryptocyst of colonial bryozoans. The specialization for feeding on sedentary prey with thick
629 integument may explain the origin of the cystiscid type of radula. The firm odontophoral hoods
630 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

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FIGURE CAPTIONS

- 800 **Figure 1.** Live marginelliform gastropods (not shown to scale). **A.** *Ticofurcilla mariolysae*
 801 (MNHN, MADIBENTHOS St. AB360, 14°46'73"N, 61°00'26"W, 12 m depth). **B.** *Crithe* aff.
 802 *marianoi* (MNHN-IM-2013-2989, PAPUA NIUGINI St. PB18, 05°06.3'S, 145°49.1'E, 26 m depth).
 803 **C.** *Cystiscus* sp. (MNHN- IM-2013-3692, PAPUA NIUGINI St. PB21 5°1'26.89"S, 145°48'2"E, 5 m
 804 depth). **D.** '*Gibberula*' sp. (MNHN-IM-2013-4208, PAPUA NIUGINI St. PB26, 04°59.1'S,
 805 145°47.7'E, 22 m depth). **E.** '*Gibberula*' aff. *moscatellii* (MNHN-IM-2013-56965, ILES DU SALUT
 806 St. SS01, 05°16.9'N, 52°35.1'W, 8 m depth). **F.** *Canalispira* sp. (MNHN-IM-2013-1838, PAPUA
 807 NIUGINI St. PS09, 05°12.3'S, 145°48.8'E, 8–10 m depth). **G.** *Marginella festiva* (MNHN-IM-2013-
 808 43709, Dakar'09 St. 09, 14°39.9'N, 17°24.0'W, 7 m depth). **H.** *Eratoidea* cf. *hematita* (MNHN-
 809 IM-2013-60596, KARUBENTHOS 2 St. DW4559, 16°24.5'N, 60°51.8'W, 72–111 m depth). **I.**
 810 '*Dentimargo*' sp. (MNHN-IM-2013-3409, PAPUA NIUGINI St. PS15, 5°5'47.4"S, 145°48'11.7"E, 12
 811 m depth). **J.** '*Marginella*' *cloveri* (MNHN-IM-2013-56775, GUYANE 2014 St. CP4402, 6°18'N,
 812 52°13.3'W, 95–97 m depth). **K.** *Volvarina* aff. *avena* (MNHN-IM-2013-60828, KARUBENTHOS 2

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

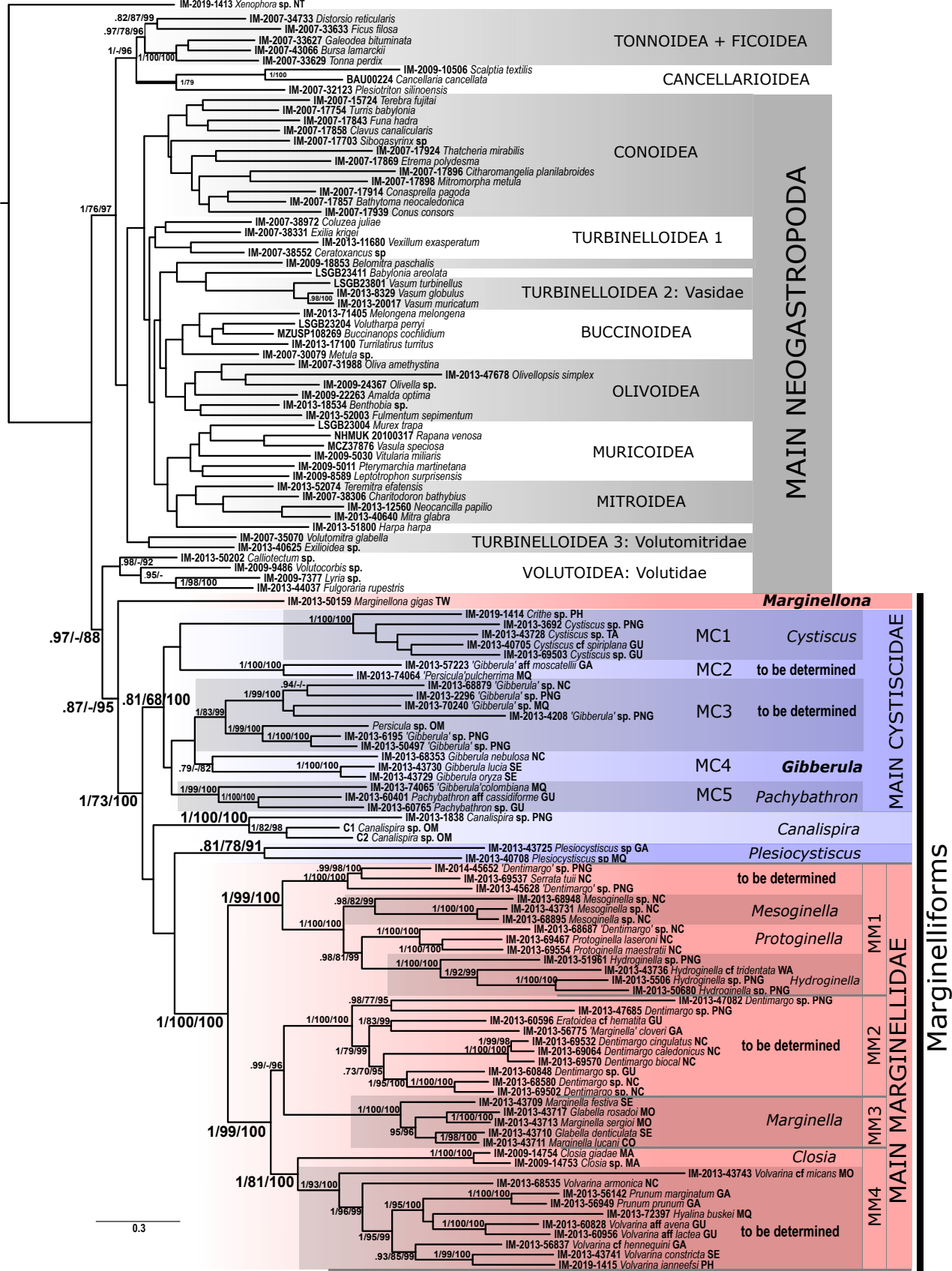
815 **Figure 2.** ML phylogeny of the Neogastropoda showing cystiscid (blue shading) and marginellid
816 (red shading) lineages (tree reconstructed by RaxML). Dark and light shading in the
817 marginelliform part of the tree (*Marginellona* + 'Main Cysticidae' + *Canalispira* + *Plesiocystiscus*
818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

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

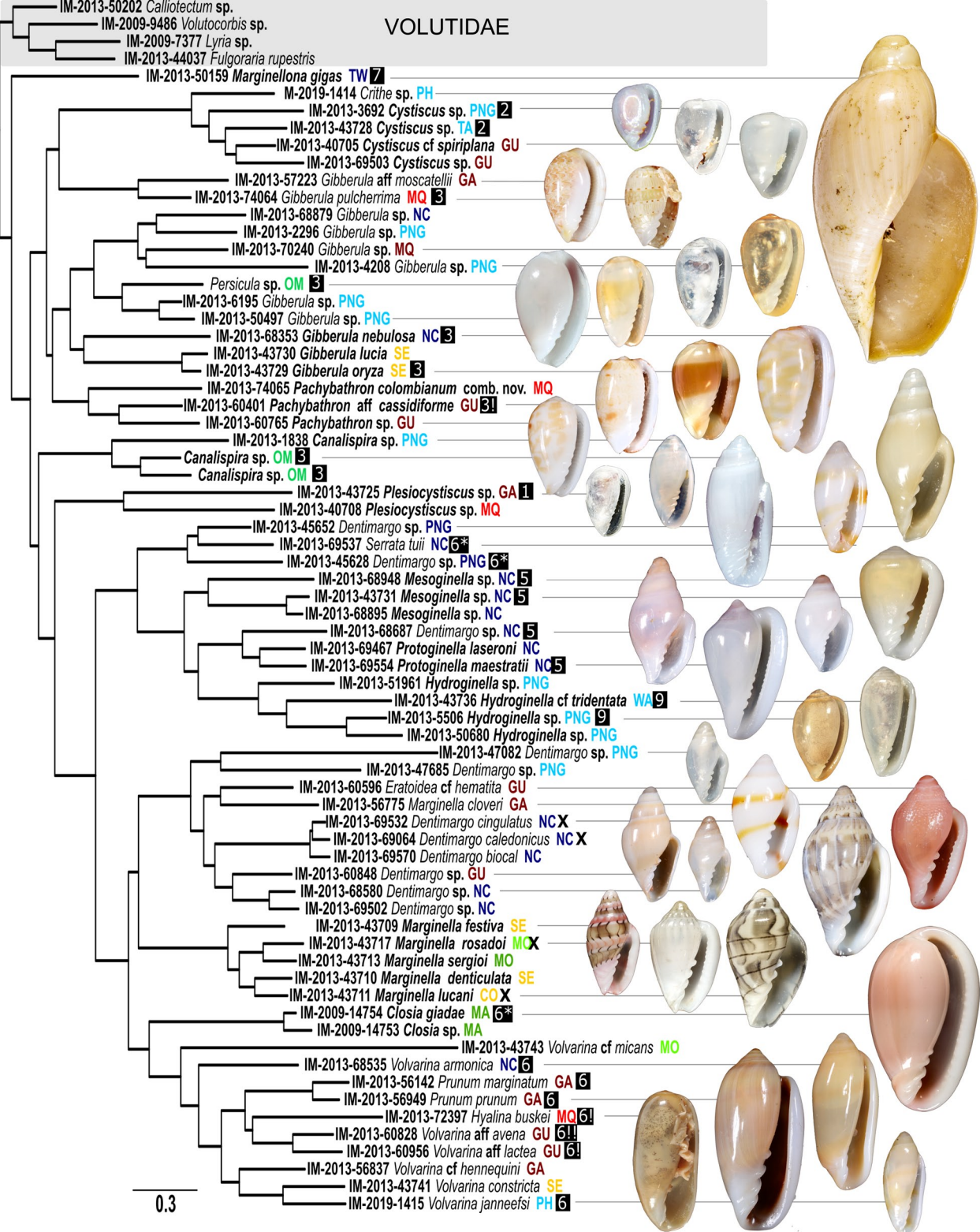
833 **Figure 4.** Radulae of studied marginelliform specimens. Numbers under the scale bars below the
834 radula images indicate scale units. **A, B.** Type 1, *Plesiocystiscus* sp. (MNHN-IM-2013-43724,
835 GUYANE St. CP4380, 6°31'N, 52°27'W, 102–104m depth), showing intact (**A**) and older, worn (**B**)
836 areas of radula. **C, D.** Type 2, *Cystiscus* sp. (MNHN-IM-2013-43726, TASMANIA St. TA44,
837 41°18.2'S, 148°18.8'E, 3–6 m depth), showing frontal (**C**) and lateral (**D**) views. **E.** Type 3,
838 *Gibberula oryza* (MNHN-IM-2013-43729, DAKAR St. 20, 14°40.2'N, 17°23.8'W, 12 m depth). **F,**
839 **G.** Type 3, *Gibberula nebulosa* (MNHN-IM-2013-68353, KANACONO St. DW4661, 22°48'S,
840 167°07'E, 405–410 m depth), showing intact (–) and worn, older (**G**) areas of radula. **H, I.** Type
841 3, *Canalispira* sp. (Oman, Masirah, leg. F. Boyer, 2013), showing intact (**H**) and worn, older (**I**)
842 areas of radula. **J, K.** Type 3, '*Persicula*' sp. (Oman, Masirah, leg. Franck Boyer, 2013), showing
843 intact (**J**) and worn, older (**K**) areas of radula. **L.** Type 3, *Pachybathron* cf. *cassidiforme* (MNHN-
844 IM-2013-61020, KARUBENTHOS2 St. DW4593, 15°56'N, 61°26'W, 133–152m depth). **M.** Type 4,

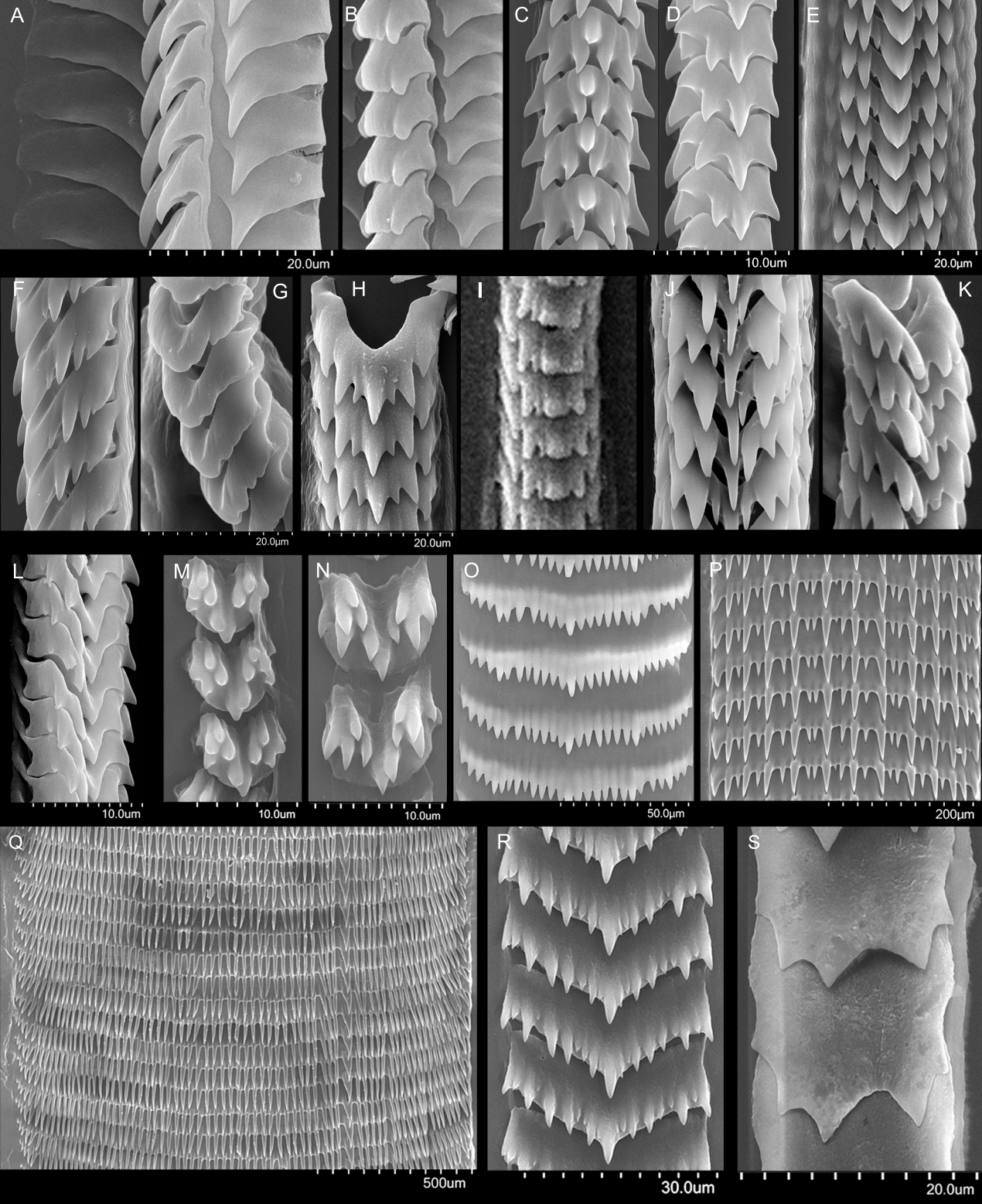
845 *Granulina liliputana* (MNHN-IM-2013-43723 Dakar'09 St. 10, 14°39.8'N, 17°23.9'W, 31 m
846 depth). **N.** Type 4, *Granulina* sp. (MNHN-IM-2013-43732, MADEEP St. DW4287, 9°12'S,
847 153°56'E, 340–375m depth). **O.** 'Modified type 6', '*Dentimargo*' sp. (MNHN-IM-2013-45652,
848 MADEEP St. DW4292, 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).





VOLUTIDAE





- 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	-	-	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>spiriplana</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>spiriplana</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>Pachyathron</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>Pachyathron</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>Protoginella 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>Protoginella 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	-	-	Philippines, Mactan Is., off Punta-Engana (lumun-lumun)	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 sp.</i>	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 sp.</i>	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)	CANCO28-10	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>Turriturris 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
Clathrellidae	<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									

