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## Molecular phylogeny and revised classification of the Buccinoidea (Neogastropoda)

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Abstract:	<p>The superfamily Buccinoidea is distributed in the world's oceans from the Arctic Ocean to the Antarctic, from intertidal to abyssal depths. It encompasses about 3,340 Recent species in 337 genera. The latest taxonomic account recognized eight full families. For the first time the monophyly of the superfamily and the relationships among the families are tested with molecular data supplemented by anatomical and radula data. Five genetic markers were used: fragments of mitochondrial <i>cox1</i>, 16S rRNA, 12S rRNA, and nuclear H3 and 28S rRNA genes (for 225 species of 117 genera). Our analysis recovered Buccinoidea monophyletic in the Bayesian analysis. The relationships between the formerly recognized families and subfamilies are drastically revised and a new classification of the superfamily is here proposed, now including 20 taxa of family rank and 23 subfamilies. Five new families (Eosiphonidae, Retimohniidae., Chauvetiidae, Dolicholatiridae, Prodotiidae) and one subfamily of Nassariidae (Tomliniinae) are described. Austrosiphonidae and Tudicidae are resurrected from synonymy and employed in a new taxonomical extension. All but 37 recent genera are reclassified. Our results demonstrate that anatomy is rather uniform within the superfamily. With exceptions, the rather uniform radular morphology alone does not allow allocating genera to a particular family without additional molecular data.</p>
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## INTRODUCTION

The superfamily Buccinoidea is one of the largest and most successful groups of Neogastropoda. It currently encompasses 3,351 accepted Recent species classified in 337 genera (MolluscaBase, 2020, accessed 19/12/2020). Among neogastropods, only the superfamily Conoidea, with 5,267 described Recent species and 379 genera (MolluscaBase, 2020, accessed 19/12/2020), outnumbers Buccinoidea in taxonomic diversity.

Buccinoidea are distributed from the Arctic Ocean to the Antarctic, from the intertidal to depths of more than 8,000 m (Kantor *et al.*, 2020b), and include several genera penetrating brackish waters and even freshwater (Strong *et al.*, 2017). They exhibit a broad range of feeding ecologies: while a majority are carrion feeders, scavengers or active predators (Taylor *et al.*, 1980), some have transitioned to herbivory (some Nassariidae and Columbelloidea; Brown, 1969, Marcus & Marcus, 1962); one lineage of buccinids is composed exclusively of specialized dwellers of biogenic substrates and hot vents (Kantor *et al.*, 2013); members of the Colubrariidae, known as vampire snails, suck blood from sleeping fishes (Bouchet & Perrine, 1996; Oliverio & Modica, 2010); and at least some species of the enigmatic genus *Chauvetia* have been found in association with starfishes (Oliver & Rolan, 2008). A number of buccinoidean species are the target of commercial fisheries in northern Europe and the North Pacific, and several species have become model organisms for the study of gastropod embryology and development (e.g. Smith & Thatje, 2013).

The superfamily has had a complex classification history, with as many as 57 family group names based on Recent genera currently attributed to the Buccinoidea. Thiele (1929) recognized five families within his “Stirps Buccinacea”: Columbelloidea, Buccinidae, Galeodidae [= Melongenidae], Nassidae [= Nassariidae], and Fascioliidae. Essentially, this was the arrangement that prevailed during the subsequent decades, with some authors additionally recognizing a separate family Buccinulidae, which was erected mostly for Southern Hemisphere Buccinoidea (Finlay, 1928).

This taxonomic hierarchy was radically revisited by Golikov & Starobogatov (1975), who raised the ranks of the taxa and recognized four superfamilies within the currently accepted extension of Buccinoidea: Fascioliarioidea, Buccinoidea (unexpectedly including, among others, the Vexillidae [= Costellariidae] and Pseudolividae), new superfamily Beringioidea, and Pyrenoidea. In total they recognized 10 families, two of which, Anachidae and Pyrenidae, were placed in different superfamilies but included genera currently classified in the family Columbelloidea (see Table 1). These viewpoints were further developed in Golikov & Starobogatov (1988), where these authors proposed a new classification of prosobranch gastropods at the rank of suborder and above. Their order Bucciniformes included the suborders Buccinoidei, Triphoroidei, Olivelloidei, and Muricoidei, while Pyrenoidei were classified in the order Mitriiformes of the superorder Coniformii. Golikov and Starobogatov's classification with inflated ranks was barely followed or even discussed by subsequent authors, especially as Ponder and Warén (1988) simultaneously recognized only two families in the Buccinoidea: Columbelloidea and Buccinidae (with the subfamilies Buccininae, Nassariinae, Melongeninae, Fascioliinae), the latter including 29 synonyms, some of which were later excluded from the Buccinoidea (e.g., Dipsaccinae, now a synonym of Ancillariidae, Olivioidea; and Latrunculinae, now a synonym of Babyloniidae).

1  
2 1 The state of the art of Buccinoidea systematics, partly based on the molecular phylogenies  
3 2 then available, is that presented by Bouchet *et al.* (2017) (Table 1), who recognized eight  
4 3 families: Buccinidae (with six subfamilies and nine tribes), Belomitridae, Colubrariidae,  
5 4 Columbelloidae (with two subfamilies), Fascioliidae (with three subfamilies), Melongenidae,  
6 5 Nassariidae (with seven subfamilies), and Pisaniidae.

7 6 The recent molecular phylogenetic studies are, however, all partial and focused on  
8 7 individual families: Belomitridae (Kantor, Puillandre, Rivasseau & Bouchet, 2012),  
9 8 Fascioliidae (Couto *et al.*, 2016), Nassariidae (Galindo *et al.*, 2016), Colubrariidae (Oliverio &  
10 9 Modica, 2010) or lower level taxa (Kantor *et al.*, 2013; 2020a; 2020b), or even biogeographic  
11 10 assemblages (Vaux *et al.*, 2017). The superfamily Buccinoidea in its entirety has in fact never  
12 11 been the subject of a comprehensive molecular phylogenetic analysis. As a consequence, in the  
13 12 absence of molecular data, the placement of many polar or temperate water lineages of the  
14 13 superfamily, such as the subfamily Beringiinae or the buccinid tribes Colini Gray, 1857,  
15 14 Volutopsiini Habe & Sato, 1973 or Prosiphonini Powell, 1951, has remained tentative.

16 15 In the present study, we reconstruct a phylogeny of the Buccinoidea based on the analysis  
17 16 of an unprecedented dataset, comprising five molecular markers and a total of 116 genera and  
18 17 231 species that cover rather comprehensively the geographic and taxonomic diversity of the  
19 18 superfamily. The outcome is a revised classification of the superfamily.

## 20 MATERIAL AND METHODS

### 21 TAXON SAMPLING

22 24 When assembling the dataset, we tried to include representatives of as many accepted and  
23 25 potentially valid family group taxa as possible. The core material for the present study was  
24 26 collected during several biodiversity surveys organized mainly by the Muséum National  
25 27 d'Histoire Naturelle (MNHN), Pro-Natura International (PNI) and the Institut de Recherche pour  
26 28 le Développement (IRD), as part of the *Our Planet Reviewed* and *Tropical Deep-Sea Benthos*  
27 29 programs (see Bouchet *et al.*, 2008 and the BasExp database at <http://expeditions.mnhn.fr/>).  
28 30 Additional material was obtained from a number of museums, institutions and private sources  
29 31 (see list of repositories). A list of sequenced material included in the analysis, with collection  
30 32 details and not-aligned gene sequences, is provided in Supplementary material Table S1.

31 33 We generated original DNA sequence data or accessed published sequences for  
32 34 representatives of 28 nominal families and subfamilies of Buccinoidea (not counting the family  
33 35 group taxa introduced in this paper), but we lack members of the subfamilies Atiliinae  
34 36 Cossmann, 1901 (Columbellidae), Liomesinae P. Fischer, 1884, and Truncariinae Cossmann,  
35 37 1901 (all probably Buccinidae).

36 38 Within the genus group, we consider only full genera. In total, we use in our analysis  
37 39 sequences (either original, or published) of 118 genera out of 339, or 35% of the recognized  
38 40 diversity. Two families are particularly diverse at the genus level: Fascioliidae (66 recognized  
39 41 genera, 17 of which are included in the current analysis) and Columbelloidae (76 recognized  
40 42 genera, 6 included in the current analysis). The former was recently studied using molecular  
41 43 phylogenetic methods and found monophyletic (Couto *et al.*, 2016), with the exception of  
42 44 several genera attributed herein to a separate family. The latter is currently being revised by E.  
43 45 Strong and M. deMaintenon and found monophyletic except one genus (personal

1 communication) and is not treated here in detail. If we only consider buccinoidean genera  
2 outside these families (194 in total), our coverage reaches 48% of the recognized diversity.

3 A genus-level revision of the families of Buccinoidea is beyond the scope of the present  
4 work, since representatives of half of the valid genera were not available for molecular study and  
5 for some even the radula is unknown. So, no new genus names are proposed herein, even when  
6 an accepted genus is demonstrated to be non-monophyletic; these cases are, however, discussed  
7 in the remarks in the taxonomic treatment of individual families. Nevertheless, we attempt to  
8 allocate all known buccinoidean genera to the family group taxon as defined herein, based either  
9 on molecular and/or morphological data. Based on the data available, we use three levels of  
10 confidence for the allocation of a genus to a family group:

11 (1) genera classified in a family based on molecular and morphological data (mostly  
12 radula); marked <sup>(1)</sup> — 103 genera;

13 (2) genera classified based on radula morphology only, and congruence between radula  
14 and molecular characters for those sequenced genera; marked <sup>(2)</sup> — 30 genera.

15 (3) genera assigned to a family based on shell characters alone, and phenetic resemblance  
16 to those genera with radula and/or molecular characters available; marked <sup>(3)</sup> — 22 genera.

17 36 genera were not attributed to any family with certainty, due to the lack of any radular or  
18 anatomical data, or when available data were deemed insufficient. For 27 of them, we  
19 nevertheless suggest a tentative classification (Supplementary material Table S2).

#### 20 21 SPECIMEN PROCESSING

22 In the field, living specimens were anaesthetized with MgCl<sub>2</sub> prior to fixation, or removed from  
23 their shells using a microwave oven following the protocol described by Galindo *et al.* (2014).  
24 Bodies were then separated from the shells, and shells were kept dry to prevent deterioration by  
25 etching and assigned the same registration number as the corresponding body (stored in 80–96%  
26 ethanol) and tissue clip (stored in 96–98% ethanol). Most of the material (shell, tissue and DNA)  
27 is vouchered in MNHN (<http://science.mnhn.fr>) unless otherwise stated.

28 Anatomy was examined by dissection. The bodies of some specimens were specially  
29 preserved in 80% ethanol after clipping a fragment of the foot for DNA extraction; others were  
30 preserved in 95% alcohol and briefly rehydrated (10–30 min) prior to dissection. In most cases  
31 this procedure allowed removal of the body from the shell and made tissues elastic enough for  
32 dissection. After dissection the bodies were returned to 95% ethanol. Radulae were cleaned using  
33 diluted bleach (NaOCl), mounted on a glass cover slip or double-sided carbon tape, air-dried,  
34 attached to aluminium stubs, coated with gold and examined by scanning electron microscope  
35 TeScan TS5130MM in the IEE RAS.

36 For size characterization we used the following arbitrary divisions: shell small < 10 mm,  
37 medium sized 10–29 mm; medium large, 30–100 mm; large, over 100 mm.

#### 38 39 40 DNA EXTRACTION AND PCR

41 Total DNA was extracted from a piece of foot using either the Dneasy96 Tissue kit (Qiagen)  
42 using automated extraction system Epmotion 5075 (Eppendorf), or manually, using Investigator  
43 Kit (Qiagen), following the manufacturer's recommendations. Five genetic markers were  
44 targeted for the phylogenetic reconstructions: the barcode fragment of the mitochondrial  
45 cytochrome *c* oxidase I (*coxI*) gene (658 bp), a ~450-bp long fragment of the mitochondrial 16S  
46

1 rRNA, a ~550 bp fragment of the mitochondrial 12S rRNA, a 328 bp fragment of the nuclear  
2 Histone 3 (H3), and a ~700 bp fragment of the nuclear 28S rRNA. The *cox1*, 12S, H3 and 28S  
3 were amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.*, 1994), 12SI  
4 and 12SIII (Simon *et al.*, 1991), H3A-H3B (Colgan *et al.*, 1998) and C1 and D2 (Jovelin &  
5 Justine, 2001), respectively. The pair of primers DY16S748R (Hayashi, 2005) – 16sbr-H  
6 (Palumbi *et al.*, 1991), the former developed specifically for Buccinidae, were used to amplify  
7 the 16S fragment. PCRs were performed in 20 µl final volume containing approximately 3 ng  
8 template DNA, 1.5 mM MgCl<sub>2</sub>, 0.26 mM of each nucleotide, 0.3 µl of each primer, 5% DMSO  
9 and 0.75 µl of either Q-Bio-Taq Polymerase (Qbiogene) or BioHYTaq DNA polymerase  
10 (Dialat). The PCR profiles were as detailed in Fedosov *et al.* (2018) and Kantor *et al.* (2020).  
11 Success of amplification was checked using an electrophoresis in agarose gel; the obtained  
12 amplicons were purified by repeated precipitation in ethanol, or using Exo/SAP Go PCR  
13 Purification Kit (Grisp, Portugal) and sequenced in both directions. Sequencing was performed  
14 by Eurofins or at the joint usage centre ‘Methods of molecular diagnostics’ of the IEE RAS on  
15 an ABI 3500 Genetic analyser (Applied Biosystems).

#### PHYLOGENETIC ANALYSIS

19 Chromatograms were examined, and forward and reverse reads were merged into consensus  
20 sequences using a SeqMan Pro v11 of the DNASTAR package (Lasergene). Our dataset of 146  
21 taxa with one specimen per species was complemented by previously published DNA sequences  
22 of 85 additional taxa of Buccinoidea or of other neogastropod lineages (Couto *et al.*, 2016;  
23 Galindo *et al.*, 2016; Fedosov *et al.*, 2015, 2019; Kantor *et al.*, 2012, 2013, 2020a, b; Oliverio &  
24 Modica, 2010; Strong *et al.*, 2017; Vaux *et al.*, 2017; Zou *et al.*, 2011), i.e. a total of 231 taxa, of  
25 which 222 were members of the superfamily Buccinoidea. Finally, only *cox1* sequences (11  
26 accessed from GanBank and ten original) were used for 13 species in the analysis aiming at  
27 confirming the placement of particular taxa.

28 Sequences were aligned for each gene independently using MAFFT v.7 (Kato *et al.*,  
29 2019). The accuracy of automatic alignments was confirmed by eye. No indels were detected in  
30 *cox1* and H3; various numbers of indels were identified in the 16S, 12S and 28S fragments,  
31 leading to the alignments of 561, 607 and 745 bp in length respectively. Alignments of 16S and  
32 12S contained regions with many indels, so we used GUIDANCE2 (Sela *et al.*, 2015) to generate  
33 best alternative alignments for each of the two markers, and to remove ambiguously aligned  
34 bases. We removed alignment columns with confidence values below 0.4, leading to alignments  
35 of 548 and 596 positions for 16S and 12S respectively, or, alternatively, below 0.9, which  
36 resulted in the alignments of 471 and 475 positions for 16S and 12S respectively. For  
37 phylogenetic inference, eight datasets were analyzed. Five of them corresponded to the five  
38 individual genes and were analyzed separately to ensure that they did not result in supported  
39 conflicting topologies. Then three concatenated datasets of the five genes were built: Buc5G  
40 with entire lengths of 16S and 12S comprising 2,899 bp, and Buc5G\_GUI40 and Buc5G\_GUI90  
41 with ambiguously aligned bases below confidence values 0.4 and 0.9 respectively removed from  
42 both 16S and 12S, resulting in a total concatenated sequences lengths of 2,875 bp and 2,677 bp  
43 respectively.

44 The single gene phylogenies were estimated by RAxML v.8.2.12 (Stamatakis, 2006), with  
45 ML (Maximum Likelihood) search and bootstrapping performed in a single run. The bootstrap

1 seed value was set to 12345, and robustness of nodes assessed by 1,000 iterations of rapid  
2 bootstrapping algorithm (Stamatakis *et al.*, 2008).

3 The concatenated datasets were subdivided into seven partitions: three corresponding to  
4 three codon positions of the *cox1*, and the remaining four to the 16S, 12S, H3 and 28S fragments  
5 respectively. We avoided coding codon positions of H3 as separate partitions, because this  
6 fragment is rather short (328 bp), so estimating separate substitution statistics set for each codon  
7 position may lead to overparametralisation and reduced accuracy of the phylogenetic inference.  
8 Concatenated datasets were then analysed by ModelFinder implemented in IQ-Tree 2.1.1  
9 (Kalyaanamoorthy *et al.*, 2017) to identify the best fit nucleotide substitution model for each  
10 initial partition, and evaluate whether any initial partitions may be merged. Based on the  
11 obtained results, seven initial partitions were merged into two partitions, which were used for  
12 both RAxML (Maximum likelihood) and BI (Bayesian Inference).

13 The ML phylogenetic tree was reconstructed for the concatenated datasets using the same  
14 parameters of RAxML v.8.2.12 as were used for the single genes trees. Bayesian analysis  
15 (Huelsenbeck & Ronquist, 2001) was performed on the concatenated datasets by running two  
16 parallel analyses in MrBayes with parameters of substitution models estimated during the run.  
17 Each run consisted of 25,000,000 generations of Markov chain, sampling frequency was set to  
18 one tree in each 1,000 generations, and chain temperature to 0.02. Convergence of each analysis  
19 was evaluated using Tracer1.4.1 (Rambaut *et al.*, 2014), where ESS (Effective Sampling Size)  
20 values were checked to ensure that they exceeded 200. A consensus tree was calculated after  
21 omitting the first 25% trees as burn-in. All analyses were performed on the Cipres Science  
22 Gateway (<http://www.phylo.org/portal2>), using IQ-Tree v. 2.1.1 on XSEDE, RAxML v.8.2.12  
23 on XSEDE and MrBayes 3.2.6 on XSEDE (Miller *et al.*, 2010).

24 The aligned datasets (*cox-1* and concatenated five genes dataset) as well, as the details of  
25 the selected best models of nucleotide evolution and output consensus trees are provided as  
26 supplementary files (File S1 – File S10).

27 Nodes with Bootstraps values (B, in percent) lower than 70 and Posterior Probabilities (PP)  
28 lower than 0.95 are considered non-supported; B values between 70 and 90 and PP values  
29 between 0.95 and 0.98 are regarded as moderately supported; and B > 90 and PP > 0.98 as well-  
30 supported.

#### 31 32 TURNING THE PHYLOGENY INTO A CLASSIFICATION

33  
34 Overall, a conservative approach was adopted and whenever possible we retained the current  
35 rank of the presently accepted family group taxa. As requested by the ICZN Code, we accepted  
36 available names even if they are based on genera considered to be junior synonyms. As much as  
37 possible, a genus-group name was applied based on the position of its type species in the tree. If  
38 the type species of a nominal genus or subgenus has not been sequenced, application of the name  
39 was determined by reference to the morphologically most similar species included in the  
40 molecular analysis.

41 Biogeographical regions follow Spalding *et al.* (2007), bathymetry ranges follow the 2009  
42 UNESCO 2009 Global Open Oceans and Deep Seabed (GOODS) Biogeographic Classification.

#### 43 44 REPOSITORIES AND ABBREVIATIONS:

45 AMS — The Australian Museum, Sydney, Australia;



- 1  
2 1 AORI — Atmosphere and Ocean Research Institute, University of Tokyo, Japan;  
3 2 BAU — Dipartimento di Biologia Animale e dell’Uomo, ‘La Sapienza’ University, Roma,  
4 3 Italy;  
5 4 BI — Bayesian inference analysis;  
6 5 CSUF — California State University, Fullerton, CA, USA;  
7 6 IEE RAS — A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of  
8 7 Sciences, Moscow, Russia;  
9 8 ICZN — International Code of Zoological Nomenclature;  
10 9 M — by monotypy (with regard to the fixation of the type species of a genus);  
11 10 ML — maximal likelihood analysis;  
12 11 MNA — Italian National Antarctic Museum, section of Genoa, Italy;  
13 12 MNHN — Muséum National d’Histoire Naturelle, Paris, France;  
14 13 MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA;  
15 14 MZUSP — Museum of Zoology, University of San Paulo, Brazil;  
16 15 NHMUK — Natural History Museum, London, UK;  
17 16 NMNZ — Museum of New Zealand Te Papa Tongarewa;  
18 17 OD — by original designation (with regard to the fixation of the type species of a genus);  
19 18 RNC — collection of R.N. Clark;  
20 19 SFKH — Simon Hill collection, later transferred to Te Papa Tongarewa Museum,  
21 20 Wellington, New Zealand;  
22 21 SPSU — Saint Petersburg State university, Saint Petersburg Russia;  
23 22 TS — type species;  
24 23 ZIN — Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;  
25 24 ZSM — Bavarian State Collection of Zoology, München, Germany;  
26 25 SD — by subsequent designation (with regard to the fixation of the type species of a  
27 26 genus);  
28 27 SL — shell length.

## 30 RESULTS

### 32 PHYLOGENETIC ANALYSIS

34 All single gene analyses resulted in generally congruent trees. Support values were extremely  
35 low for deep nodes, but moderate to high for more recent nodes. Even in trees obtained from the  
36 analyses of concatenated datasets, most deep nodes are not resolved, or lack support.  
37 Nevertheless, all four trees built from the analyses of the concatenated datasets display about the  
38 same set of well-supported clades, although (unsupported) relationships among them varied  
39 between the analyses.

40 Despite the low support values for deep nodes and some uncertain relationships,  
41 Buccinoidea was recovered as monophyletic in all analyses, but this node (Fig. 1) is only  
42 supported in the BI of the Buc5G dataset (PP=0.97 — Fig. 1). Altogether, this tree shows the  
43 highest support values and we mainly discuss the composition of revealed clades and  
44 relationships among them based on this tree, referring to others when appropriate. On the  
45 contrary the trees obtained in the analysis of the Buc5G\_GUI90 dataset displayed many  
46 polytomic nodes, with generally lower support, and will not be discussed further on.

1 To discuss the topology of the obtained multigene tree, we select 31 highly or moderately  
 2 supported clades, comprising all but seven analyzed species of Buccinoidea, which we refer to  
 3 by the name of one included genus, whenever possible the type genus of a named family. On  
 4 Figure 1, these clades are collapsed for a more convenient representation of the overall tree  
 5 topology, and the unrestrained tree is provided in Figure 2. The first split in the Buccinoidea  
 6 separates a well-supported grouping comprising two terminal clades, the *Dolicholatirus*-clade  
 7 (comprising six species of the genera *Dolicholatirus* and *Crassicantharus*) and the *Belomitra*-  
 8 clade (with two species of the genus *Belomitra*). The grouping uniting the remaining  
 9 Buccinoidea is highly supported in the analyses of the Buc5G dataset (B=94, PP=0.98) and is  
 10 subdivided into two clades. The first of them, referred to on Figure 1 as **CCBA** (for  
 11 Colubrariidae–Colidae–Biogenicsubstrates–Antarctic), comprises 1) *Colubraria*-clade (with six  
 12 species representing five genera of the family Colubrariidae), 2) *Colus*-clade (comprising eight  
 13 Arctic and northern Atlantic species of the genera *Colus* and *Turrisipho*), 3) large *Eosipho*-clade  
 14 (encompassing 21 species of Buccinoidea from hydrothermal vents, methane seeps and sunken  
 15 wood, currently classified in seven genera, with a sister group relationship with “*Aulacofusus*”  
 16 *hiranoi*), and 4) *Prosipho*-clade (formed by 15 Antarctic and southern temperate water species  
 17 currently assigned to nine genera within Buccinidae, including *Austrofusus* and, in part,  
 18 *Antarctodomus*). The remaining Buccinoidea form a cluster, hereafter called **core Buccinoidea**,  
 19 recovered in all analyses of multigene datasets, but with only moderate support in the ML  
 20 analysis of the Buc5G dataset (B=87). The first major division within the core Buccinoidea  
 21 unites the *Siphonalia*-clade (with 13 species currently attributed to five buccinid genera) and a  
 22 large, maximally supported clade referred to as the Bu–grouping. The Bu–grouping itself  
 23 encompasses five clades, among them the *Volutopsius*-clade (six species), *Neptunea*-clade (four  
 24 species), *Beringius*-clade (five species), *Bathyancistrolepis*-clade (five species), and *Buccinum*-  
 25 clade (10 species). Relationships among the clades of the Bu–grouping remain unresolved, as  
 26 does the placement of *Anomalisipho verkruezeni* within it. The second well-supported major  
 27 division of the core Buccinoidea, referred to as the Fa–grouping, unites the *Fusinus*-clade (with  
 28 15 species representing five genera mostly of the fascioliariid subfamily Fusininae), *Fasciolaria*-  
 29 clade (comprising nine species of the fascioliariid subfamily Fascioliariinae), and *Fusolatirus*  
 30 *pearsoni* in a sister relationship to the *Fasciolaria*-clade. The third well-supported division  
 31 referred to as the PB–grouping comprises the *Penion*-clade (with nine species in four genera) and  
 32 *Buccinulum*-clade (combining 17 species in the genera *Buccinulum*, *Aenator*, *Tasmeuthria* and  
 33 *Euthria*, also mostly from the Southern Hemisphere).

34 Relationships among the other clades are either not consistently detected or lack support.  
 35 Nevertheless, we mention here all divisions uniting two or more of the remaining 15 clades, and  
 36 present in at least three multigene trees. The first such group, referred to as the BB–grouping, is  
 37 well-supported in BI analyses of both the Buc5G\_GUI40 and Buc5G datasets, but absent in the  
 38 ML analysis of the Buc5G\_GUI40 dataset. It unites the *Busycon*-clade (with three large species  
 39 representing three genera from the tropical and temperate western Atlantic), *Buccinanops*-clade  
 40 (comprising two species in the South American genus *Buccinanops*), and the East-Pacific species  
 41 *Macron lividus* in a sister relationship with the *Buccinanops*-clade. The complex grouping  
 42 referred to as the NaCo–grouping (for Nassariidae–Columbellidae) is recovered in all multigene  
 43 analyses but is never supported. It comprises the *Columbella*-clade (with seven species  
 44 representing six genera of the family Columbellidae), and six terminal clades plus three species  
 45 (for a total of 23 species), all currently classified in the family Nassariidae but consistently

forming a grade in relation to the *Columbella*-clade. Four further clades show a consistent relationship to the NaCo-grouping, but again without support and without consistent branching order. These are 1) the *Melongena*-clade (with three species representing three genera of the family Melongenidae), 2) *Prodotia*-clade (comprising four small Indo-Pacific species in the genera *Prodotia*, *Caducifer* and *Clivipolia*, previously attributed to the Pisaniidae); 3) large *Pisania*-clade (including 14 species currently classified in six further genera of the Pisaniidae: *Pisania*, *Engina*, *Hesperisternia*, *Cancellopolia*, *Cantharus* and *Polia*); and 4) *Chauvetia*-clade (with three species of the temperate Northern Atlantic genus *Chauvetia*). Finally, two small clades fall in a basal polytomy of the core Buccinoidea, but do not show consistent affinity to any of the above groups: 1) the *Cominella*-clade (comprising five Southern Hemisphere species of *Cominella* and *Pareuthria*); and 2) *Retimohnia*-clade (uniting three species of the deep-water, temperate North-Pacific genera *Retimohnia* and *Fusipagoda*).

The phylogenetic position of particular taxa was checked in the extended *cox1* tree (Fig. S1, specimens sequenced only for *cox1* gene are highlighted in red), but these are unfortunately missing in the multigene datasets. *Tudicla spirillus*, *Africofusus africanus* and *Afer cumingi* clustered with *Euthria cornea* and *Euthria japonica* in the *Buccinulum*-clade, with a moderate support (B=78) for the grouping of *Tudicla*–*Euthria*–*Africofusus*. The two sequenced specimens of *Aulacofusus periscelidus* formed a group sister to the *Neptunea*-clade in the Bu-grouping, although with weak support (B=73). The sequenced specimen of *Ancistrolepis grammatus* formed a well-supported clade with *Clinopegma magnum* (B=99), *Parancistrolepis fujitai* is clustering with high support (B=100) with *Thalassoplanes moerchi* and *Pseudoliomesus canaliculatus* with *Japelion hirasei* (B=97) all in the *Bathyancistrolepis*-clade. *Metajapelion pericochlion* is clustering with high support with *Metajapelion adelphicus* (B=100). *Plicifusus rhyssus* is clustering with *Anomalisipho verkruezeni* and “*Colus*” *kujianus* (B=100). Four sequenced specimens of *Pisania striata* fell in the *Pisania*-clade, although not forming any supported grouping within it. The phylogenetic position of *Japeuthria ferrea* for which the sequences of *cox1*, 16S, and H3 (although, obtained from different individuals) were available from the GenBank was checked by adding these sequences to our Buc5G dataset. The species forms the first offshoot of *Siphonalia*-clade with the maximal support (Fig. S2).

## DISCUSSION

### IMPLICATIONS OF THE PHYLOGENETIC ANALYSIS FOR THE TAXONOMY OF BUCCINOIDEA

At this stage, pending the results of the analysis of a dataset with broader neogastropod taxon sampling and with broader genome sampling, we cannot confirm the monophyly of the superfamily Buccinoidea, which is not supported in the ML analysis. Thus, for convenience, we accept the usage of the name Buccinoidea for the currently accepted extension of this superfamily. Of the molecular clades resulting from the phylogenetic analysis, seven (*Belomitra*-clade, *Buccinum*-clade, *Colubraria*-clade, *Columbella*-clade, *Fasciolaria*-clade, *Melongena*-clade, and *Pisania*-clade) can be allocated to accepted families (Bouchet *et al.*, 2017), and the status and naming of the remaining ones is addressed in the present section.

The *Belomitra*-clade corresponds to the monotypic family Belomitridae in its current scope. Based on the supported affinity of the *Belomitra*- (and *Dolicholatirus*-) clades and their similar radulae, a possible option could be to expand Belomitridae to include *Dolicholatirus* and

1 allied genera in their own belomitrid subfamily. However, as members of *Dolicholatirus* and  
2 *Crassicantharus* show absolutely no conchological resemblance to species of *Belomitra*, we  
3 retain Belomitridae in its current scope, and establish a new family Dolicholatiridae for  
4 *Dolicholatirus* and allied genera, as defined by the contents of our *Dolicholatirus*-clade and the  
5 analysis of Couto *et al.* (2016).

6 The *Colubraria*-clade comprises the type species of *Colubraria*, *C. muricata*, as well as  
7 members of four other colubrariid genera, and therefore corresponds to the Colubrariidae, now  
8 globally accepted at the rank of family. The *Colus*- and *Eosipho*-clades of the CCBA grouping  
9 exclusively comprise taxa that are currently placed in Buccinidae, while being clearly not related  
10 to the *Buccinum*-clade (the latter recovered in the core Buccinoidea grouping, see below). Taking  
11 into account the family rank of the *Colubraria*-clade, we treat the *Colus*- and *Eosipho*-clades at  
12 the same rank. Because of differences in ecology (representatives of *Eosipho*-clade live in  
13 hydrothermal vents, methane seeps and sunken-wood habitats, while representatives of the  
14 *Colus*-clade dwell in ambient subtidal and bathyal benthic communities), distribution (only  
15 boreal and Arctic waters for *Colus*-clade, versus broad tropical and subtropical distribution for  
16 the *Eosipho*-clade), and morphology (radula) we cannot unite these two clades in a single family.  
17 The name Colusinae was established for *Colus* and some other genera and (despite  
18 nomenclatural problems discussed in the Taxonomy section) is herein applied at the rank of  
19 family to the *Colus*-clade. The *Eosipho*-clade was dealt with by Kantor *et al.* (2013), but no  
20 available name exists for it and we therefore here propose for it a new family Eosiphonidae fam.  
21 nov. For the *Prosipho*-clade, the name Prosiphoninae, established at the rank of subfamily and  
22 currently (Bouchet *et al.*, 2017) accepted as a tribe within Buccinidae, is raised to family rank as  
23 Prosiphonidae.

24 The placement of the *Buccinum*-clade naturally defines the application of the name  
25 Buccinidae. Our analysis suggests that the family in its traditional scope is paraphyletic and  
26 several of its traditional constituent taxa are here split from it at family rank. Nevertheless, we  
27 demonstrate that four phylogenetic lineages (plus the genus *Anomalisipho*), namely the  
28 *Neptunea*-clade, *Beringius*-clade, *Volutopsius*-clade, and *Bathyancistrolepis*-clade (the latter,  
29 based on *cox1*, also comprising the genus *Ancistrolepis*, *Parancistrolepis* and *Pseudoliomesus*),  
30 are closely related to the *Buccinum*-clade. These five clades, together forming the well-supported  
31 Bu-grouping, correspond to the five subfamilies traditionally recognized within the Buccinidae:  
32 Buccininae, Neptuneinae, Beringiinae, Volutopsiinae and Parancistrolepidinae (=   
33 Ancistrolepidinae). The *Siphonalia*-clade is recovered as the sister group to the Bu-grouping in  
34 our multigene analyses, also with consistently high support. *Siphonalia* is the type genus of the  
35 subfamily Siphonaliinae and this name can naturally be applied to this clade. The taxonomic  
36 extension of the family Buccinidae can be restricted to the boundaries of the Bu-grouping,  
37 leading to a family Buccinidae with five subfamilies and a subfamily Siphonaliinae, or  
38 alternatively it can be defined to include the Bu-grouping plus the *Siphonalia*-clade, leading to a  
39 single family Buccinidae. Here we favor the second option and include the *Siphonalia*-clade as a  
40 sixth subfamily. The rationale for this decision is that representatives of the *Siphonalia*-clade are  
41 rather heterogeneous morphologically and lack any morphological and anatomical characters  
42 that would allow them to be unambiguously distinguished from the Bu-grouping, itself highly  
43 morphologically heterogeneous.

44 All the members of the family Fascioliariidae included in our analysis, except the  
45 *Dolicholatirus*-clade, have clustered in the Fa-grouping. Therefore, we recognize the Fa-

1  
2 1 grouping as the family Fasciolariidae. Branching within the Fa-grouping is consistent with the  
3 2 division into three subfamilies, as was previously concluded by Couto *et al.* (2016).

4 3 Within the BB-grouping, the family group name Busyconidae — currently accepted either  
5 4 as a subfamily of Buccinidae (*e.g.* MolluscaBase, 2020) or a separate family (*e.g.* Petuch *et al.*,  
6 5 2015) — is available for the *Busycon*-clade. Based on the demonstrated lack of immediate  
7 6 relationship to the Buccinidae as circumscribed herein, we confirm the rank of the *Busycon*-clade  
8 7 as the family Busyconidae. *Buccinanops* was traditionally classified in the Nassariidae, where  
9 8 the subfamily Buccinanopsinae was established by Galindo *et al.* (2016), reflecting the isolated  
10 9 position of *Buccinanops* in their phylogenetic reconstructions. However, our results show that  
11 10 *Buccinanops* is not related to the Nassariidae, and it also differs notably in conchological and  
12 11 radula characters from members of the phylogenetically close *Busycon*-clade. Therefore, we rank  
13 12 the *Buccinanops*-clade as a separate family Buccinanopsidae. *Macron lividus* is the closest  
14 13 relative of the *Buccinanops* clade, and its placement is addressed below in the taxonomic section.

15 14 The name Cominellinae (originally a subfamily within Buccinidae) is naturally available  
16 15 for the *Cominella*-clade. As the *Cominella*-clade showed no affinity to the Buccinidae, and is not  
17 16 included in any larger, supported cluster within the core Buccinoidea, we raise it to family rank  
18 17 as Cominellidae. Members of the *Cominella*-clade and the *Retimohnia*-clade are morphologically  
19 18 highly dissimilar, and there is no family-group name available for the latter. Therefore, we  
20 19 introduce a new family Retimohniidae for the genera *Retimohnia* and *Fusipagoda*.

21 20 Australian and New Zealand species as well as north Pacific *Kelletia* spp. from the highly  
22 21 supported PB grouping were recently analysed by Vaux *et al.* (2017), who generated for these  
23 22 taxa most of the DNA sequences that are included in our analysis. Although they used rather few  
24 23 buccinoidean outgroups in their analysis, Vaux *et al.* identified a close affinity of the genera  
25 24 *Penion*, *Kelletia*, *Buccinulum*, *Aeneator* and *Antarctoneptunea*, and concluded that their  
26 25 placement in a single subfamily (Buccinulinae) is reasonable. Our analysis, however, reveals that  
27 26 the relationships of these genera are more complex, mainly because the genera *Aeneator* and  
28 27 *Buccinulum* are actually closer (in the multigene dataset) to the cosmopolitan genus *Euthria* and  
29 28 (in the expanded *cox1* dataset) to the tropical Indo-Pacific genera *Afer* and *Tudicla*, than to  
30 29 *Penion*, *Kelletia* and *Antarctoneptunea*. The members of the *Buccinulum*-clade share a  
31 30 synapomorphic feature in radular morphology: a distinct narrowing of the anterior edge of the  
32 31 central tooth, giving it a trapezoid, or sometimes nearly triangular, shape (see Fig. 18G-P). Such  
33 32 tooth shape has not been observed in species of the *Penion*-clade, nor in any other clades of the  
34 33 Buccinoidea. In light of these new results, we conclude that the two clades should be classified  
35 34 as two separate families. The family name Austrosiphonidae was proposed based on the fossil  
36 35 genus *Austrosipho*, currently considered a synonym of *Penion*. We apply it herein to the *Penion*-  
37 36 clade. Based on our results, the name Tudiclidae applies to the *Buccinulum*-clade, and has a  
38 37 priority over the junior (although widely used) name Buccinulidae. Thus, we here ascribe the  
39 38 name Tudiclidae to the *Buccinulum*-clade.

40 39 The *Melongena*-clade comprises species representing three genera currently included in the  
41 40 family Melongenidae, among them *Melongena melongena*, the type species of *Melongena*.  
42 41 Therefore, we identify this clade as the family Melongenidae. The genera currently included in  
43 42 Pisaniidae fall in two separate clades: the *Pisania*-clade and the *Prodotia*-clade (Fig. 1), and the  
44 43 tree suggests the polyphyly of the family as currently defined. All three species of the genus  
45 44 *Pisania* included in our multigene analyses were recovered in the former clade, as well as  
46 45 *Pisania striatula* (the type of the genus), included in our expanded *cox1* dataset. Although the

1 analyzed species of *Pisania* do not form a monophyletic cluster and suggest the polyphyly of the  
 2 genus, the position of *P. striatula* allows us to unequivocally apply the name Pisaniidae to the  
 3 *Pisania*-clade. In most of our reconstructions, the *Chauvetia*-clade forms a sister group to the  
 4 Pisaniidae, and species of *Chauvetia* possess a clearly divergent radula, with a unicuspid or  
 5 acuspate central tooth and with the bases of the laterals extending to form a ‘handle’ (see Fig.  
 6 20B), very unlike the radulae in the Pisaniidae examined (see Fig. 22). Despite several family-  
 7 group names have been proposed for *Chauvetia*, none of them is nomenclaturally available  
 8 (Gofas & Oliver, 2010) and the new family Chauvetiidae is established herein for the *Chauvetia*-  
 9 clade. As there is no family-group name available for the *Prodotia*-clade, we also introduce a  
 10 new family Prodotiidae for it.

11 The application of names to the clades resulting from our phylogenetic analysis is most  
 12 difficult in the NaCo-grouping, mainly because the distinctive families Nassariidae and  
 13 Columbidae are not resolved as reciprocally monophyletic clades. All analyzed members of  
 14 the family Columbidae cluster in a monophyletic *Columbella*-clade, with the name  
 15 Columbidae readily applicable to it. This clade occupies the most derived position in the  
 16 NaCo-grouping, making the traditionally accepted Nassariidae (sensu Galindo *et al.*, 2016)  
 17 paraphyletic. The *Phos*-clade, representing the subfamily Photinae, branches off first. The next  
 18 offshoot is the large nassariid cluster combining the *Bullia*-clade (consistent with the subfamily  
 19 Bullinae), the *Anentome*-clade (consistent with the subfamily Anentominae), the *Nassarius*-  
 20 clade, and three species related to it. The latter can either be entirely attributed to the subfamily  
 21 Nassariinae, or subdivided into Nassariinae and Dorsaninae. The third offshoot is a distinctive  
 22 clade combining species of the genera *Tomlinia* and *Nassaria*; no family-group name exists for  
 23 this clade. Finally, the *Cyllene*-clade (consistent with the nassariid subfamily Cylleninae) forms a  
 24 sister group to the *Columbella*-clade. Thus, the topology of our tree supports six or seven  
 25 distinctive phylogenetic clusters within what is now treated as Nassariidae, and these clusters  
 26 generally align with the currently recognized subfamilies. The lack of nodal support and  
 27 morphological criteria does not justify raising the nassariid subfamilies to full families.  
 28 Additionally, the close relationship between Columbidae and Nassariidae was not recovered in  
 29 previous molecular phylogenies. In the reconstructions of Galindo *et al.* (2016), the  
 30 Columbidae form one of the early offshoots of Buccinoidea with moderately high PP support  
 31 (0.94), while in the phylogenetic reconstruction of Strong and DeMaintenon (in preparation,  
 32 personal communication) the Columbidae form a sister group to the Fascioliariidae. This  
 33 diverging hypotheses cannot presently be resolved and, in order to minimize premature  
 34 taxonomic changes, we do not make revisions to the contents of the Nassariidae other than the  
 35 exclusion of Buccinanopsinae. The position of Columbidae within Buccinoidea remains  
 36 uncertain, and deserves further studies with broader genomic sampling.

37 Our analysis provides a phylogenetic framework which allows to test the validity of the  
 38 morphology-based family group taxa previously proposed in Buccinoidea. The latest  
 39 classification of the superfamily (Bouchet *et al.*, 2017) recognized eight families and 18  
 40 subfamilies (including four nominotypical ones). Most of the family-group taxa recognized in  
 41 that work were here proven valid, although their composition has in many cases been changed.  
 42 The present phylogeny-based classification recognizes 20 family level taxa and 22 subfamilies  
 43 (including five nominotypical ones). Several taxa previously treated in Bouchet *et al.* (2017) as  
 44 subfamilies or tribes are now raised to full families (Table 1): Colidae Gray, 1857, Prosiphonidae  
 45 Powell, 1951, Cominellidae Gray, 1857, Tudicidae Cossman, 1901, Buccinanopsidae Galindo,

1 Puillandre, Lozouet & Bouchet, 2016, and Austrosiphonidae Cotton & Godfrey, 1938.  
 2 Additionally, previously unrecognized lineages are revealed and are described below as new  
 3 taxa: Retimohniidae fam. nov., Prodotiidae fam. nov., Eosiphonidae fam. nov., and Tomliniinae  
 4 subfam. nov. (Nassariidae). We present below a revised classification of the superfamily with the  
 5 description of new taxa, including the generic composition of every family-group taxon, based  
 6 on molecular and in some cases morphological evidence. We did not consider in detail the  
 7 composition and scope of the family Fasciolariidae, because it was the subject of a molecular  
 8 phylogeny by Couto *et al.* (2016), and Columbelloidea, because it is being separately re-assessed  
 9 by M. deMaitenon and E. Strong (personal communication).

10  
 11 CLASS GASTROPODA CUVIER, 1795  
 12 SUBCLASS CAENOGASTROPODA COX, 1960  
 13 ORDER NEOGASTROPODA WENZ, 1938  
 14 SUPERFAMILY BUCCINOIDEA RAFINESQUE, 1815  
 15 FAMILY **DOLICHOLATIRIDAE FAM. NOV.**  
 16 (Figs 3A–E; 4A–C)

17  
 18 Type genus: *Dolicholatirus* Bellardi, 1884

19  
 20 Included genera:

21 *Crassicantharus* Ponder, 1972 (TS *Crassicantharus norfolkensis* Ponder, 1972; OD) <sup>(1)</sup>

22 *Dolicholatirus* Bellardi, 1884 (TS †*Fusus bronni* Michelotti, 1847; SD, Cossmann, 1901) <sup>(1)</sup>

23 *Teralatirus* Coomans, 1965 (TS *Latirus ernesti* Melvill, 1910 [= *Teralatirus roboreus* (Reeve,  
 24 1845)]; OD) <sup>(1)</sup>

25  
 26 **Diagnosis.** Shell small to medium large (60 mm), from broad to narrow fusiform or turritiform.  
 27 Spire tall, siphonal canal from very short to very long, constituting nearly half of SL. Protoconch  
 28 paucispiral, with smooth initial part and later whorls sometimes bearing axial ribs. Spiral  
 29 sculpture of fine to strong cords, sometimes pronounced only in interspaces between axial ribs.  
 30 Axial sculpture of strong, broad axial ribs present in most species. Columella sometimes with  
 31 two weak columellar plaits. Shell usually of dark colour, sometimes with brightly coloured spiral  
 32 bands. Operculum with terminal nucleus or paucispiral.

33 Radula (Fig. 4A–C) with squarish, narrow central tooth with three closely spaced cusps,  
 34 lateral cusps distinct or nearly obsolete. Lateral teeth long, with base forming about a third of  
 35 total tooth length, narrowing towards its tip, bearing two cusps, inner one much longer and  
 36 constituting about a third of total tooth length; sometimes an additional small cusp on the inner  
 37 internal side of the tooth, close to its base and not seen in dorsal view (Fig. 4B).

38 Proboscis medium long and very narrow, single or paired ventral proboscis retractor,  
 39 attached to anterior or medium part of rhynchodaeum. Salivary glands paired, large. Oesophagus  
 40 very narrow. Valve of Leiblein spherical, 6 or 7 times wider than the very narrow oesophagus,  
 41 gland of Leiblein tubular or bulky, medium to large.

42 **Distribution.** From the lower intertidal to lower bathyal depths in the tropical Pacific and  
 43 Atlantic.

44 **Remarks.** The genera included in Dolicholatiridae have traditionally been classified in  
 45 Fasciolariidae, but Ponder (1972) already noticed the uniqueness of the radula and protoconch  
 46 morphology of *Crassicantharus*. That genus was later referred to the Buccinoidea without

definite family allocation (Fraussen & Stahlschmidt, 2015), and *Dolicholatirus* was also at some point tentatively attributed to the Turbinellidae (Vermeij & Snyder, 2006: 414). Based on a multilocus molecular phylogeny, Couto *et al.* (2016) demonstrated that seven species in the genera *Dolicholatirus* and *Teralatirus* formed a clade unrelated to the rest of the Fascioliariidae, but no formal taxonomic conclusion was then made.

The radular morphology of Dolicholatiridae is very characteristic and bears some resemblance to the Belomitridae, their sister taxon in our phylogeny, in having long and narrow lateral teeth with cusps closer to the tip (Fig. 4).

The genera here included in the family need taxonomic revision, since *Dolicholatirus* was not recovered monophyletic, while *Crassicantharus noumeensis* (Crosse, 1870), sometimes referred to *Teralatirus*, did not cluster with *T. roboreus*, the type species of *Teralatirus*, in the molecular tree of Couto *et al.* (2016).

The anatomy of *Teralatirus roboreus* was examined by Simone *et al.* (2013), and of *Dolicholatirus lancea* and *Crassicantharus noumeensis* by ourselves (original unpublished data). Simone *et al.* (2013: 222) remarked the presence of an enigmatic “oesophageal gland”, not separated from the posterior oesophagus, and the absence of the gland of Leiblein. In *Dolicholatirus* and *Crassicantharus*, there is a distinct gland of Leiblein that runs dorsally along the oesophagus, and is similar to the “oesophageal gland” reported by Simone *et al.* (2013).

FAMILY BELOMITRIDAE KANTOR, PULLANDRE, RIVASSEAU & BOUCHET, 2012  
(Figs 3F, G, 4D–F)

Type genus: *Belomitra* P. Fischer, 1883

Included genera:

*Belomitra* P. Fischer, 1883 (TS *Belomitra paradoxa* P. Fischer, 1883; M) <sup>(1)</sup> (see Kantor *et al.*, 2012 for synonymy)

**Diagnosis.** Shell small (7 mm) to medium large (over 50 mm), turritiform, with high spire and short siphonal canal. Protoconch paucispiral, white. Subsutural ramp usually well pronounced, followed by distinct shoulder. Shell sculpture consisting of axial ribs present at least on spire whorls, and spiral cords, sometimes forming knobs at intersections with axial ribs. Columella sometimes with weak plaits. Shell colour white or pale olive-grey, sometimes with thick olivaceous periostracum. Operculum present or absent, when present with terminal nucleus.

Radula (Fig. 4D–F) with central tooth with rectangular or trapeziform base and 3–8 cusps; lateral teeth with very long narrow base and two small cusps closer to tip. Proboscis medium-long to long, proboscis retractors multiple, attached laterally to central portion of rhynchodaeum. Paired large salivary glands, salivary ducts follow inside oesophagus walls. Gland of Leiblein very large, valve of Leiblein well defined. Stomach without posterior mixing area. (Anatomy description based on several species studied by Kantor *et al.*, 2012).

**Distribution.** Temperate to tropical Atlantic, entire Pacific and Indian oceans at bathyal depths.

**Remarks.** The relationships of Belomitridae to other Buccinoidea were previously uncertain due to the very limited dataset used in the original molecular phylogenetic analysis (Kantor *et al.*, 2012). The present analysis shows a highly supported relationship with the family



1  
2 1 Dolicholatiridae fam. nov., from which the Belomitridae differ in having a relatively larger  
3 2 proboscis and a much thicker oesophagus, as well as a larger gland of Leiblein terminating in an  
4 3 ampulla.  
5 4

6 4  
7 5 FAMILY COLUBRARIIDAE DALL, 1904  
8 6 (Figs 5A–E, 6A–C)  
9 7

10 8 Type genus: *Colubraria* Schumacher, 1817  
11 9

12 10 = Fusidae Iredale, 1915. Type genus: *Fusus* Helbling, 1779. Invalid name: type genus placed on  
13 11 the Official Index by ICZN Opinion 1765 (1994).

14 12 = Kanamaruidae Higo & Goto, 1993. Type genus: *Kanamarua* Kuroda, 1951.  
15 13

16 14 Included genera:

17 15 *Axifex* S.-I Huang & M.-H. Lin, 2019 (TS *Axifex retis* S.-I Huang & M.-H. Lin, 2019; OD)<sup>(3)</sup>

18 16 *Bartschia* Rehder, 1943 (TS *Bartschia significans* Rehder, 1943; OD)<sup>(3)</sup>

19 17 *Colubraria* Schumacher, 1817 (TS *Colubraria granulata* Schumacher, 1817 [= *Colubraria*  
20 18 *muricata* ([Lightfoot], 1786)]; M)<sup>(1)</sup>

21 19 *Cumia* Bivona-Bernardi, 1838 (TS *Cumia decussata* Bivona-Bernardi, 1838 [= *Cumia reticulata*  
22 20 (Blainville, 1829)]; M). Synonym: *Fusus* Helbling, 1779 (TS *Murex intertextus* Helbling,  
23 21 1779; SD, Dall, 1906). Invalid: type genus placed on the Official Index by ICZN Opinion  
24 22 1765 (1994).<sup>(1)</sup>

25 23 *Cyclimetula* S.-I Huang & M.-H. Lin, 2019 (TS *Cyclimetula hsui* S.-I Huang & M.-H. Lin, 2019;  
26 24 OD)<sup>(3)</sup>

27 25 *Iredalula* Finlay, 1926 (TS †*Bela striata* Hutton, 1873; OD)<sup>(3)</sup>

28 26 *Kanamarua* Kuroda, 1951 (TS *Colus adonis* Dall, 1919; OD)<sup>(1)</sup>

29 27 *Metula* H. Adams & A. Adams, 1853 (TS *Buccinum clathratum* A. Adams & Reeve, 1850 [=  
30 28 *Metula knudseni* Kilburn, 1975]; SD, Kobelt, 1876)<sup>(1)</sup>

31 29 *Minibraria* Sarasúa, 1984 (TS *Colubraria monroei* McGinty, 1962; OD)<sup>(3)</sup>  
32 30

33 31 **Diagnosis.** Shell medium large to large, reaching over 110 mm, from narrow fusiform to broad  
34 32 fusiform, with medium to high spire and short but distinct siphonal canal. Protoconch usually  
35 33 paucispiral of 1–2.5 smooth whorls, up to 4 whorls (*Metula*). Spire whorls evenly convex,  
36 34 without pronounced shoulder. Axial sculpture present or absent, when present of distinct narrow  
37 35 and closely spaced axial ribs, crossing the spiral cords and forming reticulated sculpture pattern,  
38 36 often with regularly or irregularly spaced varices. Spiral sculpture of very weak threads, or fine,  
39 37 regularly set, beaded cords, or strong spiral cords forming knobs at intersection with axials.  
40 38 Aperture medium to high, lanceolate due to sharp posterior corner. Outer lip usually lirate inside,  
41 39 smooth in some species of *Kanamarua*. Columella smooth, often heavily callused. Operculum  
42 40 oval, spanning about half aperture, with terminal nucleus shifted leftwards.

43 41 Radula very small, variable in teeth morphology. In *Colubraria* central tooth broadly  
44 42 arcuate, with about 10, subequal, relatively long cusps; lateral teeth very broad, with 10 or 11  
45 43 subequal cusps, gradually diminishing towards inner side (Fig. 6A). In *Cumia*, *Iredalula* and  
46 44 *Metula*, teeth more narrow, central with 3–7 relatively short and broadly spaced cusps; laterals  
47 45 with 3 or 4 cusps (Fig. 6B, C). Proboscis extremely long and narrow, multiple coiled within  
48 46 rhynchocoel. Proboscis retractors paired, attached to the base or middle part of rhynchodaeum.

1 Valve of Leiblein either absent or poorly defined, gland of Leiblein absent, salivary glands  
 2 medium-sized, not fused, ducts entering oesophagus wall soon after leaving glands, and  
 3 following within it. Middle oesophagus very narrow when passing through nerve ring, posterior  
 4 oesophagus greatly expanded, muscular. Stomach large, sac-like, thin-walled, straight, tapering  
 5 posteriorly towards the very narrow intestine.

6 **Distribution.** Temperate to tropical Indo-Pacific and Atlantic, from subtidal to several  
 7 hundred meters.

8 **Remarks.** The anatomy of several species was examined by Ponder (1968) and Oliverio &  
 9 Modica (2010). At least *Colubraria* and *Cumia* are haematophagous, feeding on the blood of  
 10 sleeping parrot fishes (Scaridae) and occasionally of other fishes (Bouchet & Perrine 1996;  
 11 Oliverio & Modica, 2010). The very similar anatomy of *Metula* suggests similar feeding habits,  
 12 but these have not been observed.

#### 14 FAMILY COLIDAE GRAY, 1857 (new rank)

15 (Figs 5F–L, 6D)

17 Type genus: *Colus* Röding, 1798

19 Included genera:

20 *Colus* Röding, 1798 (TS *Murex islandicus* Mohr, 1786; SD, Dall, 1906) <sup>(1)</sup>

21 *Turrisipho* Dautzenberg & H. Fischer, 1912 (TS *Fusus lachesis* Mörch, 1869; OD) <sup>(1)</sup>

23 **Diagnosis.** Shell thin-walled, medium-large to large, reaching 200 mm, fusiform to broad  
 24 fusiform or ovate, with moderately high to very high spire and distinct, slender, moderately long  
 25 to long siphonal canal. Protoconch either medium-large, paucispiral of up to 2.5 smooth whorls  
 26 (*Colus*) or with small smooth nucleus and remaining whorls with distinct spiral keels and unclear  
 27 protoconch / teleoconch transition (*Turrisipho*). Shoulder not pronounced, whorls evenly  
 28 (sometimes strongly) convex, or with flattened abapical portion and whorl periphery. Axial  
 29 sculpture absent, spiral sculpture of cords of varying strength and width, from very weak to  
 30 distinct and evenly spaced. Aperture moderately high to high, broadly ovate; outer lip simple.  
 31 Shell covered with brown periostracum, siphonal canal and inside of aperture off-white.  
 32 Operculum large, ovate to triangular, with terminal nucleus shifted adaxially, in *Turrisipho*  
 33 nucleus drawn out into a small apical point.

34 Central tooth with rectangular or nearly square bases arcuated anteriorly, bearing 1–3  
 35 closely spaced cusps, central one largest. Lateral teeth typically with 3 cusps, outermost much  
 36 longer than others, middle one smallest (Fig. 6D). Proboscis long, straight. Proboscis retractors  
 37 numerous, arranged in bundles attached to lateral sides of rhynchodaeum. Salivary glands  
 38 moderately large, not fused. Gland of Leiblein moderately large, broad, tubular and folded  
 39 anteriorly, valve of Leiblein poorly defined. Stomach with short posterior mixing area.

40 **Distribution.** Northern Atlantic and Arctic Oceans, from subtidal to bathyal depths.

41 **Remarks.** The use of the name Colidae for this clade is fraught with nomenclatural  
 42 difficulty. The concept of the genus name *Colus* has differed significantly in the publications of  
 43 various authors, due to the late fixation of the type species by Dall (1906). When he established  
 44 the name *Colus*, Röding (1798) included in it species that are presently attributed to several  
 45 families, including Fasciolaridae (e.g. *Murex tulipa* Linnaeus, 1758 [now *Fasciolaria tulipa*])  
 46 and Buccinidae (*Murex islandicus* Mohr, 1786). When he established the subfamily Colinae of

the family Muricidae, Gray (1857: 12, as *Colusina*) also treated *Colus* as a genus mostly including species of present day Fascioliidae, but also a species of Austrosiphonidae (*Fusus dilatatus* Quoy & Gaimard, 1833 [= *Penion sulcatus* (Lamarck, 1816)]). Nevertheless he also included in the subfamily the genera *Chrysodomus* Swainson, 1840 (= *Neptunea* Röding, 1798) and *Strombella* Gray, 1857 (= *Volutopsius* Mörch, 1857); *Murex islandicus* Mohr, 1786, that later (Dall 1906) would fix as the type species of *Colus*, was attributed to *Chrysodomus*. Cotton & Godfrey (1932) used the family name Colidae in the sense of a fascioliid. Ponder & Warén (1988) treated Colinae as a synonym of Buccinidae, not Fascioliidae, while Bouchet & Rocroi (2005) and Bouchet *et al.* (2017) used it for a tribe (Colini) of Buccinidae, as a senior synonym of Neptuneinae Stimpson, 1865; the name Colinae was repeatedly used since 2005 by Kosyan and co-authors (e.g. Kosyan, 2006; Kosyan & Kantor, 2013, 2014; 2015, 2016). This is a situation covered by Art. 65.2 of the ICZN, and the case is to be referred to the Commission for a ruling. Despite this nomenclatural problem, we prefer to use at present the name Colidae in the sense already accepted by Bouchet & Rocroi (2005) and Bouchet *et al.* (2017) and later authors, with the authorship of Gray (1857), pending an application to the Commission.

At this moment, we only attribute two genera to Colidae, both based on molecular data. The shell, body morphology and radula of Colidae do not display any unique characters and hardly offer reliable proxies for family recognition. There are a number of genera that can possibly belong to Colidae, among them *Helicofusus* Dall, 1916, *Kryptos* Dautzenberg & H. Fischer, 1896, which have a radula similar to those of *Colus* species, but similar radulae are also found in Buccinidae s.s. (e.g., *Aulacofusus* Dall, 1918). For now we refrain from placing them in Colidae pending further molecular data.

#### FAMILY EOSIPHONIDAE FAM. NOV.

(Figs 6E–L, 7)

Type genus: *Eosipho* Thiele, 1929

Included genera:

*Americominella* Klappenbach & Ureta, 1972 (TS *Americominella duartei* Klappenbach & Ureta, 1972; OD)<sup>(2)</sup> — radula, see Penchaszadeh *et al.* (2019)

*Calagrassor* Kantor, Puillandre, Fraussen, Fedosov & Bouchet, 2013 (TS *Cantharus aldermenensis* Powell, 1971; OD)<sup>(1)</sup>

*Eclectofusus* Fraussen & Stahlschmidt, 2013 (TS *Pararetifusus dedonderi* Fraussen & Hadorn, 2001; OD)<sup>(1)</sup>

*Enigmaticolus* Fraussen, 2008 (TS *Enigmaticolus monnieri* Fraussen, 2008 [= *E. nipponensis* (Okutani & Fujiwara, 2000)]; OD)<sup>(1)</sup>

*Eosipho* Thiele, 1929 (TS *Chrysodomus smithi* Schepman, 1911; OD)<sup>(1)</sup>

*Gaillea* Kantor, Puillandre, Fraussen, Fedosov & Bouchet, 2013 (TS *Eosipho coriolis* Bouchet & Warén, 1986; OD)<sup>(1)</sup>

*Manaria* E.A. Smith, 1906 (TS *Manaria thurstoni* E.A. Smith, 1906; M)<sup>(1)</sup>

*Preangeria* K. Martin, 1921 (TS †*Preangeria angasanana* K. Martin, 1921; OD)<sup>(2)</sup> — radula, see Bouchet & Warén (1986: *Preangeria dentata* (Schepman, 1911), as *Eosipho dentatus*)

1 *Thermosipho* Kantor, Puillandre, Fraussen, Fedosov & Bouchet, 2013 (TS *Eosipho auzendei*  
2 Warén & Bouchet, 2001; OD) <sup>(1)</sup>

3 *Warenius* Kantor, Kosyan, Sorokin, Herbert & Fedosov, 2020 (TS *Costaria crosnieri* Bouchet &  
4 Warén, 1986; OD) <sup>(1)</sup>

5  
6  
7  
8  
9 **Diagnosis.** Shell medium-sized to large, from slightly over 10 mm to 100 mm, from ovate to  
10 narrowly fusiform. Siphonal canal from nearly absent (*Thermosipho*) to long (*Manaria*).  
11 Protoconch small, often eroded, paucispiral when known, with less than 2 whorls. Spire whorls  
12 usually evenly convex, rarely shouldered mainly due to axial sculpture. Axial sculpture either  
13 absent (*Thermosipho*, “*Aulacofusus*” *hiranoi*) or represented by very weak to strong ribs or  
14 wide, rounded folds. Spiral sculpture (except *Thermosipho* with smooth shell) of distinct cords of  
15 uneven strength, breadth and density. In *Eclectofusus* sculpture forms a reticulated pattern due to  
16 the intersection of narrow axial ribs and broadly spaced spiral cords. Aperture ovate or elongate,  
17 with smooth inner and outer lip, or a bearing labral tooth (*Preangeria*). Shell covered with  
18 periostracum, from smooth to hirsute, or forming spines (*Americominella*). Operculum leaf  
19 shaped, with terminal nucleus.

20 Radula variable (Fig. 6E–L). In most genera lateral teeth with two large cusps, subequal  
21 or outer one longer. Central with three large cusps and subrectangular base notched anteriorly  
22 (Fig. 6E–G). In *Eclectofusus* lateral teeth have three cusps, central shortest (Fig. 6H, I). In  
23 *Warenius* radula very different, with lateral teeth with three cusps with bifurcating outer one.  
24 Central tooth narrow and long, constricted anteriorly and broadened posteriorly with posterior  
25 margin bearing three cusps, central one shortest (Fig. 6K).

26 Proboscis long to very long and coiled within rhynchocoel. Salivary glands medium  
27 large, fused. Posterior oesophagus with distinct caecum. Gland of Leiblein large, bulky, broadly  
28 tubular and folded anteriorly, valve of Leiblein prominent. Stomach U-shaped with hardly  
29 discernible posterior mixing area.

30 **Distribution.** Tropical and temperate south-western Atlantic, Western and Central Indo-  
31 Pacific, and temperate northern Pacific from upper subtidal to lower bathyal depths.

32 **Remarks.** This clade combining several genera from different biogenic substrates was first  
33 discovered and characterized by Kantor *et al.* (2013) and is herein expanded to include several  
34 additional genera (*Eclectofusus*, *Americominella*, *Preangeria* and *Warenius*).

35 The anatomy of *Enigmaticolus* and *Calagrassor* has been described by Kantor *et al.*  
36 (2013).

37 The first branch of the family to diverge from the others is “*Aulacofusus*” *hiranoi*  
38 (Shikama, 1962), described as *Colus calameus hiranoi* and transferred to *Aulacofusus* by Higo *et*  
39 *al.* (1999: 229), a transfer later accepted (Hasegawa, 2009; Kosyan & Kantor, 2013). Hasegawa  
40 (2009] mentioned that “juvenile specimens smaller than ca 1.5 cm SL were found attached to  
41 pieces of sunken wood, and a similar ecology has been observed in *A. coeruleascens* (Kuroda &  
42 Habe in Habe, 1961)”. Its generic allocation is, however, unconfirmed since it is conchologically  
43 somewhat different from other *Aulacofusus* and the radula and anatomy have not been  
44 examined. “*A.*” *hiranoi* may belong to a new genus (see Discussion section of the subfamily  
45 Neptuneinae).

46 In our analysis, *Manaria* is found polyphyletic, as *Manaria fluentisona* Fraussen &  
47 Stahlschmidt, 2016 (Fig. 7F) clusters with species of *Eclectofusus*. Conchologically, it is  
48 particularly similar to *E. dedonderi* (Fraussen & Hadorn, 2001) (Fig. 7G) in the reticulated

1 sculpture pattern and strong periostracum, and we thus transfer *Manaria fluentisona* to  
2 *Eclectofusus*.

3 One specimen (MNHN IM-2013-60365; Fig. 7L) from the upper bathyal of Guadeloupe  
4 has a shell similar to *Calagrassor*, but differs in having a slightly angulated shoulder and a  
5 weakly concave subsutural region, which is evenly convex in known species of *Calagrassor*. It  
6 occupies an isolated position in the multigene tree, and probably represents a new species and  
7 genus of Eosiphonidae.

8 The genus *Americominella* includes two species and is attributed to the family on the basis  
9 of radula and, to some extent, shell similarities between the type species, *A. duartei*, and  
10 *Eclectofusus dedonderi*, as mentioned by Fraussen & Hadorn (2001).

11 Representatives of the family are colonizing three major types of biogenic substrates:  
12 hydrothermal vents, methane seeps and sunken wood (Kantor *et al.*, 2013). *Thermosipho* and  
13 *Enigmaticolus* are specialized on vents and seeps. At least one species, *Calagrassor*  
14 *aldermenensis* is known to inhabit exclusively sunken logs, hiding deep inside holes. Many other  
15 species of *Calagrassor* and *Eosipho* are often found in hauls containing sunken wood, but not  
16 attached to the logs themselves, so we only have indirect evidence of their association with  
17 wood. *Manaria* specimens, together with *Calagrassor aldermenensis*, were recovered from traps  
18 deployed in deep water off Santo, Vanuatu, containing wood and protected by a netting with a 3  
19 mm mesh, suggesting that the sunken wood is colonized by larvae or very young juveniles.  
20 *Warenius nankaiensis* is associated with seeps (Okutani & Iwasaki, 2003).

21 The marked differences in ecology (ambient bottom communities in the former and  
22 biogenic substrates in the latter), distribution (northern Atlantic and Arctic Ocean vs tropical and  
23 temperate Atlantic and Indo-Pacific) and morphology (radula with tricuspid vs bicuspid lateral  
24 teeth; stomach with short posterior mixing area vs U-shaped stomach lacking posterior mixing  
25 area) reinforces the phylogeny-derived ranking of Colidae and Eosiphonidae as full families.

26  
27 FAMILY PROSIPHONIDAE POWELL, 1951 (new rank)  
28 (Figs 8, 9)

29  
30 Type genus: *Prosipho* Thiele, 1912

31  
32 Included genera:

33 *Anomacme* Strebel, 1905 (TS *Anomacme smithi* Strebel, 1905; M)<sup>(2)</sup>; radula, see Powell (1951)

34 *Antarctodomus* Dell, 1972 (TS *Bathydomus thielei* Powell, 1958; OD)<sup>(1)</sup>

35 *Antistreptus* Dall, 1902 (TS *Antistreptus magellanicus* Dall, 1902; OD)<sup>(2)</sup>; radula, see Pastorino  
36 & Griffin (2019)

37 *Argeneuthria* Pastorino, 2016 (TS *Euthria cerealis* Rochebrune & Mabile, 1885; OD)<sup>(2)</sup>; radula,  
38 see Pastorino (2016)

39 *Austrofusus* Kobelt, 1879 (TS *Fusus nodosus* Gray, 1843 [= *Drupa glans* Röding, 1798]; SD,  
40 Martens, 1882)<sup>(1)</sup>

41 *Bathydomus* Thiele, 1912 (TS *Bathydomus obtectus* Thiele, 1912; M)<sup>(2)</sup>; radula, see Thiele  
42 (1912)

43 *Cavineptunea* Powell, 1951 (TS *Cavineptunea monstrosa* Powell, 1951; OD)<sup>(1)</sup>

44 *Chlanidota* Martens, 1878 (TS *Cominella vestita* Martens, 1878; M)<sup>(1)</sup>

- 1  
2 1 *Chlanidotella* Thiele, 1929 (TS *Cominella modesta* Martens, 1885; OD)<sup>(2)</sup>; radula, see Powell  
3 2 (1951)  
4 3 *Chlanificula* Powell, 1958 (TS *Chlanificula thielei* Powell, 1958; OD)<sup>(2)</sup>; radula, see Hain (1990)  
5 4 *Crenatosipho* Linse, 2002 (TS *Crenatosipho beaglensis* Linse, 2002; OD)<sup>(2)</sup>; radula, see Linse  
6 5 (2002)  
7 6 *Drepanodontus* Harasewych & Kantor, 2004 (TS *Drepanodontus tatyanae* Harasewych &  
8 7 Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)  
9 8 *Falsimacme* Pastorino, 2016 (TS *Euthria kobelti* Strebel, 1905; OD)<sup>(2)</sup>; radula, see Pastorino  
10 9 (2016)  
11 10 *Falsimohnia* Powell, 1951 (TS *Buccinum albozonatum* Watson, 1882; OD)<sup>(1)</sup>  
12 11 *Fusinella* Thiele, 1917 (TS *Buccinella jucunda* Thiele, 1912; by typification of replaced name  
13 12 [*Buccinella* Thiele, 1912])<sup>(2)</sup>; radula, see Thiele (1912)  
14 13 *Germonea* Harasewych & Kantor, 2004 (TS *Germonea rachelae* Harasewych & Kantor, 2004;  
15 14 OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)  
16 15 *Meteuthria* Thiele, 1912 (TS *Euthria martensi* Strebel, 1905, M)<sup>(2)</sup>; radula, see Pastorino (2016)  
17 16 *Muffinbuccinum* Harasewych & Kantor, 2004 (TS *Muffinbuccinum catherinae* Harasewych &  
18 17 Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)  
19 18 *Neobuccinum* E.A. Smith, 1879 (TS *Buccinopsis eatoni* E.A. Smith, 1875; M)<sup>(1)</sup>  
20 19 *Parabuccinum* Harasewych, Kantor & Linse, 2000 (TS *Chlanidota bisculpta* Dell, 1990; OD)<sup>(2)</sup>;  
21 20 radula, see Harasewych *et al.* (2000)  
22 21 *Probuccinum* Thiele, 1912 (TS *Neobuccinum tenerum* E.A. Smith, 1907; SD, Wenz, 1943)<sup>(1)</sup>  
23 22 *Proneptunea* Thiele, 1912 (TS *Proneptunea amabilis* Thiele, 1912; M)<sup>(1)</sup>  
24 23 *Prosipho* Thiele, 1912 (TS *Prosipho gaussianus* Thiele, 1912; SD, Powell, 1951)<sup>(1)</sup>  
25 24 *Savatieria* Rochebrune & Mabile, 1885 (TS *Savatieria frigida* Rochebrune & Mabile, 1885; M)  
26 25 <sup>(2)</sup>; radula, see Luca & Pastorino (2018)  
27 26 *Spikebuccinum* Harasewych & Kantor, 2004 (TS *Spikebuccinum stephaniae* Harasewych &  
28 27 Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)  
29 28 *Strebela* Kantor & Harasewych, 2013 (TS *Bela notophila* Strebel, 1908; OD)<sup>(2)</sup>; radula, see  
30 29 Kantor & Harasewych (2013)  
31 30  
32 31

33 **Diagnosis.** Shell from small (less than 5 mm) to medium large (over 60 mm), thin-walled,  
34 varying from oval without siphonal canal but with siphonal notch, to fusiform with distinct,  
35 attenuated canal. Protoconch when present paucispiral (in most cases dissolved), medium large  
36 of 1.5–2.5 smooth whorls, or multispiral with a small first whorl, suggesting planktonic  
37 development (*Austrofusus*). Shell usually dextral, sinistral in *Antistreptus*. Whorl profile  
38 typically evenly convex. Spiral sculpture usually dominant, represented by cords, from very fine  
39 and closely set to strong and raised or wide and flattened. Axial sculpture usually not  
40 pronounced, when present represented by weak to strong ribs, sometimes forming nodules at  
41 intersection with spiral cords. Aperture wide, with smooth outer lip. Periostracum from thin and  
42 smooth to strong, forming axial lamellae. Shell colour white, whitish, pale, or light brown, inside  
43 of aperture white. Operculum paucispiral or with terminal nucleus.

44 Radula is very variable and can be classified in six different types.

45 1. Lateral teeth with 3–5 cusps, outermost longest, inner one significantly shorter, central  
46 tooth with subsquare or subrectangular base and notched anterior edge and 3–5 sharp cusps (Fig.  
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1  
2 1 9A) — found in *Neobuccinum*, *Probuccinum*, *Chlanidota*, *Austrofusus*, *Cavineptunea*,  
3 2 *Parabuccinum*, *Chlanificula*, *Spikebuccinum*, *Bathydomus*.

4 3 2. Lateral teeth bicuspid, with subequal cusps, and outer portion of basal plate attenuated,  
5 4 long. Central tooth with square base and single, large, pointed cusp (Fig. 9B) — found in  
6 5 *Falsimohnia*, *Strebela*.

7 6 3. Lateral teeth multicuspid, with 4–7 subequal cusps, outermost shortest, sometimes with  
8 7 rows of denticles along the outer edge of outer cusp. Central tooth with subsquare or  
9 8 subrectangular base and notched anterior edge and 3 sharp cusps (Fig. 9C) — found in  
10 9 *Proneptunea*, *Maffinbuccinum*, *Chlanidotella*

11 10 4. *Prosipho* type. Lateral teeth varying in shape, but always with very long and narrow  
12 11 attenuated outer portion of basal plate, forming “handle”, and with 2–7 cusps. Central tooth  
13 12 sometimes absent, when present varying from very small, acusate to well developed, bearing  
14 13 three cusps (Fig. 9 D, F–I). Found in *Prosipho*, *Anomacme*, *Antistreptus*, *Argeneuthria*,  
15 14 *Crenatosipho*, *Falsimacme*, *Fusinella*, *Meteuthria*, *Savatieria*, *Germonea*.

16 15 5. *Antarctodomus* type. Lateral teeth with narrow base and two long, very closely spaced  
17 16 cusps, outer one slightly longer. Central tooth broad with three blunt cusps (Numanami, 1996:  
18 17 fig. 96D).

19 18 6. *Drepanodontus* type. Lateral teeth with a single large cusp (seems to be homologous to  
20 19 the outermost cusp in other genera) and small 1–3 cusplets on inner side of the cusp (Fig. 9E).

21 20 Proboscis usually not long and relatively thick, proboscis retractors either paired and  
22 21 attached laterally in the middle part of rhynchodaeum (*Falsimohnia*, *Parabuccinum*), or  
23 22 numerous and arranged in lateral bundles in mid-rhynchodaeum (others). Salivary glands  
24 23 medium-sized to very large, paired, sometimes fused (*Germonea*). Gland of Leiblein from  
25 24 vestigial (*Parabuccinum*) to very large (*Germonea*), valve of Leiblein well defined even when  
26 25 gland of Leiblein vestigial. Stomach either U-shaped, or broad U-shaped, without defined  
27 26 posterior mixing area.

28 27 **Distribution.** Antarctic and subantarctic waters, Magellan Province, from subtidal to  
29 28 abyssal depths.

30 29 **Remarks.** The concept and scope of this family is radically changed by the present study.  
31 30 Powell (1951) established the name Prosiphiinae without providing any diagnosis or statement  
32 31 about the erection of this new family group name. It was rather vaguely circumscribed as a  
33 32 subfamily of Buccinulidae, to include several Antarctic and Magellanic genera (*Meteuthria*,  
34 33 *Prosipho*, *Anomacme*, *Fusinella*, *Proneptunea* and *Chlanidotella*) with “central tooth tricuspid,  
35 34 lateral teeth multicuspid”; Powell (1951: 132) added that “typically, the laterals have a long basal  
36 35 projection, like a handle”. Other Antarctic and subantarctic buccinoid genera were attributed by  
37 36 Powell to the Buccinulidae subfamilies Buccinulinae (central and lateral teeth tricuspid) and  
38 37 Cominellinae (central tooth tricuspid, lateral teeth bicuspid). Powell himself considered this  
39 38 classification provisional, having characterized it as “probably more convenient than real”.

40 39 Our phylogeny demonstrates that the genera that Powell included in Buccinulinae  
41 40 (*Chlanidota*, *Neobuccinum*, *Probuccinum*, *Cavineptunea*, and *Bathydomus*) and Cominellinae  
42 41 (*Falsimohnia*) are actually closely related to *Prosipho*, in spite of notable differences in radular  
43 42 morphology. Beside Antarctic and subantarctic species, Prosiphonidae includes species from  
44 43 New Zealand (*Austrofusus glans*) and Tasmania (*Antarctodomus* cf. *powelli*). It should be  
45 44 emphasized that practically no Magellanic genera were available for inclusion in the molecular

analysis and these are attributed to Prosiphonidae based on radula similarities with sequenced species, but it cannot be excluded that they constitute independent phylogenetic lineages.

The anatomy was studied in the sequenced genera *Chlanidota* (Harasewych & Kantor, 1999) and *Falsimohnia* (Kantor & Harasewych, 2013), as well as in the non-sequenced genera *Drepanodontus*, *Germonea*, *Muffinbuccinum*, *Spikebuccinum* (Kantor & Harasewych, 2013) and *Parabuccinum* (Harasewych *et al.*, 2000), and our family diagnosis is based on these studies.

#### FAMILY BUCCINIDAE RAFINESQUE, 1815

(Figs 10–14)

Type genus: *Buccinum* Linnaeus, 1758

#### SUBFAMILY BUCCININAE RAFINESQUE, 1815

(Fig. 10A–F)

Included genera:

*Buccinum* Linnaeus, 1758 (TS *Buccinum undatum* Linnaeus, 1758; SD, Montfort, 1810)<sup>(1)</sup>.

Synonyms: *Volutharpa* P. Fischer, 1856 (TS *Volutharpa deshayesiana* P. Fischer, 1856; M; syn. nov.); *Bathybuccinum* Golikov & Sirenko, 1989 (TS *Bathybuccinum bicordatum* Golikov & Sirenko, 1989; OD; syn. nov.)

*Ovulatibuccinum* Golikov & Sirenko, 1989 (TS *Buccinum ovulum* Dall, 1895; OD)<sup>(1)</sup>

*Thysanobuccinum* Golikov & Gulbin, 1980 (TS *Buccinum tunicatum* Golikov & Gulbin, 1977; OD)<sup>(1)</sup>

**Diagnosis.** Shell from small to large (over 150 mm), oval to broadly fusiform, without siphonal canal and with siphonal notch. Protoconch paucispiral. Whorls convex to (sub)cylindrical, shouldered, sometimes with strong keel at shoulder. Shell sculpture pronounced in most cases, spiral sculpture from microscopic threads to prominent keels; axial sculpture, when present, of distinct, broad, sigmoid or arcuated axial ribs. Shell covered with ciliated periostracum, sometimes very thick and forming lamellae. Aperture wide, ovate with simple outer lip. Operculum small to large, with subcentral nucleus.

Radula with central tooth with broad rectangular base, notched anteriorly, and with nearly straight posterior margin with 4–8 cusps; lateral teeth with 3–4 cusps, intermediate one much shorter than outer and inner ones. Proboscis long, proboscis retractors multiple, attached laterally to posterior portion of rhynchodaeum. Paired small salivary glands. Gland of Leiblein small, tubular, valve of Leiblein small. Stomach with long posterior mixing area (Kantor, 2003).

Individual hemispherical egg capsules forming large ball-shaped clusters. Direct development with nurse eggs and adelphophagy (Fretter & Graham, 1962).

**Distribution.** Temperate northern Atlantic and temperate northern Pacific to Arctic, from intertidal to abyssal depths.

**Remarks.** The molecular phylogenetic analysis did not resolve *Volutharpa* and *Bathybuccinum* as separate genera and they are accepted as synonyms of *Buccinum* (for clarity we use the name of the synonyms on the tree, Fig. 2). The status of *Plicibuccinum* Golikov & Gulbin, 1977 (TS *Plicibuccinum plicatum* Golikov & Gulbin, 1977 [= *Buccinum ochotense*



1  
2 1 *declivis* Habe & Ito, 1976]; OD) and *Corneobuccinum* Golikov & Gulbin, 1977 (TS *Colus*  
3 2 (*Latisipho*) *lepidus* Dall, 1918; OD) remains uncertain.  
4  
5 3

6 4 SUBFAMILY BERINGIINAE GOLIKOV & STAROBOGATOV, 1975  
7 5 (Figs 10G–K, 11C)  
8  
9 6

10 7 Type genus: *Beringius* Dall, 1887  
11 8

12 9 = Metajapelioninae Goryachev, 1987 (as subfamily of Beringiidae). Type genus: *Metajapelion*  
13 10 Goryachev, 1987.  
14  
15 11

16 12 Included genera:

17 13 *Beringius* Dall, 1887 (TS *Chrysodomus crebricostatus* Dall, 1877; M) <sup>(1)</sup>

18 14 *Metajapelion* Goryachev, 1987 (TS *Tritonium pericochlion* Schrenck, 1862; OD) <sup>(1)</sup>

19 15 *Neoberingius* Habe & Ito, 1965 (TS *Beringius frielei* Dall, 1895, OD) <sup>(2)</sup>; radula, see Habe &  
20 16 Sato (1973)  
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23 18 **Diagnosis.** Shell large, reaching 140 mm, broadly fusiform, with high spire and very short to  
24 19 obsolete siphonal canal. Protoconch paucispiral, of about 2–2.5 whorls, very large, diameter  
25 20 similar to, or even exceeding, that of first teleoconch whorls. Whorl profile subcylindrical to  
26 21 evenly convex. Shell sculpture pronounced in most cases, spiral sculpture from microscopic  
27 22 threads to prominent keels; axial sculpture, when present, of distinct, broad, arcuated axial ribs.  
28 23 Aperture wide, ovate. Shell pale or brownish, covered with smooth periostracum. Operculum  
29 24 very large, may exceed aperture length, detached from foot on large, oldest portion, with  
30 25 terminal nucleus.

31 26 Radula (Fig. 11C) with cusplless, subrectangular, plate-like central tooth; lateral teeth long,  
32 27 with narrow base of about 1/3 of tooth height, with 3, rarely 4, cusps, outermost one much  
33 28 longer. Proboscis long, thick, proboscis retractors multiple, attaching laterally to posterior  
34 29 portion of rhynchodaeum. Paired, medium-sized, salivary glands. Salivary ducts very thick.  
35 30 Gland of Leiblein small, tubular, valve of Leiblein rounded, medium-sized.  
36 31

37 32 Individual egg capsules very large, rounded, with one convex and another concave surface,  
38 33 reaching more than 50 mm, with stalk, attached to substrate. Capsules aggregate in linear  
39 34 clusters. Capsule wall multilayered. Development direct, with nurse eggs, emerging molluscs  
40 35 very large, reaching more than 15 mm in SL (Gulbin, 2018).  
41 36

42 37 **Distribution.** Temperate northern Atlantic and temperate northern Pacific to Arctic, from  
43 38 subtidal to lower bathyal depths.  
44 39

45 40 **Remarks.** In addition to three species of *Beringius*, “*Japelion*” *adelphicus* (Dall, 1907)  
46 41 and “*Beringius*” *aleuticus* Dall, 1895 are clustering together in our multigene analysis.  
47 42

48 43 “*Japelion*” *adelphicus* has a radula (Fig. 11C) morphologically similar to *Beringius* spp.  
49 44 (Bouchet & Warén, 1985: fig. 467, sic!; Habe & Sato, 1973: fig. 13). The radula of “*B.*”  
50 45 *aleuticus* is unknown. “*Beringius*” *aleuticus* is different in shell shape from other species of  
51 46 *Beringius*, particularly in having an ovoid, non-sculptured shell with very short canal. The  
52 47 isolated position of this species in our tree suggests that it may represent a previously  
53 48 unrecognized lineage worthy of a separate genus status.  
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The genus *Japelion* Dall, 1916 currently includes several species with channelled suture. The type species (OD), *Buccinum hirasei* Pilsbry, 1901, belongs to the subfamily Parancistrolepidinae, as proved by molecular analysis and radular morphology (see Fig. 11D). Another conchologically very similar species, “*Japelion*” *pericochlion* (included only in our *cox1* tree; radula, see Habe & Sato, 1973: fig. 14; shell see Fig. 10K herein) is clustering together with “*Japelion*” *adelphicus* and is nesting in the subfamily Beringiinae. *Tritonium pericochlion* is the type species of *Metajapelion*, and thus “*Japelion*” *adelphicus* is transferred to *Metajapelion*.

SUBFAMILY NEPTUNEINAE STIMPSON, 1865  
(Figs 10L–O, 11A)

Type genus: *Neptunea* Röding, 1798

= Chrysodominae Dall, 1870. Type genus: *Chrysodomus* Swainson, 1840.

Included genera:

*Aulacofusus* Dall, 1918 (TS *Fusus spitzbergensis* Reeve, 1855 [= *Fusus brevicauda* Deshayes, 1832]; OD) <sup>(1)</sup>

*Neptunea* Röding, 1798 (TS *Murex antiquus* Linnaeus, 1758; SD, Sandberger (1861). Synonym: *Chrysodomus* Swainson, 1840; TS *Murex despectus* Linnaeus, 1758; SD, Cossmann (1901b: 98)) <sup>(1)</sup>

**Diagnosis.** Shell large, reaching 240 mm, broadly fusiform, with high spire and short to medium-long, siphonal canal often bent abaxially. Protoconch paucispiral, moderately large. Whorl profile convex to distinctly shouldered. Shell sculpture pronounced in most species, spiral sculpture from microscopic threads to prominent bulging keels; axial sculpture rarely present, then of indistinct axial ribs or sometimes distinct, raised, axial lamellae producing prominent nodules at shoulder. Aperture very wide. Shell covered with smooth periostracum. Operculum large, spanning most of aperture, with terminal nucleus.

Radula with multicuspid (2–8 cusps) central tooth with rectangular and anteriorly arcuate base; lateral teeth broad, with 2–7 cusps, outermost longest (Fig. 11A). Proboscis from long to very long and coiled within rhynchodaeum, thick, proboscis retractors from paired to multiple, attached laterally to median portion of rhynchodaeum, in *Neptunea* can pass through salivary glands. Paired medium-sized salivary glands. Gland of Leiblein from obsolete to medium large, tubular, valve of Leiblein from very small to large and rounded. Stomach large, with medium to long posterior mixing area.

Individual egg capsules large, of varying shape, usually with ornamented surface, aggregated in clusters of various shapes — ball-shaped, corn cob, or single-layered with capsules individually attached to substrate. Development direct, with nurse eggs, emerging molluscs large, reaching over 7 mm in SL (Pearse & Thorson, 1967).

**Distribution.** Temperate northern Pacific through Arctic to temperate northern Atlantic, from subtidal to lower bathyal depths.

**Remarks.** In our multigene analysis, “*Aulacofusus*” *hiranoi* (Shikama, 1962) was recovered in a clade uniting buccinoideans from biogenic substrates (*Eosiphonidae* fam. nov.).

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1 However, in addition to “*Aulacofusus*” *hiranoi*, two specimens of a second species of the same  
2 genus, *A. periscelidus* (Dall, 1891), were included in the analysis based on *cox1* alone: whereas  
3 the placement of *A. hiranoi* remained the same as in the multigene tree, *A. periscelidus* was sister  
4 to *Neptunea* (B=70). No data on radula or anatomy of “*A.*” *hiranoi* are available, but the  
5 conchological similarity with other members of the Eosiphonidae, particularly with *Eosipho*, was  
6 noted by Kosyan & Kantor (2013). Beside, *A. periscelidus* is rather similar in shell morphology  
7 and radula (see Fig. 13B) to *A. brevicauda*, the type species of the genus (Kosyan & Kantor,  
8 2013). For this reason, we here include *Aulacofusus* in the subfamily Neptuneinae, whereas “*A.*”  
9 *hiranoi* should be excluded from *Aulacofusus* and reassigned to a new genus within  
10 Eosiphonidae.

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SUBFAMILY VOLUTOPSIINAE HABE & SATO, 1973  
(Figs 11H, 12A–D)

15 Type genus: *Volutopsius* Mörch, 1857

17 Included genera:

18 *Habevolutopsius* Kantor, 1983 (TS *Volutopsius hirasei* Pilsbry, 1907; OD)<sup>(1)</sup>

19 *Lussivolutopsius* Kantor, 1983 (TS *Lussivolutopsius hydractiniferus* Kantor, 1983; OD)<sup>(1)</sup>

20 *Pyrulofusus* Mörch, 1869 (TS *Fusus deformis* Reeve, 1847; M)<sup>(1)</sup>

21 *Volutopsius* Mörch, 1857 (TS *Fusus largillierti* Petit de la Saussaye, 1851 [= *Strombus*  
22 *norwegicus* Gmelin, 1790]; M)<sup>(1)</sup>

24 **Diagnosis.** Shell large, reaching 160 mm, from fusiform to broadly fusiform or ovate, with very  
25 short to medium high spire and short to very short, nearly obsolete siphonal canal. Protoconch  
26 paucispiral, always retained in adults, of about two whorls, medium sized (3.5–5 mm in  
27 diameter) to very large (up to 13 mm). Whorl profile convex to subcylindrical. Shell sculpture  
28 pronounced in most species, spiral sculpture from microscopic threads to prominent bulging  
29 keels; axial sculpture sometimes present, from knobs on shoulder and axial lamellae (some  
30 species of *Volutopsius*) to distinct axial ribs. Shell covered with smooth periostracum. Aperture  
31 ovate, wide, often with strongly calloused inner lip. Shell colour from ivory to orange or dark-  
32 brown, parietal callus and/or inside aperture often light- to dark-brown. Operculum small to  
33 medium-sized, spanning half of aperture or less, with terminal nucleus shifted leftwards.

34 Radula (Fig. 11H) with multicuspid (3–8 cusps) central tooth, with rectangular or nearly  
35 square, anteriorly arcuate, base; laterals varying in width from narrow to broad, typically with 2  
36 cusps of varying length and rarely with indistinct intermediate cusplet. Proboscis from short to  
37 long, proboscis retractors multiple, attached laterally to median portion of rhynchodaeum. Paired  
38 salivary glands large, rarely fused. Gland and valve of Leiblein absent. Stomach variable, from  
39 sac-like with large posterior mixing area, to expanded, tubular, with very short mixing area.  
40 (Anatomy description based on Kantor, 1990).

41 Individual egg capsules very large, from 16 to 66 mm in diameter, hemispherical to  
42 lenticular, solitary, usually smooth, covered by thin chalky layer when newly laid. Development  
43 direct, with very few nurse eggs and a large amount of proteinaceous substance filling the  
44 capsule, emerging molluscs large to very large, reaching 19.5 mm in SL [*Pyrulofusus harpa*  
45 (Mörch, 1857), see Cowan (1965)].

**Distribution.** Temperate northern Pacific through Arctic to temperate northern Atlantic from subtidal to upper bathyal depths.

SUBFAMILY PARANCISTROLEPIDINAE HABE, 1972

(Figs 11E, F, I, 12E–K)

Type genus: *Parancistrolepis* Azuma, 1965.

= Brevisiphoniinae Lus, 1973. Type genus: *Brevisiphonia* Lus, 1973

= Ancistrolepidinae Habe & Sato, 1973. Type genus: *Ancistrolepis* Dall, 1895.

Included genera:

*Ancistrolepis* Dall, 1895 (TS *Chrysodomus eucosmius* Dall, 1891; OD) <sup>(1)</sup>

*Bathyancistrolepis* Habe & Ito, 1968 (TS *Chrysodomus trochoideus* Dall, 1907; OD) <sup>(1)</sup>

*Clinopegma* Grant & Gale, 1931 (TS *Buccinum unicum* Pilsbry, 1905; OD) <sup>(1)</sup>

*Japelion* Dall, 1916 (TS *Buccinum hirasei* Pilsbry, 1901; OD) <sup>(1)</sup>

*Neancistrolepis* Habe & Sato, 1973 (TS *Ancistrolepis beringianus* Dall, 1919; OD) <sup>(2)</sup>

*Parancistrolepis* Azuma, 1965 (TS *Japelion kinoshitai* Kuroda, 1931; M) <sup>(1)</sup>; radula, see Habe (1972) (Fig. 13I, herein)

*Pseudoliomesus* Habe & Sato, 1973 (TS Type species: *Tritonium ooides* Middendorff, 1848; OD) <sup>(1)</sup>

*Thalassoplanes* Dall, 1908 (TS: *Troschelia moerchi* Dall, 1908; OD) <sup>(1)</sup>. Synonym:

*Brevisiphonia* Lus, 1973 (TS *Brevisiphonia circumreta* Lus, 1973 [= *Thalassoplanes moerchii*]; OD)

**Diagnosis.** Shell medium-sized to large, reaching 120 mm, from oval with very short spire to fusiform with high spire. Shell base obliquely truncated, without defined siphonal canal but with siphonal notch of varying depth. Protoconch of 2.5–3 whorls, large, diameter up to 3 mm. Whorl profile from evenly convex to angulated at shoulder. Suture canaliculate in *Japelion*. Shell sculpture pronounced in most species, spiral sculpture from microscopic threads to prominent bulging keels; axial sculpture limited to growth lines, sometimes thickened and forming reticulated pattern at intersection with spiral cords. Shell covered with smooth or ciliated periostracum, whitish to light brown; inside of aperture white. Operculum large, spanning most of aperture, sometimes exceeding its length, narrow, with terminal nucleus and detached along most of its length, or very small (*Parancistrolepis* only), spanning about 1/5 of aperture length (Fig. 12K).

Central tooth in most species with rectangular and anteriorly arcuate to notched base; lateral teeth most often with three cusps, outermost longest, sometimes with additional intermediate cusps (Fig. 11F). In *Thalassoplanes* (Fig. 11E) central tooth very narrow and long, lateral teeth broad, with 7 or 8 short cusps of subequal length. Proboscis from long to very long and coiled within rhynchodaeum, thick to thin; proboscis retractors from paired to multiple, attached laterally to posterior portion of rhynchodaeum. Salivary glands medium-sized, fused. Gland of Leiblein large, extended, tubular and coiled, valve of Leiblein large. Stomach large, with medium-sized posterior mixing area.

1 Egg capsules solitary, large, elongate-oval with very long stalk. Capsule smooth, length  
 2 52–60 mm, with stalk 195–205 mm. On concave side of capsule there is an operculum for the  
 3 release of hatching juveniles. Newly laid capsule filled by white proteinous substance. Stalk  
 4 rounded in section and triangular at its base, expanding into irregularly shaped flattened plate,  
 5 attaching to substrate. Up to 8 embryos per capsule, ready to hatch juveniles with SL 8.5–9.5  
 6 mm (Kantor, 1988).

7 **Distribution.** Temperate northern Pacific from subtidal to abyssal depths.

8 **Remarks.** Our multigene dataset did not include any *Ancistrolepis* species, but in the *cox1*-  
 9 based tree *Ancistrolepis grammatus* (Dall, 1907) (Fig. 12E) clusters with other members of the  
 10 subfamily, being sister with maximal support to *Clinopegma unicum*, the type species of  
 11 *Clinopegma*.

12 Similarly *Parancistrolepis* was included only in the *cox1*-based tree and clustered with  
 13 maximal support with *Thalassoplanes*. The radula of *Parancistrolepis* (Fig. 13I) shows some  
 14 similarity to that of *Thalassoplanes* (Fig. 13E), but differs in the morphology of the central tooth.  
 15 Therefore the name Parancistrolepidinae Habe, 1972 (original spelling Parancistrolepisinae) has  
 16 priority over Ancistrolepidinae Habe & Sato, 1973. The subfamily was raised to family level by  
 17 Goryachev (1987) who included in it *Parancistrolepis*, *Thalassoplanes*, and *Brevisiphonia*.

#### 18 SUBFAMILY SIPHONALIINAE FINLAY, 1928

19 (Figs 13, 14)

20 Type genus: *Siphonalia* A. Adams, 1863.

21 Included genera:

22 *Bayerius* Olsson, 1971 (TS *Fusinus fragilissimus* Dall, 1908; OD) <sup>(1)</sup>

23 *Japeuthria* Iredale, 1918 (TS *Buccinum ferreum* Reeve, 1847; OD) <sup>(1)</sup>

24 *Mohnia* Friele, 1878 (TS *Fusus mohni* Friele, 1877; M) <sup>(2)</sup>

25 *Pararetifusus* Kosuge, 1967 (TS *Phymorhynchus tenuis* Okutani, 1966; OD) <sup>(1)</sup>

26 *Phaenomenella* Fraussen, 2006 (TS *Manaria inflata* Shikama, 1971; OD) <sup>(1)</sup>

27 *Siphonalia* A. Adams, 1863 (TS *Buccinum cassidariaeforme* Reeve, 1846; SD, Cossmann,  
 28 1889) <sup>(1)</sup>

29 **Diagnosis.** Shell small (10 mm) to medium large (over 60 mm), very thin-walled and fragile to  
 30 robust, oval to broadly fusiform. Protoconch paucispiral, sometimes large and bulbous  
 31 (*Phaenomenella*), sometimes with small smooth initial part, followed by strong axial and spiral  
 32 sculpture on the upper teleoconch whorls, forming a reticulated pattern (*Mohnia*, *Bayerius*).  
 33 Whorl outline from evenly, gently or strongly convex, to distinctly shouldered. Spiral sculpture  
 34 always present, of uniform or unequal spiral cords. Axial sculpture present at least on upper  
 35 whorls in *Phaenomenella* and *Siphonalia*, represented by low, rounded ribs, stronger on earlier  
 36 whorls, on later whorls more pronounced at shoulder. Aperture wide to very wide. Siphonal  
 37 canal short to moderately long, often bent abaxially. Operculum from oval paucispiral to  
 38 elongate with terminal nucleus.

39 Radula (Fig. 14) comprising central tooth with rectangular base notched anteriorly and 3  
 40 cusps; lateral teeth with 2–4 cusps, typically 3, central shortest. Proboscis medium-long to long,  
 41 proboscis retractors multiple, attach laterally to central portion of rhynchodaeum. Paired large  
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1 salivary glands. Gland of Leiblein very large, valve of Leiblein well defined. Stomach with long  
2 to very long posterior mixing area (based on anatomical description in Kantor *et al.* (2020a,  
3 2020b).

4 **Distribution.** Temperate northern Atlantic and Arctic to temperate northern Pacific at  
5 upper subtidal to hadal depths.

6 **Remarks.** The subfamily Siphonaliinae was originally erected as a subfamily of  
7 Buccinulidae and, in addition to the type genus, included *Penion*, *Aeneator* and *Glaphyrina*.  
8 Later molecular phylogenetic analyses (Vaux *et al.*, 2017; Kantor *et al.*, 2020a) have shown that  
9 none of these latter genera is phylogenetically close to *Siphonalia*. Neither are they close to each  
10 other and all three are here placed in different families. The family name Siphonaliidae was  
11 again independantly established by Goryachev (1987: 33, 35).

12 Based on the sequences of three genes (*cox1*, 16S, and H3) *Japeuthria ferrea* is here  
13 confidently placed in the subfamily (Fig. S2), where it is recovered in a sister position to all other  
14 taxa. These taxa are in turn form two maximally supported clades, one uniting representatives of  
15 *Siphonalia* and *Phaenomenella*, and the other all remaining genera. The affinity of *Japeuthria*  
16 and *Siphonalia* has previously been proposed by Hayashi (2005) based on the analysis of a 1,3  
17 Kb fragment of 16S rRNA, while the close relationship of *Mohnia dalli*, *Pararetifusus* and  
18 *Bayerius* to the genera *Siphonalia* and *Phaenomenella* was shown and briefly discussed in  
19 Kantor *et al.* (2020b).

20 The taxonomic position of *Mohnia dalli* (Friele, 1881) needs an additional remark.  
21 Originally described in the genus *Sipho* Klein, 1753 (an unavailable name), it was transferred to  
22 *Turrisipho* Dautzenberg & H. Fischer, 1912 by Bouchet & Warén (1985). The radula remains  
23 unknown. We tentatively transfer it to *Mohnia* based on overall shell similarity, paucispiral  
24 operculum (Kantor *et al.*, 2020b) and similar protoconch morphology (for the protoconch of *M.*  
25 *mohni*, see Bouchet & Warén, 1985: fig. 531, of *M. dalli*, fig. 559).

#### UNASSIGNED BUCCINIDAE

29 In our multigene analysis type species of *Anomalisipho*, *A. verkruezeni* constitutes its own  
30 branch, while in *cox1* based tree it is clustering together with *P. rhyssus* (Dall, 1907) and  
31 «*Colus*» *kujianus* Tiba, 1973 with maximal support (Fig. S1). Due to very limited material we  
32 abstain at the moment of taking taxonomic decision, but these genera may constitute a separate  
33 subfamily.

34  
35 *Anomalisipho* Dautzenberg & H. Fischer, 1912 (TS *Sipho verkruezeni* Kobelt, 1876; OD) <sup>(1)</sup>  
36 (Figs 13G, 14K, L)

37 **Remark.** The type species of *Anomalisipho* from the subtidal depths of the northern Atlantic is  
38 included in the analysis and ends up isolated in the tree, forming a long branch sister to  
39 *Buccinum*, albeit without support. The radula of *Anomalisipho virgata* (Friele, 1879) (Fig 13G),  
40 a morphologically very similar species, is similar to the radulae encountered in different genera,  
41 e.g. *Aulacofusus*, *Clinopegma*, *Ancistrolepis*, *Buccinum* and others, and thus does not clarify the  
42 position of the genus. The operculum, with terminal nucleus, differs from the operculum of  
43 Buccininae with subcentral nucleus, and speaks against including *Anomalisipho* in that  
44 subfamily. In the expectation of additional data, we refrain from allocating *Anomalisipho* to any  
45 subfamily.

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2 *Plicifusus* Dall, 1902 (TS *Fusus kroeyeri* Möller, 1842; OD) <sup>(1)</sup>  
3 (Fig. 12N)

4 **Remark.** The single species, *P. rhyssus* (Dall, 1907) was included in *coxI* based analysis and  
5 clusters together with *Anomalisipho verkruezeni* and “*Colus*” *kujianus* Tiba, 1973. *Plicifusus* is  
6 species rich and morphologically variable genus, including about dozen of species and is  
7 distributed in the Arctic and north Pacific (Kosyan, Kantor, 2012). Its radula is very similar to  
8 that of *Anomalisipho*. “*Colus*” *kujianus* according to our tree clearly does not belong to *Colus*.  
9 In shell characters (Fig. 12O) it resembles both *Plicifusus* (Fig. 12N) and *Anomalisipho*. Its  
10 generic placement is not defined yet pending the results of multigene analysis.

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BUCCINIDAE INSERTAE SEDIS

14 As circumscribed herein the family Buccinidae includes mostly boreal and, to a lesser extent,  
15 temperate to subtropical taxa of Northern Hemisphere Buccinoidea. Notwithstanding, there  
16 remains numerous, sometimes common, boreal genera that the lack of suitable material  
17 prevented us from including in the molecular analysis. Among them are *Troschelia* Mörch, 1876,  
18 *Helicofusus* Dall, 1916, and *Latisipho* Dall, 1916. Their taxonomic position remain uncertain,  
19 since shell and radula characters that were the basis for earlier placement appear to be weakly  
20 informative due to their high homoplasy.

21 Besides, representatives of two nominal subfamilies described within Buccinidae are not  
22 present in our analysis and therefore their status remains unconfirmed.

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SUBFAMILY LIOMESINAE P. FISCHER, 1884  
(Fig. 14O)

= Buccinopsidae G. O. Sars, 1878 (invalid: type genus [*Buccinopsis* Jeffreys, 1867] a junior  
homonym)]

Type genus: *Liomesus* Stimpson, 1865 (TS †*Buccinum dalei* J. de C. Sowerby, 1825; OD).  
Synonym: *Buccinopsis* Jeffreys, 1867 (TS †*Buccinum dalei*; M)

**Remarks.** The radula of *Liomesus ovum* (Turton, 1825), was illustrated by G.O. Sars (1878: tab.  
X, fig. 15) as *Buccinopsis eburnea* (M. Sars, 1851). It is characterized by acuspate  
subrectabgular central tooth and unicuspidate lateral ones. This morphology is very different  
from other buccinoidean radulae, and has led Habe & Sato (1973) to suggest close relationships  
to *Beringius*, which was included by them together with *Liomesus* in the subfamily  
Liomesusinae. Bouchet & Warén (1985: fig. 461) provided a line drawing of a very different  
radula of *Liomesus ovum*, from an egg capsule, with muticuspidate central and lateral teeth.  
Because of this ambiguity, and the lack of molecular and anatomical data, we cannot propose  
any plausible hypothesis on the position of *Liomesus*.

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SUBFAMILY TRUNCARIINAE COSSMANN, 1901  
(Fig. 14M)

1  
2 1 Type genus: *Truncaria* A. Adams & Reeve, 1850 (TS *Buccinum filosum* A. Adams & Reeve,  
3 2 1850; M)  
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5 3

6 4 **Remarks.** The anatomy and radula of the type (and only included) genus remains unstudied  
7 5 (Olsson, 1971) and molecular data are lacking as well. The peculiar shell shape (Fig. 14M) does  
8 6 not provide any clue on the possible relationships of *Truncaria*, and even its position within  
9 7 Buccinidae remains to be confirmed.  
10 7

11 8  
12 9 FAMILY FASCIOLARIIDAE GRAY, 1853  
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15 11 SUBFAMILY FASCIOLARIINAE GRAY, 1853  
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18 13 Type genus: *Fasciolaria* Lamarck, 1799 (TS *Murex tulipa* Linnaeus, 1758; M)  
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20 15 = Latiridae Iredale, 1929. Type genus *Latirus* Montfort, 1810 (TS *Latirus aurantiacus* Montfort,  
21 16 1810; OD).  
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24 18 SUBFAMILY FUSININAE WRIGLEY, 1927  
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27 20 Type genus: *Fusinus* Rafinesque, 1815 (TS *Murex colus* Linnaeus, 1758; by typification of  
28 21 replaced name [*Fusus* Bruguière, 1789])  
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31 23 = Fusinae Swainson, 1840 (inv.). Type genus: *Fusus* Bruguière, 1789 (inv.) (TS *Murex colus*  
32 24 Linnaeus, 1758; by subsequent monotypy, Lamarck, 1799).  
33 24

34 25 = Cyrtulidae MacDonald, 1869. Type genus: *Cyrtulus* Hinds, 1843 (TS *Cyrtulus serotinus*  
35 26 Hinds, 1843; M).  
36 26  
37 27

38 28 SUBFAMILY PERISTERNIINAE TRYON, 1880  
39 29  
40 29

41 30 Type genus: *Peristernia* Mörch, 1852 (TS *Turbinella nassatula* Lamarck, 1822; SD, Martens,  
42 31 1868)  
43 32

44 33 **Remarks.** The 5-gene molecular phylogeny of the Fasciolariidae of Couto *et al.* (2016) revealed  
45 34 four major lineages. Three of these cluster together and are generally consistent with the widely  
46 35 accepted subfamilies Peristerniinae, Fasciolariinae and Fusininae (the latter further analysed by  
47 36 Kantor *et al.*, 2018), but with a significantly altered content mostly due to the transfer of several  
48 37 genera from Peristerniinae to the other two subfamilies. The analysis is congruent with that of  
49 38 Couto *et al.* (2016), the results of which are followed here with additions and corrections based  
50 39 on Kantor *et al.* (2018).  
51 38  
52 39

53 40 Vaux *et al.* (2017) attributed *Pararetifusus* to the Fasciolariidae, based on the erroneous  
54 41 assignment of *Microfulgur carinatus* Ponder, 1970 to *Pararetifusus*. Our analysis demonstrates  
55 42 that *M. carinatus* belongs to the Fasciolariidae (Fusininae), while *Pararetifusus*, represented in  
56 43 our dataset by its type species *P. tenuis*, belongs to the Buccinidae (Siphonaliinae).  
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The morphology, anatomy and radula of a number of species of Fasciolaridae were recently described in detail by Couto & Simone (2019). For the genus level taxonomy, see Snyder & Callomon (2021).

FAMILY BUSYCONIDAE WADE, 1917 (1867)  
(Figs 15A–C, 16A, B)

SUBFAMILY BUSYCONINAE WADE, 1917 (1867)

Type genus: *Busycon* Röding, 1798

= Fulguridae Stoliczka, 1867. Type genus *Fulgur* Montfort, 1810.

Included genera:

*Busycoarctum* Hollister, 1958 (TS *Pyrula coarctata* G.B. Sowerby I, 1825; OD)<sup>(3)</sup>

*Busycon* Röding, 1798 (TS *Busycon muricatum* Röding, 1798 [= *Murex carica* Gmelin, 1791]; SD, B. Smith, 1938). Synonym: *Fulgur* Montfort, 1810 (TS *Fulgur eliceans* Montfort, 1810; OD)<sup>(1)</sup>

*Lindafulgur* Petuch, 2004 (TS †*Busycon lindajoyceae* Petuch, 1991; OD)<sup>(3)</sup>

*Sinistrofulgur* Hollister, 1958 (TS *Busycon sinistrum* Hollister, 1958; OD)<sup>(3)</sup>

SUBFAMILY BUSYCOTYPINAE PETUCH, 1994

Type genus *Busycotypus* Wenz, 1943

Included genera:

*Busycotypus* Wenz, 1943 (TS *Murex canaliculatus* Linnaeus, 1758; OD)<sup>(1)</sup>

*Fulguropsis* Marks, 1950 (TS *Bulla pyrum* Dillwyn, 1817; OD)<sup>(1)</sup>

**Diagnosis.** Shell large to very large (over 400 mm), dextral or sinistral, with low or very low spire and long siphonal canal. Protoconch paucispiral, medium-sized. Suture often canalliculated. Spire whorls shouldered, or concave due to wide concave shoulder slope terminating at lower suture. Spiral sculpture often with a keel on shoulder, and uniform or unequal spiral cords on rest of the whorl. Axial sculpture present or absent, of knobs or tubercles on shoulder. Aperture high, elongate-pyriform due to broad siphonal canal. Periostracum from thin to thick, ciliated. Operculum large and thick, spanning most of aperture, leaf shaped with terminal nucleus.

Radula (Fig. 16A, B) with central tooth with rectangular base, deeply arcuated anteriorly and bearing 3–5 subequal cusps on posterior edge; lateral teeth with 3 or 4 cusps, outermost longest, intermediate much shorter. Proboscis long and thick, posteriorly with a septum, isolating the proboscis inner cavity from body haemocoel, salivary ducts and oesophagus passing through septum (Kosyan & Kantor, 2004). Proboscis retractors multiple, attached laterally to posterior portion of rhynchodaeum. Paired medium-sized salivary glands. Gland of Leiblein from small and narrow, tubular to large and folded, terminating in ampulla; valve of Leiblein well defined. Stomach with posterior mixing area medium-long to long (Kantor, 2003).

Individual oval egg capsules with sculptured surface and short stalk forming long string egg clusters. Development intracapsular.

**Distribution.** Tropical and temperate western North Atlantic, from intertidal to shelf edge.

**Remarks.** The subfamilial and generic classification follows Petuch *et al.* (2015).

FAMILY BUCCINANOPSIDAE GALINDO, PUILLANDRE, LOZOUET & BOUCHET, 2016 (NEW RANK)  
(Figs 15D, 16I)

Type genus: *Buccinanops* d'Orbigny, 1841

Included genera:

*Buccinanops* d'Orbigny, 1841 (TS *Buccinum cochlidium* Dillwyn, 1817; OD) <sup>(1)</sup>

**Diagnosis.** Shell thick-walled, medium-large, buccinoid, with low to moderately high spire and distinct siphonal notch giving it a truncated appearance. Protoconch large, smooth, paucispiral, of about 1.5–2.5 whorls. Whorl profile usually evenly convex, or with bulging subsutural keel, but occasionally rather flat. Sculpture lacking or represented by axial ribs on early teleoconch whorls, and later mainly by growth lines, occasionally with spines on shoulder. Siphonal canal very short, robust, heavily calloused, usually demarcated from shell base by furrow or narrow depression, Inner aperture lip with strongly developed parietal callus, and terminal columellar fold. Operculum large, leaf-shaped, with smooth margins and terminal nucleus.

Radula (Fig. 16I) with multicuspidate arcuated central tooth with 7–9 cusps decreasing abaxially in size, one prominent cusp, not always the central one. Lateral teeth with 3–5 cusps, intermediate(s) much shorter than longest outer and inner ones.

Anatomy (after Simone, 1996). Foot with a single metapodial tentacle. Adults eyeless. Proboscis long to very long, proboscis retractors numerous, lateral. Valve of Leiblein vestigial, gland of Leiblein small, tubular. Salivary glands small, not fused. Stomach not large, with short posterior mixing area. Non-planktotrophic development.

**Distribution.** Temperate waters of South America, intertidal.

**Remarks.** The genus *Buccinanops* was traditionally (Cernohorsky, 1984) included in the nassariid subfamily Dorsaninae and segregated as a separate subfamily by Galindo *et al.* (2016). In the phylogeny of Galindo *et al.*, *Buccinanops* was recovered as sister to all the other Nassariidae. In our analysis, however, it is sister to *Macron* and together with it form a highly supported clade with Busyconidae, none of which were included in Galindo *et al.*'s analysis.

FAMILY COMINELLIDAE GRAY, 1857  
(Figs 15E–J, 16C–E)

Type genus: *Cominella* Gray, 1850

Included genera:

*Cominella* Gray, 1850 (TS *Buccinum testudineum* Bruguière, 1789 [= *Buccinum maculosum* Martyn, 1784]; SD, Iredale, 1918) <sup>(1)</sup>

*Falsitromina* Dell, 1990 (TS *Tromina bella* Powell, 1951, OD) <sup>(2)</sup>; radula, see Powell (1951)

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2 1 *Lusitromina* Harasewych & Kantor, 2004 (TS *Tromina abyssorum* Lus, 1993, OD)<sup>(2)</sup>; radula,  
3 2 see Harasewych & Kantor (2004)  
4 3 *Pareuthria* Strebel, 1905 (TS *Fusus plumbeus* Philippi, 1844 [= *Pareuthria fuscata* (Bruguière,  
5 4 1789)]; SD, Tomlin, 1932)<sup>(1)</sup>  
6 5 *Parficulina* Powell, 1958 (TS *Notoficula problematica* Powell, 1951, OD)<sup>(2)</sup>; radula, see Powell  
7 6 (1951)  
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11 8 **Diagnosis.** Shell from small (5 mm) to medium-sized (to 75 mm), from broadly-ovate to  
12 9 elongate oval or nearly biconical, with very short siphonal canal and often distinct siphonal  
13 10 notch. Protoconch paucispiral. Shoulder from weakly defined to distinct, with concave  
14 11 subsutural ramp. Axial sculpture absent or represented by rounded ribs, strongest on shoulder  
15 12 and whorl periphery. Spiral sculpture absent or composed of cords or striae varying in strength  
16 13 and number per whorl; cancellate sculpture rarely present. Operculum with terminal nucleus or  
17 14 paucispiral.

18 15 Radula (Fig. 16C–E) with central tooth almost square, deeply notched on anterior margin,  
19 16 with three closely spaced cusps; bicuspid lateral teeth with subequal cusps, or outer cusp longer.

20 17 **Distribution.** Intertidal to abyssal depths in the Southern Hemisphere: Magellanic region,  
21 18 New Zealand, Antarctica.

22 19 **Remarks.** Powell initially considered Cominellidae as a full family (Powell, 1929), but  
23 20 later (Powell, 1951) treated it as a subfamily of Buccinulidae, a viewpoint followed by many  
24 21 later authors (e.g., Harasewych & Kantor, 2004; Pastorino, 2016). Our analysis clearly  
25 22 demonstrates that this clade deserves family rank and is not closely related to Buccinulidae.

26 23 Only two genera (*Cominella* and *Pareuthria*) were included in our analysis, while three  
27 24 others are included in the family merely based on radular characters. However, similar radulae  
28 25 with bicuspid lateral teeth and tricuspid central ones are also found in unrelated Buccinoidea  
29 26 (e.g. in *Phos*, Photinae) and the aforementioned genera may in fact belong to other family(ies).

30 27 Kantor & Harasewych (2013) argued that most Antarctic species attributed to *Pareuthria*  
31 28 (Dell, 1990; Numanami, 1996) in fact belong to *Falsimohnia* (confirmed herein to be a  
32 29 Prosiphonidae) and *Strebela* (suggested herein to be a Prosiphonidae), both restricted to the area  
33 30 of the Antarctic convergence. The position of *Pareuthria turriiformis* Egorova, 1982 from the  
34 31 Ross Sea was considered doubtful since its anatomy was not studied and its shell does not  
35 32 resemble any other species of *Pareuthria*. Our molecular analysis, nevertheless, confirmed that  
36 33 this species is closely related to *P. fuscata*, the type species of the genus, and thus we confirm the  
37 34 inclusion of *P. turriiformis* in *Pareuthria*.

#### 38 37 FAMILY RETIMOHNIIDAE FAM. NOV.

39 38 (Figs 15 K–O, 16 F–H)

40 39 Type genus: *Retimohnia* McLean, 1995

41 40 Included genera:

42 41 *Fusipagoda* Habe & Ito, 1965 (TS *Mohnia exquisita* Dall, 1913; OD)<sup>(1)</sup>

43 42 *Retifusus* Dall, 1916 (TS *Tritonium jessoense* Schrenck, 1867; OD)<sup>(2)</sup>; radula, see Kosyan &  
44 43 Kantor (2014)  
45 44

1 *Retimohnia* McLean, 1995 (TS *Mohnia frielei* Dall, 1891; OD) <sup>(1)</sup>

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5 **Diagnosis.** Shell thin-walled, small to medium-sized, 12–37 mm in adults, oval to narrowly  
6 fusiform, with moderately long to long siphonal canal. Teleoconch whorls convex or shouldered.  
7 Axial sculpture usually present at least on earlier whorls, of prominent rounded axial ribs. Spiral  
8 sculpture typically of numerous, closely spaced, cords, sometimes with strong keel on shoulder.  
9 Shell pale, yellowish or light brown, due to thin periostracum; inside of aperture white.  
10 Operculum oval, paucispiral or with adaxial terminal nucleus.

11 Radula (Fig. 16F–H). Central tooth with 3–6 cusps and deeply anteriorly notched basal  
12 plate. Lateral teeth with 3–5 (typically 3) cusps. Proboscis short, gland of Leiblein large, valve of  
13 Leiblein well developed. Salivary glands moderately developed or large, sometimes fused.  
14 Stomach large, with small or moderately large posterior mixing area.

15 **Distribution.** North Pacific, northwards from Oregon along the American coast, and northwards  
16 from Japan to Chukchi Sea on the Asian side, from subtidal to abyssal depths.

17 **Remarks.** The genera that are included in the family were previously classified in the subfamily  
18 Colinae (then included in Buccinidae – Kosyan & Kantor, 2014, 2016). Our analysis clearly  
19 demonstrates that they are related neither to Colidae nor to Buccinidae. Their position in the  
20 phylogeny of Buccinoidea as a clade sister to Cominellidae is only marginally supported.

21 The only specimen of *Fusipagoda* included in the analysis represents a species new to  
22 science. It differs from other species of *Fusipagoda* (for review, see Kosyan & Kantor, 2015) in  
23 the presence of axial sculpture and we attribute it to the genus with some doubts; consequently,  
24 the allocation of *Fusipagoda* in the family Retimohniidae is itself a little doubtful.

25 The anatomy of *Retimohnia* and *Retifusus* was recently described by Kosyan & Kantor  
26 (2014, 2016).

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FAMILY AUSTROSIPHONIDAE COTTON & GODFREY, 1938  
(Figs 17A–E, 18A–E)

Type genus: *Austrosipho* Cossmann, 1906.

Included genera:

*Antarctoneptunea* Dell, 1972 (TS *Fusitriton aurora* Hedley, 1916; OD) <sup>(1)</sup>

*Kelletia* Bayle, 1884 (TS *Fusus kelletii* Forbes, 1852; M) <sup>(1)</sup>

*Penion* P. Fischer, 1884 (TS *Fusus dilatatus* Quoy & Gaimard, 1833; M). Synonym after Ponder  
(1973): *Austrosipho* Cossmann, 1906 (TS †*Fusus roblini* Tenison Woods, 1876; OD; Miocene of  
South Australia) <sup>(1)</sup>

*Serratifusus* Darragh, 1969 (TS †*Fusus craspedotus* Tate, 1888; OD) <sup>(1)</sup>

**Diagnosis.** Shell medium-sized to very large, from 35 to 220 mm in adults, broad to narrowly  
fusiform, with moderately long to very long siphonal canal. Protoconch varying in size, reaching  
4 whorls and nearly 4 mm in diameter. Teleoconch whorls evenly convex, shouldered or  
distinctly pagodiform. Axial sculpture usually present at least on adapical whorls, consisting of  
ribs, knobs or spines on shoulder, rarely absent (*Antarctoneptunea aurora*). Spiral sculpture of  
multiple cords varying in strength and density, rarely absent on subsutural ramp (*Serratifusus*).  
Operculum leaf shaped, with terminal nucleus.

Radula (Fig. 18A–F). Central tooth with subrectangular, narrow to medium-broad, and anteriorly notched basal plate, usually bearing 3 cusps. Lateral teeth with 3–7 (most often three) cusps, outer one longest. Proboscis short to long, gland of Leiblein large, subdivided into compartments, valve of Leiblein well developed. Salivary glands large. Stomach either tubular, U-shaped, without posterior mixing area, or sac-like with small posterior mixing area.

Development with (*Kelletia*: Rosenthal, 1970) or without planktotrophic larvae.

**Distribution.** Antarctica, Australasia, tropical Pacific, western America from Baja California to Monterey Bay, Japan, in subtidal to bathyal depths.

**Remarks.** Since its original description, the family name Austrosiphonidae was rarely used as valid and appeared only in checklists without diagnosis or description (Macpherson & Chapple, 1951; Iredale & McMichael, 1962). Ponder (1973) considered it, together with Buccinulidae, a synonym of Buccinidae, and Bouchet *et al.* (2017) a synonym of Siphonaliinae. As demonstrated by our molecular analysis, all these groups constitute independent phylogenetic lineages.

A close relationship of *Serratifusus* to *Penion* had been suggested by Harasewych (1991). Vaux *et al.* (2017) for the first time revealed a close relationship between the Antarctic, initially monotypic, genus *Antarctoneptunea* and *Penion benthicola* Dell, 1956, and transferred the latter to *Antarctoneptunea*.

#### FAMILY TUDICLIDAE COSSMANN, 1901

(Figs 17F–P, 18G–L)

Type genus: *Tudicla* Röding, 1798

[= Buccinulidae Finlay, 1928. Type genus: *Buccinulum* Deshayes, 1830]

Included genera:

*Aneator* Finlay, 1926 (TS *Verconella marshalli* Murdoch, 1924; OD) <sup>(1)</sup>

*Afer* Conrad, 1858 (TS *Murex afer* Gmelin, 1791; by tautonomy) <sup>(1)</sup>; radula, see Harasewych, 2018

*Buccinulum* Deshayes, 1830 (TS *Murex lineatus* Gmelin, 1791 [= *Fusus linea* Martyn, 1784]; SD, Iredale, 1921) <sup>(1)</sup>. Synonyms: *Evarnula* Finlay, 1926 (TS *Cominella striata* Hutton, 1875; OD); *Chathamina* Finlay, 1928 (TS *Cantharus fuscozonatus* Suter, 1908; OD)

*Euthria* Gray, 1850 (TS *Murex corneus* Linnaeus, 1758; SD [Art. 70.3], Petit, 2012) <sup>(1)</sup>

*Euthriostoma* Marche-Marchad & Brébion, 1977 (TS *Euthriostoma gliberti* Marche-Marchad & Brébion, 1977 [= *Euthria saharica* Locard, 1897]; OD) <sup>(2)</sup>; radula, see Bouchet & Warén, 1986

*Lirabuccinum* Vermeij, 1991 (TS *Buccinum dirum* Reeve, 1846, OD) <sup>(2)</sup>; radula, see Callomon & Lawless, 2013

?*Siphonofusus* Kuroda & Habe, 1954 (TS *Siphonalia lubrica* Dall, 1918; M) <sup>(2)</sup>; radula, see Shuto, 1978

*Tasmeuthria* Iredale, 1925 (TS *Siphonalia clarkei* Tenison Woods, 1876; OD) <sup>(1)</sup>; radula, see Cooke, 1917

*Tudicla* Röding, 1798 (TS *Murex spirillus* Linnaeus, 1767; SD, Angas, 1878) <sup>(1)</sup>; radula, see Harasewych, 2018

**Diagnosis.** Shell medium-sized to medium-large, from 10 to about 100 mm in adults, with very short to very long siphonal canal, sometimes twisted or strongly inclined abaxially. Protoconch paucispiral, usually large to very large and bulbous. Axial sculpture usually present at least on adapical whorls, of rounded axial ribs or knobs varying in strength, rarely absent. Spiral sculpture completely absent, or represented by striae or cords of variable strength and density. Outer aperture lip smooth or lirate inside, inner lip calloused, sometimes bearing a parietal knob. Operculum oval, with terminal nucleus.

Radula (Fig. 18G–L) with trapezoidal central tooth, medium- to deeply arcuated anteriorly, and with attenuated narrow posterior portion bearing three closely spaced cusps. Lateral teeth with three strong cusps, outermost longest. Proboscis long, gland of Leiblein medium-large, subdivided into compartments, valve of Leiblein well developed. Salivary glands large, salivary ducts embedded in oesophagus wall. Stomach broad tubular, U-shaped, without posterior mixing area (in *Buccinulum*).

**Distribution.** Tropical (West Africa) and temperate (Mediterranean) Atlantic, tropical Indo-Pacific, northern Pacific, subtidal to upper bathyal depths.

**Remarks.** The subfamily Tudiclinae was classified in the Turbinellidae until Harasewych (2018) provided data on the anatomy and radula of *Tudicla spirillus*, the type species of the monotypical type genus, and transferred it to the Buccinoidea. He also pointed to strong similarities between *Tudicla*, *Afer*, *Euthria* and *Euthriostoma*.

Representatives of *Tudicla* (*T. spirillus*), *Afer* (*Afer cumingii* (Reeve, 1848)) and *Africofusus* Vermeij & Snyder, 2018 (*A. africanus* (G. B. Sowerby III, 1897)) were included in our extended *cox1* analysis and fall in the same clade as *Buccinulum*. Similarly, based on the sequence of 16S gene, *Afer cumingii* was recovered as sister to *Buccinulum* in the analysis of Li *et al.* (2013). The radulae of *Afer* (Fig. 18L) and *Tudicla* are very similar to those of *Euthria* and *Buccinulum* (Li *et al.*, 2013; Fraussen & Hadorn, 2000; Harasewych, 2018), having a characteristic and unique central tooth, leaving no doubt that *Tudicla*, *Afer*, and *Buccinulum* belong to the same family. The name Tudicliidae Cossmann, 1901 has priority over Buccinulidae Finlay, 1928.

The position of *Africofusus* (TS *Fusus ocellifer* Lamarck, 1816; OD) remains doubtful due to the lack of molecular data and radula description for the type species, which is conchologically rather different from the sequenced *A. africanus* and may be not congeneric. Vermeij & Snyder (2018) only conditionally attributed *Fulgur africanus* to the genus.

The extension of the family Tudicliidae (as Buccinulidae Finlay, 1928) has drastically changed over time. Beside *Buccinulum*, the Recent genera *Evarnula* Finlay, 1926, *Chathamina* Finlay, 1928, and *Tasmeuthria* Iredale, 1925 were originally placed by Finlay in the family, and all three were later considered synonyms of *Buccinulum* by Ponder (1971).

Powell (1951) extended the scope of the family to encompass the entire radiation of Southern Hemisphere Buccinoidea. However, Vaux *et al.* (2017) demonstrated that southern buccinoideans are not monophyletic, a conclusion corroborated by our analysis. Tudicliidae as circumscribed herein includes species from both the Southern and Northern Hemispheres.

The genus *Euthria* in its current scope is conchologically very heterogeneous and our analysis did not recover it monophyletic. The species of *Euthria* included in our analysis form two clades. The first one (to which the name *Euthria* can be restricted) includes the type species, *E. cornea*, *E. japonica*, and *E. walleri*. The second one includes *Tasmeuthria clarkei* (Tenison Woods, 1876) (TS of *Tasmeuthria*), and a subclade comprising “*Euthria*” *scepta*, “*E.*”

1 *cummulata* and “*E.*” *solifer*. *Tasmeuthria* was synonymized with *Buccinulum* by Ponder (1971),  
 2 but our analysis demonstrates that it is worthy of a full generic status. However, *T. clarkei* (Fig.  
 3 17J) is conchologically very different from the other three species (see, e.g., Fig. 17M), in  
 4 particular in having a much shorter siphonal canal. Therefore, it is possible that “*Euthria*” *scepta*,  
 5 “*E.*” *cummulata* and “*E.*” *solifer* should be classified in a different genus. One possible name for  
 6 this subclade is *Siphonofusus*, also previously considered a synonym of *Euthria*. The type  
 7 species, *S. lubrica*, possesses a medium-long canal inclined abaxially, and is conchologically  
 8 rather similar to *E. solifer*. Furthermore, *S. lubrica* possesses a radula similar to other Tudicliidae  
 9 species (Shuto, 1978). The validity of *Siphonofusus* is at present not confirmed, pending  
 10 molecular data, but we tentatively include it as valid genus of Tudicliidae.

11 *Buccinulum* was recovered monophyletic neither in our, nor in Vaux *et al.* (2017) analyses.  
 12 Its taxonomy can not be resolved at the moment, since the type species of the genus was not  
 13 included in the analysis.

14 *Lirabuccinum* had been considered closely related to *Buccinulum* by Vermeij (1991). In  
 15 the revision of the genus by Callomon and Lawless (2013), the radulae of several species were  
 16 illustrated. Whereas the radula of the type species, *L. dirum*, is similar to that in Tudicliidae  
 17 (Callomon & Lawless, 2013: fig. 18), the radula of *Lirabuccinum musculus* Callomon &  
 18 Lawless, 2013 (fig. 21) is markedly different in the shape of the central tooth and *L. musculus*  
 19 may not be congeneric with *L. dirum*. Pending molecular data, we tentatively attribute the genus  
 20 to Tudicliidae after Vermeij (1991).

#### 21 22 FAMILY MELONGENIDAE GILL, 1871 (1854)

23  
24 Type genus: *Melongena* Schumacher, 1817

25  
26 = Cassidulidae Gray, 1854 (inv.). Type genus: *Cassidulus* Gray, 1854

27 = Galeodidae Thiele, 1925 (inv.). Type genus: *Galeodes* Röding, 1798

28 = Volemidae Winckworth, 1945. Type genus: *Volema* Röding, 1798

29 = Heligmotomidae Adegoke, 1977. Type genus: *Heligmotoma* Mayer-Eymar, 1896]

30  
31 Included genera:

32 *Brunneifusus* Dekkers, 2018 (TS *Murex ternatanus* Gmelin, 1791; OD) <sup>(3)</sup>

33 *Heligmotoma* Mayer-Eymar, 1896 (TS †*Melongena nilotica* Mayer-Eymar, 1896; M) <sup>(3)</sup>

34 *Hemifusus* Swainson, 1840 (TS *Fusus colosseus* Lamarck, 1822; SD, Gray, 1847) <sup>(1)</sup>

35 *Lenifusus* Dekkers, 2018 (TS *Pyrula elongata* Lamarck, 1822; OD) <sup>(3)</sup>

36 *Melongena* Schumacher, 1817 (TS *Melongena fasciata* Schumacher, 1817 [= *Murex melongena*  
 37 Linnaeus, 1758]; M). Synonym: *Galeodes* Röding, 1798 (TS *Murex melongena* Linnaeus,  
 38 1758; SD, Dall, 1906) <sup>(1)</sup>

39 *Pugilina* Schumacher, 1817 (TS *Murex morio* Linnaeus, 1758; SD, Herrmannsen, 1848).

40 Objective synonym: *Cassidulus* Gray, 1854 (TS *Murex morio* Linnaeus, 1758; M) <sup>(1)</sup>

41 *Saginafusus* Wenz, 1943 (TS *Fusus pricei* E.A. Smith, 1887; OD) <sup>(3)</sup>

42 *Taphon* H. Adams & A. Adams, 1853 (TS *Fusus striatus* G.B. Sowerby I, 1833; M) <sup>(3)</sup>

43 *Volegalea* Iredale, 1938 (TS *Volegalea wardiana* Iredale, 1938; OD) <sup>(3)</sup>

44 *Volema* Röding, 1798 (TS *Volema paradisiaca* Röding, 1798; SD, Iredale, 1917) <sup>(3)</sup>

**Diagnosis.** Shell medium-sized to very large, over 400 mm, varying from broadly ovate with very short canal to fusiform with moderately long canal, or narrowly fusiform with very long siphonal canal. Protoconch paucispiral, medium-large. Axial sculpture from very weak to strong, from growth lines to prominent axial ribs, knobs or long spines on shoulder. Spiral sculpture represented by strong cords of variable strength. Aperture elongate, inner lip often with pronounced parietal callus. Shell colour varying from light to dark brown, sometimes with spiral bands; shell often covered with periostracum, sometimes very thick with axial lamellae and cilia. Operculum thick, large, spanning entire aperture, with terminal nucleus.

Radula (Fig. 22A) with central tooth with rectangular base, shallowly arcuate on anterior margin, and usually with three, broadly spaced, long cusps; lateral teeth bicuspid, with curved cusps, outer one longest. Head characteristically long, tubular, with short tentacles on its tip. Proboscis long, often coiled within rhynchocoel, valve and gland of Leiblein absent. Salivary glands medium-large, salivary ducts tightly attached to oesophagus on most of their length. Posterior oesophagus sometimes forming a pouch. Stomach broad, tubular, U-shaped, without posterior mixing area (Kantor, 2003).

Development direct. Irregularly oval egg capsules attached individually to substrate with short stalk, grouped in single-layered egg cluster.

**Distribution.** Tropical Atlantic, tropical and western Indo-Pacific at subtidal to lower shelf depths.

**Remarks.** The anatomy of several representatives was studied by Kosyan & Kantor (2004) and Abbate & Simone (2015).

#### FAMILY **PRODOTIIDAE** FAM. NOV.

(Figs 19, 20C–F)

Type genus *Prodotia* Dall, 1924

Included genera:

*Caducifer* Dall, 1904 (TS *Triton truncatus* Hinds, 1844; OD) <sup>(1)</sup>

*Clivipollia* Iredale, 1929 (TS *Clivipollia imperita* Iredale, 1929 [= *Clivipollia pulchra* (Reeve, 1846)]; M) <sup>(1)</sup>

*Enzinopsis* Iredale, 1940 (TS *Engina gannita* Hedley, 1914 [= *Ricinula contracta* Reeve, 1846]; OD) <sup>(3)</sup>

*Falsilatirus* Emerson & Moffitt, 1988 (TS *Falsilatirus pacificus* Emerson & Moffitt, 1988; OD) <sup>(3)</sup>

*Minioniella* Fraussen & Stahlschmidt, 2016 (TS *Minioniella heleneae* Fraussen & Stahlschmidt, 2016; OD) <sup>(3)</sup>

*Prodotia* Dall, 1924 (TS *Phos billeheusti* Petit de la Saussaye, 1853 [= *Prodotia iostoma* (Gray, 1833)]; OD) <sup>(1)</sup>

*Speccapollia* Fraussen & Stahlschmidt, 2016 (TS *Ricinula revurva* Reeve, 1846; OD) <sup>(3)</sup>

**Diagnosis.** Shell small to medium-sized, varying from narrowly fusiform, nearly turritiform to broadly biconic with short to medium long siphonal canal. Protoconch medium large, with up to 4 smooth, glossy whorls. Axial sculpture of broad rounded axial ribs of varying strength. Spiral sculpture of distinct, closely spaced cords forming spirally elongated nodules, or raised minute



tubercles at intersection with spiral cords. Aperture ovate or elongated; outer aperture lip liriate, or distinctly denticulated; inner lip calloused, with parietal and anal knobs, often bearing denticles. Operculum with terminal nucleus.

Radula (Fig. 20C–F) of two types. In *Prodotia* (Fig. 20C, D), central tooth with broad arcuate base, with 5–9 cusps, sometimes with additional cusplets. Lateral teeth narrow, with very long outer cusp, bicuspid or with additional very small intermediate cusplet. In *Clivipollia* and *Caducifer* (Fig. 20E, F), central tooth with narrow subsquare base, arcuate on anterior margin, bearing three large cusps; lateral teeth tricuspid, outer cusp longest, intermediate cusp sometimes longer than inner cusp. Proboscis long, narrow, single large proboscis retractor emerging ventrally from posterior third of rhynchodaeum. Odontophore with radula relatively small, spanning anterior half of proboscis length. Valve of Leiblein well defined, gland of Leiblein expanded, tubular. Salivary glands medium-large to large, not fused. Salivary ducts tightly attached to oesophagus on most of their length.

**Distribution.** Tropical Indo-Pacific, tropical Atlantic, at intertidal to subtidal depths.

**Remarks.** The three genera attributed to the new family based on molecular data are rather heterogeneous conchologically as well as in radula morphology (Fig. 20). The radula of *Caducifer* is quite similar to that of some Pisaniidae, nevertheless differing consistently in central tooth morphology: in Pisaniidae the three central cusps are abutting much smaller cusps or serration, which are absent in Prodotiidae.

Four additional genera are attributed to Prodotiidae based on their conchological similarity to *Clivipollia* (Ponder, 1972; Fraussen & Stahlschmidt, 2016). It is possible that broader taxonomic sampling of the Pisaniidae will result in the transfer of some other genera and species to the Prodotiidae. Due to the lack of support of the deeper nodes, the relationships of Prodotiidae are unclear.

#### FAMILY CHAUVETIIDAE FAM. NOV.

(Figs 20B, 21O, P)

Type genus: *Chauvetia* Monterosato, 1884

= *Lachesinae* Bellardi, 1877. Type genus: *Lachesis* Risso, 1826 (invalid: junior homonym of *Lachesis* Daudin, 1803 [Reptilia])

= *Donovaniidae* T. L. Casey, 1904. Type genus: *Donovania* Bucquoy, Dautzenberg & Dollfus, 1883 (invalid: junior homonym of *Donovania* Leach, 1814 [Crustacea])

= *Chauvetiinae* F. Nordsieck, 1968. Type genus: *Chauvetia* Monterosato, 1884 (not available; see Bouchet *et al.*, 2017)]

Included genus:

*Chauvetia* Monterosato, 1884 (nom. nov. pro *Nesaea* Risso, 1826, non Lamarck, 1812, nec Leach, 1814) (TS *Lachesis mamillata* Risso, 1826; by typification of replaced name, Bucquoy, Dautzenberg & Dollfus (1883). Synonyms: *Lachesis* Risso, 1826 (TS *Lachesis mamillata* Risso, 1826; M); *Donovania* Bucquoy, Dautzenberg & Dollfus, 1883 (TS: *Lachesis mamillata* Risso, 1826; by typification of replaced name [*Lachesis* Risso, 1826])

(1)

**Diagnosis.** Shell small, 5 to 13 mm in adults, narrowly fusiform, with high spire and very short siphonal canal. Protoconch small, paucispiral, of about 1.5 whorls, sculptured with spiral threads and in later part by axial ribs. Whorl outline convex; shoulder not pronounced. Axial sculpture of strong and closely spaced ribs, pronounced throughout whorl height. Spiral sculpture of distinct cords, forming nodules at intersection with axial ribs. Aperture oval, low, outer lip with denticles inside. Operculum spanning entire aperture, oval, with subcentral nucleus.

Central tooth (Fig. 20B) with square base and single large cusp, or cusplless. Lateral teeth with long and narrow attenuated outer portion of basal plate, forming “handle”, and with 3 cusps, inner one shorter.

**Distribution.** Mediterranean and adjacent NE Atlantic from the English Channel to Senegal, intertidal to subtidal.

**Remarks.** The isolated position of *Chauvetia* was recognized by many authors, as reflected by three previous attempts to name the family, all of them invalid nomenclaturally. The complex taxonomic history and nomenclature of *Chauvetia* are discussed in detail by Gofas & Oliver (2010).

Although molecular phylogenetic data clearly indicate that Chauvetiidae belongs to Buccinoidea, the relationships of the family are not yet resolved due to lack of support of deeper nodes.

At least one species, *Chauvetia tenuisculpta* (Dautzenberg, 1891), was found parasitizing the sea star *Oreaster clavatus* Müller & Troschel, 1842 (Oliver & Rolán, 2008).

#### FAMILY PISANIIDAE GRAY, 1857

(Figs 21, 22)

Type genus: *Pisania* Bivona-Bernardi, 1832

[= Pusiostomatidae Iredale, 1940. Type genus: *Pusiostoma* Swainson, 1840 (TS *Voluta mendicaria* Linnaeus, 1758, SD, Herrmannsen, 1848 (in 1846–1852))]

Included genera:

*Aplus* De Gregorio, 1885 (TS †*Murex plicatus* Brocchi, 1814; SD, Vokes, 1971)<sup>(1,2)</sup>; see Aissaoui *et al.* (2016)

*Cancellopollia* Vermeij & Bouchet, 1998 (TS *Cancellopollia gracilis* Vermeij & Bouchet, 1998; OD)<sup>(1)</sup>

*Cantharus* Röding, 1798 (TS *Buccinum tranquebaricum* Gmelin, 1791; SD, Cossmann, 1889)<sup>(1)</sup>

*Ecmanis* Gistel, 1848 (TS *Buccinum igneum* Gmelin, 1791; by typification of replaced name, nom. nov. pro *Proboscidea* Möller, 1832, non *Proboscidea* Bruguière, 1791)<sup>(1)</sup>

*Engina* Gray, 1839 (TS *Engina zonata* Gray, 1839 [= *Purpura turbinella* Kiener, 1836]; SD, Gray, 1847)<sup>(1)</sup>

*Gemophos* Olsson & Harbison, 1953 (TS *Buccinum gemmatum* Reeve, 1846, OD)<sup>(1)</sup>

*Hesperisternia* J. Gardner, 1944 (TS †*Hesperisternia waltonia* J. Gardner, 1944; OD)<sup>(1)</sup>

*Pisania* Bivona-Bernardi, 1832 (TS *Pisania striatula* Bivona-Bernardi, 1832 [= *Pisania striata* (Gmelin, 1791)]; SD, Opinion 740 (1965))<sup>(1)</sup>

*Pollia* Gray, 1834 (TS *Buccinum undosum* Linnaeus, 1758; M)<sup>(1)</sup>

1 *Sinetectula* Fraussen & Vermeij, 2021 (TS *Buccinum (Polia) farinosum* Gould, 1850; OD) <sup>(1)</sup>

2  
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4  
5 **Diagnosis.** Shell medium-sized to medium large, exceptionally reaching 100 mm (*Cantharus*),  
6 from fusiform to broadly fusiform or biconic, with low to medium-high spire and short to nearly  
7 obsolete siphonal canal. Protoconch small, paucispiral or multispiral, comprising 1.5 to more  
8 than 3.5 whorls. Whorl outline flattened, weakly or strongly convex. Axial sculpture of strong  
9 and closely spaced ribs, rarely absent (*Pisania*). Spiral sculpture ranging from fine striation to  
10 distinct prominent cords, sometimes keels forming nodules at intersection with axial ribs.  
11 Aperture high, outer lip typically thickened, striated or denticulated inwards. Inner lip often  
12 heavily calloused, often with distinct anal denticle or knob, sometimes bearing multiple denticles  
13 or lirae. Shell sometimes covered with very thick hirsute periostracum. Operculum spanning  
14 entire aperture, assymetrical, drop-shaped, thick, with terminal nucleus.

15 Radula (Fig. 22) central tooth with relatively narrow, rectangular or trapeziform base,  
16 bearing 5 cusps, outer pair very weak, sometimes obsolete (Fig. 20B). Lateral teeth with 2, 3  
17 (usually) or 4 cusps, intermediate cusps always smaller, sometimes inner cusp longer (Fig. 20B,  
18 C), but usually shorter than outer cusp; inner cusp sometimes with serrated inner edge. Proboscis  
19 medium to long; large, paired proboscis retractors emerging laterally from posterior part of  
20 rhynchodaeum, numerous additional lateral bundles of retractors can be present at mid-length of  
21 rhynchodaeum. Odontophore with radula long, spanning entire proboscis length, and can  
22 protrude backwards from proboscis. Valve of Leiblein from small to well defined, pear-shaped,  
23 gland of Leiblein small and flaccid to large, folded anteriorly. Salivary glands medium-large to  
24 large, not fused. Stomach long, with very short posterior mixing area. The anatomical account is  
25 based on studies of *Gemophos tinctus* (Conrad, 1846) (Kosyan & Kantor, 2004), *Polia undosa*  
26 (Linnaeus, 1758), *P. fumosa* (Dillwyn, 1817), and *Ecmanis fasciculatus* (Reeve, 1846) (herein).

27 **Distribution.** Tropical and temperate northern Atlantic, Indo-Pacific, temperate northern  
28 Pacific and temperate Australasia, at intertidal to subtidal depths.

29 **Remarks.** The Pisaniidae are a large group of mainly tropical Buccinoidea that exhibit a  
30 significant range of conchological and morphological (radula) forms. The Pisaniidae were  
31 generally recognized as a subfamily of Buccinidae (e.g. Cernohorsky, 1971; Watters & Finlay,  
32 1989; Vermeij, 2001; Bouchet & Rocroi, 2005; Fraussen & Stahlschmidt, 2016), but was ranked  
33 as a full family, distinct from Buccinidae by Bouchet *et al.* (2017), based on the molecular tree  
34 of Galindo *et al.* (2016). This is confirmed by our molecular phylogeny.

35 Eight of the genera traditionally included in the family were represented in our multigene  
36 analysis. The genus level taxonomy was reviewed by Vermeij (2001) and is mostly followed  
37 here, with the exception of several genera transferred to Prodotiidae. In total 15 valid genera are  
38 attributed to the family (see also Table 3).

39 The family is in need of a revision based on molecular data, since our data reveal the  
40 polyphyly of at least *Pisania* and *Engina*; furthermore, some of the genera currently assigned to  
41 the family may belong to Prodotiidae. Three species of “*Pisania*” were included in our multigene  
42 analyses, two of them [“*Pisania*” *decollata* (G. B. Sowerby I, 1833) and “*P.*” *ignea* (Gmelin,  
43 1791)] cluster together with maximal support, while “*P.*” *pusio* (Linnaeus, 1758) forms a  
44 separate branch. In the analysis of extended *cox1* dataset, *P. striata* (Gmelin, 1791), the type  
45 species of the genus, did not cluster with any of these other three species. A revision of *Pisania*  
is beyond the scope of the present study and requires a much more extensive dataset. We can  
nevertheless state that the name *Pisania* cannot be applied to any of the species included into our

1 multigene analyses. Instead, *Ecmanis* Gistel, 1848 [nom. nov. pro *Proboscidea* Möller, 1832,  
 2 non Bruguière, 1791; type species *Buccinum igneum* Gmelin, 1791] is applicable to the clade  
 3 uniting “*P.*” *decollata* and “*P.*” *ignea*. Based on the characteristic spiral sculpture of broadly  
 4 spaced strong keels in *P. decollata* (Fig. 21H), Dall (1904) proposed the subgenus *Taeniola*  
 5 [invalid, non *Taeniola* Pallas, 1760 [Cestoda] = *Taenia* Linnaeus, 1758]. Furthermore, the radula  
 6 of “*P.*” *decollata* (Fig. 22B) is rather similar to the radula of “*P.*” *fasciculata* (Reeve, 1846) [= *P.*  
 7 *montrouzieri* Crosse, 1862] (Fig. 22C), the type species of *Appisania* Thiele, 1929, a name that  
 8 may be applicable to “*P.*” *decollata*.

9 Four species of “*Engina*” (in the currently accepted scope) were included in our multigene  
 10 analysis. Three of them — the type species *Engina turbinella*, *E. mendicaria* and *E. alveolata* —  
 11 form a highly supported clade that includes both western Atlantic and Indo-West Pacific species.  
 12 Their radulae are very different from each other (Fig. 22E, F; Cernohorsky, 1971: fig. 65 for *E.*  
 13 *alveolata*), thus suggesting its low taxonomic value. Previously accepted as an *Engina*,  
 14 *Sinetectula egregia* (Reeve, 1844) forms an independent long branch, recovered in our tree in a  
 15 position sister to all other Pisaniidae. “*Engina*” *corinnae* (Fig. 21E) despite being  
 16 conchologically similar to *Engina* s.s. also shows no immediate relationship to it, and should also  
 17 be excluded from the genus.

#### 18 FAMILY NASSARIIDAE IREDALE, 1916 (1835)

19 (Figs 23, 24)

20 Type genus: *Nassarius* Duméril, 1805

#### 21 SUBFAMILY NASSARIINAE IREDALE, 1916 (1835)

- 22 = Nassinae Swainson, 1835. Type genus *Nassa* Lamarck, 1799. Invalid: type genus a junior  
 23 homonym of *Nassa* Röding, 1798 [Gastropoda]  
 24 = Cyclopsidae Chenu, 1859. Type genus *Cyclops* Montfort, 1810. Invalid: type genus a junior  
 25 homonym of *Cyclops* O. F. Müller, 1776 [Crustacea]  
 26 = Cyclonassinae Gill, 1871. Type genus: *Cyclonassa* Swainson, 1840  
 27 = Aletrionidae Dall, 1908. Type genus: *Aletrion* Montfort, 1810  
 28 = Arculariidae Iredale, 1915. Type genus: *Arcularia* Link, 1807]

29 Included genera:

- 30 *Caesia* H. Adams & A. Adams, 1853 (TS *Nassa perpinguis* Hinds, 1844; SD, Wenz, 1943) <sup>(3)</sup>  
 31 *Demoulia* Gray, 1838 (TS *Buccinum retusum* Lamarck, 1822; SD, Herrmannsen, 1847) <sup>(3)</sup>  
 32 *Nassarius* Duméril, 1805 (TS *Buccinum arcularia* Linnaeus, 1758; by subsequent monotypy,  
 33 Froriep, 1806). Synonyms: *Aletrion* Montfort, 1810 (TS *Buccinum papillosum* Linnaeus,  
 34 1758; OD); *Arcularia* Link, 1807 (TS *Buccinum gibbosulum* Linnaeus, 1758; SD,  
 35 Cossmann, 1901b: 215)<sup>(1)</sup>  
 36 *Nassodonta* H. Adams, 1867 (TS *Nassodonta insignis* H. Adams, 1867; M) <sup>(1)</sup>  
 37 *Naytia* H. Adams and A. Adams, 1853 (TS *Strombus glabratus* G.B. Sowerby II, 1842; SD,  
 38 Cossmann, 1901) <sup>(1)</sup>  
 39 *Phrontis* H. Adams and A. Adams, 1853 (TS *Buccinum tiarula* Kiener, 1841; SD, Cossmann,  
 40 1901) <sup>(1)</sup>

1 *Reticunassa* Iredale, 1936 (TS *Nassa paupera* Gould, 1850; OD)<sup>(1)</sup>  
 2 *Tritia* Risso, 1826 (TS *Buccinum reticulatum* Linnaeus, 1758; SD, Gray, 1847). Synonyms:  
 3 *Nassa* Lamarck, 1799 (non Röding, 1798) (TS *Buccinum mutabile* Linnaeus, 1758; M);  
 4 *Cyclops* Montfort, 1810 (non O. F. Müller, 1776) (TS *Cyclops asterizans* Montfort, 1810;  
 5 OD); *Cyclonassa* Swainson, 1840 (TS *Buccinum neriteum* Linnaeus, 1758; M)<sup>(1)</sup>

6  
 7 **Diagnosis.** Shell from small to medium-large, very variable in shape, normally bucciniform, but  
 8 from fusiform to broadly fusiform and oval, and occasionally (*e.g.* *Tritia neritea* (Linnaeus,  
 9 1758)) discoidal with nearly flat spire, without siphonal canal and with distinct siphonal notch.  
 10 Spire from very short to high. Parietal callus can be hypertrophied to form a glossy shield,  
 11 covering entire ventral side of the shell. Protoconch paucispiral or multispiral, development  
 12 planktotrophic, lecithotrophic, or ovoviviparous. Axial sculpture usually present, of variously  
 13 developed ribs at least on adapical teleoconch whorls, and sometimes forming distinct knobs at  
 14 intersection with spiral cords, but can be completely absent (*Nassodonta*). Spiral sculpture from  
 15 well developed to nearly obsolete. In *Nassodonta* distinct spiral sulcus at shell base. Aperture  
 16 with smooth or lirate outer lip, inner lip can bear a parietal knob. Operculum with a terminal  
 17 nucleus, with simple or serrated edges; in *Nassodonta* with two spines.

18 Radula (Fig. 24E) central tooth broadly arcuated, with numerous even-sized cusps. Lateral  
 19 teeth in most representatives bicuspid, but irregularly multicuspid in *Hebra* H. Adams & A.  
 20 Adams, 1853 (considered a synonym of *Nassarius* by Galindo *et al.*, 2016) (Cernohorsky, 1984:  
 21 figs 43–45). At the inner corner of the lateral teeth a cusplless, irregular, intermediate lateral  
 22 accessory plate is present in some species (Cernohorsky, 1984: figs 27, 28). Proboscis long, not  
 23 coiled within rhynchocoel, valve of Leiblein distinct, gland of Leiblein tubular, medium-large.  
 24 Salivary glands small, not fused. In some species, stomach with a crystalline style (*e.g.*, *Tritia*  
 25 *obsoleta* (Say, 1822); see Brown, 1969). Foot with paired metapodial tentacles.

26 **Distribution.** Cosmopolitan, except Arctic and Southern Ocean, from intertidal to about  
 27 2,000 m (Cernohorsky, 1984).

28 **Remarks.** Galindo *et al.* (2016) revised the classification of the Nassariidae based on five  
 29 molecular markers obtained for 218 nassariid species. Several genera formerly included in the  
 30 Buccinidae (*Antillophos*, *Engoniophos*, *Phos*, *Nassaria*, *Tomlinia* and *Anentome*) were included  
 31 in the analysis and found to belong in Nassariidae. Nassariidae were recovered monophyletic. In  
 32 the resulting classification, Galindo *et al.* (2016) recognized seven subfamilies of Nassariidae,  
 33 including the new subfamily Buccinanopsinae. In our analysis, Nassariidae sensu Galindo is  
 34 paraphyletic: Buccinanopsidae are clustering with *Macron* and *Busyconidae*, while  
 35 Columbellidae are nested within Nassariidae *s.l.* as sister to *Cylleninae*. There are also a number  
 36 of other differences with Galindo's tree, such as *Dorsanum* then nested within Nassariinae and  
 37 now constituting its own subfamily Dorsaninae.

38 Due to a dataset of Nassariidae *s.l.* herein much more limited in comparison with that of  
 39 Galindo *et al.* (2016), we overall follow their system with the exception of Buccinanopsidae  
 40 being segregated and the erection of the new subfamily Tomliniinae.

#### 41 SUBFAMILY BULLIINAE ALLMON, 1990

42  
 43  
 44 Type genus: *Bullia* Gray, 1833

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1 Included genera:

2 *Bullia* Gray, 1833 (TS *Bullia semiplicata* Gray, 1833; M) <sup>(1)</sup>

3  
4 **Diagnosis.** Shell from medium-sized to medium-large, variable in shape, from fusiform to  
5 narrow fusiform, normally bucciniform, without siphonal canal and with distinct siphonal notch,  
6 usually glossy. Spire from high to very high. Parietal callus can be strongly thickened and  
7 forming an oblique ridge overlaying the suture. Protoconch smooth, large, of about 3 whorls.  
8 Development direct with nurse eggs, or ovoviviparous. Axial sculpture absent or limited to short  
9 subsutural ribs. Spiral sculpture either absent, or of spiral, broadly spaced grooves, rarely of  
10 raised cords. Aperture smooth inside. Operculum often very small, with a terminal nucleus, with  
11 simple or serrated edges.

12 Radula central tooth broadly arcuated, with very numerous (up to 20) cusps gradually  
13 diminishing towards the edge of tooth; lateral teeth with 4 or 5 cusps, outer one largest and  
14 intermediate much smaller. Proboscis short and broad, valve and gland of Leiblein absent.  
15 Stomach with medium-long posterior mixing area (anatomy based on description of *Bullia*  
16 *laevissima* (Gmelin, 1791); Abbate & Simone, 2016). Foot with paired metapodial tentacles.  
17 Eyes absent.

18 **Distribution.** South Africa and western Indian Ocean, intertidal and shallow subtidal.

20 SUBFAMILY ANENTOMINAE STRONG, GALINDO & KANTOR, 2017

22 Type genus: *Anentome* Cossmann, 1901

24 Included genera:

25 *Anentome* Cossmann, 1901 (TS *Melania helena* von dem Busch, 1847; by typification of  
26 replaced name (*Canidia* H. Adams, 1862 non J. Thomson, 1857 [Coleoptera])) <sup>(1)</sup>

27 *Clea* H. Adams & A. Adams, 1855 (TS *Clea nigricans* A. Adams, 1855; M) <sup>(1)</sup>

28 *Oligohalinophila* Neiber & Glaubrecht, 2019 (TS *Canidia dorri* Watterbled, 1886, OD) <sup>(1)</sup>

30 **Diagnosis.** Shell medium-sized, variable in shape, from nearly oval to fusiform, without siphonal  
31 canal and with distinct siphonal notch. Spire from medium-high to high. Axial sculpture usually  
32 present, of distinct sigmoidal ribs, absent in *Clea*. Spiral sculpture of distinct, albeit low, cords,  
33 present at least on shell base, often on entire shell surface. Aperture smooth inside. Operculum  
34 large, with terminal nucleus, with simple edges, in *Anentome* with thickened, pointed, elevated  
35 process behind nucleus.

36 Radula (Fig. 24C, D) variable, either with arcuated central tooth with 5–7 medium-sized or  
37 small cusps (*Clea*, *Anentome*) and tricuspid lateral teeth, outer cusp largest; or with central tooth  
38 with about 10 cusps (*Oligohalinophila*, Fig. 24D) and multicusp lateral teeth with 6 or 7 cusps,  
39 innermost serrated along inner edge. Proboscis medium to long, numerous proboscis retractors  
40 forming bundles attached laterally to mid-rhynchodaeum, in *Anentome* with very large additional  
41 paired retractors at base of rhynchodaeum. Valve of Leiblein distinct, gland of Leiblein absent.  
42 Stomach with very long posterior mixing area and closely spaced ducts of digestive gland  
43 (anatomy after Strong *et al.*, 2017). Foot metapodial tentacles absent.

44 **Distribution:** Fresh and low salinity waters in South and South-East Asia.

## SUBFAMILY DORSANINAE COSSMANN, 1901

Type genus: *Dorsanum* Gray, 1847

[= Duplicatinae Muskhelishvili, 1967. Type genus: *Duplicata* Korobokov, 1955]

Included genus:

*Dorsanum* Gray, 1847 (TS *Buccinum politum* Lamarck, 1822 [= *Dorsanum miran* (Bruguère, 1789)]; OD). Synonym: *Duplicata* Korobokov, 1955 (TS *Buccinum duplicatum* J. de C. Sowerby, 1832; OD)<sup>(1)</sup>

**Diagnosis.** Shell medium-sized, elongate-fusiform, without siphonal canal and with distinct siphonal notch. Spire high. Protoconch elongated, smooth, shining, of ca 2 whorls. Axial sculpture present on adapical spire whorls, vanishing on last whorls, of broad folds, rounded on top, spiral sculpture absent. Aperture weakly lirated inside. Operculum small, oval, with simple edge and subcentral nucleus shifted to low edge of operculum.

Radula with broad arcuated central tooth with numerous (15–20) small cusps, and bicuspid lateral teeth. Proboscis long, not coiled within rhynchocoel, valve of Leiblein small, distinct, gland of Leiblein tubular, medium large. Salivary glands small, not fused. Stomach with long posterior mixing area and three closely spaced ducts to digestive gland (anatomy after Simone & Pastorino, 2014). Foot with short paired metapodial tentacles.

**Distribution.** West Africa, subtidal.

**Remarks.** *Dorsanum miran* (Bruguère, 1789) is the only known Recent species.

## SUBFAMILY PHOTINAE GRAY, 1857

Type genus: *Phos* Montfort, 1810.

Included genera:

*Antillophos* Woodring, 1928 (TS *Cancellaria candeana* d'Orbigny, 1842; OD)<sup>(1)</sup>

*Engoniophos* Woodring, 1928 (TS † *Phos erectus* Guppy, 1873; OD)<sup>(1)</sup>

*Northia* Gray, 1847 (TS *Buccinum pristis* Deshayes, 1844; OD)<sup>(1)</sup>

*Phos* Montfort, 1810 (TS *Murex senticosus* Linnaeus, 1758; OD)<sup>(1)</sup>

**Diagnosis.** Shell medium-large, reaching 80 mm (*Northia*), fusiform, with medium-high spire and nearly obsolete siphonal canal with distinct siphonal notch. Some species with periodical varices. Protoconch small, from paucispiral to multispiral with carinae. Axial sculpture of strong and closely spaced, sometimes sharp, ribs, in *Northia* present on adapical spire whorls; spiral sculpture of distinct prominent cords, sometimes forming nodules at intersection with axial ribs. In *Northia* spiral cords present only on adapical spire whorls and shell base. Aperture high, lirated inside. Operculum spanning most or all of aperture, lanceolate, with terminal nucleus.

Radula (Fig. 24F–H) central tooth of two types: tricuspid with arcuated basal plate (*Phos*, *Northia*) (Fig. 24F, G), or very broad, multicuspid (*Engoniophos*) (Fig. 24H); lateral teeth bicuspid, outer cusp longest. Anatomy studied in *Engoniophos uncinatus* (Say, 1826) (Abbate *et al.*, 2018), several species of *Phos* and *Northia pristis* (this paper). Metapodium with or without

1 single tentacle. Head tentacles long with eyes situated at mid-length on poorly defined lobes.  
 2 Proboscis long, usually not coiled within rhynchoocoel, partially coiled in *Northia*. Proboscis  
 3 retractors lateral, either a single pair or several on each side, detached from rhynchodaeum at  
 4 mid-length. Valve of Leiblein distinct, gland of Leiblein tubular, not large, with long constricted  
 5 duct. Salivary glands small, fused (*Phos*), or separate (*Engoniophos*, *Northia*), salivary ducts  
 6 very thin. Stomach (*Phos*, *Northia*) very small, broadly U-shaped with very small posterior  
 7 mixing area.

8 **Distribuion.** Tropical Atlantic and Indo Pacific, subtidal.

9 **Remarks.** Galindo *et al.* (2016) first included the subfamily Photinae (previously included  
 10 in Buccinidae) in Nassariidae, as the second offshoot of the family in their tree, but the  
 11 corresponding node was not supported. In our tree, the subfamily is sister to the rest of the  
 12 Nassaridae + Columbellidae.

#### 13 14 SUBFAMILY TOMLINIINAE SUBFAM. NOV.

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16 Type genus: *Tomlinia* Peile, 1937

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18 Included genera:

19 *Nassaria* Link, 1807 (TS *Nassaria lyrata* Link, 1807 [= *Nassaria pusilla* (Röding, 1798)]; SD,  
 20 Eames, 1952)<sup>(1)</sup>

21 *Tomlinia* Peile, 1937 (TS *Buccinum rapulum* Reeve, 1846; OD)<sup>(1)</sup>

22 ? *Trajana* J. Gardner, 1948 (TS †*Trajana pyta* J. Gardner, 1948; OD)<sup>(3)</sup>

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24 **Diagnosis.** Shell medium-large, reaching 50 mm, fusiform to broad-fusiform or nearly oval, with  
 25 medium to high spire and from obsolete to short siphonal canal, with distinct siphonal notch,  
 26 siphonal canal can be closed (*Trajana*). Protoconch small, paucispiral, off 1.5–3 whorls. Axial  
 27 sculpture of strong and closely spaced, sometimes sharp, ribs, absent in *Tomlinia*. In addition to  
 28 ribs periodical varices can be present. Spiral sculpture normally distinct on entire shell, but only  
 29 on shell base in *Tomlinia*. Aperture medium to high, from narrow to broad. Outer lip lirate in  
 30 *Nassaria* and *Trajana*, smooth in *Tomlinia*. Columella smooth or with low denticles. Operculum  
 31 oval, with terminal nucleus, sometimes with serrated edge.

32 Radula (Fig. 24A, B) central tooth multicuspid, with rectangular base in *Nassaria* and  
 33 narrow, arcuate in *Tomlinia*; in the latter additional, much smaller, cusplets between larger  
 34 cusps; lateral teeth bicuspid, outer cusp longest.

35 **Distribution.** Estuarine areas in Vietnam, Malaysia and Indonesia (*Tomlinia*), entire  
 36 tropical Indo-Pacific, temperate eastern Pacific, subtidally to bathyal depths (*Nassaria* and  
 37 *Trajana*; Cernohorsky, 1981).

38 **Remarks.** This subfamily unites rather heterogeneous genera. While *Nassaria* lives  
 39 subtidally to over 900 m throughout the Indo-Pacific, *Tomlinia* is one of a few genera of  
 40 Buccinoidea that penetrates estuarine and fresh waters in South East Asia. *Nassaria* and *Trajana*  
 41 on one hand, and *Tomlinia* on the other, are conchologically markedly different. This clade with  
 42 high support in our analysis was also recovered by Galindo *et al.* (2016) (albeit without support)  
 43 as sister to *Cyllene* and included by them in the subfamily Cylleninae. In our analysis it is  
 44 recovered, albeit without support, as a sister to the clade (*Cyllene* (Columbellidae)). We have



1  
2 1 chosen to form the name of the subfamily based on the genus *Tomlinia* to avoid the confusion of  
3 2 having two family group names based on the genera *Nassarius* and *Nassaria*.

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SUBFAMILY CYLLENINAE BELLARDI, 1882

6 Type genus: *Cyllene* Gray, 1834

8 Included genera:

9 *Cyllene* Gray, 1834 (TS *Cyllene owenii* Gray, 1834; M) <sup>(1)</sup>

10 *Neoterion* Pilsbry & Lowe, 1932 (TS *Hindsia ariel* Pilsbry & Lowe, 1932; M) <sup>(2)</sup>; radula, see  
11 D'Attilio (1981)

13 **Diagnosis.** Shell medium-sized, reaching 20 mm, bucciniform, with low spire, without siphonal  
14 canal, and with distinct siphonal notch. Suture grooved. Protoconch small, paucispiral or  
15 multispiral, smooth. Axial sculpture of variously developed ribs, sometimes sigmoidal, on last  
16 whorl may be present adapically only. Spiral sculpture of distinct prominent cords, present on  
17 spiral whorls and at least in adapical part of last whorl and shell base. Aperture elongate and  
18 narrow, outer lip thick, interior prominently lirate; columella calloused and distinctly plicate.  
19 Operculum brown, elongated and pointed, margins even, with terminal nucleus.

20 Radula (Fig. 24I) central tooth broad, with arcuated base, multicuspid, with up to 20 cusps,  
21 gradually diminishing in length from center to sides; lateral teeth with narrow and thickened  
22 base, outer cusp long, inner cusp absent or very reduced to a mere subtriangular protrusion.

23 **Distribution.** West Africa, tropical Indo-West Pacific and S.E. Australia (Cernohorsky,  
24 1984).

25 **Remarks.** The taxonomic position of the enigmatic genus *Neoterion* is problematic.  
26 Conchologically the shell is more similar to Muricidae than to any Buccinoidea (Fig. 23C).  
27 Galindo *et al.* (2016: 350) included it in Photinae based on the “reconstruction of ancestral  
28 characters”, probably protoconch morphology. The radula was examined by D'Attilio (1981) and  
29 although the drawing (reproduced herein on Fig. 24I, lower panel, with some alteration in the  
30 position of the lateral tooth) was not supplemented by any description, it is in most details  
31 similar to the characteristic radula of *Cyllene* (Fig. 24I, upper panel) and *Neoterion* is thus  
32 transferred herein to Cyllenidae.

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FAMILY COLUMBELLIDAE SWAINSON, 1840

37 = Anachidae Golikov & Starobogatov, 1972. Type genus: *Anachis* H. Adams & A. Adams, 1853

38 = Pyrenidae Suter, 1909. Type genus: *Pyrene* Röding, 1798 (TS *Pyrene rhombiferum* Röding,  
39 1798; M)]

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SUBFAMILY COLUMBELLINAE SWAINSON, 1840

43 Type genus: *Columbella* Lamarck, 1799 (TS *Voluta mercatoria* Linnaeus, 1758; M)

SUBFAMILY ATILIINAE COSSMANN, 1901

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2 Type genus: *Atilia* H. Adams & A. Adams, 1853 (TS *Columbella suffusa* G. B. Sowerby I, 1844; SD, Pace, 1902). Synonym: *Anachis* H. Adams & A. Adams, 1853. Type genus: *Anachis* H. Adams & A. Adams, 1853 (TS *Columbella scalarina* G.B. Sowerby I, 1832; SD, Tate, 1868)

7 **Remarks.** Columbelloidea is a very speciose family, currently including 76 valid genera and 911 Recent species (MolluscaBase, accessed 20.12.2020) and represented in our analysis by only seven species in six genera. It is recovered monophyletic with maximal support and sister to Cylleninae of Nassariidae (without support). Columbelloidea possess a radula unique for Buccinoidea, with a rectangular acuspate central tooth and lateral teeth with very narrow base and 3–5 cusps along the inner edge (see, e.g. Bandel, 1984). In *Pseudanachis basedowi* (Hedley, 1918) (not included in the analysis) the radula is markedly different in having multicuspidate central teeth and nearly subtriangular lateral teeth with more than 10 small cusps (Guralnick & deMaitenon, 1997).

#### UNASSIGNED BUCCINOIDEA

19 *Macron* H. Adams & A. Adams, 1853 (TS *Buccinum aethiops* Reeve, 1847; M)

21 **Remarks.** The position of *Macron* has been debated for a rather long time. It was initially described as a subgenus of *Pseudoliva* Swainson, 1840, and remained included in Pseudolividae until Thiele (1929) illustrated the typically buccinoidean radula of *M. lividus* (A. Adams, 1855) and *M. aethiops* (Reeve, 1847) [as *M. trochlea* (Gray, 1839)] (herein, Fig. 16J) and transferred it to the Buccinidae. The placement proposed by Thiele was followed by some authors (e.g. by Wenz, 1938–1944 and Keen, 1971), but later Vermeij (1998) re-assigned *Macron* to Pseudolividae on conchological grounds despite acknowledging the buccinoidean radular morphology. Kantor *et al.* (2017) removed the genus from Pseudolividae and, after Landau *et al.* (2013), suggested affinities to the Nassariidae. The present results clearly indicate that *Macron* is a genus of Buccinoidea, as it is recovered in a highly supported grouping with Buccinanopsidae. However, in shell and radular characters, *Macron lividus* is very different from *Buccinanops* and we do not include *Macron* in Buccinanopsidae. The affinities of the southern African genus *Burnupena* Iredale, 1918 (TS *Buccinum porcatum* Gmelin, 1791 [= *Burnupena cincta* (Röding, 1798)]; OD; see Orr, 1956) are also uncertain, and the genus shows rather strong similarities to *Macron* in shell and radular morphology. It is possible that future studies will confirm the relationships between the two genera and a new taxon of the family group will be established.

#### MORPHOLOGY AND ITS TAXONOMIC VALUE

41 The soft body morphology of the Buccinoidea studied herein is rather uniform. Some families are characterized by specific characters, e.g. the very long and tubular head of Melongenidae, or the presence of metapodial tentacle(s) in Nassariidae. In general, it is difficult to recognize *a priori* the structures that bear a strong phylogenetic signal. For example, opercula are rather morphologically heterogeneous. In most groups they have a terminal nucleus, but in some a concentric operculum with subcentral nucleus (so far found only in the subfamily

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2 1 Buccininae) or a paucispiral one are present, the latter found in several unrelated groups (some  
3 2 Dolicholatiridae, some Cominellidae, some Siphonaliinae, Retimohniidae, and some  
4 3 Prosiphonidae). Nevertheless, within Buccinidae the opercular morphology seems to be a  
5 4 reliable diagnostic character for subfamily level taxa: in Beringiinae, the operculum closes  
6 5 entirely the aperture with a terminal nucleus strongly shifted adaxially; in Buccininae, the  
7 6 operculum is concentric, while in Volutopsiinae the operculum, with a nucleus strongly shifted  
8 7 adaxially, is very small in comparison to the large aperture; in Neptuneinae, the operculum is  
9 8 large, closing nearly entirely the aperture, drop-shaped, with terminal nucleus shifted adaxially.

10 9 The digestive tract is also rather uniform with regard to its main components: anterior  
11 10 foregut, containing proboscis, salivary glands, valve and gland of Leiblein, and mid-gut  
12 11 (stomach). Accessory salivary glands are absent in all Buccinoidea. The proboscis is long to very  
13 12 long, the valve of Leiblein is usually present (absent in some Colubrariidae, all Melongenidae,  
14 13 and in the buccinid subfamily Volutopsiinae). The presence of the gland of Leiblein is usually  
15 14 correlated with the presence of the valve of Leiblein, although the gland can be absent even  
16 15 when the valve is still recognizable, although very reduced (some Colubrariidae, Neptuneinae of  
17 16 Buccinidae, Anentominae of Nassariidae). The salivary glands are paired (and can be fused),  
18 17 acinous, and the salivary ducts usually follow freely along the oesophagus, but they can enter the  
19 18 walls of the oesophagus shortly after leaving the glands (Belomitridae, Colubrariidae,  
20 19 Tudicliidae). Beyond these shared traits, some families have a very distinctive digestive system,  
21 20 e.g. Colubrariidae with an extremely long and thin proboscis coiled within the rhynchodaeum,  
22 21 an extended mid-oesophagus without traces of gland and valve of Leiblein, and, finally, a  
23 22 uniquely shaped stomach in which the intestine is opening posterior to the oesophagus.

24 23 Stomach morphology is potentially important in phylogenetic inference, although it  
25 24 remains poorly studied. A single comparative study of the stomach anatomy of different  
26 25 Buccinoidea was made by Kantor (2003), and there are numerous descriptions of different  
27 26 representatives in the literature. Important characters are the presence and size of the posterior  
28 27 mixing area defining the general outline of the stomach, the position and number of ducts of the  
29 28 digestive gland, or the presence of a gastric shield. When available, brief descriptions of the  
30 29 stomach are provided above in the diagnoses of the family group taxa.

31 30 The radula is one of the best studied morphological characters in Buccinoidea and,  
32 31 compared to other morphological structures, is least dependent of preservation conditions, and it  
33 32 was often used for taxonomic decisions. The radula of Buccinoidea usually consists of three  
34 33 teeth per transverse row, rarely the central tooth is reduced or even absent (some Prosiphonidae).  
35 34 Conversely, in the Nassariinae there is an additional cusplless intermediate lateral accessory plate  
36 35 between the central and lateral teeth. The function and homology of these plates are unknown.

37 36 In the most common radula type of Buccinoidea, found in many unrelated lineages, the  
38 37 central tooth with a rectangular base bears 3–6 cusps, and the lateral teeth are moderately  
39 38 multicuspid (3–6 cusps), with the outer cusp longest. Such radulae are recorded in  
40 39 Austrosiphonidae, Buccinidae (Buccininae, Neptuneinae, some Parancistrolepidinae),  
41 40 Busyconidae, Retimohniidae, some Nassariidae, Prodotiidae and some Prosiphonidae (e.g.  
42 41 *Neobuccinum* and *Chlanidota*). A very peculiar shape of the lateral teeth is found in some genera  
43 42 of Prosiphonidae and in the unrelated Chauvetiidae; there, the outer portion of the basal plate is  
44 43 long, narrow and attenuated, forming a “handle” (Figs 9F–I, 20B). In many cases the rows of  
45 44 teeth are strongly overlapping and this attenuated portion is seen only in oblique view. The  
46 45 number of cusps on the lateral teeth is not correlated with the presence of the handle, nor is the

1 central tooth morphology. The latter can be well developed, with squarish base and well  
2 developed cusp(s) (e.g. some *Prosipho*, see Numanami, 1996; *Argeneuthria*, Fig. 9G, H herein,  
3 both Prosiphonidae; or *Chauvetia*, Fig. 20B, Chauvetiidae), or it can be very reduced to rather a  
4 single obtuse cusp (e.g. *Antistreptus*, Prosiphonidae, Fig. 9I), or it can altogether be absent  
5 (*Met euthria martensi* (Strebel, 1905), Pastorino, 2016).

6 Few of the family group taxa are characterized by a unique radula type. In Tudicliidae the  
7 radula is very uniform (Fig. 17F–P) throughout all genera and possesses a very characteristic  
8 central tooth with trapeziform basal plate, narrowing towards the posterior edge, with three cusps  
9 that occupy the width of the entire basal plate. Columbelloids possess a more variable although  
10 still similar radulae, with an acusate central tooth rectangular plate and laterals characterized by  
11 a very narrow, constricted base attached to the membrane, so that tooth length exceeds several  
12 times the width of the base, while normally 3–5 distinct cusps emanate from the inner edge of  
13 the tooth. Superficially similar acusate central teeth are found in the unrelated subfamily  
14 Beringiinae (Buccinidae) (Fig. 11 C).

15 Other families characterized by a unique morphology of lateral radular teeth are the  
16 Dolicholatiridae and Belomitridae (Fig. 4), with long and narrow teeth base with the cusps  
17 shifted close to the tips. All species of Melongenidae studied so far are characterized by bicuspid  
18 lateral teeth (Fig. 20A), although similar teeth are found in the unrelated Volutopsiinae  
19 (Buccinidae), Eosiphonidae and some other buccinoidean lineages. Special attention should be  
20 paid to the radula of Pisaniidae. While the lateral teeth are rather variable in shape, the number of  
21 cusps (2–4) and the presence or absence of serration on the inner side of the inner cusp and the  
22 central teeth are markedly uniform. In all species studied in this respect (except *Cancellopolia*  
23 *ustulata* Vermeij & Bouchet, 1998, see Vermeij & Bouchet, 1998) the central tooth is  
24 rectangular, with three major cusps on the posterior edge abated by distinct much smaller cusps  
25 on each side (Fig. 22 herein; Cernohorsky, 1971: figs 17–20, 23, 28; Ponder, 1972: figs 1–5, 9–  
26 12). These additional cusps can be reduced together with the major cusps (as in “*Engina*”  
27 *egregia*). On the contrary, in Prodotiidae (which encompass genera previously classified in  
28 Pisaniidae) these lateral secondary cusps are absent (Fig. 20C–F herein; Cernohorsky, 1971: fig.  
29 27; Ponder, 1972: figs 6, 7, 13). After further studies, this may appear to be a reliable  
30 morphological character distinguishing the two families. Also this is questioning the generic  
31 assignment of *Cancellopolia ustulata* that may belong to a new genus of Prodotiidae.

32 Opposite examples are also numerous. The family Prosiphonidae exhibits the most diverse  
33 array of radulae of any buccinoideans (Fig. 9). Our tree includes sequenced representatives  
34 possessing at least three different radula types, which Powell (1951) thought were characterizing  
35 families/subfamilies. Our data however demonstrate that radula morphology of Prosiphonidae is  
36 not correlated with the evolutionary history of the group. Likewise, in Buccinidae the disparity  
37 of radula morphology is high, with some subfamilies characterized by a rather specific  
38 morphology — e.g. Beringiinae with strongly modified lateral teeth and acusate central teeth  
39 (Fig. 11C) and Volutopsiinae with always bicuspid lateral teeth (Fig. 11H) (Kantor, 1990).  
40 Nassariidae also exhibit a high disparity of radular morphology (Fig. 24) with multicupid vs  
41 tricuspid central tooth found in the same subfamily Photinae (Fig. 24F–H).

42 Summing up, we conclude that with the exception of some families, the rather uniform  
43 radular morphology alone does not allow the allocation of genera to a particular family without  
44 additional molecular data. The radula nevertheless remains a valuable taxonomic character in  
45 some groups in combination with the morphology of the digestive tract.

## ON THE RELATIONSHIPS OF POLAR BUCCINOIDEAN FAUNAS

Buccinoidea contribute prominently to the molluscan faunas of high latitudes, and it is interesting to comments on the biogeographic patterns emerging from the reconstructed phylogeny of the superfamily. First, we observe a clear latitudinal pattern, with no bipolar families as circumscribed herein, neither shared between any of the poles and the tropics.

The routes of colonization of the Arctic and the connections between the Arctic fauna and adjacent oceans have been previously discussed (e.g., Durham & MacNeil, 1967; Vermeij, 1991; Vermeij *et al.*, 2019). It is well established that throughout the Cenozoic, the Arctic fauna was mainly influenced by migrations from the Atlantic, and the shelf fauna of the Arctic Ocean was repeatedly extirpated during glaciations (Hardy *et al.*, 2010). Then, starting 3.5 MYA, when Bering Strait opened, not only the Northern Pacific fauna poured into the Arctic Ocean, but also faunal exchange became possible via cross-Arctic invasion of the Atlantic by Pacific taxa, and vice versa. The analysis of recent faunas suggests that expansion of originally Pacific taxa to the Atlantic was notably more frequent than the cross-Arctic invasion of the Pacific by Atlantic taxa (Vermeij, 1991).

Two buccinoidean families reach the Arctic: Colidae and Buccinidae, the latter represented in the Arctic by members of four subfamilies: Buccininae, Neptuneinae, Beringiinae and Volutopsiinae. Colidae is represented in our dataset by eight species from the genera *Colus* and *Turrisipho*, all collected off Iceland or off the Russian coast of the Barents Sea. Kosyan (2007) mentions three species of *Colus* that occur in the North-West Pacific: *Colus islandicus*, *C. minor* (Dall, 1925), and *C. kujianus* Tiba, 1973. One more species, *Colus bukini* Kantor, 1984 was described from the southern Kuril Islands. Unfortunately, none of the latter species, which are restricted to the Pacific, was available to test the monophyly of *Colus*, but as there are no data, to our knowledge, to doubt it, we provisionally accept it as monophyletic. Based on the examination of Miocene and Pliocene fossil material, Vermeij (1991) concluded that *Colus* is a genus that originated in the Atlantic, which implies that *C. minor* and *C. kujianus* are the result of a cross-Arctic invasion.

The situation is opposite in the Buccinidae. Among the 37 species of Buccinidae (as redefined herein) included in the multigene and extended COI analyses, 28 were sampled in the North Pacific and nine (three *Buccinum*, two *Neptunea*, two *Beringius*, one *Anomalisipho*, and one *Mohnia*) in the North Atlantic or the European sector of the Arctic Ocean. The highest diversity of the living Buccinidae is recorded in the temperate North Pacific (Golikov, 1963, 1980; Kantor, 1990; Okutani, 2017), and the buccinid fossil record in the Pacific can be traced back to the Eocene (Gladenkov *et al.*, 1988; Vermeij *et al.*, 2019). It is clear that the family Buccinidae is a lineage originating from the Pacific that has invaded the Atlantic only after the opening of Bering Strait. In conclusion, our results suggest that originally there has been two unrelated buccinoidean radiations at high latitudes in the Northern Hemisphere, one per ocean.

Clarke and Crame (1989: 264) suggested that the Antarctic has continuously been an arena of molluscan faunal evolution: "Overall the fauna has had a long evolutionary history and thus has no single origin. In a sense, it has always been there". Beu (2009) stressed that an Antarctic molluscan fauna similar to the recent one was well established by early Cenozoic times, and the Buccinoidea were a prominent element thereof: "The most diverse families of Antarctic larger gastropods have remained largely unchanged since Paleocene and Eocene time: Trochidae,

1 Naticidae, Conoidea and, above all, Buccinoidea (sensu lato)'. However, as suggested by Beu  
2 (2009), composition of buccinid fauna of Antarctica as per early Eocene was a result of an earlier  
3 faunal change. In this change, in particular, larger forms referred by Beu to Busyconidae and  
4 Melongenidae (Beu, 2009), which were worldwide distributed in Mesozoic and Paleocene  
5 gradually decline in abundance. Previous studies by Vaux and co-authors (2017, 2018) and our  
6 present results identify at least three lineages of Buccinoidea that have independently originated  
7 in or colonized the Antarctic: the Prosiphonidae, Cominellidae and Austrosiphonidae.

8 The Prosiphonidae comprise mainly Antarctic taxa, with some members in Magellanic and  
9 temperate Australian faunas. The latter are represented in our dataset by *Antarctodomus cf.*  
10 *powelli* from off Tasmania, and *Austrofuscus glans* from New Zealand. Dates of the family  
11 diversification are to be determined, but Beu (2009) remarked that at least three genera,  
12 *Prosipho*, *Probuccinum* and *Chlanidota*, were already diversified in Antarctica by the Eocene.  
13 The distribution of the recent family members reflects close connections between Antarctica,  
14 Australia and New Zealand throughout the early Cenozoic, and is consistent with an origin of  
15 Prosiphonidae on a Southern Ocean shelf of breaking up Gondwana.

16 Cominellidae are represented in our dataset by *Pareuthria turiformis* from the Antarctic  
17 and *P. fuscata* from Patagonia, whereas most species of *Cominella* inhabit the temperate  
18 Australia–New Zealand region (Donald *et al.*, 2015). Vaux *et al.* dated the diversification of the  
19 *Cominella* crown group at ~55 MYA, and Beu (2009) mentioned that *Pareuthria* (representing  
20 another subclade of Cominellidae in our tree) was among the genera present in the Antarctic  
21 fauna by the Eocene. This suggests that Cominellidae as circumscribed herein originated in the  
22 Cretaceous–Paleocene, and the distribution of recent members of the family, as in Prosiphonidae,  
23 does not reject an origin on continental shelves and slopes bordering the Southern Ocean.

24 The family Austrosiphonidae is mainly represented by Australia–New Zealand taxa but,  
25 based on the analysis of Vaux *et al.* (2018), it includes the Antarctic *Antarctoneptunea aurora*  
26 and, based on our data, also *Seratifusus lineatus* from Norfolk Ridge off New Caledonia. The  
27 evolutionary history of this group is discussed in detail by Vaux *et al.* (2017), and the inferred  
28 origin of its temperate water subclade (~78 MYA) predates the Cretaceous–Paleogene boundary.  
29 The distribution of the recent members of this clade (including the species of *Seratifusus*  
30 reaching subtropical latitudes) is also consistent with an origin of this lineage in the Southern  
31 Ocean.

32 The hypothesis of a Southern Hemisphere origin of the entire Austrosiphonidae–Tudicliidae  
33 clade needs to be revisited in the light of the new phylogenetic hypotheses obtained in the  
34 present study. Vaux *et al.* (2017) recovered the genera *Buccinulum*, *Aeneator*, *Antarctoneptunea*,  
35 *Penion* and *Kelletia* as a single clade, with an estimated origin at ~116 MYA in the Aptian–  
36 Albian. The Recent species of the former three genera inhabit Southern temperate or polar water,  
37 whereas *Kelletia* by early Miocene has extended its distribution to the Northern Hemisphere  
38 (Hayashi, 2005), and its living species occur in NE and NW Pacific. Nevertheless, Vaux *et al.*  
39 (2017) noted the possible paraphyly of this group in relation to some Northern Hemisphere  
40 buccinoidean lineage(s). Our results confirm this suspicion and change the concept of  
41 Buccinulidae, in particular by demonstrating a close affinity of the *Buccinulum*–*Aeneator*  
42 subclade of the former Buccinulidae to the East African *Afer*, Indian *Tudicla*, and widely  
43 distributed *Euthria*. However, the taxa from temperate Australia (*Tasmeuthria clarkei*) and  
44 Norfolk Ridge (three species formerly placed in *Euthria*) are sister to the rest of the Tudicliidae.  
45 Thus, if we accept an origin of the Austrosiphonidae–Tudicliidae clade in the Southern Ocean, in

1 the most parsimonious scenario, one northward dispersal event for the *Afer–Tudicla–Euthria*  
2 lineage (see the *cox1* tree on Fig. S1) is required to explain the current distribution of the  
3 Tudicliidae. If we hypothesize that the family has originated elsewhere, three independent  
4 southward dispersals are required: for the ancestral Austrosiphonidae, for *Tasmeuthria*, and for  
5 the *Aeneator–Buccinulum* subclade of the Tudicliidae. The first scenario certainly seems more  
6 plausible. The northwards dispersal of *Afer–Tudicla–Euthria* might have been a ‘hitchhike’ with  
7 the concurrent drift of the Indian plate, with subsequent spread of taxa to the Tethys, temperate  
8 Pacific and East Africa, or could have proceeded along the eastern continental shelf of Africa. As  
9 remarked by Vaux *et al.* (2017), also based on previous conclusions (Donald *et al.*, 2015), the  
10 Southern Hemisphere whelk lineages have non-planktotrophic larval development (except  
11 probably *Austrofusus*), thus implying limited dispersal abilities in timeframes of one or few  
12 generations, but range shifts happen over millions of years.

13 Thus, our results support the notion that, in the late Mesozoic and early Cenozoic,  
14 Southern Ocean waters were an arena of buccinoidean diversification that coincided with major  
15 diversification events in other lineages of carnivorous gastropods in the Aptian–Albian ages of  
16 the late Early Cretaceous (Taylor *et al.*, 1980; Strong *et al.*, 2019).

#### 17 18 FUTURE WORK

19  
20 Priority should now be given to expand taxonomic sampling by including genera of  
21 uncertain affinities, such as the Antarctic and Magellanic *Falsitromina*, *Anomacme*,  
22 *Drepanodontus*, *Met euthria*, etc., and the Arctic–North Pacific *Liomesus*, *Latisipho*, *Troschelia*,  
23 etc., which may well result in the detection of additional family-level lineages. In a broader  
24 context, further efforts are needed to generate a supported backbone phylogeny of Buccinoidea,  
25 infer timing of the lineage diversification and review the fossil record in light of the inferred  
26 phylogenetic relationships.

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## SUPPORTING INFORMATION

Fig. S1. Buccinoidea phylogenetic relationships obtained with the Maximum Likelihood (ML) of the *cox1* gene. The species not included in multigene analysis are highlighted in red.

Fig. S2. Buccinoidea phylogenetic relationships obtained with the Maximum Likelihood (ML) of the multigene dataset (concatenated alignment *cox1*, 12S, 16S, 28S and H3 genes). For



- 1  
2 1 *Japeuthria ferrea* (highlighted in red) concatenated alignment of three genes (*cox1*, 16S,  
3 and H3) was used.  
4 2  
5 3  
6 4 Table S1. List of sequenced species included in the molecular analysis with collecting details and  
7 not-aligned sequences.  
8 5  
9 6  
10 7 Table S2. List of genera of Buccinoidea with uncertain familiar allocation.  
11 8  
12 9  
13 9 *Cox1* dataset:  
14 10  
15 11 File S1\_Buc2021\_COI\_all.fas. *Cox1* alignment used to reconstruct a phylogenetic tree on the  
16 Fig. S1.  
17 12  
18 13 File S2\_Buc2021\_COI\_all\_GTR.contree. IQtree output consensus tree (Fig. S1)  
19 14  
20 15 5 genes dataset:  
21 16 File S3\_Buc5G\_230\_GUI40c.fas. Concatenated alignment of 5 genes (*cox1*-16S-12S-H3-28S)  
22 after removal of the columns with confidence values below 0.4 from 16S and 12S.  
23 17  
24 18 File S4\_Buc5G\_230\_GUI90.fas. Concatenated alignment of 5 genes (*cox1*-16S-12S-H3-28S)  
25 after removal of the columns with confidence values below 0.9 from 16S and 12S.  
26 19  
27 20 File S5\_Buc5G\_231\_final.fas. Concatenated alignment of 5 genes (*cox1*-16S-12S-H3-28S) used  
28 for final Bayesian and RaxML analyses on the 5 genes dataset (Figs 1, 2).  
29 21  
30 22 File S6\_Buc5G\_231\_final\_best\_models.txt. Output of the Model finder as implemented in the  
31 IQtree for the final 5 genes dataset.  
32 23  
33 24 File S7\_Buc231\_5Gbest\_model\_RAxML\_bipartitions.result. Output tree file produced by  
34 RaxML for the dataset Buc5G\_231\_final.fas with partitions as specified in  
35 Buc5G\_231\_final\_best\_models.txt.  
36 26  
37 27 File S8\_Buc231\_5Gbest\_model\_BA.nex.con. Consensus tree file generated after summing two  
38 \*.t files from the Bayesian analysis of the dataset Buc5G\_231\_final.fas with partitions as  
39 specified in Buc5G\_231\_final\_best\_models.txt, and discarding 25% trees from first  
40 generations of MCMC.  
41 30  
42 31 File S9\_Buc5G\_232\_final\_Japeuthria.fas. Alignment Buc5G\_231\_final.fas, with additional  
43 hymeric entry for *Japeuthria ferrea*, represented by 3 genes, *cox1*, 16S, and H3, all  
44 obtained from GenBank. Used for analysis to generate the tree on the fig S2.  
45 33  
46 34 File S10\_Buc5G-6\_Japeuthria.contree. IQtree consensus tree resulting from the analysis of the  
47 Buc5G\_232\_final\_Japeuthria.fas with partitions as specified in  
48 Buc5G\_231\_final\_best\_models.txt.  
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## FIGURE CAPTIONS

Figure 1. Buccinoidea phylogenetic relationships obtained with the Bayesian Inference (BI) of the multigene Buc5G dataset (concatenated alignment *cox1*, 12S, 16S, 28S and H3 genes). Bootstrap values (B >70%) and posterior probabilities (PP ≥ 0.95) are shown above each nodes. The clades containing multiple samples are collapsed.

Figure 2 (3 parts). Buccinoidea phylogenetic relationships obtained with the Maximum Likelihood (ML) and the Bayesian Inference (BI) of the multigene dataset (concatenated alignment *cox1*, 12S, 16S, 28S and H3 genes). Bootstrap values (B >70%) and posterior probabilities (PP ≥ 0.95) are shown above each nodes. The names of the family group taxa are provided according to the classification accepted in the present work.

Figure 3. Shells of Dolicholatiridae (A-D) and Belomitridae (E-F). **A.** *Dolicholatirus* sp., Western Australia, Esperance, 11 m, MNHN IM-2009-29739, sequenced specimen (radula, see Fig. 4A). **B.** *Dolicholatirus spiceri* (Tenison Woods, 1876), MNHN IM-2013-42515. **C.** *Dolicholatirus lancea* (Gmelin, 1791), Vietnam, Nha-Trang Bay, Mun I., south side, SL 42.5 mm (radula, see Fig. 4C). **D.** *Crassicantharus noumeensis*, Marshall Is., Gehh I., Kwajalein Atoll, 16 m, SL 18.2 mm (photo Scott Johnson). **E.** *Dolicholatirus* n.sp., southern New Caledonia, KANACONO st. DW4661, 22°45'S, 167°13'E, 400-405 m, SL 7.0 mm, MNHN IM-2013-68545, sequenced specimen. **F.** *Belomitra paschalis* (Thiele, 1925), Mozambique, MAINBAZA sta. CC3172, 25°59'S, 34°35'E, 630-638 m, MNHN IM-2009-18856, sequenced specimen, SL 15.0 mm (radula, see Fig. 4D). **G.** *Belomitra bouteti* Kantor, Puillandre, Rivasseau & Bouchet, 2012, holotype, French Polynesia, Society Is., TARASOC st. 3436, 16°43'S, 151°26'W, 430 m, MNHN IM-2007-24478, SL 32.6 mm (radula, see Fig. 4E).

Figure 4. Radulae of Dolicholatiridae and Belomitridae. **A.** *Dolicholatirus* sp., Western Australia, Esperance, 11 m, MNHN IM-2009-29739 (shell, see Fig. 3A). **B.** *Dolicholatirus cayhuesonicus* (G.B.Sowerby II, 1879), Guadeloupe, KARUBENTHOS 2012 st. GS07, 12 m, MNHN IM-2013-20291. **C.** *Dolicholatirus lancea* (Gmelin, 1791), Vietnam, Nha-Trang Bay, Mun I., south side, SL 43.5 mm (shell, see Fig. 3C). **D.** *Belomitra paschalis* (Thiele, 1925), Mozambique, MAINBAZA sta. CC3172, 25°59'S, 34°35'E, 630-638 m, MNHN IM-2009-18856 (shell, see Fig. 3F). **E.** *Belomitra bouteti* Kantor, Puillandre, Rivasseau & Bouchet, 2012, holotype, French Polynesia, Society Is., TARASOC st. 3436, 16°43'S, 151°26'W, 430 m, MNHN IM-2007-24478, SL 32.6 mm (shell, see Fig. 3G). **F.** *Belomitra brachytoma* (Schepman, 1913), Taiwan 2000 st. CP32, 22°01.7'S, 120°16.4'E, 904 m, MNHN unregistered.

Scale bars A-D – 10 µm, E-F – 50 µm.

Figure 5. Shells of Colubrariidae (A-E) and Colidae (F-L). **A.** *Colubraria muricata* ([Lightfoot, 1786]), Philippines, Mactan I., Punta Engaño, 10-25 m, SL 77.1 mm, © Guido & Philippe Poppe – www.conchology.be. **B.** *Cumia reticulata* (Blainville, 1829), Mediterranean France, SL 41.3 mm, © Guido & Philippe Poppe – www.conchology.be. **C.** *Kanamarua adonis* (Dall, 1919), Philippines, AURORA 2007 st. CP2663, 15°45'N, 121°45'E, MNHN IM-2007-34640, SL 25.8 mm, sequenced specimen. **D.** *Metula inflata* (Houbrick, 1984), Philippines, PANGLAO 2005. st. CP2348, 9°30'N, 123°52'E, 196-216 m, MNHN IM-2007-30079 SL 42.6

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2 1 mm, sequenced specimen. **E.** *Metula* sp., Philippines, AURORA 2007 st. CP2709, 15°12'N,  
3 121°34'E, 244-296 m, MNHN IM-2007-34641, SL 37 mm, sequenced specimen. **F.** *Colus*  
4 *islandicus* (Møller, 1842), Iceland, 67°16'N, 15°26'W, 296-306 m, MNHN IM-2013-78004, SL  
5 100.3 mm, sequenced specimen. **G.** *Colus gracilis* (da Costa, 1778), Iceland, 66°33'N, 25°03'W,  
6 187-222 m, MNHN IM-2013-78018, SL 53.8 mm, sequenced specimen. **H.** *Colus turigulus*  
7 (Friele, 1877), Iceland, 67°25'N, 17°24.5'W, 906-942 m, MNHN IM-2013-78007, SL 61.2 mm,  
8 sequenced specimen. **I.** *Colus holboelli* (Møller, 1842), Iceland, 67°02'N, 23°00'W, 236-243 m,  
9 MNHN IM-2013-78017, SL 35.7 mm, sequenced specimen. **J.** *Colus sabinii* (Gray, 1824),  
10 Iceland, 64°34'N, 10°28'W, 451-478 m, MNHN IM-2013-78014, sequenced specimen. **K.**  
11 *Turrisipho voeringii* Bouchet & Warén, 1985, Iceland, 67°18'N, 23°30.5'W, 395-408 m, MNHN  
12 IM-2013-78002, SL 40.4 mm, sequenced specimen. **L.** *Turrisipho moebii* (Dunker & Metzger,  
13 1875), Iceland, 64°21'N, 12°56'W, 149-152 m, MNHN IM-2013-78009, SL 35.4 mm, sequenced  
14 specimen.

15 Figure 6. Radulae of Colubrariidae (A-C), Colidae (D) and Eosiphonidae fam. nov. (E-L).  
16 **A.** *Colubraria muricata* ([Lightfoot, 1786]) (after Oliverio & Modica, 2010, photo A. Kosyan).  
17 **B.** *Cumia mestayerae* (Iredale, 1915) (7) and *Iredalula striata* (Hutton, 1873) (9) (after Ponder,  
18 1968). **C.** *Metula* sp., South India, off Tutticorin, from fishermen, IEE uncataloged, SL 35.2 mm.  
19 **D.** *Colus islandicus* (after Kosyan & Kantor 2009: fig. 41). **E.** *Enigmaticolus nipponensis*  
20 (Okutani & Fujiwara, 2000), Madagascar, MIRIKY st. CP3279, 15°21'S, 45°57'E, 780-1020 m,  
21 MNHN IM-2009-7079 (shell see on Fig. 7A). **F.** *Manaria kuroharai* Azuma, 1960, China Sea,  
22 ZHONGSHA 2015 st. CP4152, 16°5'N, 113°55'E, 410-412 m, MNHN IM-2013-59292, SL 47.7  
23 mm (shell see on Fig. 7I). **G.** *Gaillaea cf canetae* (Clench & Aguayo, 1944), Guadeloupe,  
24 KARUBENTHOS 2 st. CP4513, 16°13'N, 61°54'W, 406-644 m, MNHN IM-2013-60080  
25 (sequenced specimen). **H.** *Eclectofusus* sp., Papua-New Guinea, PAPUA NIUGINI st. CP3949,  
26 5°12'S, 145°51'E, 380-407 m, MNHN IM-2013-4813 (sequenced specimen). **I.** *Eclectofusus*  
27 *dedonderi* (Fraussen & Hadorn, 2001), paratype, Philippines, Balicasag I., tangle nets at 120-150  
28 m, coll. KF-3206 (shell, see Fig. 7G). **J.** Eosiphonidae Gen. sp., Guadeloupe, KARUBENTHOS  
29 2 st. CP4543, 16°40'N, 61°34'W, 385-399 m, MNHN IM-2013-60365 (shell, see Fig. 7L). **K.**  
30 *Warenius* sp., China Sea, ZHONGSHA 2015 st. CP4134, 19°50'N, 116°27'E, 1128-1278 m,  
31 MNHN IM-2013-61665 (sequenced specimen). **L.** *Americominella longisetosa* (Castellanos &  
32 Fernandez, 1972) (after Penchaszadeh *et al.*, 2019, photo G. Pastorino

33 Scale bars: A, K – 50 µm, C, H, J – 20 µm, D – 500 µm, E, F, G, L – 100 µm

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35 Figure 7. Shells of Eosiphonidae fam. nov. **A.** *Enigmaticolus nipponensis* (Okutani &  
36 Fujiwara, 2000), Madagascar, MIRIKY st. CP3279, 15°21'S, 45°57'E, 780-1020 m, MNHN IM-  
37 2009-7079, SL 99.4 mm, sequenced specimen (radula, see Fig. 6A). **B.** *Thermosipho auzendei*  
38 (Warén & Bouchet, 2001), holotype, central Pacific, Rehu hydrothermal site, Nautilite dive  
39 NAUDUR: stn ND18°0-1B, 17°24.85'S 113°12.15'W, 2578 m, MNHN IM-2000-7049, SL 62  
40 mm. **C.** *Eosipho smithi* (Schepman, 1911), Vanuatu, SANTO 2006 st. AT103, 15°0'38"S;  
41 166°51'E, 373-721 m, MNHN IM-2007-32983, SL 56.1 mm. **D.** *Calagrassor bacciballus*  
42 Fraussen & Stahlschmidt, 2016, Philippines, Bohol Sea, PANGLAO 2005 st. CP2356, 9°21'N ;  
43 124°9'E, 1764 m, MNHN IM-2007-32940, SL 13.2 mm. **E.** *Calagrassor aldermenensis* (Powell,  
44 1971), Philippines, AURORA 2007 st. CP2673, 15°1'N, 121°45'E, 431-493 m, MNHN IM-  
45 2007-34635, SL 20.7 mm, sequenced specimen. **F.** “*Manaria*” *fluentisona* Fraussen &

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1 Stahlschmidt, 2016, holotype, Solomon Is., SALOMONBOA 3 st. DW2790, 8°19'S, 160°37'E,  
2 314-586 m, MNHN IM-2007-35942, SL 15.4 mm. **G.** *Eclectofusus dedonderi* (Fraussen &  
3 Hadorn, 2001) paratype 12, Philippines, Balicasag I., tangle nets at 120-150 m, coll. KF-3206,  
4 SL 11.6 mm. **H.** *Manaria formosa* Bouchet & Warén, 1986, Madagascar, MIRIKY st. CP3183,  
5 12°38'S, 48°14'E, 420-436 m, MNHN IM-2007-36855, SL 55 mm. **I.** *Manaria kuroharai*  
6 Azuma, 1960, China Sea, ZHONGSHA 2015 st. CP4152, 16°5'N, 113°55'E, 410-412 m, MNHN  
7 IM-2013-59292, SL 47.7 mm, sequenced specimen (radula see Fig. 6F). **J.** *Gaillea coriolis*  
8 (Bouchet & Warén, 1986), Philippines, AURORA 2007 st. CP2699, 14°50'N, 123°35'E, 541-  
9 583 m, MNHN IM-2007-34637, SL 31 mm. **K.** *Calagrassor* sp. 2, Papua-New Guinea, PAPUA  
10 NIUGINI st. CP4048, 3°20'S, 143°28'E, 325-345 m, MNHN IM-2013-18794, sequenced  
11 specimen. **L.** Eosiphonidae Gen. sp., Guadeloupe, KARUBENTHOS 2 st. CP4543, 16°40'N,  
12 61°34'W, 385-399 m, MNHN IM-2013-60365, SL 11.3 mm, sequenced specimen (radula, see  
13 Fig. 6J). **M.** *Aulacofusus hiranoi* (Shikama, 1962), Japan, 37°00'N, 141°39'E, 557-561 m,  
14 AORI\_YK#3406, SL 35.4 mm, sequenced specimen. **N.** *Preangeria dentata* (Schepman, 1911),  
15 Philippines, PANGLAO 2005 st. CP2349, 9°32'N, 123°56'E, 219-240 m, IM-2007-32656, SL  
16 22.8 mm. **O.** *Warenus crosnieri* (Bouchet & Warén, 1986), holotype, Madagascar,  
17 N/O"Vauban" st. CH138, 13°49'S 47°29'E, 1800-2000 m, MNHN IM-2000-6369, SL 33.7 mm.  
18 **P.** *Americominella longisetosa* (Castellanos & Fernandez, 1972) (after Penchaszadeh *et al.*,  
19 2019), SL 98 mm, photo G. Pastorino.

21 Figure 8. Shells of Prosiphonidae. **A-B.** *Antarctodomus thielei* (Powell, 1958), Ross Sea,  
22 Antarctica, 65°25'S, 160°53'E. 114 m, MNA00183, SL 18 mm, sequenced specimen. **C.**  
23 *Antarctodomus cf. powelli* Dell, 1995, Tasmania, NC0009, SL 42.1 mm, sequenced specimen. **D.**  
24 *Austrofusus glans* (Röding, 1798), New Zealand, South Island, Nelson, Collingwood, Pakawai,  
25 USNM 601959, SL 40 mm. **E.** *Cavineptunea cf. monstrosa* Powell, 1951, Bransfield Strait,  
26 Antarctica, MNA11734, SL 39.8 mm, sequenced specimen. **F.** *Chlanidota signeyana* Powell,  
27 1951, Bransfield Strait, Antarctica, MNA6718. SL 33.5 mm, sequenced specimen. **G.**  
28 *Falsimohnia innocens* (E.A.Smith, 1907), Bransfield Strait, Antarctica, MNA11387, SL 5.6 mm,  
29 sequenced specimen. **H.** *Falsimohnia minor* (Strebel, 1908), Bransfield Strait, Antarctica,  
30 MNA11409, SL 6.5 mm, sequenced specimen. **I.** *Proneptunea* sp., Bransfield Strait, Antarctica,  
31 MNA11364, SL 6.1 mm, sequenced specimen. **J.** *Probuccinum tenerum* (E.A.Smith, 1907),  
32 Bransfield Strait, Antarctica, MNA11740, SL 17.4 mm. **K.** *Prosipho spiralis* Thiele, 1912,  
33 Bransfield Strait, Antarctica, MNA11398, SL 7.1 mm, sequenced specimen. **L.** *Prosipho mundus*  
34 E.A.Smith, 1915, Ross Sea, Antarctica, 454 m, MNA6308, SL 7.6 mm, sequenced specimen. **M.**  
35 *Drepanodontus tatyanae* Harasewych & Kantor, 2004, holotype, Scotia Sea, Antarctica, 59°2'S,  
36 51°53'W, 3010-3510 m, USNM 1010544, SL 43.1 mm. **N.** *Neobuccinum eatoni* (E.A.Smith,  
37 1875), Antarctica, South Shetland Is., King George I., 62°10'S, 57°44'W, 610-625 m, USNM  
38 897630, SL 39 mm. **O.** *Germonea rachelae* Harasewych & Kantor, 2004, holotype, Antarctica,  
39 off South Georgia I., 58°02'S, 37°57'W, 3197-3239 m, USNM 896594, SL 61.8 mm. **P.**  
40 *Muffinbuccinum catherinae* Harasewych & Kantor, 2004, holotype, South Atlantic Ocean  
41 [Argentine Abyssal Plain], 47°17'S, 47°46'W, 5685-5798 m, USNM 1010623, SL 26.4 mm.

43 Figure 9. Radulae of Prosiphonidae. **A.** *Neobuccinum eatoni* (E.A.Smith, 1875),  
44 Antarctica, Adélie Land, 66°35'S, 143°5'E, 862-875 m, MNHN IM-2009-8220. **B.** *Falsimohnia*  
45 *minor* (Strebel, 1908), syntype, South Georgia I., outer Cumberland Bay, 54°11'S, 36°18'W,

1 252–310 m, SMNH Type-1057. **C.** *Muffinbuccinum catherinae* Harasewych & Kantor, 2004,  
 2 paratype 1, South Atlantic Ocean [Argentine Abyssal Plain], 47°17' S, 47°46'W, 5685–5798 m,  
 3 USNM 1010624. **D.** *Germonea rachelae* Harasewych & Kantor, 2004, holotype, off South  
 4 Georgia I., 58°02' S, 37°57'W, 3197–3239 m, USNM 896594. **E.** *Drepanodontus tatyanae*  
 5 Harasewych & Kantor, 2004, paratype 1, E of South Sandwich Is., 57°00'S, 26°10'W, 2740–2757  
 6 m, USNM 881529. **F.** *Falsimacme kobelti* (Strebel, 1905), Argentina, photo G. Pastorino. **G–H.**  
 7 *Argeneuthria cerealis* (Rochebrune & Mabile, 1885), Tierra del Fuego, photo G. Pastorino. **I.**  
 8 *Antistreptus magellanicus* (Dall, 1902), Argentina, 37°35'S, 56°25'W, 73 m, photo G. Pastorino  
 9 Scale bars: A, C, D, E – 100 µm, B, I – 10 µm, F, G, H – 30 µm.

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 11 Figure 10. Shells of Buccinidae. **A.** *Buccinum chishimanum* Pilsbry, 1904, Japan,  
 12 Hokkaido, 42°58'N, 144°53'E, intertidal, AORI\_YK#3988, SL 29.0 mm, sequenced specimen.  
 13 **B.** *Buccinum nipponense* Dall, 1907, Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m,  
 14 AORI\_YK#3989, SL 40.8 mm, sequenced specimen. **C.** *Thysanobuccinum* sp., Japan, Honshu I.,  
 15 39°25'N, 143°10'E, 1950–2051 m, AORI\_YK#3408, SL 22.4 mm, sequenced specimen. **D.**  
 16 *Ovulatibuccinum cf. fimbriatum* (Golikov & Sirenko, 1988), Japan, Honshu I., 38°25'N,  
 17 142°00'E, 342–343 m, SL 9.0 mm, sequenced specimen. **E.** *Bathybuccinum bicordatum* Golikov  
 18 & Sirenko, 1988, Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, AORI\_YK#3992, SL 8.4  
 19 mm, sequenced specimen. **F.** *Thysanobuccinum* n. sp., Japan, 38°16'N, 143°32'E, 3302–3311 m,  
 20 AORI\_YK#3402, SL 20.3 mm, sequenced specimen. **G.** *Beringius crebricostatus* (Dall, 1877),  
 21 Aleutian Is., 54°05'N, 166°23'W, 88 m, RNC\_4149, SL 127.7 mm, sequenced specimen. **H.**  
 22 *Beringius aleuticus* Dall, 1895, holotype, Aleutian Is., SE of Seguam I., 52°15'N, 171°40'W, 454  
 23 m, USNM 106999, SL 65 mm. **I.** *Beringius turtoni* (Bean, 1834), Iceland, 67°00'N, 23°14'W,  
 24 246–247 m, MNHN IM-2013-78021, SL 108.4 mm, sequenced specimen. **J.** *Metajapelion*  
 25 *adelphicus* (Dall, 1907), Japan, Kyushu Is., 32°06'N, 129°29'E, 606–610 m, AORI\_YK#3975, SL  
 26 54.1 mm, sequenced specimen (radula, see Fig. 13C). **K.** *Metajapelion pericochlion* (Schrenck,  
 27 1863), Japan, AORI\_YK#4142, SL 117.7 mm, specimen sequenced for *cox-1*. **L.** *Neptunea*  
 28 *kurosio* Oyama, 1959, Japan, Kyushu I., 32°10'N, 129°30'E, 470–487 m, AORI\_YK#3985, SL  
 29 86.4 mm, sequenced specimen. **M.** *Neptunea fukueae* Kira, 1959, Japan, Kyushu I., 32°10'N,  
 30 129°30'E, 470–487 m, AORI\_YK#3658, SL 61.7 mm, sequenced specimen. **N.** *Neptunea*  
 31 *despecta* (Linnaeus, 1758), Iceland, 67°49'N, 21°44.5'W, 755–770 m, MNHN IM-2013-78010,  
 32 SL 41.2 mm, sequenced specimen. **O.** *Aulacofusus periscelidus* (Dall, 1891), Kurile Is., Urup Is.,  
 33 45°55.2'N, 150°15.8'E, 169–150 m, IEE BUC270, SL 58.5 mm, specimen sequenced for *cox-1*.

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 35 Figure 11. Radulae of Buccinidae. **A.** *Neptunea costaria* Fraussen & Terryn, 2007,  
 36 holotype of *Costaria borealis* Golikov, 1977, Iturup I. [South Kurile Is.], 414 m, ZIN 30873/1.  
 37 **B.** *Aulacofusus periscelidus* (Dall, 1891), Kurile Is., Urup I., Kitovy Cape, 50 m, ZIN 55945  
 38 (after Kosyan & Kantor, 2013: fig. 5 E). **C.** *Metajapelion adelphicus* (Dall, 1907), Japan,  
 39 Kyushu Is., 32°06'N, 129°29'E, 606–610 m, AORI\_YK#3975, SL 54.1 mm (shell, see Fig. 10 I).  
 40 **D.** *Japelion hirasei* (Pilsbry, 1901), Japan, Honshu I., 39°22'N, 142°15'E, 479–484 m,  
 41 AORI\_YK#3449, SL 95.8 mm (shell, see Fig. 14F). **E.** *Thalassoplanes moerchi* (Dall, 1908),  
 42 Kurile-Kamchatka Trench, 43°58'N, 157°19'E, 5422–5379 m, ZSM, uncatalogued (IEE  
 43 BUC144) (shell, see Fig. 14I). **F.** *Clinopegma magnum unicum* (Pilsbry, 1905), form *damon*,  
 44 south-eastern Sakhalin, 46°28'N, 142°52'E, in 44 m, Zoological Museum of Moscow State  
 45 University, uncatalogued, SL 97.8 mm. **G.** *Anomalisipho virgatus* (Friele, 1879), 80°57'N,

1 47°05'E, Icebraker *Litke st. 22*, 124 m, ZIN, uncatalogued (shell see Fig. 14K). **H.** *Volutopsius*  
 2 *regularis* (Dall, 1873) (after Kantor, 1990: fig. 32). **I.** *Parancistrolepis fujitai* (Kuroda, 1931) (2)  
 3 and *P. kinoshitai* (Kuroda, 1931) (3) (after Habe, 1972).

4 Scale bars: A, B-E, G – 100 µm; F – 200 µm.

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 6 Figure 12. Shells of Buccinidae. **A.** *Habevolutopsius hirasei* (Pilsbry, 1907), Japan,  
 7 Honshu I., 40°58'N, 141°46'E, 459–498 m, AORI\_YK#3657, SL 62.4 mm, sequenced  
 8 specimen. **B.** *Lussivolutopsius filiosus* (Dall, 1919), Bering Sea, 60°01'N, 168°39'W, 37 m,  
 9 RNC\_4493, SL 52.8 mm, sequenced specimen. **C.** *Volutopsius fragilis* (Dall, 1891), Chukchi  
 10 Sea, 71°31'N, 157°23'W, 88 m, RNC\_4552, SL 74.2 mm, sequenced specimen. **D.** *Pyrulofusus*  
 11 *dexius* Dall, 1907, Aleutian Is, 52°56'N, 170°59'E, 185 m, RNC\_4870, SL 148 mm, sequenced  
 12 specimen. **E.** *Ancistrolepis grammatus* (Dall, 1907), Okhotsk Sea, Kurile Is., Onkotan I.,  
 13 49°31'N, 154°25'E, 571–580 m, IEE Bu-OS-1188, SL 21.4 mm, specimen sequenced for *cox-1*.  
 14 **F.** *Japelion hirasei* (Pilsbry, 1901), Japan, Honshu I., 39°22'N, 142°15'E, 479–484 m,  
 15 AORI\_YK#3449, SL 95.8 mm (radula, see Fig. 13D). **G.** *Clinopegma magnum unicum* (Pilsbry,  
 16 1905), Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, AORI\_YK#3403, SL 75.7 mm,  
 17 sequenced specimen. **H.** *Bathyancistrolepis trochoideus* (Dall, 1907), Japan, Honshu I.,  
 18 38°47'N, 143°10'E, 1887–1919 m, AORI\_YK#3377, SL 38.4 mm, sequenced specimen. **I.**  
 19 *Thalassoplanes moerchi* (Dall, 1908), Kurile-Kamchatka Trench, 43°58'N, 157°19'E, 5422–5379  
 20 m, ZSM, uncatalogued (IEE BUC144), SL 31.4 mm, sequenced specimen (radula, see Fig. 13E).  
 21 **J.** *Pseudoliomesus canaliculatus* (Dall, 1874), Japan, AORI\_YK#4141, SL 32.2 mm, specimen  
 22 sequenced for *cox-1*. **K.** *Parancistrolepis fujitai* (Kuroda, 1931), Japan, AORI\_YK#3401, SL  
 23 81.4 mm, specimen sequenced for *cox-1*. **L.** *Anomalisipho virgatus* (Friele, 1879), Spitzbergen,  
 24 80°57'N, 47°05'E, Icebraker *Litke st. 22*, 124 m, ZIN, uncatalogued, SL 40.3 mm (radula, see  
 25 Fig. 13G). **M.** *Anomalisipho verkruzeni* (Kobelt, 1876), Iceland, 67°06'N, 23°14'W, 246 m,  
 26 MNHN IM-2013-78020, SL 61.5 mm, sequenced specimen. **N.** *Plicifusus rhyssus* (Dall, 1907),  
 27 Japan, AORI\_YK#4211, SL 46.7 mm, specimen sequenced for *cox-1*. **O.** “*Colus*” *kujianus* Tiba,  
 28 1973, Japan, AORI\_YK#4210, SL 57.7 mm, specimen sequenced for *cox-1*. **P.** *Liomesus ovum*  
 29 (Turton, 1825), Scotland, SL 29.1 mm © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). **Q.**  
 30 *Truncaria filosa* (A. Adams & Reeve, 1850) (holotype of *Cominella brunneocincta* Dall, 1896),  
 31 *Albatross st. 3390*, Gulf of Panama, 102 m, USNM 123009, SL 31.5 mm (photo USNM).

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 33 Figure 13. Shells of Siphonaliidae. **A.** *Pararetifusus tenuis* (Okutani, 1966), off  
 34 Kesenuma, Miyagi, Honshu I., Japan, 38°47'N, 143°10'E, 1887–1919 m, SL 11.6 mm,  
 35 sequenced spm (BUC 181). **B.** *Bayerius holoserica* (Lus, 1971), KURAMBIO I st. AGT 6–9,  
 36 north-western Pacific, 42°29'N, 154°00'E, 5293–5307 m, SL 48.9 mm, sequenced specimen  
 37 (radula, see Fig. 11A). **C.** *Bayerius knudseni* (Bouchet & Warén, 1986). KURAMBIO I st. AGT  
 38 12–5, north-western Pacific, 39°44'N, 147°10'E, 5229–5217 m, SL 23.9 mm, sequenced  
 39 specimen (radula, see Fig. 11B). **D.** *Phaenomenella insulapratasensis* (Okutani & Lan, 1994),  
 40 South China Sea, DONGSHA 2014 st. CP4129, 20°29'N, 116°8'E, 590–633 mm, MNHN IM-  
 41 2013-50203, SL 38.7 mm, sequenced specimen. **E.** *Phaenomenella nicoi* Kantor, Kosyan,  
 42 Sorokin & Fedosov, 2020, holotype, South China Sea, SW off Dong Sha, ZHONGSHA 2015; st.  
 43 CP4132, 20°07'N, 116°22'E, 958–988 m, MNHN IM-2013-61585, SL 41.1 mm, sequenced  
 44 specimen (radula, see Fig. 11D). **F.** *Siphonalia spadicea* (Reeve, 1847), South China Sea,  
 45 TAIWAN 2004 st. CP244, 24°53'N, 121° 56'E, 122–123 m, MNHN IM-2007-32856, SL 51.8

1 mm, sequenced specimen. **G.** *Mohnia dalli* (Friele, 1881), Barents Sea, 72°23'N, 14°58'E, 702 m, SL 24.6 mm, sequenced specimen.

Figure 14. Radulae of Siphonaliidae. **A.** *Bayerius holoserica* (Lus, 1971), KURAMBIO I st. AGT 6–9, north-western Pacific, 42°29'N, 154°00'E, 5293–5307 m (shell, see Fig. 10B). **B.** *Bayerius knudseni* (Bouchet & Warén, 1986). KURAMBIO I st. AGT 12–5, north-western Pacific, 39°44'N, 147°10'E, 5229–5217 m (shell, see on Fig. 10C). **C.** *Pararetifusus tenuis* (Okutani, 1966), Kurile Is., off Iturup I., 44°20'N, 148°24'E, 414 m, ZIN 58795/6 (after Kosyan, 2006, fig. 3A). **D–E.** *Phaenomenella nicoi* Kantor, Kosyan, Sorokin & Fedosov, 2020, D – holotype, South China Sea, SW off Dong Sha, ZHONGSHA 2015 st. CP4132, 20°07'N, 116°22'E, 958–988 m, MNHN IM-2013-61585 (shell, see Fig. 10E); E – South China Sea, ZHONGSHA 2015 st. CP4134, 19°50'N, 116°27'E, 1128–1278 m, MNHN-IM-2013-61673. **F.** *Siphonalia cassidariaeformis* (Reeve, 1846), Japan, Off Hashima, Miyazaki Prefecture, Kyushu (after Kantor et al., 2020a: fig. 11A).

Scale bars: A,B, D, E – 100 µm, C – 50 µm, F – 200 µm.

Figure 15. Shells of Busyconidae (A–C), Buccinanopsidae (D), Cominellidae (E–J), and Retimohniidae (K–O). **A.** *Busycotypus canaliculatus* (Linnaeus, 1758), USA, South Carolina, MNHN IM-2013-40689, sequenced specimen. **B.** *Busycon carica* (Gmelin, 1791), USA, South Carolina, MNHN IM-2013-40690, sequenced specimen. **C.** *Fulguropsis pyruloides* (Say, 1822), USA, South Carolina, MNHN IM-2013-40692, sequenced specimen. **D.** *Buccinanops deformis* (P. P. King, 1832), Argentina, Isla de los Pajaros, 42°25.4'S, 64°32.2'W, intertidal, IEE uncatalogued, SL 27.7 mm (radula, see Fig. 16I). **E.** *Pareuthria fuscata* (Bruguière, 1789), Tierra del Fuego, San Sebastian Bay, 53°16.8'S, 68°13.2'W, USNM 898376, SL 21.6 mm (photo USNM). **F.** *Pareuthria turriiformis* Egorova, 1982, Antarctica, Ross Sea, 71°19'S, 170°30'E, 243 m, MNA168, SL 16.1 mm, sequenced specimen. **G.** *Cominella virgata* H. Adams & A. Adams, 1853, New Zealand, Ahipara Bay, Reef Point, Te Papa Tongareva (M.278752), SL 31.3 mm. **H.** *Cominella glandiformis* (Reeve, 1847), New Zealand, Mangere Inlet, SE of Auckland, 36°56'S, 174°49'E, AORI\_YK#3987, 25.6 mm, sequenced specimen. **I.** *Lusitromina abyssorum* (Lus, 1993), off Saunders I., South Sandwich Is., 57°39'S, 26°00'W, 2380–2609 m, USNM 1010536, SL 29.2 mm (photo USNM) (radula, see Fig. 16E). **J.** *Falsitromina bella* (Powell, 1951), South Shetland Is., 61°45'S, 61°14'W, 4758 m, USNM 881870, SL 5.1 mm. **K.** *Retimohnia bella* (Ozaki, 1958), Japan, off Tokachi, Hokkaido I., 42°11'N, 144°11'E, 1210–1248 m. AORI\_YK#3977, SL 24.5 mm, sequenced specimen. **L.** *Retimohnia micra* (Dall, 1907), Japan, off Otsuchi, Iwate, Honshu I., 39°20'N, 142°23'E, 849–864 m, AORI\_YK#3978, SL 11.7 mm, sequenced specimen. **M.** *Fusipagoda exquisita* (Dall, 1913), Eastern Kamchatka, 55°52'N, 164°8'E, 4382 m, R/V *Vityaz* sta. 524, SL 23.5 mm (radula, see Fig. 16G) (after Kosyan & Kantor, 2015: fig. 1B). **N.** *Fusipagoda* sp., Japan, off Onagawa, Miyagi, Honshu I., 38°16'N, 143°32'E, 3302–3311 m, AORI\_YK#3981, SL 29.1 mm, sequenced specimen. **O.** *Retifusus jessoensis* (Schrenck, 1863), Sea of Japan, Peter the Great Bay, ZIN 34121/16, SL 22.1 mm (radula, see Fig. 16H) (after Kosyan & Kantor, 2014: fig. 1B).

Figure 16. Radulae of Busyconidae (A–B), Cominellidae (C–E), Retimohniidae (F–H), Buccinanopsidae (I), and Buccinoidea insertae sedis (J–K). **A.** *Busycon carica* (Gmelin, 1791), USA, Lewes, Delaware (after Kosyan & Kantor, 2004: fig. 11A). **B.** *Fulguropsis spirata*

1 (Lamarck, 1816), Mexico, Yucatan (after Kosyan & Kantor, 2004: fig. 11C). **C.** *Pareuthria*  
 2 *fuscata* (Bruguière, 1789) (after Pastorino, 2016; photo G. Pastorino). **D.** *Cominella virgata* H.  
 3 Adams & A. Adams, 1853, New Zealand, Wellington Bay, New Zealand (after Cernohorsky,  
 4 1971: fig. 93). **E.** *Lusitromina abyssorum* (Lus, 1993), off Saunders I., South Sandwich Is.,  
 5 57°39'S, 26°00'W, 2380-2609 m, SL 29.2 mm, USNM 1010536 (shell, see Fig 15I). **F.**  
 6 *Retimohnia micra* (Dall, 1907), Sea of Japan, R/V *Vityaz* st. 7490, 39°51'N, 133°47'E, 560 m  
 7 (after Kosyan & Kantor, 2016: fig. 9B). **G.** *Fusipagoda exquisita* (Dall, 1913), eastern  
 8 Kamchatka, R/V *Vityaz*, st. 524, 55°52'N, 164°08'E, 4382 m (shell, see Fig. 15M) (after Kosyan  
 9 & Kantor, 2015: fig. 3A). **H.** *Retifusus jessoensis* (Schrenck, 1863 in 1862-63), Sea of Japan,  
 10 Peter the Great Bay, ZIN 34121/16, SL 22.1 mm (shell, see Fig. 15O) (after Kosyan & Kantor,  
 11 2014: fig. 4A). **I.** *Buccinanops deformis* (P. P. King, 1832), Argentina, Isla de los Pajaros,  
 12 42°25.4'S, 64°32.2'W, intertidal, IEE uncatalogued (shell, see Fig. 15D). **J.** *Macron* spp. – (350)  
 13 *M. lividus* (A. Adams, 1855); (352) *Macron aethiops* (Reeve, 1847) (after Thiele, 1929). **K.**  
 14 *Burnupena* spp – (b) **B.** *cincta* (Röding, 1798); (d) *Burnupena papyracea* (Bruguière, 1789)  
 15 (after Orr, 1956: fig. 1).

16 Scale bars: A,B – 500 µm; C – 80 µm. E, F, G, H, I – 100 µm.

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 18 Figure 17. Shells of Austrosiphonidae (A-E) and Tudicliidae (F-P). **A.** *Penion cuvierianus*  
 19 (Powell, 1927), New Zealand, off White I., NMNZ M.132414. **B.** *Penion chathamensis* Powell,  
 20 1938, New Zealand, E of Mernoo Bank, Chatham Rise, NMNZ M.118863. **C.** *Antarctoneptunea*  
 21 *benthicola* (Dell, 1956), New Zealand, Chatham Rise, NMNZ M.009775, SL 95 mm. **D.**  
 22 *Antarctoneptunea aurora* (Hedley, 1916), Antarctica, 77°00'S, 161°59'W, 525-537 m, USNM  
 23 898682, SL 68.9 mm (photo USNM). **E.** *Serratifusus lineatus* Harasewych, 1991, holotype, New  
 24 Caledonia, Grand Passage, 18°55'S, 163°24'E, 460 m, MNHN IM-2000-6527, SL 35.5 mm. **F.**  
 25 *Aeneator recens* (Dell, 1951), New Zealand, NE slope of Mernoo Bank, Chatham Rise, NMNZ  
 26 M.127027. **G.** *Aeneator benthicolus* Dell, 1963, New Zealand, off Cape Kidnappers, NMNZ  
 27 M.147010. **H.** *Buccinulum linea* (Martyn, 1784), neotype, New Zealand, head of Titirangi Bay,  
 28 NE of Havelock, NMNZ M.046477, SL 35.4 mm. **I.** *Euthria walleri* (Ladd, 1976), Vanuatu,  
 29 15°33'S, 167°17'E, 120-156 m, MNHN IM-2007-32887, SL 57.5 mm, sequenced specimen. **J.**  
 30 *Tasmeuthria clarkei* (Tenison Woods, 1876), Western Australia, Esperance, Woody I., 33°58'S,  
 31 122°01'E, 11 m, MNHN IM-2013-63028, SL 9.9 mm, sequenced specimen (radula, see Fig.  
 32 18K). **K.** *Afer cumingii* (Reeve, 1848), Taiwan, SL 88.9 mm, © Guido & Philippe Poppe –  
 33 www.conchology.be. **L.** *Euthria japonica* (Shuto, 1978), E Taiwan, 24°34'N, 122°2'E, 195-207  
 34 m, IM-2013-78127, sequenced specimen (radula, see Fig. 18J). **M.** *Euthria cummulata* Fraussen  
 35 & Hadorn, 2003, New Caledonia, Norfolk Ridge, 23°17'S, 168°14'E, 275-348 m, IM-2007-  
 36 34931, SL 46.2 mm, sequenced specimen. **N.** *Euthriostoma saharicum* (Locard, 1897), Western  
 37 Sahara, © Guido & Philippe Poppe – www.conchology.be. **O.** *Tudicla spirillus* (Linnaeus,  
 38 1767), trawled between Porto Novo and Pondicherry, India, 13–15 m, USNM 894130, SL 76.7  
 39 mm (after Harasewych, 2018). **P.** *Lirabuccinum dirum* (Reeve, 1846), USA, SL 26 mm, ©  
 40 Guido & Philippe Poppe – www.conchology.be.

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 42 Figure 18. Radulae of Austrosiphonidae (A-F) and Tudicliidae (G-P). **A.** *Antarctoneptunea*  
 43 *aurora* (Hedley, 1916), Antarctica, Adélie Land, 66°34'S, 145°21'E, 401-416 m, MNHN IM-  
 44 2009-7893. **B.** *Antarctoneptunea benthicola* (Dell, 1956), New Zealand, 48°49'S, 167°27'E, 560  
 45 m, MNNZ M.95190. **C.** *Antarctoneptunea benthicola* (Dell, 1956), New Zealand, 43°03.7'S,



1 177°00'E, 350 m, MNMZ M.117007. **D.** *Kelletia lischkei* Kuroda, 1938 (after Kang, 1976). **E.**  
 2 *Penion cuvierianus* (Powell, 1927), New Zealand, Peach Cove, Bream Bay, Northland,  
 3 35°51.9'S, 174°34.1'E, 24 m, NMNZ M.98018. **F.** *Serratifusus lineatus* Harasewych, 1991,  
 4 northern New Caledonia, 18°59'S, 163°24'E, 320-335 m, MNHN IM-2007-34666 (sequenced  
 5 specimen). **G.** *Aeneator* spp. (A) *Aeneator elegans* (Suter, 1917), st. VUZ83, off Palliser Bay,  
 6 1000 m, NMNZ M.11115; (B) *A. valedictus* (R. B. Watson, 1886), Chatham Islands Expedition  
 7 st. 6, Chatham Rise, 400 m, NMNZ (after Beu, 1979). **H.** *Buccinulum linea* (Martyn, 1784), New  
 8 Zealand, NMNZ. **I.** *Euthria cornea* (Linnaeus, 1758), Mediterranean, Capri I., IEE  
 9 uncatalogued. **J.** *Euthria japonica* (Shuto, 1978), E Taiwan, 24°34'N, 122°02'E, 195-207 m, IM-  
 10 2013-78127 (shell, see Fig. 17L). **K.** *Tasmeuthria clarkei* (Tenison Woods, 1876), Western  
 11 Australia, Esperance, Woody I., 33°58'S, 122°01'E, 11 m, MNHN IM-2013-63028 (shell, see  
 12 Fig. 17J). **L.** *Afer cumingii* (Reeve, 1848) (after Li *et al.*, 2013: fig. 2).

13 Scale bars: A,B,H-J – 100 µm; C, E, K – 250 µm; F – 50 µm

15 Figure 19. Shells of Prodotiidae fam. nov. (A-I). **A.** *Clivipolia pulchra* (Reeve, 1846),  
 16 Philippines, Pamilacan I., 09°29.4'N, 123°56.0'E, 17 m, MNHN IM-2007-32529, SL 22.4 mm,  
 17 sequenced specimen. **B.** *Caducifer decapitatus* (Reeve, 1844), Vanuatu, 15°33.0'S, 167°09.6'E,  
 18 20 m, MNHN IM-2007-32728, SL 13 mm, sequenced specimen. **C.** *Caducifer decapitatus*  
 19 (Reeve, 1844), Papua-New Guinea, Madang lagoon, S Sek I., 05°06.4'S, 145°49'21.2"E, MNHN  
 20 IM-2013-18102, SL 8.3 mm (young specimen with intact spire). **D-E.** *Prodotia lannumi*  
 21 (Schwengel, 1950), Vanuatu, Santo, south of Aoré I., 15°36.6'S, 167°10.0'E, 10-18 m, **D** –  
 22 MNHN IM-2007-32839, SL 11.6 mm, sequenced specimen; **E** – MNHN IM-2007-32859, SL  
 23 14.1 mm. **F.** *Enzinopsis contracta* Reeve, 1846 (holotype of *Engina gannita* Hedley, 1914),  
 24 Australia, Queensland, Torres Strait, Darnley I., AMS C.7468, SL 17.2 mm. **G.** *Speccapollia*  
 25 *africana* Fraussen & Stahlschmidt, 2016, holotype, Mozambique, Nacala Bay, 3-5 m, MNHN  
 26 IM- 2000-31691, SL 10 mm. **H.** *Minioniella heleneae* Fraussen & Stahlschmidt, 2016, holotype,  
 27 Tuamotu Islands, IM- 2000-31692, SL 6.7 mm. **I.** *Prodotia iostoma* (Gray, 1833), New  
 28 Caledonia, Koumac, KOUMAC 2.3 st. KB617, 20°44.7'S, 164°15.8'E, 13 m, SL 22.1 mm  
 29 (radula, see Fig. 20D).

31 Figure 20. Radulae of Melongenidae (A), Chauvetiidae fam. nov. (B) and Prodotiidae fam.  
 32 nov. (C-F) **A.** *Volegalea cochlidium* (Linnaeus, 1758), Vietnam, Haiphong, fishermen market  
 33 (after Kosyan & Kantor. 2004: fig. 3C, as *Pugilina pugilina* (Born, 1778)). **B.** *Chauvetia*  
 34 *mamillata* (Risso, 1826) (after Gofas & Oliver, 2010: fig. 2). **C.** *Prodotia lannumi* (Schwengel,  
 35 1950), New Ireland, Kavieng. **D.** *Prodotia iostoma* (Gray, 1833), New Caledonia, Koumac,  
 36 KOUMAC 2.3 st. KB617, 20°44.7'S, 164°15.8'E, 13 m (shell, see Fig. 19I). **E.** *Clivipollia*  
 37 *pulchra* (Reeve, 1846), New Caledonia, Grand récif de Koumac, KOUMAC 2.3 st. KL39,  
 38 20°45.1'S, 164°14.0'E, 26 m, MNHN IM-2019-8415. **F.** *Caducifer decapitatus* (Reeve, 1844),  
 39 New Caledonia, Grand récif de Koumac, KOUMAC 2.3 st. KB645, 20°40.5'S, 164°13.0'E, 16 m,  
 40 MNHN IM-2019-9119.

41 Scale bars: A – 100 µm, B – 10 µm; C – 20 µm; D, E, F – 50 µm

43 Figure 21. Shells of Pisaniidae (A-N) and Chauvetiidae fam. nov. (O-P). **A.** “*Engina*”  
 44 *egregia* (Reeve, 1844), Vanuatu, Santo, SE Aesi I., 15°26.9'S, 167°15.8'E, 11 m, IM-2007-  
 45 32918, SL 14 mm, sequenced specimen. **B.** *Engina mendicaria* (Linnaeus, 1758), Vanuatu, S

1 coast of Santo I., 15°34.9'S, 167°02.4'E, 0-1 m, MNHN IM-2007-32893, SL 15.9 mm. **C.** *Engina*  
 2 *alveolata* (Kiener, 1836), Vanuatu, Santo, E. of Malo I., 15°43.4'S, 167°15.0'E, 6 m, MNHN IM-  
 3 2007-32919, SL 12.4 mm, sequenced specimen. **D.** *Hesperisternia karinae* (Nowell-Usticke,  
 4 1959), Guadeloupe, 16°24'N, 60°52'W, 72 -111 m, MNHN IM-2013-60604, sequenced  
 5 specimen. **E.** “*Engina*” *corinnae* Crovo, 1971, Martinique, Ste Luce, Grand Caye, 14°27.3'N,  
 6 60°55.5'W, 15 m, MNHN IM-2013-70604, SL 9.3 mm, sequenced specimen. **F.** *Pisania striata*  
 7 (Gmelin, 1791), Greece, SL 16.5 mm, © Guido & Philippe Poppe – www.conchology.be. **G.**  
 8 “*Pisania*” *pusio* (Linnaeus, 1758), Guadeloupe, SL 34.2 mm, © Guido & Philippe Poppe –  
 9 www.conchology.be. **H.** “*Pisania*” *decollata* (G.B. Sowerby I, 1833), Papua New Guinea,  
 10 05°11'S, 145°50'E, 5 m, MNHN IM-2013-18270, SL 20.7 mm, sequenced specimen. **I.**  
 11 “*Pisania*” *ignea* (Gmelin, 1791), N Madagascar, 25°17'S, 46°31'E, 53-54 m, MNHN IM-2009-  
 12 14631, sequenced specimen. **J.** *Gemophos tinctus* (Conrad, 1846), Guadeloupe, 16°20'N,  
 13 61°32'W, 1 m, MNHN IM-2013-8012, SL 16.4 mm, sequenced specimen. **K.** *Cancellopolia*  
 14 *gracilis* Vermeij & Bouchet, 1998, holotype, New Caledonia, Norfolk Ridge, 435 m, MNHN  
 15 IM-2000-6329, SL 29.8 mm. **L.** *Polia fumosa* (Dillwyn, 1817), South Madagascar, 25°28.1'S,  
 16 44°56.4'E, 12-14 m, MNHN IM-2009-14575. **M.** *Cantharus melanostoma* (G.B. Sowerby I,  
 17 1825), Philippines, SL 59.2 mm © Guido & Philippe Poppe – www.conchology.be. **N.** *Polia*  
 18 *imprimelata* Fraussen & Rosado, 2011, South Madagascar, 24°23'S, 47°32'E, 154-168 m, IM-  
 19 2009-14603, sequenced specimen. **O.** *Chauvetia mamillata* (Risso, 1826), Spain, Malaga, 0-5 m,  
 20 IEE BUC 193, SL 5.5 mm. **P.** *Chauvetia procerula* (Monterosato, 1889), Spain, Malaga, 0-5 m,  
 21 IEE BUC 210, SL 4.2 mm

23 Figure 22. Radulae of Pisaniidae. **A.** *Pisania striata* (Gmelin, 1791), Mediterranean (after  
 24 Troschel, 1867, pl. 7, fig. 2). **B.** “*Pisania*” *decollata* (G.B. Sowerby I, 1833), New Caledonia,  
 25 Koumac, MNHN unregistered. **C.** “*Pisania*” *fasciculata* (Reeve, 1846), New Caledonia,  
 26 Koumac, KOUMAC 2.3 st. KB517, 20°37.6'S, 164°17.3'E, 0 m, MNHN unregistered. **D.**  
 27 “*Pisania*” (= *Ecmanis*) *ignea* (Gmelin, 1791) (after Ponder, 1972: text fig. 2). **E.** *Engina*  
 28 *turbinella* (Kiener, 1836), French Guiana, 05°17.5'N, 52°35.2'W, 7 m, MNHN IM-2013-57184  
 29 (sequenced specimen). **F.** *Engina mendicaria* (Linnaeus, 1758), Papua New Guinea, Laing I.,  
 30 IEE unregistered. **G.** *Polia fumosa* (Dillwyn, 1817), Vietnam, Nha-Trang Bay, Mun I., IEE  
 31 unregistered. **H.** *Polia undosa* (Linnaeus, 1758), Vietnam, Nha-Trang Bay, Mun I., IEE  
 32 unregistered. **I.** “*Engina*” *egregia* (Reeve, 1844), Papua New Guinea, Madang Lagoon,  
 33 05°13.8'S, 145°48.0'E, 15 m, MNHN IM-2013-12540.

34 Scale bars: B, C, G, H – 100 µm; E, F – 20 µm, I – 50 µm.

36 Figure 23. Shells of Nassariidae. Cylleninae: **A.** *Cyllene owenii* Gray, 1834 (syntype of  
 37 *Cyllene senegalensis* Petit de la Saussaye, 1853), Senegal, MNHN IM-2000-6364, SL 16 mm. **B.**  
 38 *Cyllene parvula* Bozzetti, 2014, Madagascar, holotype, MNHN IM-2000-27891, SL 12.5 mm. **C.**  
 39 *Neoterion ariel* (Pilsbry & Lowe, 1932), holotype, ANSP 155564, Nicaragua, SL 6.5 mm (photo  
 40 ANSP). Tomliniinae: **D.** *Nassaria acuminata* (G.B. Sowerby III, 1913), Vanuatu, 15°37'S,  
 41 167°15'E, 140-153 mm, MNHN IM-2007-32730, SL 23.6 mm, sequenced specimen. **E.** *Tomlinia*  
 42 *fraussenii* Thach, 2014, Vietnam, MNHN IM-2013-53362. Bulliinae: **F.** *Bullia perlucida*  
 43 Bozzetti, 2014, holotype, Madagascar, MNHN IM-2000-27493, SL 19.9 mm. Dorsaninae: **G.**  
 44 *Dorsanum miran* (Bruguière, 1789), Senegal, SL 22.5 mm, © Guido & Philippe Poppe –  
 45 www.conchology.be. Anentominae: **H.** *Oligohalinophila dorri* (Wattebled, 1886), syntype,  
 46 MNHN IM-2000-6321, Vietnam, lagune de Koa-hai, SL 13.9 mm. **I.** *Anentome* sp. D, Vietnam,

1 vicinities of Nha-Trang city, middle part of Kai river, IM-2009-29658, sequenced specimen.  
 2 Nassariinae: **J.** *Naytia glabrata* (G.B. Sowerby II, 1842), Cameroon, SL 7.2 mm, © Guido &  
 3 Philippe Poppe – www.conchology.be. **K.** *Phrontis complanata* (Powys, 1835), Costa Rica, SL  
 4 7.1 mm, © Guido & Philippe Poppe –www.conchology.be. Photinae: **L.** *Engoniophos uncinatus*  
 5 (Say, 1826) (syntype of *Nassa guadelupensis* Petit de la Saussaye, 1852), Guadeloupe, MNHN  
 6 IM-2000-6713, SL 27.1 mm. **M.** *Antillophos candeanus* (d'Orbigny, 1842) (syntype of *Phos*  
 7 *antillarum* Petit de la Saussaye, 1853), Guadeloupe, MNHN IM-2000-6584, SL 28.5 mm. **N.**  
 8 *Phos senticosus* (Linnaeus, 1758), Papua New Guinea, Laing I., intertidal, SL 33.5 mm (radula,  
 9 see Fig. 24G). **O.** *Northia pristis* (Deshayes, 1844), Panama, Venado I., intertidal, IEE BUC  
 10 YK1 (radula, see Fig. 24F).

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Figure 24. Radulae of Nassariidae. **A.** *Tomlinia fraussenii* Thach, 2014, Vietnam, MNHN.  
**B.** *Nassaria* sp., Bismarck Sea, W Kairiru I., 03°20'S, 143°28'E, 325-345 m, PAPUA NIUGINI  
 st. CP4048, MNHN IM-2013-18779. **C.** *Anentome* sp. D, Vietnam, vicinities of Nha-Trang city,  
 middle part of Kai river, MNHN IM-2009-29661. **D.** *Oligohalinophila dorri* (Wattebled, 1886),  
 Vietnam (after Kantor & Kilburn, 2001: fig. 18). **E.** *Tritia reticulata* (Linnaeus, 1758), Black  
 Sea, Gelendzhik, IEE uncatalogued. **F.** *Northia pristis* (Deshayes, 1844), Panama, Venado I.,  
 intertidal, IEE BUC YK1 (shell, see Fig. 21M). **G.** *Phos senticosus* (Linnaeus, 1758), Papua-  
 New Guinea, Laing Id., intertidal, IEE uncatalogued, SL 33.5 mm (shell, see Fig. 21L). **H.**  
*Engoniophos uncinatus* (Say, 1826) (after Abbate *et al.*, 2018: fig. 5). **I.** Radulae of Nassariidae,  
 Cylleninae. Upper panel – *Cyllene fuscata* A.Adams, 1851 (after Yang & Zang, 2011: pl. 1r).  
 lower panel – *Neoterion ariel* (Pilsbry & Lowe, 1932), after D'Attilio (1981). Scale bars: A-E, G,  
 I – 100 µm, F – 200 µm.

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For Review Only

Table 1. Comparison of previous classifications of Buccinoidea with the classification accepted in the present paper.

Golikov & Starobogatov, 1975	This paper	Bouchet <i>et al.</i> 2017
	SPF Buccinoidea Rafinesque, 1815	SPF Buccinoidea Rafinesque, 1815
<u>Superfamily Pyrenoidea Suter, 1913</u> Pyrenidae Suter, 1913	Columbellidae Swainson, 1840	Columbellidae Swainson, 1840
<u>Superfamily Beringioidea Golikov &amp; Starobogatov, 1975 (part)</u> Anachidae Golikov & Starobogatov, 1975	SF Columbellinae SF Atiliinae Cossmann, 1901	SF Columbellinae SF Atiliinae Cossmann, 1901
<u>Superfamily Beringioidea Golikov &amp; Starobogatov, 1975 (part)</u> Beringiidae Golikov & Starobogatov, 1975	Buccinidae Rafinesque, 1815 SF Beringiinae Golikov & Starobogatov, 1975 SF Buccininae	Buccinidae Rafinesque, 1815 SF Beringiinae Golikov & Starobogatov, 1975 SF Buccininae
<u>Superfamily Buccinoidea Rafinesque, 1815 (part)</u> Buccinidae Rafinesque, 1815 Neptuneidae Troschel, 1869	SF Volutopsiinae Habe & Sato, 1973 SF Parancistrolepidinae Habe, 1972 SF Neptuneinae Stimpson, 1865 ? SF Liomesini P. Fischer, 1884 ? SF Truncariinae Cossmann, 1901 SF Siphonaliinae Finlay, 1928 Colidae Gray, 1857 Prosiphonidae Powell, 1951 Cominellidae Gray, 1857 <b>Eosiphonidae fam. nov.</b> <b>Retimohniidae fam. nov.</b>	T Buccinini T Parancistrolepidini Habe, 1972 T Colini Gray, 1857 T Ancistrolepidini Habe & Sato, 1973 T Liomesini P. Fischer, 1884
Buccinulidae Powell, 1929	Tudicidae Cossmann, 1901 Busyconidae Wade, 1917 SF Busyconinae Wade, 1917 SF Busycotypinae Petuch, 1994	T Prosiphonini Powell, 1951 T Cominellini Gray, 1857 SF Buccinulinae Finlay, 1928 SF Busyconinae Wade, 1917 T Busyconini Wade, 1917 T Busycotypini Petuch, 1994
(?) Pseudolividae Thiele, 1929 Vexillidae Thiele, 1929	<b>Chauvetiidae fam. nov.</b> Austrosiphonidae Cotton & Godfrey, 1938	SF Donovaninae Casey, 1904 SF Siphonaliinae Finlay, 1928
<u>Superfamily Buccinoidea Rafinesque, 1815 (part)</u> Melongenidae Gill, 1871	Melongenidae Gill, 1871	Melongenidae Gill, 1871
<u>Superfamily Buccinoidea Rafinesque, 1815 (part)</u> Nassariidae Iredale, 1916	Nassariidae Iredale, 1916 SF Nassariinae SF Anentominae Strong, Galindo & Kantor, 2017 SF Bulliinae Allmon, 1990 SF Dorsaninae Cossmann, 1901 SF Cylleninae Bellardi, 1882 <b>SF Tomliniinae subfam. nov.</b> SF Photinae Gray, 1857	Nassariidae Iredale, 1916 SF Nassariinae SF Anentominae Strong, Galindo & Kantor, 2017 SF Bulliinae Allmon, 1990 SF Dorsaninae Cossmann, 1901 SF Cylleninae Bellardi, 1882 SF Photinae Gray, 1857
<u>Superfamily Fasciolarioidea Gray, 1853</u> Fasciolaridae Gray, 1853 Fusinidae Wrigley, 1927	Buccinanopsidae Galindo, Puillandre, Lozouet & Bouchet, 2016 Fasciolaridae Gray, 1853 SF Fasciolarinae SF Fusininae Wrigley, 1927 SF Peristerniinae Tryon, 1880 <b>Dolicholatiridae fam. nov.</b>	SF Buccinanopsinae Galindo, Puillandre, Lozouet & Bouchet, 2016 Fasciolaridae Gray, 1853 SF Fasciolarinae SF Fusininae Wrigley, 1927 SF Peristerniinae Tryon, 1880
	Belomitridae Kantor, Puillandre, Rivasseau & Bouchet, 2012 Colubrariidae Dall, 1904 Pisaniidae Gray, 1857 <b>Prodotiidae fam. nov.</b>	Belomitridae Kantor, Puillandre, Rivasseau & Bouchet, 2012 Colubrariidae Dall, 1904 Pisaniidae Gray, 1857

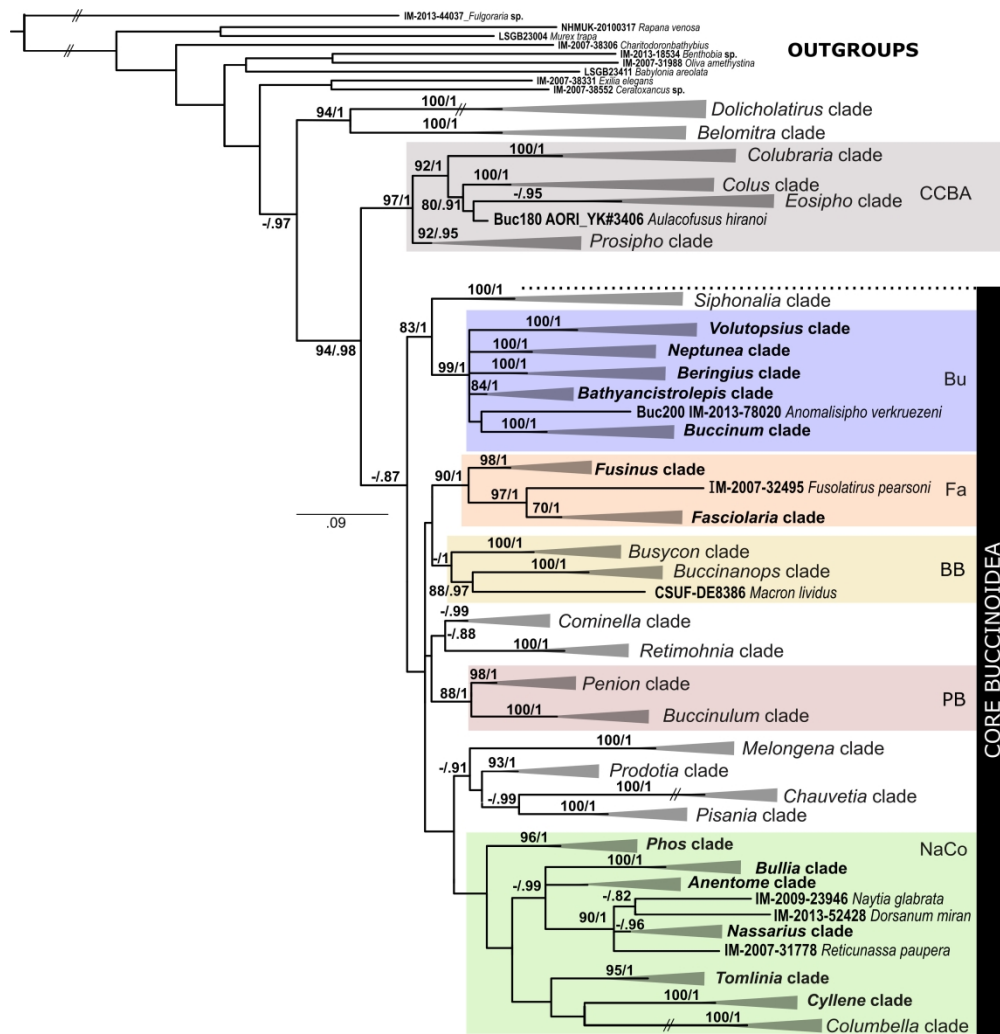


Figure 1. Buccinoidea phylogenetic relationships obtained with the the Bayesian Inference (BI) of the multigene Buc5G dataset (concatenated alignment *cox1*, 12S, 16S, 28S and H3 genes). Bootstrap values ( $B > 70\%$ ) and posterior probabilities ( $PP \geq 0.95$ ) are shown above each nodes. The clades containing multiple samples are collapsed.

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Figure 2 (3 parts). Buccinoidea phylogenetic relationships obtained with the Maximum Likelihood (ML) and the Bayesian Inference (BI) of the multigene dataset (concatenated alignment cox1, 12S, 16S, 28S and H3 genes). Bootstrap values (B >70%) and posterior probabilities (PP ≥ 0.95) are shown above each nodes. The names of the family group taxa are provided according to the classification accepted in the present work.

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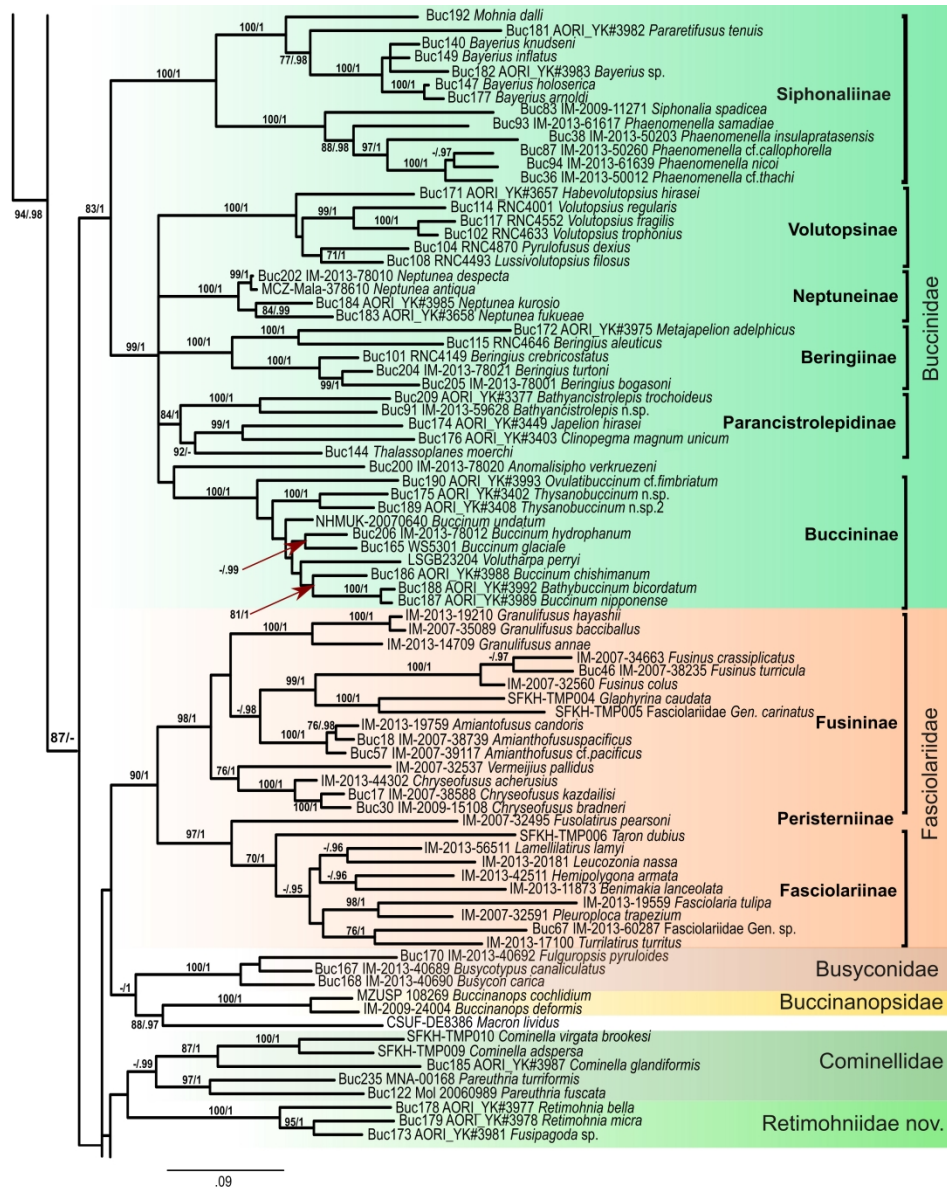


Figure 2 continued

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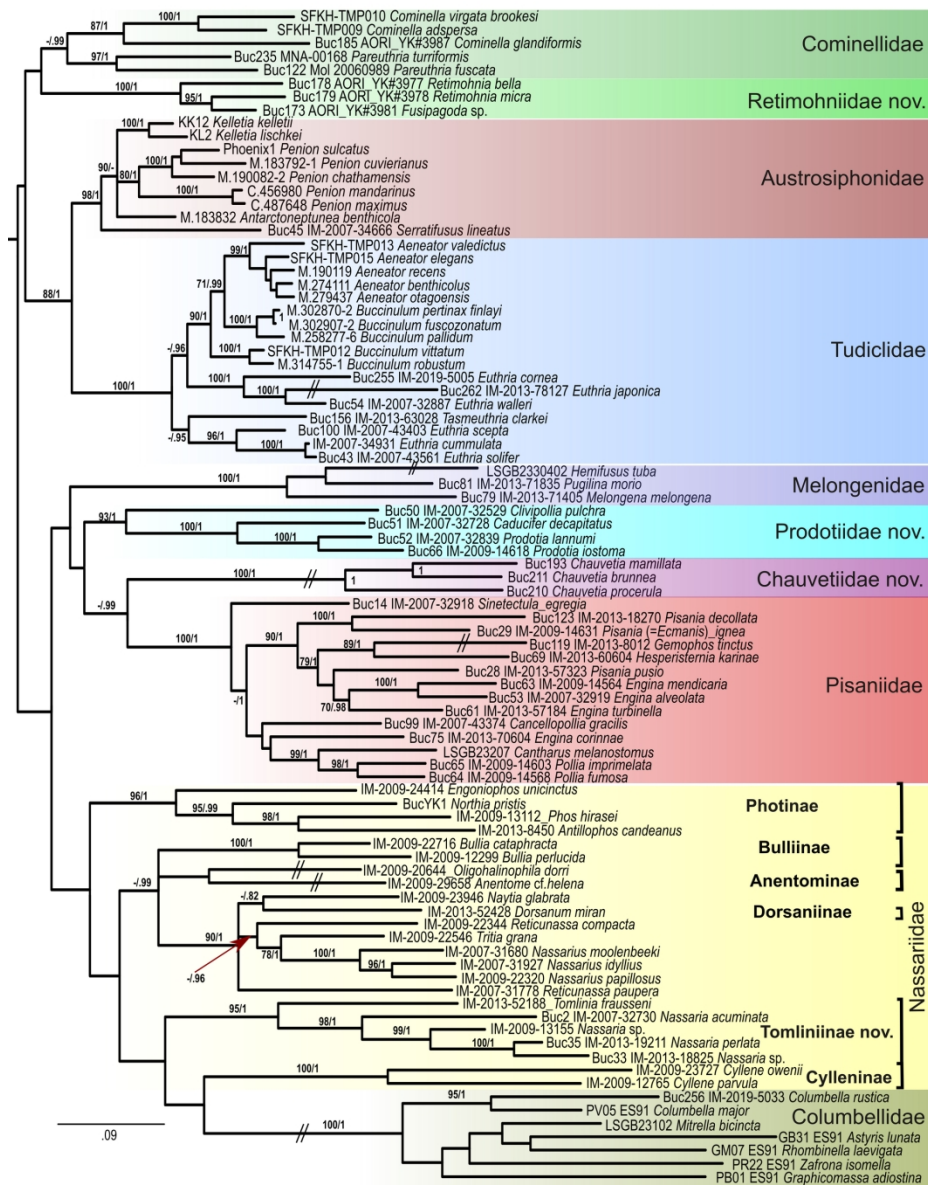


Figure 2 (completed)

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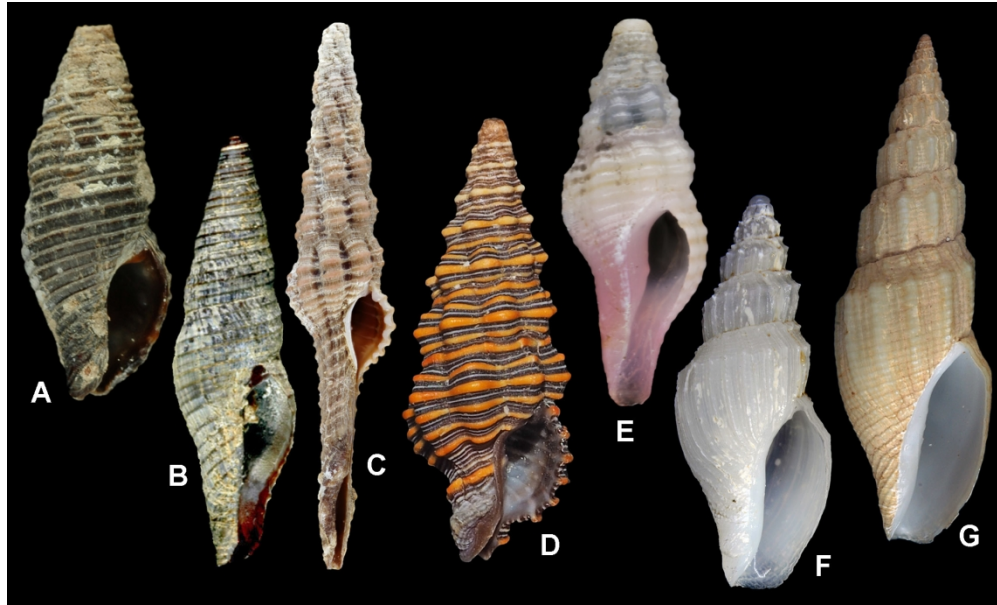


Figure 3. Shells of Dolicholatiridae (A-D) and Belomitridae (E-F). A. *Dolicholatirus* sp., Western Australia, Esperance, 11 m, MNHN IM-2009-29739, sequenced specimen (radula, see Fig. 4A). B. *Dolicholatirus spiceri* (Tenison Woods, 1876), MNHN IM-2013-42515. C. *Dolicholatirus lancea* (Gmelin, 1791), Vietnam, Nha-Trang Bay, Mun I., south side, SL 42.5 mm (radula, see Fig. 4C). D. *Crassicantharus noumeensis*, Marshall Is., Gehh I., Kwajalein Atoll, 16 m, SL 18.2 mm (photo Scott Johnson). E. *Dolicholatirus* n.sp., southern New Caledonia, KANACONO st. DW4661, 22°45'S, 167°13'E, 400-405 m, SL 7.0 mm, MNHN IM-2013-68545, sequenced specimen. F. *Belomitra paschalis* (Thiele, 1925), Mozambique, MAINBAZA sta. CC3172, 25°59'S, 34°35'E, 630-638 m, MNHN IM-2009-18856, sequenced specimen, SL 15.0 mm (radula, see Fig. 4D). G. *Belomitra bouteti* Kantor, Puillandre, Rivasseau & Bouchet, 2012, holotype, French Polynesia, Society Is., TARASOC st. 3436, 16°43'S, 151°26'W, 430 m, MNHN IM-2007-24478, SL 32.6 mm (radula, see Fig. 4E).

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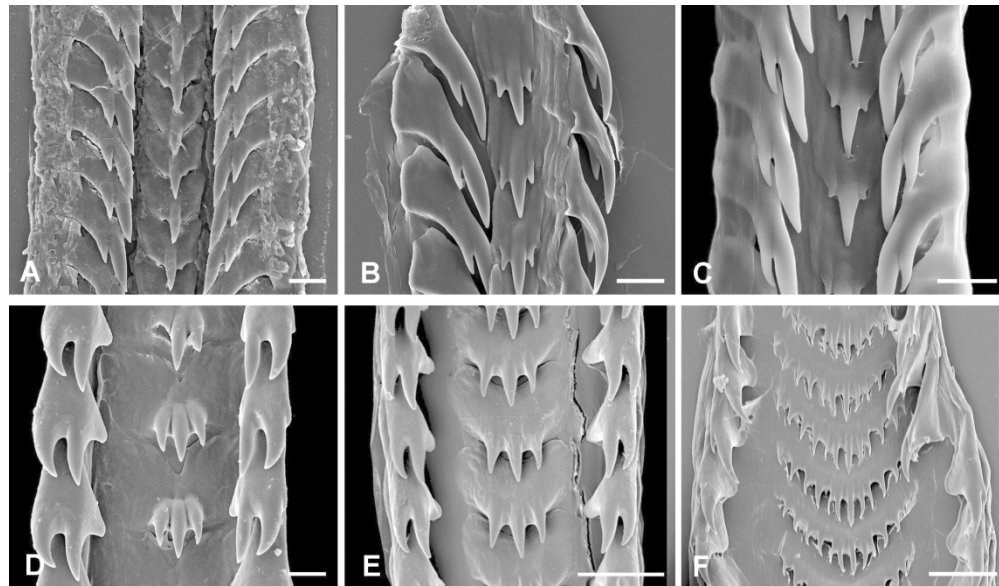


Figure 4. Radulae of Dolicholatiridae and Belomitridae. A. *Dolicholatirus* sp., Western Australia, Esperance, 11 m, MNHN IM-2009-29739 (shell, see Fig. 3A). B. *Dolicholatirus cayhuesonicus* (G.B.Sowerby II, 1879), Guadeloupe, KARUBENTHOS 2012 st. GS07, 12 m, MNHN IM-2013-20291. C. *Dolicholatirus lancea* (Gmelin, 1791), Vietnam, Nha-Trang Bay, Mun I., south side, SL 43.5 mm (shell, see Fig. 3C). D. *Belomitra paschalis* (Thiele, 1925), Mosambique, MAINBAZA sta. CC3172, 25°59'S, 34°35'E, 630–638 m, MNHN IM-2009-18856 (shell, see Fig. 3F). E. *Belomitra bouteti* Kantor, Puillandre, Rivasseau & Bouchet, 2012, holotype, French Polynesia, Society Is., TARASOC st. 3436, 16°43'S, 151°26'W, 430 m, MNHN IM-2007-24478, SL 32.6 mm (shell, see Fig. 3G). F. *Belomitra brachytoma* (Schepman, 1913), Taiwan 2000 st. CP32, 22°01.7'S, 120°16.4'E, 904 m, MNHN unregistered. Scale bars A-D – 10  $\mu$ m, E-F – 50  $\mu$ m.

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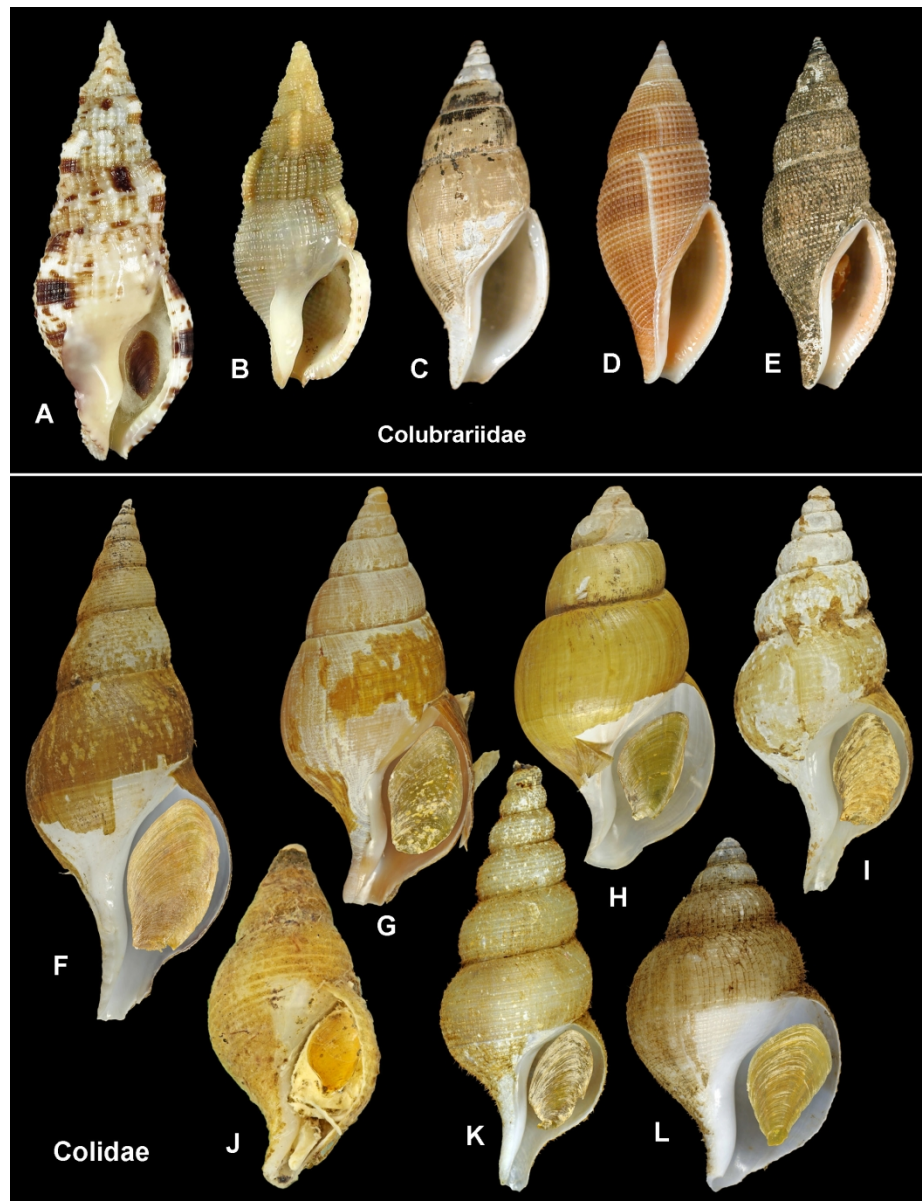


Figure 5. Shells of Colubrariidae (A-E) and Colidae (F-L). A. *Colubraria muricata* ([Lightfoot, 1786]), Philippines, Mactan I., Punta Engaño, 10-25 m, SL 77.1 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). B. *Cumia reticulata* (Blainville, 1829), Mediterranean France, SL 41.3 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). C. *Kanamarua adonis* (Dall, 1919), Philippines, AURORA 2007 st. CP2663, 15°45'N, 121°45'E, MNHN IM-2007-34640, SL 25.8 mm, sequenced specimen. D. *Metula inflata* (Houbrick, 1984), Philippines, PANGLAO 2005. st. CP2348, 9°30'N, 123°52'E, 196-216 m, MNHN IM-2007-30079 SL 42.6 mm, sequenced specimen. E. *Metula* sp., Philippines, AURORA 2007 st. CP2709, 15°12'N, 121°34'E, 244 -296 m, MNHN IM-2007-34641, SL 37 mm, sequenced specimen. F. *Colus islandicus* (Møller, 1842), Iceland, 67°16'N, 15°26'W, 296-306 m, MNHN IM-2013-78004, SL 100.3 mm, sequenced specimen. G. *Colus gracilis* (da Costa, 1778), Iceland, 66°33'N, 25°03'W, 187-222 m, MNHN IM-2013-78018, SL 53.8 mm, sequenced specimen. H. *Colus turigulus* (Friele, 1877), Iceland, 67°25'N, 17°24.5'W, 906-942 m, MNHN IM-2013-78007, SL 61.2 mm, sequenced specimen. I. *Colus holboellii* (Møller, 1842), Iceland, 67°02'N, 23°00'W, 236-243 m, MNHN IM-2013-78017, SL 35.7 mm, sequenced specimen. J. *Colus sabinii* (Gray, 1824), Iceland, 64°34'N, 10°28'W, 451-478 m, MNHN IM-2013-78014, sequenced specimen. K. *Colus* sp., Iceland, 67°25'N, 17°24.5'W, 906-942 m, MNHN IM-2013-78007, SL 61.2 mm, sequenced specimen. L. *Colus* sp., Iceland, 67°25'N, 17°24.5'W, 906-942 m, MNHN IM-2013-78007, SL 61.2 mm, sequenced specimen.

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Turrisipho voeringii Bouchet & Warén, 1985, Iceland, 67°18'N, 23°30.5'W, 395-408 m, MNHN IM-2013-78002, SL 40.4 mm, sequenced specimen. L. Turrisipho moebii (Dunker & Metzger, 1875), Iceland, 64°21'N, 12°56'W, 149-152 m, MNHN IM-2013-78009, SL 35.4 mm, sequenced specimen.

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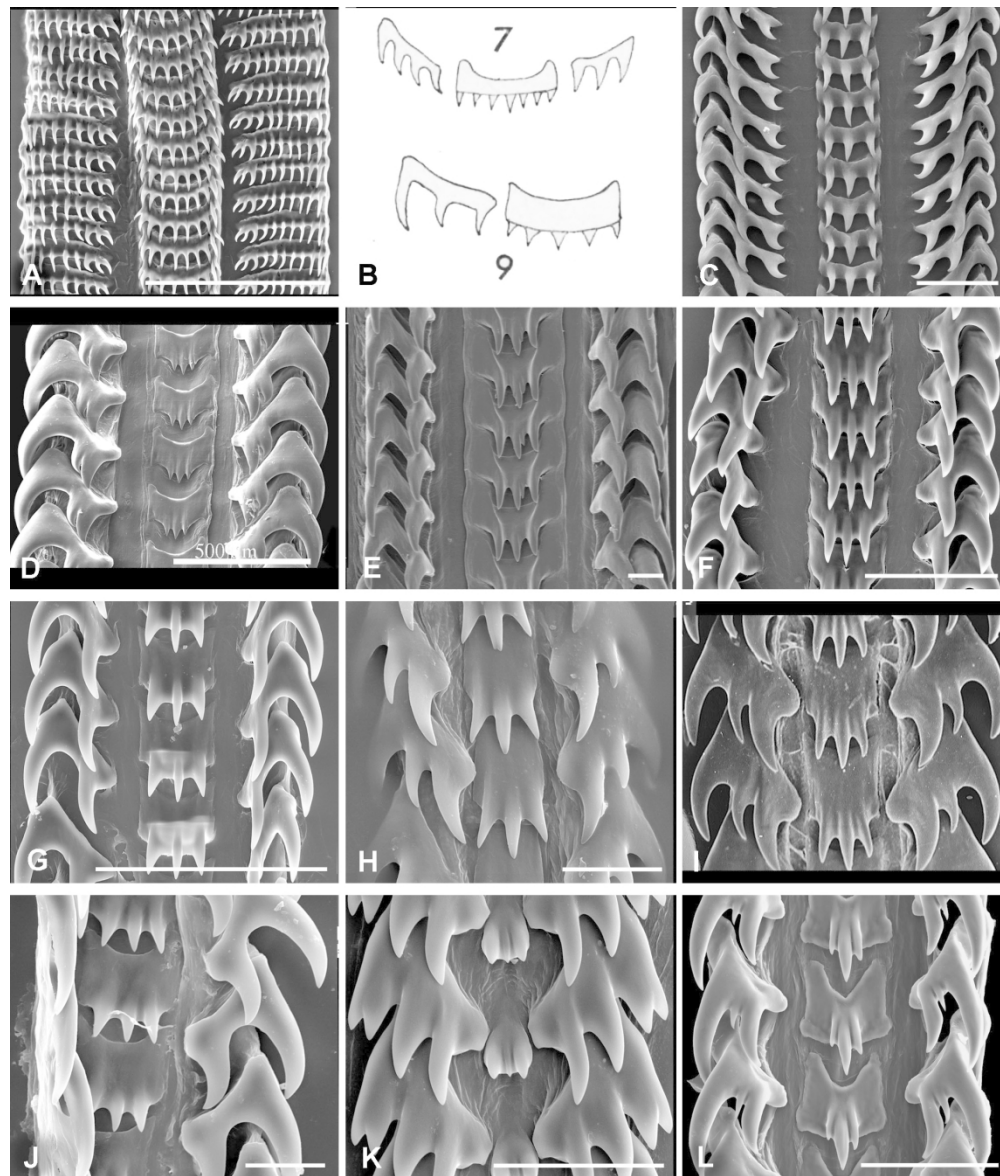


Figure 6. Radulae of Colubrariidae (A-C), Colidae (D) and Eosiphonidae fam. nov. (E-L). A. *Colubraria muricata* ([Lightfoot, 1786]) (after Oliverio & Modica, 2010, photo A. Kosyan). B. *Cumia mestayerae* (Iredale, 1915) (7) and *Iredalula striata* (Hutton, 1873) (9) (after Ponder, 1968). C. *Metula* sp., South India, off Tutticorin, from fishermen, IEE uncataloged, SL 35.2 mm. D. *Colus islandicus* (after Kosyan & Kantor 2009: fig. 41). E. *Enigmaticolus nipponensis* (Okutani & Fujiwara, 2000), Madagascar, MIRIKY st. CP3279, 15°21'S, 45°57'E, 780-1020 m, MNHN IM-2009-7079 (shell see on Fig. 7A). F. *Manaria kuroharai* Azuma, 1960, China Sea, ZHONGSHA 2015 st. CP4152, 16°5'N, 113°55'E, 410-412 m, MNHN IM-2013-59292, SL 47.7 mm (shell see on Fig. 7I). G. *Gaillea* cf. *canetae* (Clench & Aguayo, 1944), Guadeloupe, KARUBENTHOS 2 st. CP4513, 16°13'N, 61°54'W, 406-644 m, MNHN IM-2013-60080 (sequenced specimen). H. *Eclctofusus* sp., Papua-New Guinea, PAPUA NIUGINI st. CP3949, 5°12'S, 145°51'E, 380-407 m, MNHN IM-2013-4813 (sequenced specimen). I. *Eclctofusus dedonderi* (Fraussen & Hadorn, 2001), paratype, Philippines, Balicasag I., tangle nets at 120-150 m, coll. KF-3206 (shell, see Fig. 7G). J. Eosiphonidae Gen. sp., Guadeloupe, KARUBENTHOS 2 st. CP4543, 16°40'N, 61°34'W, 385-399 m, MNHN IM-2013-60365 (shell, see Fig. 7L). K. *Warenius* sp., China Sea, ZHONGSHA 2015 st. CP4134, 19°50'N, 116°27'E, 1128-1278 m, MNHN IM-2013-61665 (sequenced specimen). L. *Americominella longisetosa* (Castellanos & Fernandez,

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1972) (after Penchaszadeh et al., 2019, photo G. Pastorino  
Scale bars: A, K – 50 µm, C, H, J – 20 µm, D – 500 µm, E, F, G, L – 100 µm.

170x199mm (300 x 300 DPI)



Figure 7. Shells of Eosiphonidae fam. nov. A. *Enigmaticolus nipponensis* (Okutani & Fujiwara, 2000), Madagascar, MIRIKY st. CP3279, 15°21'S, 45°57'E, 780–1020 m, MNHN IM-2009-7079, SL 99.4 mm, sequenced specimen (radula, see Fig. 6A). B. *Thermosipho auzendei* (Warén & Bouchet, 2001), holotype, central Pacific, Rehu hydrothermal site, Nautilite dive NAUDUR: stn ND18'0-1B, 17°24.85'S 113°12.15'W, 2578 m, MNHN IM-2000-7049, SL 62 mm. C. *Eosipho smithi* (Schepman, 1911), Vanuatu, SANTO 2006 st. AT103, 15°0'38''S; 166°51'E, 373–721 m, MNHN IM-2007-32983, SL 56.1 mm. D. *Calagrassor bacciballus* Fraussen & Stahlschmidt, 2016, Philippines, Bohol Sea, PANGLAO 2005 st. CP2356, 9°21'N ; 124°9'E, 1764 m, MNHN IM-2007-32940, SL 13.2 mm. E. *Calagrassor aldermenensis* (Powell, 1971), Philippines, AURORA 2007 st. CP2673, 15°1'N, 121°45'E, 431–493 m, MNHN IM-2007-34635, SL 20.7 mm, sequenced specimen. F. "*Manaria*" *fluentisona* Fraussen & Stahlschmidt, 2016, holotype, Solomon Is., SALOMONBOA 3 st. DW2790, 8°19'S, 160°37'E, 314–586 m, MNHN IM-2007-35942, SL 15.4 mm. G. *Eclectofusus dedonderi* (Fraussen & Hadorn, 2001) paratype 12, Philippines, Balicasag I., tangle nets at 120–150 m, coll. KF-3206, SL 11.6 mm. H. *Manaria formosa* Bouchet & Warén, 1986, Madagascar, MIRIKY st. CP3183, 12°38'S, 48°14'E, 420–436 m, MNHN IM-2007-36855, SL 55 mm. I. *Manaria kuroharai* Azuma, 1960, China Sea,



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3 ZHONGSHA 2015 st. CP4152, 16°5'N, 113°55'E, 410-412 m, MNHN IM-2013-59292, SL 47.7 mm,  
4 sequenced specimen (radula see Fig. 6F). J. *Gaillea coriolis* (Bouchet & Warén, 1986), Philippines, AURORA  
5 2007 st. CP2699, 14°50'N, 123°35'E, 541-583 m, MNHN IM-2007-34637, SL 31 mm. K. *Calagrassor* sp. 2,  
6 Papua-New Guinea, PAPUA NIUGINI st. CP4048, 3°20'S, 143°28'E, 325-345 m, MNHN IM-2013-18794,  
7 sequenced specimen. L. *Eosiphonidae* Gen. sp., Guadeloupe, KARUBENTHOS 2 st. CP4543, 16°40'N,  
8 61°34'W, 385-399 m, MNHN IM-2013-60365, SL 11.3 mm, sequenced specimen (radula, see Fig. 6J). M.  
9 *Aulacofusus hiranoi* (Shikama, 1962), Japan, 37°00'N, 141°39'E, 557-561 m, AORI\_YK#3406, SL 35.4 mm,  
10 sequenced specimen. N. *Preangeria dentata* (Schepman, 1911), Philippines, PANGLAO 2005 st. CP2349,  
11 9°32'N, 123°56'E, 219 -240 m, IM-2007-32656, SL 22.8 mm. O. *Warenius crosnieri* (Bouchet & Warén,  
12 1986), holotype, Madagascar, N/O"Vauban" st. CH138, 13°49'S 47°29'E, 1800-2000 m, MNHN IM-2000-  
13 6369, SL 33.7 mm. P. *Americominella longisetosa* (Castellanos & Fernandez, 1972) (after Penchaszadeh et  
14 al., 2019), SL 98 mm, photo G. Pastorino.

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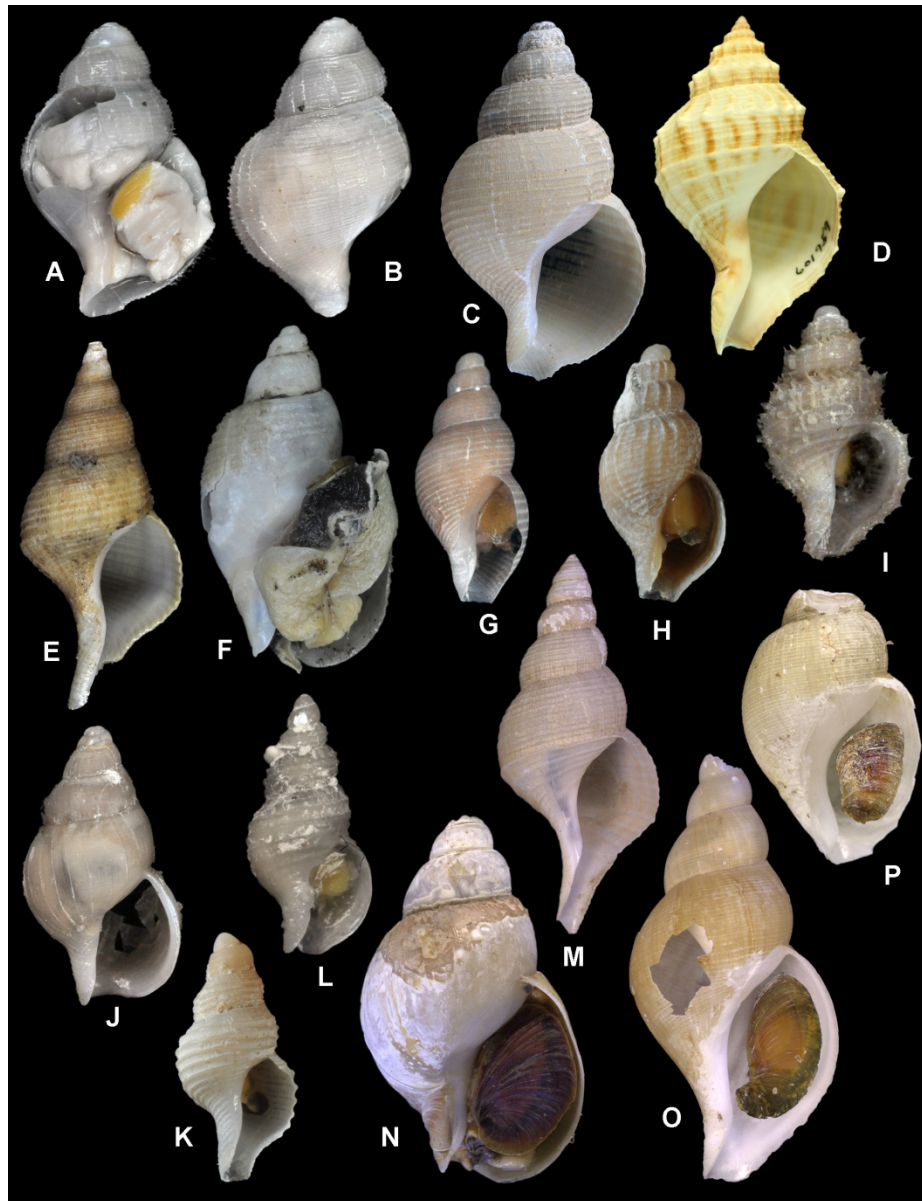


Figure 8. Shells of Prosiphonidae. A-B. *Antarctodomus thielei* (Powell, 1958), Ross Sea, Antarctica, 65°25'S, 160°53'E. 114 m, MNA00183, SL 18 mm, sequenced specimen. C. *Antarctodomus* cf. *powelli* Dell, 1995, Tasmania, NC0009, SL 42.1 mm, sequenced specimen. D. *Austrofusius glans* (Röding, 1798), New Zealand, South Island, Nelson, Collingwood, Pakawai, USNM 601959, SL 40 mm. E. *Cavineptunea* cf. *monstrosa* Powell, 1951, Bransfield Strait, Antarctica, MNA11734, SL 39.8 mm, sequenced specimen. F. *Chlanidota signeyana* Powell, 1951, Bransfield Strait, Antarctica, MNA6718. SL 33.5 mm, sequenced specimen. G. *Falsimohnia innocens* (E.A.Smith, 1907), Bransfield Strait, Antarctica, MNA11387, SL 5.6 mm, sequenced specimen. H. *Falsimohnia minor* (Strebel, 1908), Bransfield Strait, Antarctica, MNA11409, SL 6.5 mm, sequenced specimen. I. *Proneptunea* sp., Bransfield Strait, Antarctica, MNA11364, SL 6.1 mm, sequenced specimen. J. *Probuccinum tenerum* (E.A.Smith, 1907), Bransfield Strait, Antarctica, MNA11740, SL 17.4 mm. K. *Prosipho spiralis* Thiele, 1912, Bransfield Strait, Antarctica, MNA11398, SL 7.1 mm, sequenced specimen. L. *Prosipho mundus* E.A.Smith, 1915, Ross Sea, Antarctica, 454 m, MNA6308, SL 7.6 mm, sequenced specimen. M. *Drepanodontus tatyanae* Harasewych & Kantor, 2004, holotype, Scotia Sea, Antarctica, 59°2'S, 51°53'W, 3010-3510 m, USNM 1010544, SL 43.1 mm. N. *Neobuccinum eatoni*

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(E.A.Smith, 1875), Antarctica, South Shetland Is., King George I., 62°10'S, 57°44'W, 610-625 m, USNM 897630, SL 39 mm. *O. Germonea rachelae* Harasewych & Kantor, 2004, holotype, Antarctica, off South Georgia I., 58°02'S, 37°57'W, 3197-3239 m, USNM 896594, SL 61.8 mm. *P. Muffinbuccinum catherinae* Harasewych & Kantor, 2004, holotype, South Atlantic Ocean [Argentine Abyssal Plain], 47°17'S, 47°46'W, 5685-5798 m, USNM 1010623, SL 26.4 mm.

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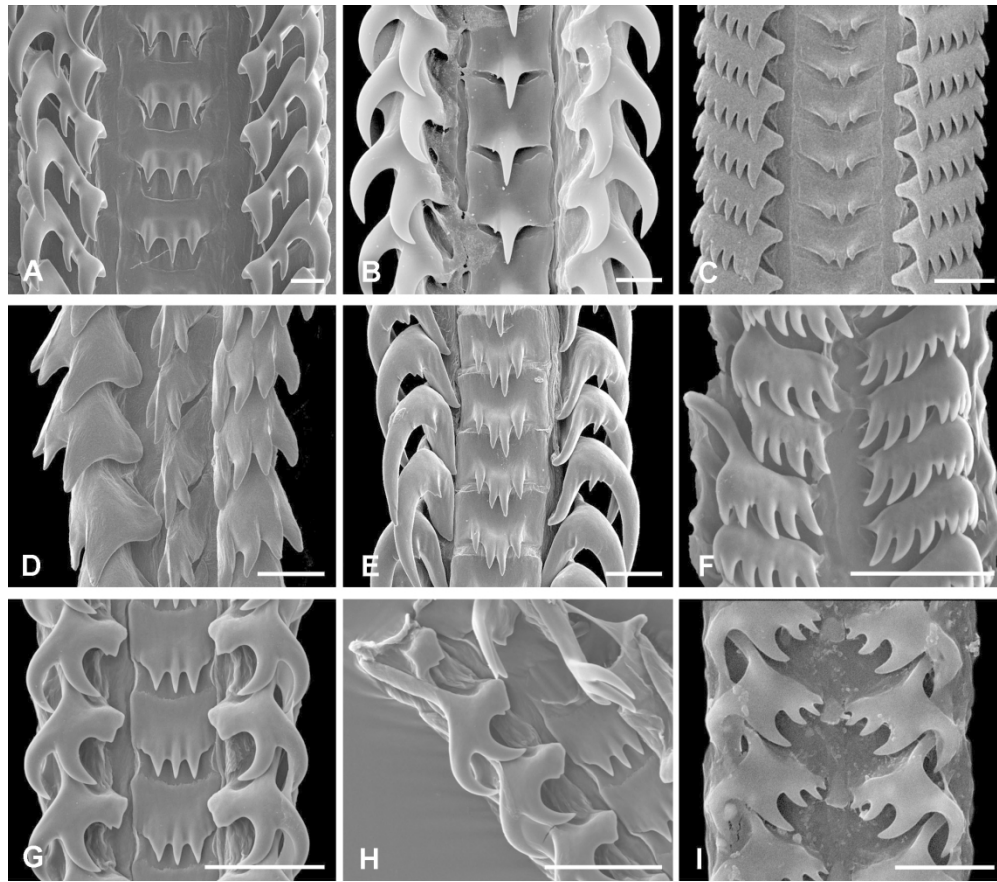


Figure 9. Radulae of Prosiphonidae. A. *Neobuccinum eatoni* (E.A.Smith, 1875), Antarctica, Adélie Land, 66°35'S, 143°5'E, 862–875 m, MNHN IM-2009-8220. B. *Falsimohnia minor* (Strebel, 1908), syntype, South Georgia I., outer Cumberland Bay, 54°11'S, 36°18'W, 252–310 m, SMNH Type-1057. C. *Muffinbuccinum catherinae* Harasewych & Kantor, 2004, paratype 1, South Atlantic Ocean [Argentine Abyssal Plain], 47°17' S, 47°46'W, 5685–5798 m, USNM 1010624. D. *Germonea rachelae* Harasewych & Kantor, 2004, holotype, off South Georgia I., 58°02' S, 37°57'W, 3197–3239 m, USNM 896594. E. *Drepanodontus tatyanae* Harasewych & Kantor, 2004, paratype I, E of South Sandwich Is., 57°00'S, 26°10'W, 2740–2757 m, USNM 881529. F. *Falsimacme kobelti* (Strebel, 1905), Argentina, photo G. Pastorino. G–H. *Argeneuthria cerealis* (Rochebrune & Mabile, 1885), Tierra del Fuego, photo G. Pastorino. I. *Antistreptus magellanicus* (Dall, 1902), Argentina, 37°35'S, 56°25'W, 73 m, photo G. Pastorino. Scale bars: A, C, D, E – 100  $\mu$ m, B, I – 10  $\mu$ m, F, G, H – 30  $\mu$ m.

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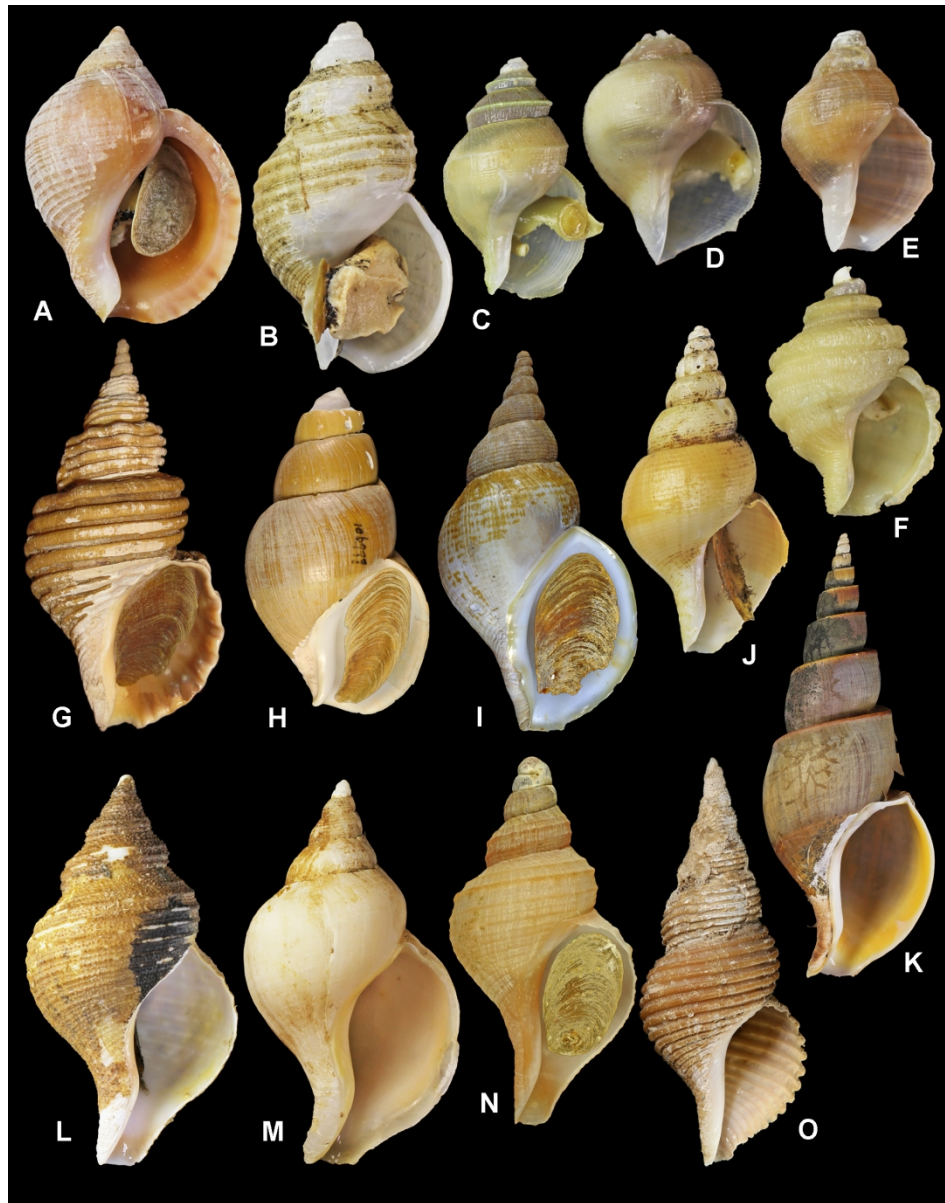


Figure 10. Shells of Buccinidae. A. *Buccinum chishimanum* Pilsbry, 1904, Japan, Hokkaido, 42°58'N, 144°53'E, intertidal, AORI\_YK#3988, SL 29.0 mm, sequenced specimen. B. *Buccinum nipponense* Dall, 1907, Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, AORI\_YK#3989, SL 40.8 mm, sequenced specimen. C. *Thysanobuccinum* sp., Japan, Honshu I., 39°25'N, 143°10'E, 1950–2051 m, AORI\_YK#3408, SL 22.4 mm, sequenced specimen. D. *Ovulatibuccinum* cf. *fimbriatum* (Golikov & Sirenko, 1988), Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, SL 9.0 mm, sequenced specimen. E. *Bathybuccinum bicordatum* Golikov & Sirenko, 1988, Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, AORI\_YK#3992, SL 8.4 mm, sequenced specimen. F. *Thysanobuccinum* n. sp., Japan, 38°16'N, 143°32'E, 3302–3311 m, AORI\_YK#3402, SL 20.3 mm, sequenced specimen. G. *Beringius crebricostatus* (Dall, 1877), Aleutian Is., 54°05'N, 166°23'W, 88 m, RNC\_4149, SL 127.7 mm, sequenced specimen. H. *Beringius aleuticus* Dall, 1895, holotype, Aleutian Is., SE of Seguam I., 52°15'N, 171°40'W, 454 m, USNM 106999, SL 65 mm. I. *Beringius turtoni* (Bean, 1834), Iceland, 67°00'N, 23°14'W, 246–247 m, MNHN IM-2013-78021, SL 108.4 mm, sequenced specimen. J. *Metajapelion adelphicus* (Dall, 1907), Japan, Kyushu Is., 32°06'N, 129°29'E, 606–610 m, AORI\_YK#3975, SL 54.1 mm, sequenced specimen (radula, see Fig. 13C). K. *Metajapelion*

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3 pericochlion (Schrenck, 1863), Japan, AORI\_YK#4142, SL 117.7 mm, specimen sequenced for cox-1. L.  
4 Neptunea kurosio Oyama, 1959, Japan, Kyushu I., 32°10'N, 129°30'E, 470–487 m, AORI\_YK#3985, SL 86.4  
5 mm, sequenced specimen. M. Neptunea fukueae Kira, 1959, Japan, Kyushu I., 32°10'N, 129°30'E, 470–487  
6 m, AORI\_YK#3658, SL 61.7 mm, sequenced specimen. N. Neptunea despecta (Linnaeus, 1758), Iceland,  
7 67°49'N, 21°44,5'W, 755-770 m, MNHN IM-2013-78010, SL 41.2 mm, sequenced specimen. O. Aulacofusus  
8 periscelidus (Dall, 1891), Kurile Is., Urup Is., 45°55.2'N, 150°15.8'E, 169-150 m, IEE BUC270, SL 58.5 mm,  
9 specimen sequenced for cox-1.

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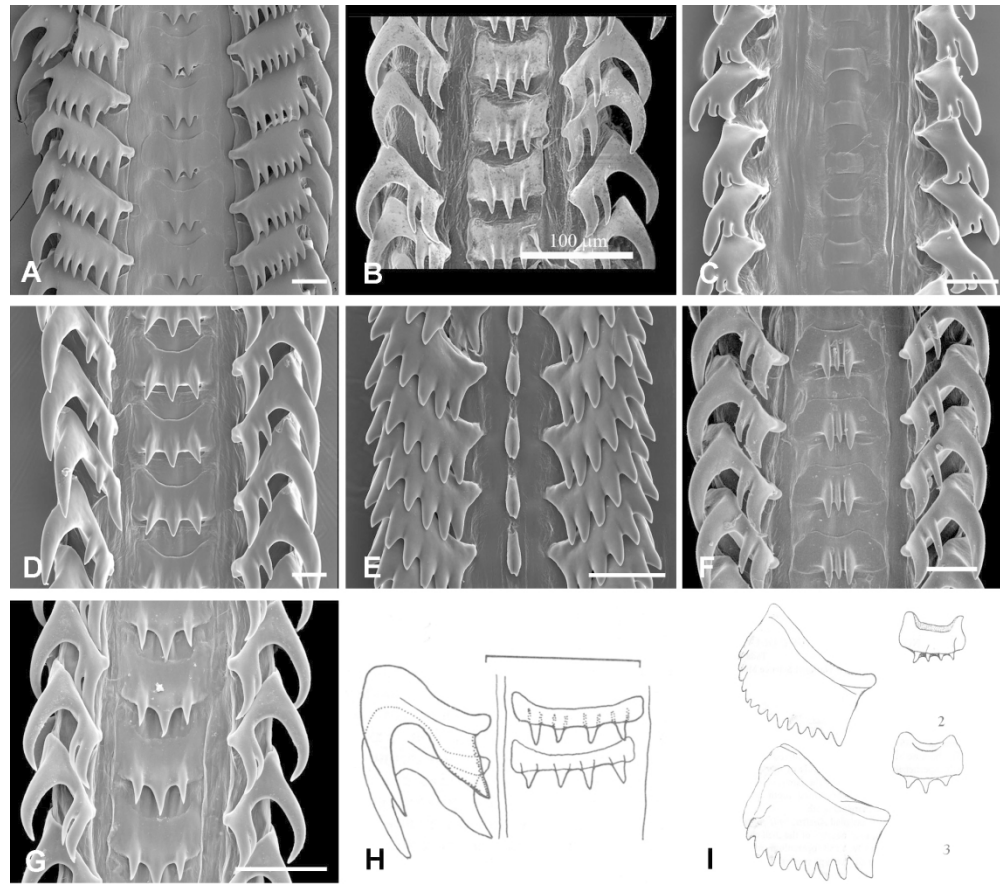


Figure 11. Radulae of Buccinidae. A. *Neptunea costaria* Fraussen & Terryn, 2007, holotype of *Costaria borealis* Golikov, 1977, Iturup I. [South Kurile Is.], 414 m, ZIN 30873/1. B. *Aulacofusus periscelidus* (Dall, 1891), Kurile Is., Urup I., Kitovy Cape, 50 m, ZIN 55945 (after Kosyan & Kantor, 2013: fig. 5 E). C. *Metajapelion adelphicus* (Dall, 1907), Japan, Kyushu Is., 32°06'N, 129°29'E, 606–610 m, AORI\_YK#3975, SL 54.1 mm (shell, see Fig. 12I). D. *Japelion hirasei* (Pilsbry, 1901), Japan, Honshu I., 39°22'N, 142°15'E, 479–484 m, AORI\_YK#3449, SL 95.8 mm (shell, see Fig. 14F). E. *Thalassoplanes moerchi* (Dall, 1908), Kurile-Kamchatka Trench, 43°58'N, 157°19'E, 5422–5379 m, ZSM, uncatalogued (IEE BUC144) (shell, see Fig. 14I). F. *Clinopegma magnum unicum* (Pilsbry, 1905), form *damon*, south-eastern Sakhalin, 46°28'N, 142°52'E, in 44 m, Zoological Museum of Moscow State University, uncatalogued, SL 97.8 mm. G. *Anomalisipho virgatus* (Friele, 1879), 80°57'N, 47°05'E, Icebraker Litke st. 22, 124 m, ZIN, uncatalogued (shell see Fig. 14K). H. *Volutopsius regularis* (Dall, 1873) (after Kantor, 1990: fig. 32). I. *Parancistrolepis fujitai* (Kuroda, 1931) (2) and *P. kinoshitai* (Kuroda, 1931) (3) (after Habe, 1972).  
Scale bars: A, B–E, G – 100  $\mu$ m; F – 200  $\mu$ m.

170x150mm (300 x 300 DPI)



Figure 12. Shells of Buccinidae. A. *Habevolutopsius hirasei* (Pilsbry, 1907), Japan, Honshu I., 40°58'N, 141°46'E, 459–498 m, AORI\_YK#3657, SL 62.4 mm, sequenced specimen. B. *Lussivolutopsius filusos* (Dall, 1919), Bering Sea, 60°01'N, 168°39'W, 37 m, RNC\_4493, SL 52.8 mm, sequenced specimen. C. *Volutopsius fragilis* (Dall, 1891), Chukchi Sea, 71°31'N, 157°23'W, 88 m, RNC\_4552, SL 74.2 mm, sequenced specimen. D. *Pyrulofusus dexius* Dall, 1907, Aleutian Is, 52°56'N, 170°59'E, 185 m, RNC\_4870, SL 148 mm, sequenced specimen. E. *Ancistrolepis grammatus* (Dall, 1907), Okhotsk Sea, Kurile Is., Onkotan I., 49°31'N, 154°25'E, 571–580 m, IEE Bu-OS-1188, SL 21.4 mm, specimen sequenced for *cox-1*. F. *Japelion hirasei* (Pilsbry, 1901), Japan, Honshu I., 39°22'N, 142°15'E, 479–484 m, AORI\_YK#3449, SL 95.8 mm (radula, see Fig. 13D). G. *Clinopegma magnum unicum* (Pilsbry, 1905), Japan, Honshu I., 38°25'N, 142°00'E, 342–343 m, AORI\_YK#3403, SL 75.7 mm, sequenced specimen. H. *Bathyanastrolepis trochoideus* (Dall, 1907), Japan, Honshu I., 38°47'N, 143°10'E, 1887–1919 m, AORI\_YK#3377, SL 38.4 mm, sequenced specimen. I. *Thalassoplanes moerchi* (Dall, 1908), Kurile-Kamchatka Trench, 43°58'N, 157°19'E, 5422–5379 m, ZSM, uncataloged (IEE BUC144), SL 31.4 mm, sequenced specimen (radula, see Fig. 13E). J. *Pseudoliomesus canaliculatus* (Dall, 1874), Japan, AORI\_YK#4141, SL 32.2 mm, specimen



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3 sequenced for cox-1. K. *Parancistrolepis fujitai* (Kuroda, 1931), Japan, AORI\_YK#3401, SL 81.4 mm,  
4 specimen sequenced for cox-1. L. *Anomalisipho virgatus* (Friele, 1879), Spitzbergen, 80°57'N, 47°05'E,  
5 Icebraker Litke st. 22, 124 m, ZIN, uncatalogued, SL 40.3 mm (radula, see Fig. 13G). M. *Anomalisipho*  
6 *verkruzeni* (Kobelt, 1876), Iceland, 67°06'N, 23°14'W, 246 m, MNHN IM-2013-78020, SL 61.5 mm,  
7 sequenced specimen. N. *Plicifusus rhyssus* (Dall, 1907), Japan, AORI\_YK#4211, SL 46.7 mm, specimen  
8 sequenced for cox-1. O. "Colus" *kujianus* Tiba, 1973, Japan, AORI\_YK#4210, SL 57.7 mm, specimen  
9 sequenced for cox-1. P. *Liomesus ovum* (Turton, 1825), Scotland, SL 29.1 mm © Guido & Philippe Poppe –  
10 [www.conchology.be](http://www.conchology.be). Q. *Truncaria filosa* (A. Adams & Reeve, 1850) (holotype of *Cominella brunneocincta*  
11 Dall, 1896), Albatross st. 3390, Gulf of Panama, 102 m, USNM 123009, SL 31.5 mm (photo USNM).

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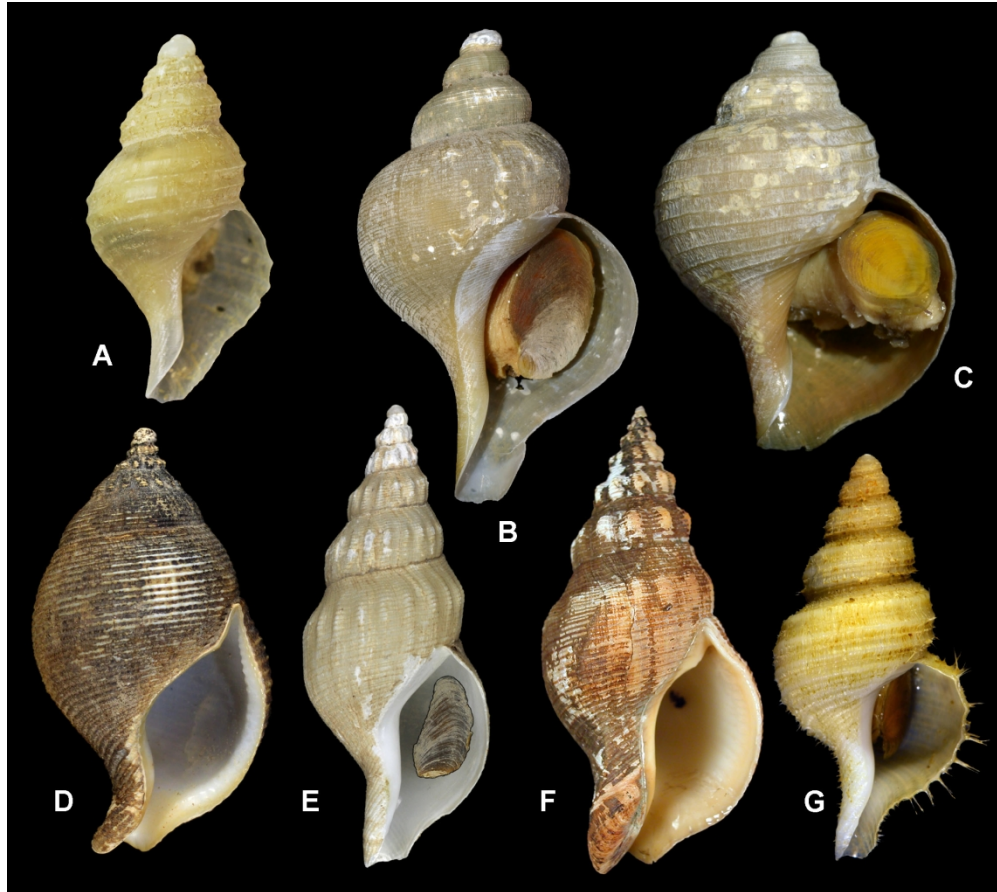


Figure 13. Shells of Siphonaliidae. A. *Pararetifusus tenuis* (Okutani, 1966), off Kesenuma, Miyagi, Honshu I., Japan, 38°47'N, 143°10'E, 1887-1919 m, SL 11.6 mm, sequenced spm (BUC 181). B. *Bayerius holoserica* (Lus, 1971), KURAMBIO I st. AGT 6-9, north-western Pacific, 42°29'N, 154°00'E, 5293-5307 m, SL 48.9 mm, sequenced specimen (radula, see Fig. 11A). C. *Bayerius knudseni* (Bouchet & Warén, 1986), KURAMBIO I st. AGT 12-5, north-western Pacific, 39°44'N, 147°10'E, 5229-5217 m, SL 23.9 mm, sequenced specimen (radula, see Fig. 11B). D. *Phaenomenella insulapratasensis* (Okutani & Lan, 1994), South China Sea, DONGSHA 2014 st. CP4129, 20°29'N, 116°8'E, 590-633 m, MNHN IM-2013-50203, SL 38.7 mm, sequenced specimen. E. *Phaenomenella nicoi* Kantor, Kosyan, Sorokin & Fedosov, 2020, holotype, South China Sea, SW off Dong Sha, ZHONGSHA 2015; st. CP4132, 20°07'N, 116°22'E, 958-988 m, MNHN IM-2013-61585, SL 41.1 mm, sequenced specimen (radula, see Fig. 11D). F. *Siphonalia spadicea* (Reeve, 1847), South China Sea, TAIWAN 2004 st. CP244, 24°53'N, 121° 56'E, 122-123 m, MNHN IM-2007-32856, SL 51.8 mm, sequenced specimen. G. *Mohnia dalli* (Friele, 1881), Barents Sea, 72°23'N, 14°58'E, 702 m, SL 24.6 mm, sequenced specimen.

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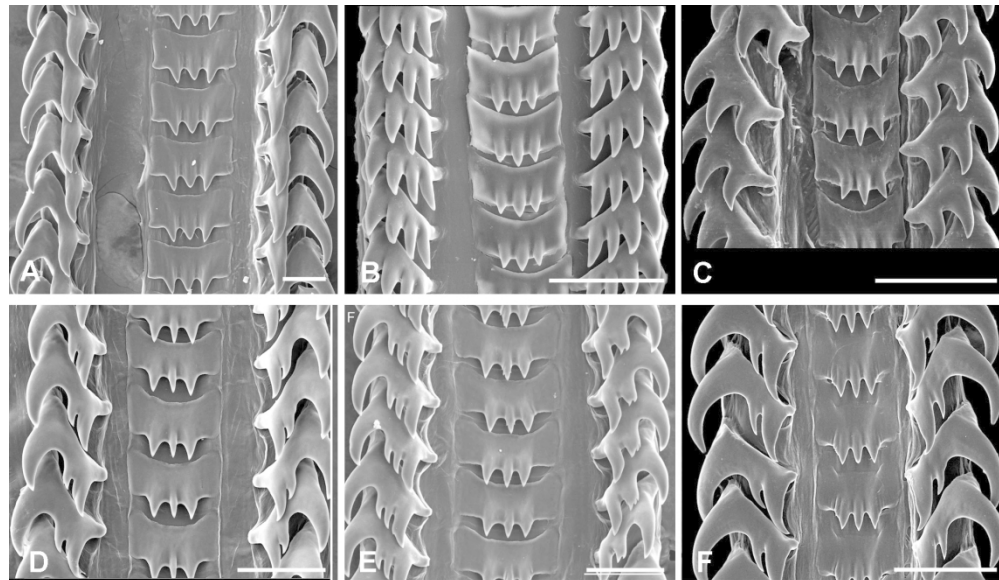


Figure 14. Radulae of Siphonaliidae. A. *Bayerius holoserica* (Lus, 1971), KURAMBIO I st. AGT 6–9, north-western Pacific, 42°29'N, 154°00'E, 5293–5307 m (shell, see Fig. 10B). B. *Bayerius knudseni* (Bouchet & Warén, 1986). KURAMBIO I st. AGT 12–5, north-western Pacific, 39°44'N, 147°10'E, 5229–5217 m (shell, see on Fig. 10C). C. *Pararetifusus tenuis* (Okutani, 1966), Kurile Is., off Iturup I., 44°20'N, 148°24'E, 414 m, ZIN 58795/6 (after Kosyan, 2006, fig. 3A). D–E. *Phaenomenella nicoi* Kantor, Kosyan, Sorokin & Fedosov, 2020, D – holotype, South China Sea, SW off Dong Sha, ZHONGSHA 2015 st. CP4132, 20°07'N, 116°22'E, 958–988 m, MNHN IM-2013-61585 (shell, see Fig. 10E); E – South China Sea, ZHONGSHA 2015 st. CP4134, 19°50'N, 116°27'E, 1128–1278 m, MNHN-IM-2013-61673. F. *Siphonalia cassidariaeformis* (Reeve, 1846), Japan, Off Hashima, Miyazaki Prefecture, Kyushu (after Kantor et al., 2020a: fig. 11A). Scale bars: A, B, D, E – 100 µm, C – 50 µm, F – 200 µm.

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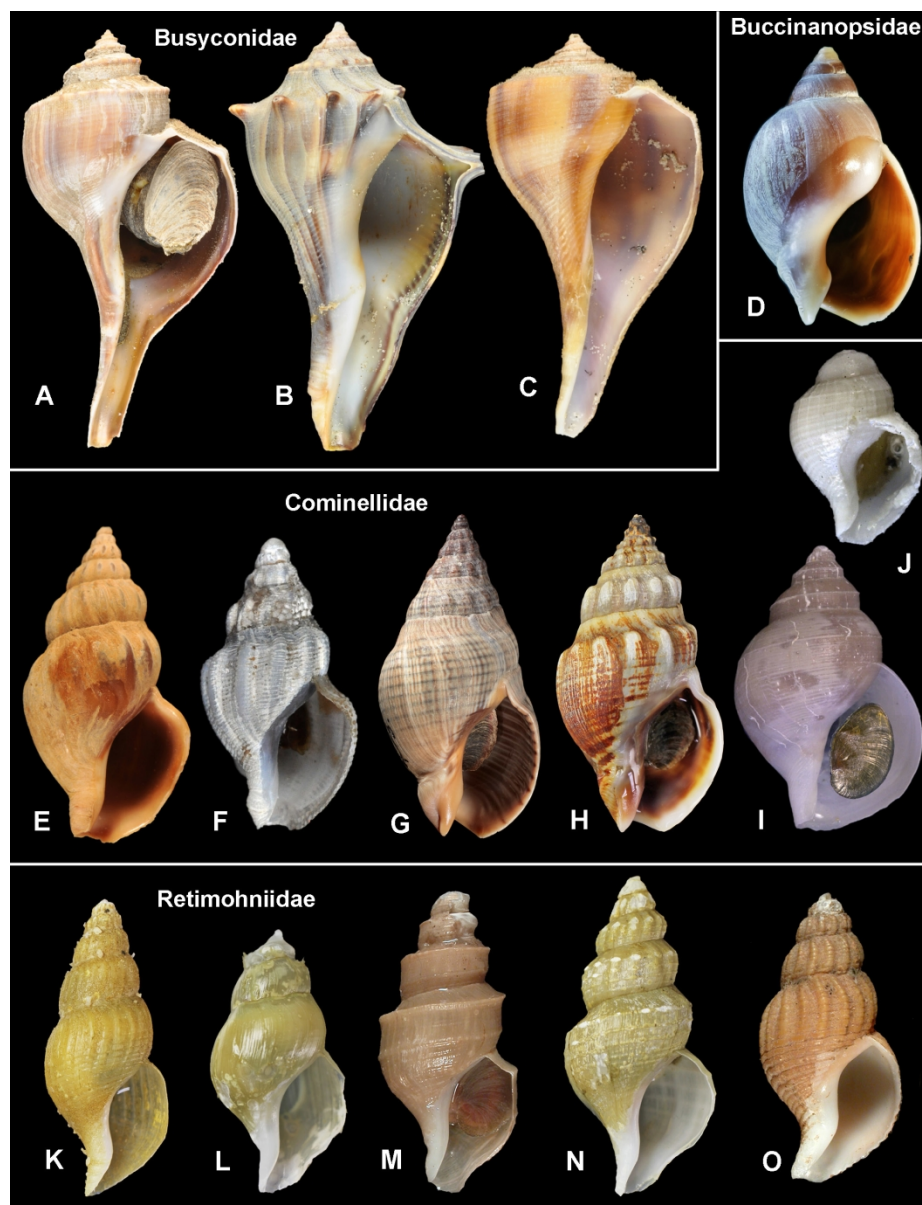


Figure 15. Shells of Busyconidae (A-C), Buccinanopsidae (D), Cominellidae (E-J), and Retimohniidae (K-O).  
 A. *Busycotypus canaliculatus* (Linnaeus, 1758), USA, South Carolina, MNHN IM-2013-40689, sequenced specimen. B. *Busycon carica* (Gmelin, 1791), USA, South Carolina, MNHN IM-2013-40690, sequenced specimen. C. *Fulguropsis pyruloides* (Say, 1822), USA, South Carolina, MNHN IM-2013-40692, sequenced specimen. D. *Buccinanops deformis* (P. P. King, 1832), Argentina, Isla de los Pajaros, 42°25.4'S, 64°32.2'W, intertidal, IEE uncatalogued, SL 27.7 mm (radula, see Fig. 16I). E. *Pareuthria fuscata* (Bruguière, 1789), Tierra del Fuego, San Sebastian Bay, 53°16.8'S, 68°13.2'W, USNM 898376, SL 21.6 mm (photo USNM). F. *Pareuthria turriformis* Egorova, 1982, Antarctica, Ross Sea, 71°19'S, 170°30'E, 243 m, MNA168, SL 16.1 mm, sequenced specimen. G. *Cominella virgata* H. Adams & A. Adams, 1853, New Zealand, Ahipara Bay, Reef Point, Te Papa Tongareva (M.278752), SL 31.3 mm. H. *Cominella glandiformis* (Reeve, 1847), New Zealand, Mangere Inlet, SE of Auckland, 36°56'S, 174°49'E, AORI\_YK#3987, 25.6 mm, sequenced specimen. I. *Lusitromina abyssorum* (Lus, 1993), off Saunders I., South Sandwich Is., 57°39'S, 26°00'W, 2380-2609 m, USNM 1010536, SL 29.2 mm (photo USNM) (radula, see Fig. 16E). J. *Falsitromina bella* (Powell, 1951), South Shetland Is., 61°45'S, 61°14'W, 4758 m, USNM 881870, SL 5.1 mm. K. *Retimohnia*

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3 bella (Ozaki, 1958), Japan, off Tokachi, Hokkaido I., 42°11'N, 144°11'E, 1210–1248 m. AORI\_YK#3977, SL  
4 24.5 mm, sequenced specimen. L. Retimohnia micra (Dall, 1907), Japan, off Otsuchi, Iwate, Honshu I.,  
5 39°20'N, 142°23'E, 849–864 m, AORI\_YK#3978, SL 11.7 mm, sequenced specimen. M. Fusipagoda  
6 exquisita (Dall, 1913), Eastern Kamchatka, 55°52'N, 164°8'E, 4382 m, R/V Vityaz sta. 524, SL 23.5 mm  
7 (radula, see Fig. 16G) (after Kosyan & Kantor, 2015: fig. 1B). N. Fusipagoda sp., Japan, off Onagawa,  
8 Miyagi, Honshu I., 38°16'N, 143°32'E, 3302–3311 m, AORI\_YK#3981, SL 29.1 mm, sequenced specimen.  
9 O. Retifusus jessoensis (Schrenck, 1863), Sea of Japan, Peter the Great Bay, ZIN 34121/16, SL 22.1 mm  
10 (radula, see Fig. 16H) (after Kosyan & Kantor, 2014: fig. 1B).

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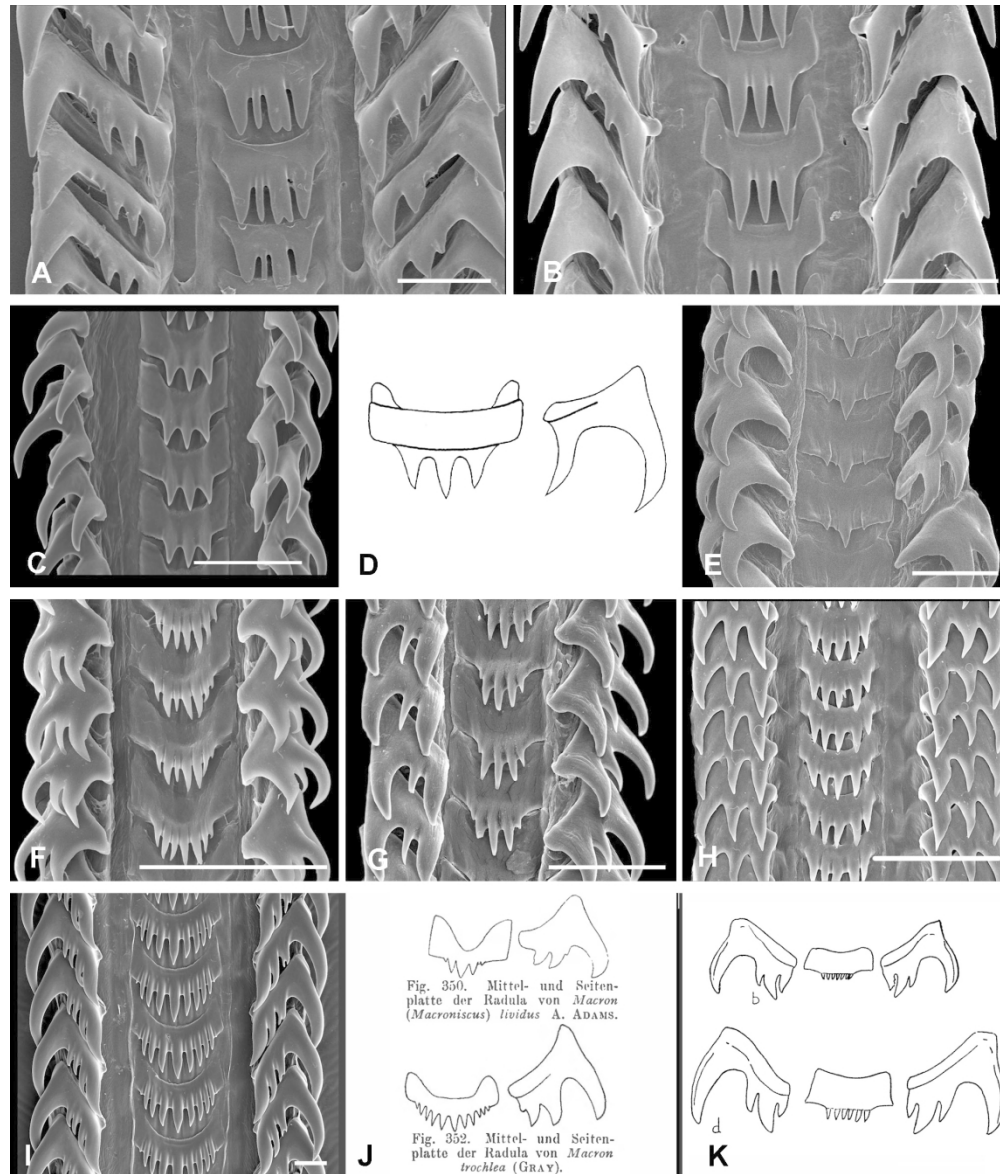


Figure 16. Radulae of Busyconidae (A-B), Cominellidae (C-E), Retimohniidae (F-H), Buccinanopsidae (I), and Buccinoidea insertae sedis (J-K). A. *Busycon carica* (Gmelin, 1791), USA, Lewes, Delaware (after Kosyan & Kantor, 2004: fig. 11A). B. *Fulguopsis spirata* (Lamarck, 1816), Mexico, Yucatan (after Kosyan & Kantor, 2004: fig. 11C). C. *Pareuthria fuscata* (Bruguière, 1789) (after Pastorino, 2016; photo G. Pastorino). D. *Cominella virgata* H. Adams & A. Adams, 1853, New Zealand, Wellington Bay, New Zealand (after Cernohorsky, 1971: fig. 93). E. *Lusitromina abyssorum* (Lus, 1993), off Saunders I., South Sandwich Is., 57°39'S, 26°00'W, 2380-2609 m, SL 29.2 mm, USNM 1010536 (shell, see Fig 15I). F. *Retimohnia micra* (Dall, 1907), Sea of Japan, R/V Vityaz st. 7490, 39°51'N, 133°47'E, 560 m (after Kosyan & Kantor, 2016: fig. 9B). G. *Fusipagoda exquisita* (Dall, 1913), eastern Kamchatka, R/V Vityaz, st. 524, 55°52'N, 164°08'E, 4382 m (shell, see Fig. 15M) (after Kosyan & Kantor, 2015: fig. 3A). H. *Retifusus jessoensis* (Schrenck, 1863 in 1862-63), Sea of Japan, Peter the Great Bay, ZIN 34121/16, SL 22.1 mm (shell, see Fig. 15O) (after Kosyan & Kantor, 2014: fig. 4A). I. *Buccinanops deformis* (P. P. King, 1832), Argentina, Isla de los Pajaros, 42°25.4'S, 64°32.2'W, intertidal, IEE uncatalogued (shell, see Fig. 15D). J. *Macron* spp. – (350) *M. lividus* (A. Adams, 1855); (352) *Macron aethiops* (Reeve, 1847) (after Thiele, 1929). K. *Burnupena* spp. – (b) *B. cincta* (Röding, 1798); (d) *Burnupena papyracea* (Bruguière, 1789) (after Orr, 1956: fig. 1).

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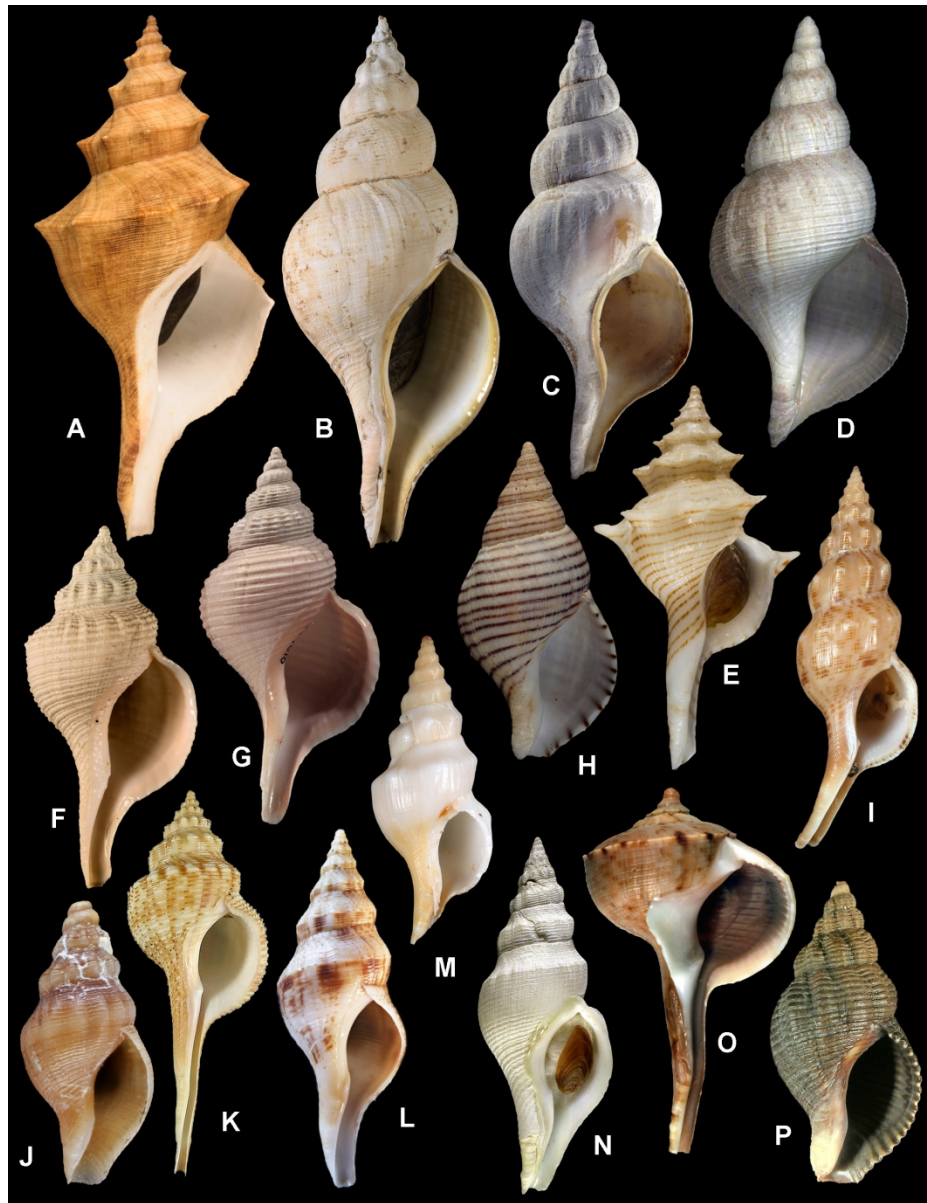


Figure 17. Shells of Austrosiphonidae (A-E) and Tudicidae (F-P). A. *Penion cuvierianus* (Powell, 1927), New Zealand, off White I., NMNZ M.132414. B. *Penion chathamensis* Powell, 1938, New Zealand, E of Mernoo Bank, Chatham Rise, NMNZ M.118863. C. *Antarctoneptunea benthicola* (Dell, 1956), New Zealand, Chatham Rise, NMNZ M.009775, SL 95 mm. D. *Antarctoneptunea aurora* (Hedley, 1916), Antarctica, 77°00'S, 161°59'W, 525-537 m, USNM 898682, SL 68.9 mm (photo USNM). E. *Serratifusus lineatus* Harasewych, 1991, holotype, New Caledonia, Grand Passage, 18°55'S, 163°24'E, 460 m, MNHN IM-2000-6527, SL 35.5 mm. F. *Aeneator recens* (Dell, 1951), New Zealand, NE slope of Mernoo Bank, Chatham Rise, NMNZ M.127027. G. *Aeneator benthicolus* Dell, 1963, New Zealand, off Cape Kidnappers, NMNZ M.147010. H. *Buccinum linea* (Martyn, 1784), neotype, New Zealand, head of Titirangi Bay, NE of Havelock, NMNZ M.046477, SL 35.4 mm. I. *Euthria walleri* (Ladd, 1976), Vanuatu, 15°33'S, 167°17'E, 120-156 m, MNHN IM-2007-32887, SL 57.5 mm, sequenced specimen. J. *Tasmeuthria clarkei* (Tenison Woods, 1876), Western Australia, Esperance, Woody I., 33°58'S, 122°01'E, 11 m, MNHN IM-2013-63028, SL 9.9 mm, sequenced specimen (radula, see Fig. 18K). K. *Afer cumingii* (Reeve, 1848), Taiwan, SL 88.9 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). L. *Euthria japonica* (Shuto, 1978), E Taiwan, 24°34'N, 122°2'E, 195-207 m,



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3 IM-2013-78127, sequenced specimen (radula, see Fig. 18J). M. Euthria cummulata Fraussen & Hadorn,  
4 2003, New Caledonia, Norfolk Ridge, 23°17'S, 168°14'E, 275-348 m, IM-2007-34931, SL 46.2 mm,  
5 sequenced specimen. N. Euthriostoma saharicum (Locard, 1897), Western Sahara, © Guido & Philippe  
6 Poppe – www.conchology.be. O. Tudicla spirillus (Linnaeus, 1767), trawled between Porto Novo and  
7 Pondicherry, India, 13–15 m, USNM 894130, SL 76.7 mm (after Harasewych, 2018). P. Lirabuccinum dirum  
8 (Reeve, 1846), USA, SL 26 mm, © Guido & Philippe Poppe – www.conchology.be.

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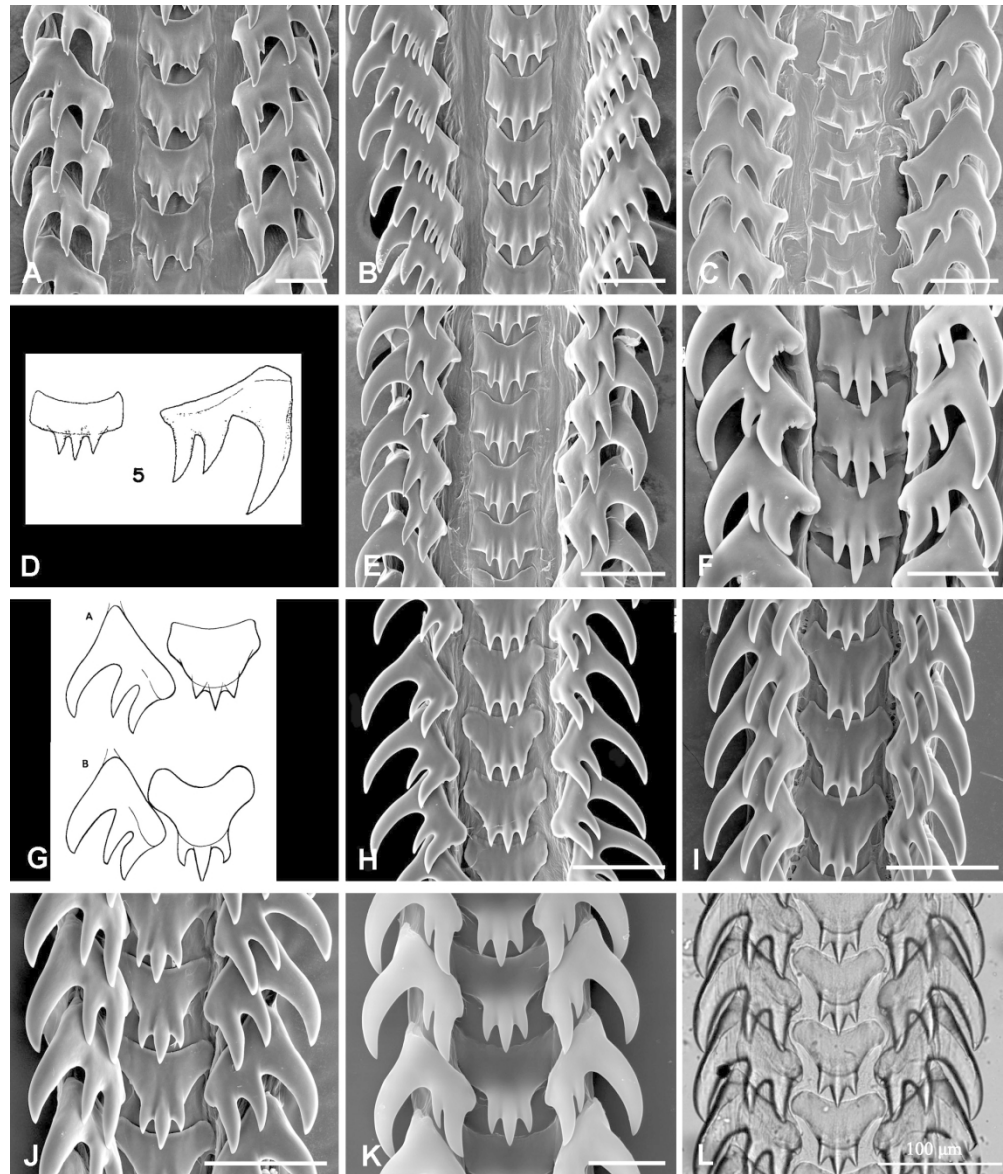


Figure 18. Radulae of Austrosiphonidae (A-F) and Tudicliidae (G-P). A. *Antarctoneptunea aurora* (Hedley, 1916), Antarctica, Adélie Land, 66°34'S, 145°21'E, 401-416 m, MNHN IM- 2009-7893. B. *Antarctoneptunea benthicola* (Dell, 1956), New Zealand, 48°49'S, 167°27'E, 560 m, MNNZ M.95190. C. *Antarctoneptunea benthicola* (Dell, 1956), New Zealand, 43°03.7'S, 177°00'E, 350 m, MNNZ M.117007. D. *Kelletia lischkei* Kuroda, 1938 (after Kang, 1976). E. *Penion cuvierianus* (Powell, 1927), New Zealand, Peach Cove, Bream Bay, Northland, 35°51.9'S, 174°34.1'E, 24 m, NMNZ M.98018. F. *Serratifusus lineatus* Harasewych, 1991, northern New Caledonia, 18°59'S, 163°24'E, 320-335 m, MNHN IM-2007-34666 (sequenced specimen). G. *Aeneator* spp. (A) *Aeneator elegans* (Suter, 1917), st. VUZ83, off Palliser Bay, 1000 m, NMNZ M.11115; (B) *A. valedictus* (R. B. Watson, 1886), Chatham Islands Expedition st. 6, Chatham Rise, 400 m, NMNZ (after Beu, 1979). H. *Buccinum linea* (Martyn, 1784), New Zealand, NMNZ. I. *Euthria cornea* (Linnaeus, 1758), Mediterranean, Capri I., IEE uncatologued. J. *Euthria japonica* (Shuto, 1978), E Taiwan, 24°34'N, 122°02'E, 195-207 m, IM-2013-78127 (shell, see Fig. 17L). K. *Tasmeuthria clarkei* (Tenison Woods, 1876), Western Australia, Esperance, Woody I., 33°58'S, 122°01'E, 11 m, MNHN IM-2013-63028 (shell, see Fig. 17J). L. *Afer cumingii* (Reeve, 1848) (after Li et al., 2013: fig. 2).

Scale bars: A,B,H-J – 100 μm; C, E, K – 250 μm; F – 50 μm

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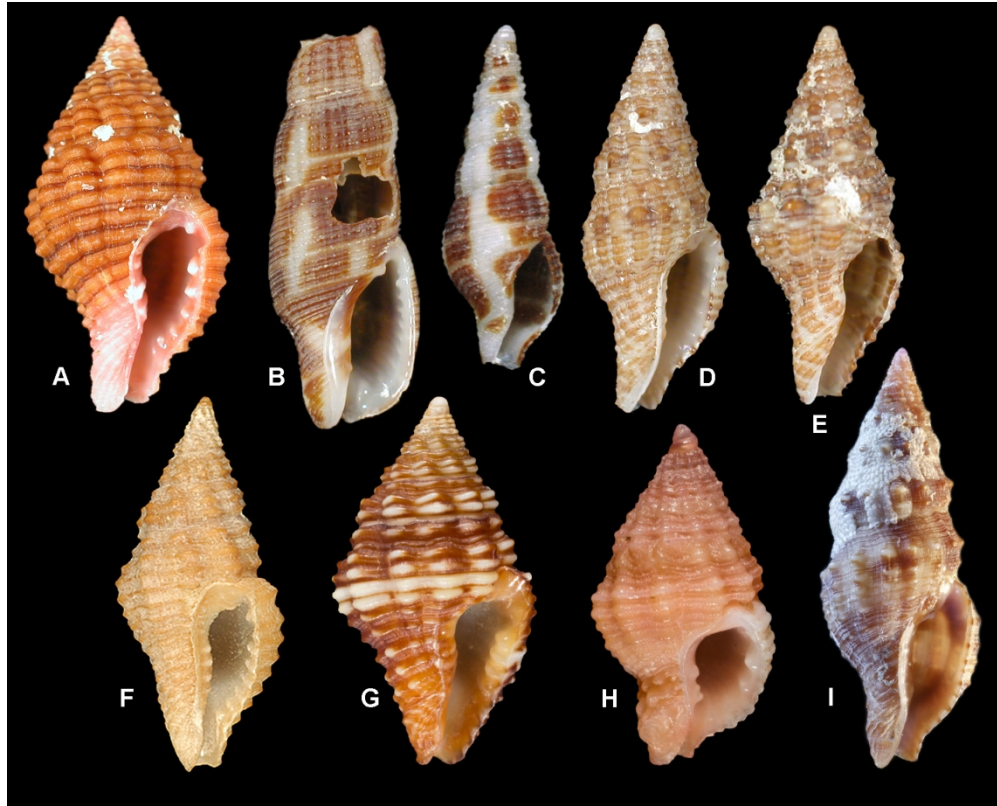


Figure 19. Shells of Prodotiidae fam. nov. (A-I). A. *Clivipolia pulchra* (Reeve, 1846), Philippines, Pamilacan I., 09°29.4'N, 123°56.0'E, 17 m, MNHN IM-2007-32529, SL 22.4 mm, sequenced specimen. B. *Caducifer decapitatus* (Reeve, 1844), Vanuatu, 15°33.0'S, 167°09.6'E, 20 m, MNHN IM-2007-32728, SL 13 mm, sequenced specimen. C. *Caducifer decapitatus* (Reeve, 1844), Papua-New Guinea, Madang lagoon, S Sek I., 05°06.4'S, 145°49'21.2"E, MNHN IM-2013-18102, SL 8.3 mm (young specimen with intact spire). D-E. *Prodotia lannumi* (Schwengel, 1950), Vanuatu, Santo, south of Aoré I., 15°36.6'S, 167°10.0'E, 10-18 m, D – MNHN IM-2007-32839, SL 11.6 mm, sequenced specimen; E – MNHN IM-2007-32859, SL 14.1 mm. F. *Enzinopsis contracta* Reeve, 1846 (holotype of *Engina gannita* Hedley, 1914), Australia, Queensland, Torres Strait, Darnley I., AMS C.7468, SL 17.2 mm. G. *Speccapollia africana* Fraussen & Stahlschmidt, 2016, holotype, Mozambique, Nacala Bay, 3-5 m, MNHN IM- 2000-31691, SL 10 mm. H. *Minioniella heleneae* Fraussen & Stahlschmidt, 2016, holotype, Tuamotu Islands, IM- 2000-31692, SL 6.7 mm. I. *Prodotia iostoma* (Gray, 1833), New Caledonia, Koumac, KOUMAC 2.3 st. KB617, 20°44,7'S, 164°15,8'E, 13 m, SL 22.1 mm (radula, see Fig. 20D).

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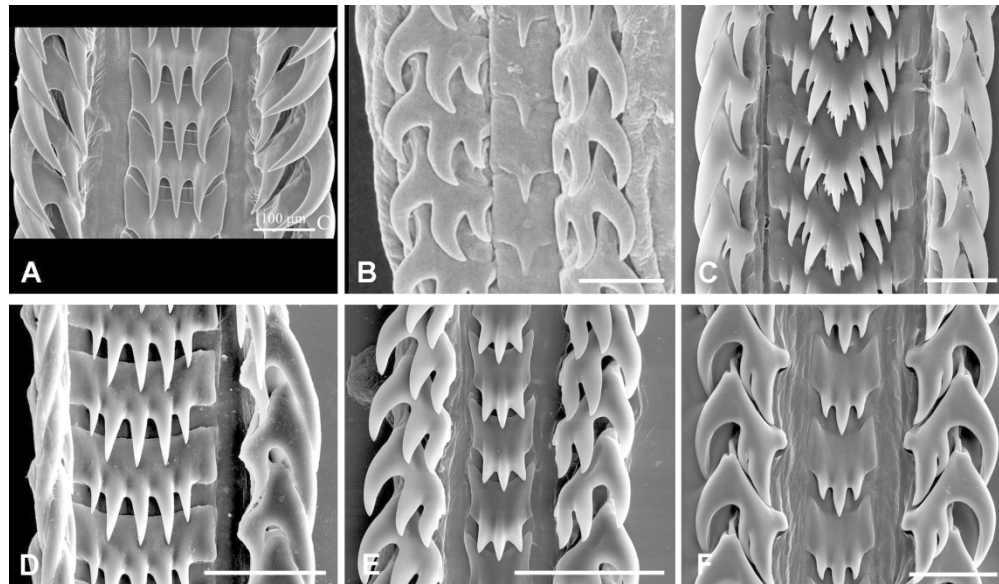


Figure 20. Radulae of Melongenidae (A), Chauvetiidae fam. nov. (B) and Prodotiidae fam. nov. (C-F) A. *Volegalea cochlidium* (Linnaeus, 1758), Vietnam, Haiphong, fishermen market (after Kosyan & Kantor, 2004: fig. 3C, as *Pugilina pugilina* (Born, 1778)). B. *Chauvetia mamillata* (Risso, 1826) (after Gofas & Oliver, 2010: fig. 2). C. *Prodotia lannumi* (Schwengel, 1950), New Ireland, Kavieng. D. *Prodotia iostoma* (Gray, 1833), New Caledonia, Koumac, KOUMAC 2.3 st. KB617, 20°44.7'S, 164°15.8'E, 13 m (shell, see Fig. 19I). E. *Clivipollia pulchra* (Reeve, 1846), New Caledonia, Grand récif de Koumac, KOUMAC 2.3 st. KL39, 20°45.1'S, 164°14.0'E, 26 m, MNHN IM-2019-8415. F. *Caducifer decapitatus* (Reeve, 1844), New Caledonia, Grand récif de Koumac, KOUMAC 2.3 st. KB645, 20°40.5'S, 164°13.0'E, 16 m, MNHN IM-2019-9119. Scale bars: A – 100 µm, B – 10 µm; C – 20 µm; D, E, F – 50 µm

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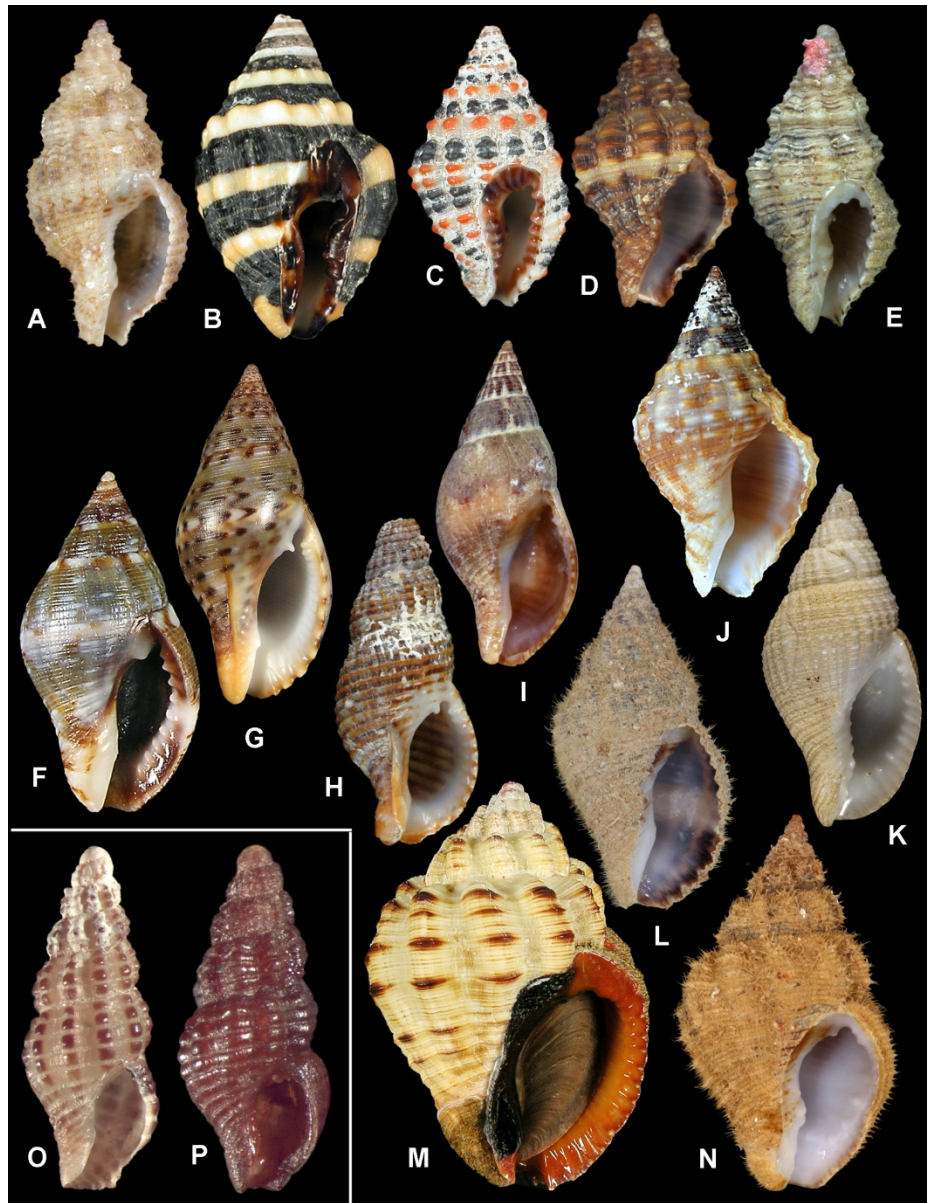


Figure 21. Shells of Pisaniidae (A-N) and Chauvetiidae fam. nov. (O-P). A. "*Engina*" *egregia* (Reeve, 1844), Vanuatu, Santo, SE Aesi I., 15°26.9'S, 167°15.8'E, 11 m, IM-2007-32918, SL 14 mm, sequenced specimen. B. *Engina mendicaria* (Linnaeus, 1758), Vanuatu, S coast of Santo I., 15°34.9'S, 167°02.4'E, 0-1 m, MNHN IM-2007-32893, SL 15.9 mm. C. *Engina alveolata* (Kiener, 1836), Vanuatu, Santo, E. of Malo I., 15°43.4'S, 167°15.0'E, 6 m, MNHN IM-2007-32919, SL 12.4 mm, sequenced specimen. D. *Hesperisternia karinae* (Nowell-Usticke, 1959), Guadeloupe, 16°24'N, 60°52'W, 72 -111 m, MNHN IM-2013-60604, sequenced specimen. E. "*Engina*" *corinnae* Crovo, 1971, Martinique, Ste Luce, Grand Caye, 14°27.3'N, 60°55.5'W, 15 m, MNHN IM-2013-70604, SL 9.3 mm, sequenced specimen. F. *Pisania striata* (Gmelin, 1791), Greece, SL 16.5 mm, © Guido & Philippe Poppe – www.conchology.be. G. "*Pisania*" *pusio* (Linnaeus, 1758), Guadeloupe, SL 34.2 mm, © Guido & Philippe Poppe – www.conchology.be. H. "*Pisania*" *decollata* (G.B. Sowerby I, 1833), Papua New Guinea, 05°11'S, 145°50'E, 5 m, MNHN IM-2013-18270, SL 20.7 mm, sequenced specimen. I. "*Pisania*" *ignea* (Gmelin, 1791), N Madagascar, 25°17'S, 46°31'E, 53-54 m, MNHN IM-2009-14631, sequenced specimen. J. *Gemophos tinctus* (Conrad, 1846), Guadeloupe, 16°20'N, 61°32'W, 1 m, MNHN IM-2013-8012, SL 16.4 mm, sequenced specimen. K. *Cancellopollia gracilis* Vermeij & Bouchet,

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3 1998, holotype, New Caledonia, Norfolk Ridge, 435 m, MNHN IM-2000-6329, SL 29.8 mm. *L. Pollia fumosa*  
4 (Dillwyn, 1817), South Madagascar, 25°28.1'S, 44°56.4'E, 12-14 m, MNHN IM-2009-14575. *M. Cantharus*  
5 *melanostoma* (G.B. Sowerby I, 1825), Philippines, SL 59.2 mm © Guido & Philippe Poppe –  
6 www.conchology.be. *N. Pollia imprimelata* Fraussen & Rosado, 2011, South Madagascar, 24°23'S, 47°32'E,  
7 154-168 m, IM-2009-14603, sequenced specimen. *O. Chauvetia mamillata* (Risso, 1826), Spain, Malaga, 0-  
8 5 m, IEE BUC 193, SL 5.5 mm. *P. Chauvetia procerula* (Monterosato, 1889), Spain, Malaga, 0-5 m, IEE BUC  
9 210, SL 4.2 mm

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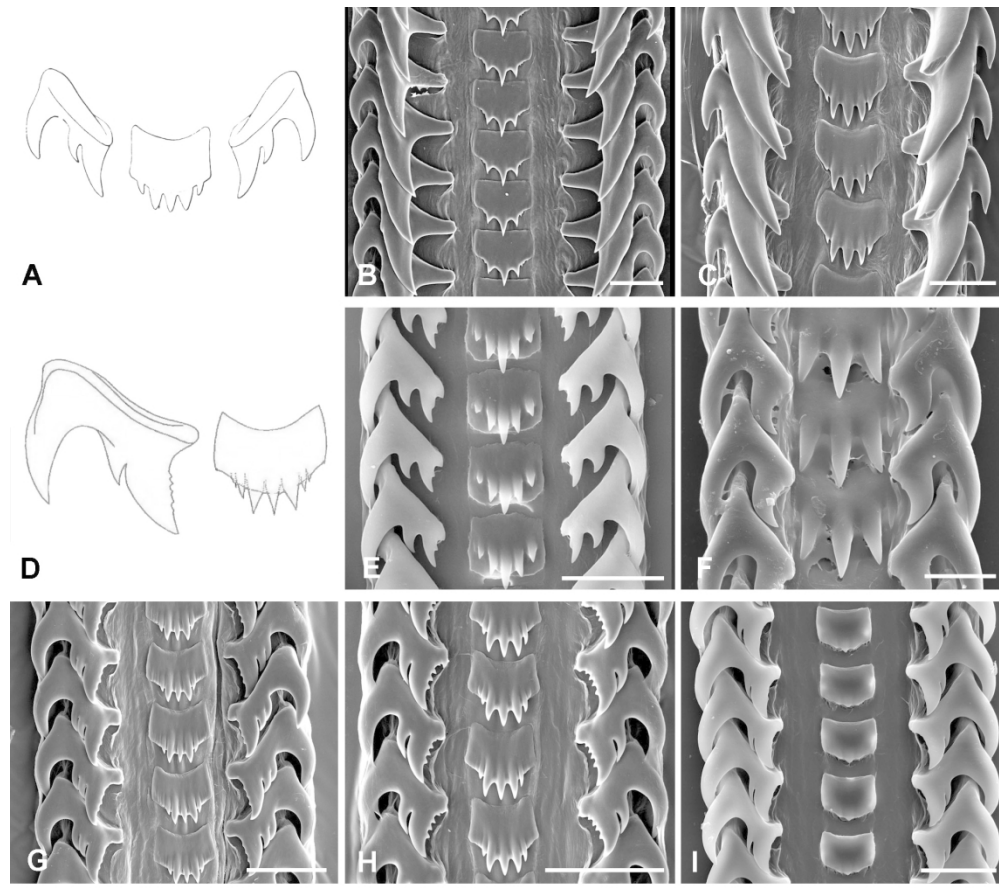


Figure 22. Radulae of Pisaniidae. A. *Pisania striata* (Gmelin, 1791), Mediterranean (after Troschel, 1867, pl. 7, fig. 2). B. "*Pisania*" *decollata* (G.B. Sowerby I, 1833), New Caledonia, Koumac, MNHN unregistered. C. "*Pisania*" *fasciculata* (Reeve, 1846), New Caledonia, Koumac, KOUMAC 2.3 st. KB517, 20°37.6'S, 164°17.3'E, 0 m, MNHN unregistered. D. "*Pisania*" (= *Ecmanis*) *ignea* (Gmelin, 1791) (after Ponder, 1972: text fig. 2). E. *Engina turbinella* (Kiener, 1836), French Guiana, 05°17.5'N, 52°35.2'W, 7 m, MNHN IM-2013-57184 (sequenced specimen). F. *Engina mendicaria* (Linnaeus, 1758), Papua New Guinea, Laing I., IEE unregistered. G. *Pollia fumosa* (Dillwyn, 1817), Vietnam, Nha-Trang Bay, Mun I., IEE unregistered. H. *Pollia undosa* (Linnaeus, 1758), Vietnam, Nha-Trang Bay, Mun I., IEE unregistered. I. "*Engina*" *egregia* (Reeve, 1844), Papua New Guinea, Madang Lagoon, 05°13.8'S, 145°48.0'E, 15 m, MNHN IM-2013-12540. Scale bars: B, C, G, H – 100 µm; E, F – 20 µm, I – 50 µm.

170x151mm (300 x 300 DPI)





Figure 23. Shells of Nassariidae. Cylleninae: A. *Cyllene owenii* Gray, 1834 (syntype of *Cyllene senegalensis* Petit de la Saussaye, 1853), Senegal, MNHN IM-2000-6364, SL 16 mm. B. *Cyllene parvula* Bozzetti, 2014, Madagascar, holotype, MNHN IM-2000-27891, SL 12.5 mm. C. *Neoterion ariel* (Pilsbry & Lowe, 1932), holotype, ANSP 155564, Nicaragua, SL 6.5 mm (photo ANSP). Tomliniinae: D. *Nassaria acuminata* (G.B. Sowerby III, 1913), Vanuatu, 15°37'S, 167°15'E, 140-153 mm, MNHN IM-2007-32730, SL 23.6 mm, sequenced specimen. E. *Tomlinia frausseni* Thach, 2014, Vietnam, MNHN IM-2013-53362. Bulliinae: F. *Bullia perlucida* Bozzetti, 2014, holotype, Madagascar, MNHN IM-2000-27493, SL 19.9 mm. Dorsaninae: G. *Dorsanum miran* (Bruguère, 1789), Senegal, SL 22.5 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). Anentominae: H. *Oligohalinophila dorri* (Wattebled, 1886), syntype, MNHN IM-2000-6321, Vietnam, lagune de Koa-hai, SL 13.9 mm. I. *Anentome* sp. D, Vietnam, vicinities of Nha-Trang city, middle part of Kai river, IM-2009-29658, sequenced specimen. Nassariinae: J. *Naytia glabrata* (G.B. Sowerby II, 1842), Cameroon, SL 7.2 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). K. *Phrontis complanata* (Powys, 1835), Costa Rica, SL 7.1 mm, © Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). Photinae: L. *Engoniophos uncinatus* (Say, 1826) (syntype of *Nassa guadelupensis* Petit de la Saussaye, 1852), Guadeloupe, MNHN IM-2000-6713, SL

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3 27.1 mm. *M. Antillophos candeanus* (d'Orbigny, 1842) (syntype of *Phos antillarum* Petit de la Saussaye,  
4 1853), Guadeloupe, MNHN IM-2000-6584, SL 28.5 mm. *N. Phos senticosus* (Linnaeus, 1758), Papua New  
5 Guinea, Laing I., intertidal, SL 33.5 mm (radula, see Fig. 24G). *O. Northia pristis* (Deshayes, 1844),  
6 Panama, Venado I., intertidal, IEE BUC YK1 (radula, see Fig. 24F).

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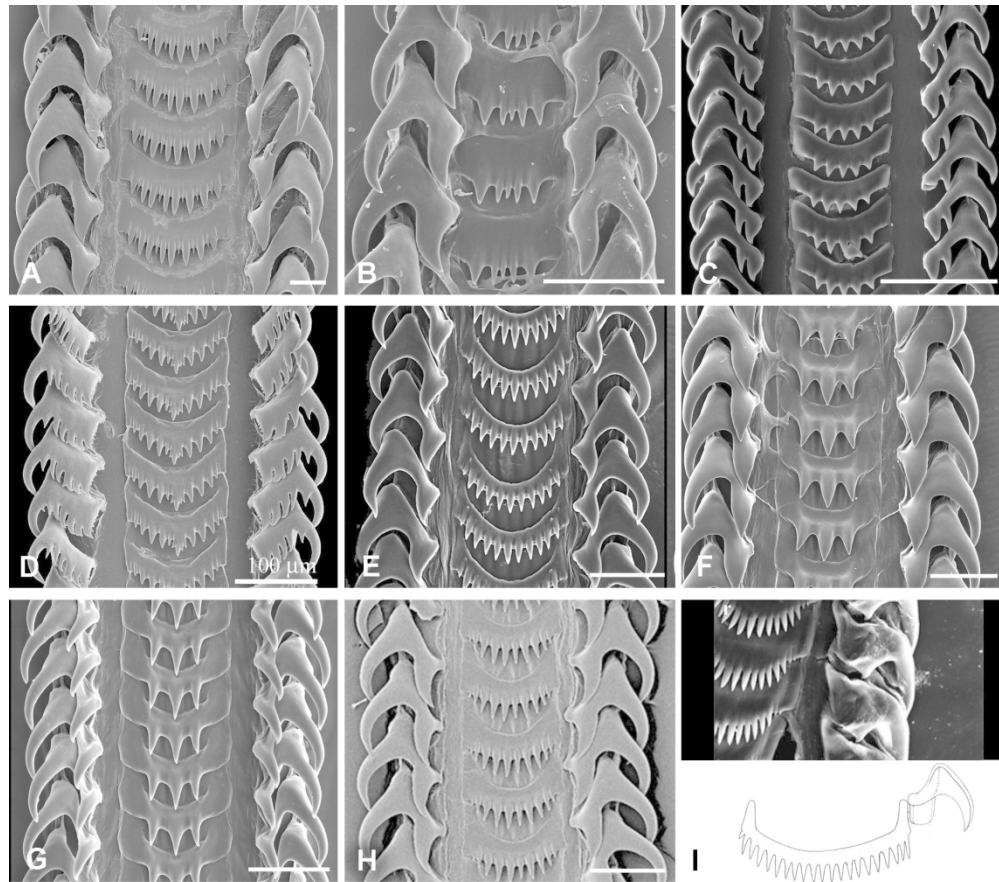


Figure 24. Radulae of Nassariidae. A. *Tomlinia fraussenii* Thach, 2014, Vietnam, MNHN. B. *Nassaria* sp., Bismarck Sea, W Kairiru I., 03°20'S, 143°28'E, 325-345 m, PAPUA NIUGINI st. CP4048, MNHN IM-2013-18779. C. *Anentome* sp. D, Vietnam, vicinities of Nha-Trang city, middle part of Kai river, MNHN IM-2009-29661. D. *Oligohalinophila dorri* (Wattebled, 1886), Vietnam (after Kantor & Kilburn, 2001: fig. 18). E. *Tritia reticulata* (Linnaeus, 1758), Black Sea, Gelendzhik, IEE uncatalogued. F. *Northia pristin* (Deshayes, 1844), Panama, Venado I., intertidal, IEE BUC YK1 (shell, see Fig. 21M). G. *Phos senticosus* (Linnaeus, 1758), Papua-New Guinea, Laing Id., intertidal, IEE uncatalogued, SL 33.5 mm (shell, see Fig. 21L). H. *Engoniophos uncinatus* (Say, 1826) (after Abbate et al., 2018: fig. 5). I. Radulae of Nassariidae, Cylleninae. Upper panel – *Cyllene fuscata* A.Adams, 1851 (after Yang & Zang, 2011: pl. 1r). lower panel – *Neoterion ariel* (Pilsbry & Lowe, 1932), after D'Attilio (1981). Scale bars: A-E, G, I – 100  $\mu$ m, F – 200  $\mu$ m.

170x149mm (300 x 300 DPI)