

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

YURI I. KANTOR<sup>1,5,\*</sup>, ALEXANDER E. FEDOSOV<sup>1,5,□</sup>, ALISA R. KOSYAN<sup>1</sup>,  
NICOLAS PUILLANDRE<sup>2</sup>, PAVEL A. SOROKIN<sup>1</sup>, YASUNORI KANO<sup>3</sup>,  
ROGER CLARK<sup>4</sup> and PHILIPPE BOUCHET<sup>2</sup>

<sup>1</sup>*A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninski prospect, Moscow 119071, Russian Federation*

<sup>2</sup>*Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles. 57 rue Cuvier, CP 51, 75005 Paris, France*

<sup>3</sup>*Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan*

<sup>4</sup>*Santa Barbara Museum of Natural History, 2559 Puesta Del Sol, Santa Barbara, California, 93105 USA*

<sup>5</sup>*Correspondants du Muséum, Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles. 57 rue Cuvier, CP 51, 75005 Paris, France*

Received 20 January 2021; revised 23 March 2021; accepted for publication 15 April 2021

The superfamily Buccinoidea is distributed across the oceans of the world from the Arctic Ocean to the Antarctic and from intertidal to abyssal depths. It encompasses 3351 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 *COI*, 16S rRNA, 12S rRNA and nuclear Histone 3 (*H3*) and 28S rRNA genes (for 225 species of 117 genera). Our analysis recovered Buccinoidea monophyletic in Bayesian analyses. 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 (**Chauvetiidae**, **Dolicholatiridae**, **Eosiphonidae**, **Prodotiidae** and **Retimohniidae**) and one subfamily of Nassariidae (**Tomliniinae**) are described. Austrosiphonidae and Tudicidae are resurrected from synonymy and employed in a new taxonomical extension. All but 40 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 the allocation of genera to a particular family without additional molecular data.

**ADDITIONAL KEYWORDS:** anatomy – Bayesian inference – zoogeography – shell morphology – *COI* mtDNA – molecular phylogeny.

## INTRODUCTION

The superfamily Buccinoidea is one of the largest and most successful groups of Neogastropoda. It currently encompasses 3351 accepted recent species

classified in 337 genera (MolluscaBase, 2020, accessed 19/12/2020). Among neogastropods, only the superfamily Conoidea, with 5267 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 seas, from the intertidal to depths of more than 8000 m (Kantor *et al.*, 2020b), and include several genera penetrating brackish waters and even

\*Corresponding author. E-mail: [kantor.yuri1956@gmail.com](mailto:kantor.yuri1956@gmail.com)  
[Version of record, published online 17 July 2021; <http://zoobank.org/> urn:lsid:zoobank.org:pub: F017D269-C17D-4A17-AA77-BE4299EEA7F8]

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 Columbelloidae; Marcus & Marcus, 1962; Brown, 1969); 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* Monterosato, 1884 have been found in association with starfishes (Oliverio & 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 Buccinoidea. Thiele (1929) recognized five families within his 'Stirps Buccinacea': Buccinidae, Columbelloidae, Fascioliidae, Galeodidae (= Melongenidae) and Nassariidae (= Nassariidae). 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: new superfamily Beringioidea, Buccinoidea [unexpectedly including, among others, Vexillidae (= Costellariidae) and Pseudolivididae], Fascioliarioidea and Pyrenoidea. In total they recognized ten families, two of which, Anachidae and Pyrenidae, were placed in different superfamilies but included genera currently classified in the family Columbelloidae (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, Muricoidei, Olivelloidei and Triphoroidei, while Pyrenoidei were classified in the order Mitriformes of the superorder Coniformii. Golikov & Starobogatov's classification with inflated ranks was barely followed or even discussed by subsequent authors, especially as Ponder & Warén (1988) simultaneously recognized only two families in Buccinoidea: Columbelloidae and Buccinidae (with the subfamilies Buccininae, Nassariinae, Melongeninae and Fascioliinae), the latter including 29 synonyms, some of which were later excluded from

the Buccinoidea [e.g. Dipsaccinae, now a synonym of Ancillariidae (Olivoidea); and Latrunculinae, now a synonym of Babyroniidae].

The state of the art of Buccinoidea systematics, partly based on published molecular phylogenies then available, is that presented by Bouchet *et al.* (2017) (Table 1), who recognized eight families: Buccinidae (with six subfamilies and nine tribes), Belomitridae, Colubrariidae, Columbelloidae (with two subfamilies), Fascioliariidae (with three subfamilies), Melongenidae, Nassariidae (with seven subfamilies) and Pisaniidae. However, the recent molecular phylogenetic studies are all partial and focused on individual families: Belomitridae (Kantor *et al.*, 2012), Fascioliariidae (Couto *et al.*, 2016), Nassariidae (Galindo *et al.*, 2016), Colubrariidae (Oliverio & Modica, 2010) or lower level taxa (Kantor *et al.*, 2013, 2020a, b) or even biogeographic assemblages (Vaux *et al.*, 2017). The superfamily Buccinoidea in its entirety has, in fact, never been the subject of a comprehensive molecular phylogenetic analysis. As a consequence, in the absence of molecular data, the placement of many polar or temperate water lineages of the superfamily, such as the subfamily Beringiinae or the buccinid tribes Colini Gray, 1857, Volutopsiini Habe & Sato, 1973 or Prosiphonini Powell, 1951, has remained tentative.

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

## MATERIAL AND METHODS

### TAXON SAMPLING

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

**Table 1.** Comparison of previous classifications of Buccinoidea with the classification accepted in the present paper (arrows indicate accordance of the taxa split in several in the present paper).

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

Downloaded from https://academic.oup.com/zoolinnean/article/194/3/789/6323346 by guest on 24 April 2024

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

Within the genus group, we consider only full genera. In total, we use in our analysis sequences (either original or published) of 118 genera out of 339, or 35% of the recognized diversity. Two families are particularly diverse at the genus level: Fasciolaridae (66 recognized genera, 17 of which are included in the current analysis) and Columbellidae (76 recognized genera, six included in the current analysis). The former was recently studied using molecular phylogenetic methods and found to be monophyletic (Couto *et al.*, 2016), with the exception of several genera attributed herein to a separate family. The latter is currently being revised by E. Strong and M. deMaintenon and found monophyletic except for one genus (personal communication) and is not treated here in detail. If we only consider buccinoidean genera outside these families (194 in total), our coverage reaches 48% of the recognized diversity.

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

1. Genera classified in a family based on molecular and morphological data (mostly radula); marked <sup>(1)</sup> – 103 genera.
2. Genera classified based on radula morphology only, and congruence between radula and molecular characters for those sequenced genera; marked <sup>(2)</sup> – 30 genera.
3. Genera assigned to a family based on shell characters alone, and phenetic resemblance to those genera with radula and/or molecular characters available; marked <sup>(3)</sup> – 22 genera.

Forty genera were not attributed to any family with certainty, due to the lack of any radular or anatomical data, or when available data were deemed

insufficient. For 32 of them, we nevertheless suggest a tentative placement in the classification (Supporting Information, Table S2).

#### SPECIMEN PROCESSING

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

Anatomy was examined by dissection. The bodies of some specimens were specially preserved in 80% ethanol after clipping a fragment of the foot for DNA extraction; others were preserved in 95% alcohol and briefly rehydrated (10–30 min) prior to dissection. In most cases, this procedure allowed removal of the body from the shell and made tissues elastic enough for dissection. After dissection, the bodies were returned to 95% ethanol. Radulae were cleaned using diluted bleach (NaOCl), mounted on a glass cover-slip or double-sided carbon tape, air-dried, attached to aluminium stubs, coated with gold and examined by scanning electron microscope TeScan TS5130MM in the IEE RAS. For size characterization we used the following arbitrary divisions: shell small < 10 mm, medium-sized 10–29 mm, medium-large 30–100 mm, large > 100 mm.

#### DNA EXTRACTION AND POLYMERASE CHAIN REACTION (PCR)

Total DNA was extracted from a piece of foot using either the Dneasy96 Tissue kit (Qiagen) using automated extraction system Epmotion 5075 (Eppendorf), or manually using Investigator Kit (Qiagen), following the manufacturer's recommendations. Five genetic markers were targeted for the phylogenetic reconstructions: the barcode fragment of the mitochondrial cytochrome *c* oxidase I (*cox1*) gene (658 bp), a ~450-bp long fragment of the mitochondrial 16S rRNA, a ~550 bp fragment of the mitochondrial 12S rRNA, a 328 bp fragment of the nuclear Histone 3 (*H3*) and a ~700 bp fragment of the nuclear 28S rRNA. The *cox1*, 12S, *H3* and 28S were amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.*, 1994), 12SI and 12SIII (Simon *et al.*, 1991), *H3A-H3B* (Okusu *et al.*, 2003) and C1 and D2 (Jovelin & Justine, 2001), respectively. The pair of primers DY16S748R (Hayashi, 2005) – 16sbr-H

(Palumbi *et al.*, 1991), the former developed specifically for Buccinidae, were used to amplify the 16S fragment. Polymerase chain reactions were performed in 20 µL final volume containing approximately 3 ng template DNA, 1.5 mmol/L MgCl<sub>2</sub>, 0.26 mmol/L of each nucleotide, 0.3 µL of each primer, 5% DMSO and 0.75 µL of either Q-Bio-Taq Polymerase (Qbiogene) or BioHYTaq DNA polymerase (Dialat). The PCR profiles were as detailed in Fedosov *et al.* (2020) and Kantor *et al.* (2020a). Success of amplification was checked using an electrophoresis in agarose gel; the obtained amplicons were purified by repeated precipitation in ethanol or using Exo/SAP Go PCR Purification Kit (Grisp, Portugal) and sequenced in both directions. Sequencing was performed by Eurofins or at the joint usage centre 'Methods of molecular diagnostics' of the IEE RAS on an ABI 3500 Genetic analyser (Applied Biosystems).

#### PHYLOGENETIC ANALYSIS

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

Sequences were aligned for each gene independently using MAFFT v.7 (Katoh *et al.*, 2019). The accuracy of automatic alignments was confirmed by eye. No indels were detected in *cox1* and *H3*; various numbers of indels were identified in the 16S, 12S and 28S fragments, leading to the alignments of 561, 607 and 745 bp in length, respectively. Alignments of 16S and 12S contained regions with many indels, so we used GUIDANCE2 (Sela *et al.*, 2015) to generate best alternative alignments for each of the two markers, and to remove ambiguously aligned bases. We removed alignment columns with confidence values below 0.4, leading to alignments of 548 and 596 positions for 16S and 12S, respectively, or, alternatively, below 0.9, which resulted in the alignments of 471 and 475 positions for 16S and 12S, respectively. For phylogenetic inference, eight datasets were analysed. Five of them corresponded to the five individual genes and were analysed separately to ensure that they did not result in supported conflicting topologies. Then three

concatenated datasets of the five genes were built: Buc5G with entire lengths of 16S and 12S comprising 2899 bp, and Buc5G\_GUI40 and Buc5G\_GUI90 with ambiguously aligned bases below confidence values 0.4 and 0.9, respectively, removed from both 16S and 12S, resulting in a total concatenated sequences lengths of 2875 bp and 2677 bp, respectively.

The single-gene phylogenies were estimated by RAxML v.8.2.12 (Stamatakis, 2006), with ML (maximum likelihood) search and bootstrapping performed in a single run. The bootstrap seed value was set to 12 345, and robustness of nodes assessed by 1000 iterations of rapid bootstrapping algorithm (Stamatakis *et al.*, 2008).

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

The ML phylogenetic tree was reconstructed for the concatenated datasets using the same parameters of RAxML v.8.2.12 as were used for the single-gene trees. Bayesian analysis (Huelsenbeck & Ronquist, 2001) was performed on the concatenated datasets by running two parallel analyses in MrBayes with parameters of substitution models estimated during the run. Each run consisted of 25 000 000 generations of Markov chain, sampling frequency was set to one tree in each 1000 generations and chain temperature to 0.02. Convergence of each analysis was evaluated using TRACER v.1.4.1 (Rambaut *et al.*, 2018), where ESS (effective sampling size) values were checked to ensure that they exceeded 200. A consensus tree was calculated after omitting the first 25% trees as burn-in. All analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using IQ-Tree v. 2.1.1 on XSEDE, RAxML on XSEDE and MrBayes 3.2.6 on XSEDE (Miller *et al.*, 2010). The aligned datasets (*cox1* and concatenated five-gene dataset) and the details of the selected best models of nucleotide evolution and output consensus trees are provided in the Supporting Information (Files S1–S10). Nodes with bootstraps values (B, in per cent)

lower than 70 and posterior probabilities (PP) lower than 0.95 are considered non-supported; B values between 70 and 90 and PP values between 0.95 and 0.98 are regarded as moderately supported; and B > 90 and PP > 0.98 as well-supported.

#### TURNING THE PHYLOGENY INTO A CLASSIFICATION

Overall, a conservative approach was adopted and, whenever possible, we retained the current rank of the presently accepted family-group taxa. As requested by the [International Code of Zoological Nomenclature - International Commission on Zoological Nomenclature \(ICZN\), 1999](#), we accepted available names, even if they are based on genera considered to be junior synonyms. As much as possible, a genus-group name was applied based on the position of its type species in the tree. If the type species of a nominal genus or subgenus has not been sequenced, application of the name was determined by reference to the morphologically most similar species included in the molecular analysis. Biogeographical regions follow [Spalding \*et al.\* \(2007\)](#), bathymetry ranges follow the [UNESCO 2009 Global Open Oceans and Deep Seabed \(GOODS\) Biogeographic Classification](#).

#### REPOSITORIES AND ABBREVIATIONS

AMS, The Australian Museum, Sydney, Australia; AORI, Atmosphere and Ocean Research Institute, University of Tokyo, Japan; BAU, Dipartimento di Biologia Animale e dell'Uomo, 'La Sapienza' University, Roma, Italy; BI, Bayesian inference analysis; CSUF, California State University, Fullerton, CA, USA; IEE RAS, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia; ICZN, International Code of Zoological Nomenclature; M, by monotypy (with regard to the fixation of the type species of a genus); ML, maximal likelihood analysis; MNA, Italian National Antarctic Museum, section of Genoa, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MZUSP, Museum of Zoology, University of San Paulo, Brazil; NHMUK, Natural History Museum, London, UK; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; OD, by original designation (with regard to the fixation of the type species of a genus); RNC, collection of R. N. Clark; SFKH, Simon Hill collection, later transferred to Te Papa Tongarewa Museum, Wellington, New Zealand; SPSU, St. Petersburg State university, St. Petersburg, Russia; TS, type species; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZSM, Bavarian State Collection of Zoology, Munich, Germany; SD, by subsequent designation (with regard

to the fixation of the type species of a genus); SL, shell length.

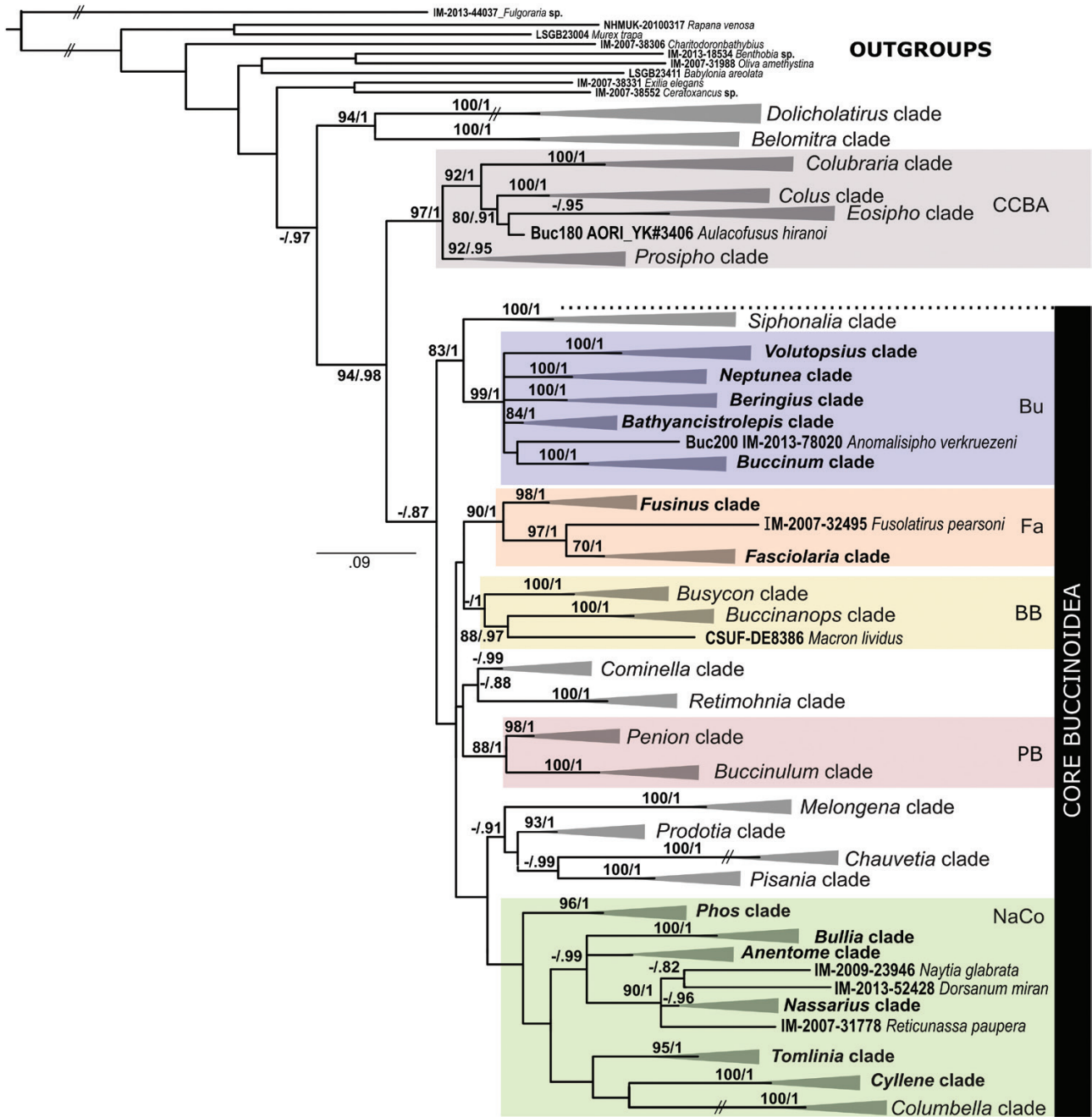
## RESULTS

#### PHYLOGENETIC ANALYSIS

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

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

To discuss the topology of the obtained multigene tree, we have selected 31 highly or moderately supported clades, comprising all but seven analysed species of Buccinoidea, which we refer to by the name of one included genus, whenever possible the type genus of a named family. On [Figure 1](#), these clades are collapsed for a more convenient representation of the overall tree topology, and the unrestrained tree is provided in [Figure 2](#). The first split in the Buccinoidea separates a well-supported grouping comprising two terminal clades, the *Dolicholatirus*-clade (comprising six species of the genera *Crassicantharus* [Ponder, 1972](#) and *Dolicholatirus* [Bellardi, 1886](#)) and the *Belomitra*-clade (with two species of the genus *Belomitra* [P. Fischer, 1882](#)). The grouping uniting the remaining Buccinoidea is highly supported in the analyses of the Buc5G dataset (B = 94, PP = 0.98) and is subdivided into two clades. The first of them, referred to on [Figure 1](#) as CCBA (for Colubrariidae–Colidae–Biogenicsubstrates–Antarctic), comprises: (1) *Colubraria*-clade (with six species representing five genera of the family Colubrariidae); (2) *Colus*-clade (comprising eight Arctic and northern Atlantic species of the genera *Colus* [Röding, 1798](#) and *Turrisipho* [Dautzenberg & H. Fischer, 1912](#)); (3) large *Eosipho*-clade [encompassing 21 species of Buccinoidea from

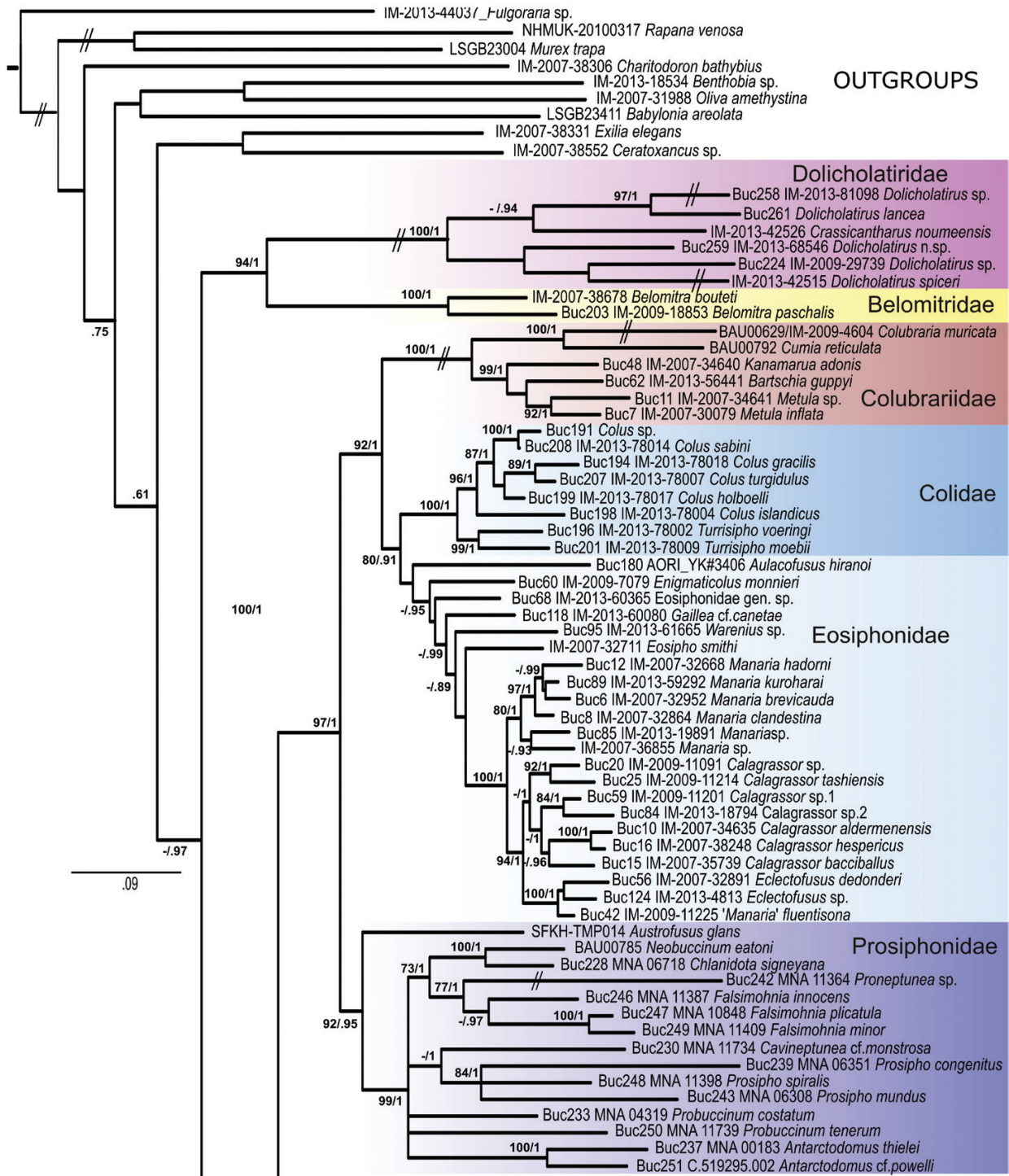


**Figure 1.** Buccinoidea phylogenetic relationships obtained with Bayesian inference (BI) of the multigene Buc5G dataset (concatenated alignment *cox1*, 12S, 16S, 28S and *H3* genes). Bootstrap values (B > 70%) and posterior probabilities (PP ≥ 0.95) are shown above each nodes. The clades containing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

hydrothermal vents, methane seeps and sunken wood, currently classified in seven genera, with a sister-group relationship with ‘*Aulacofusus*’ *hiranoi* (Shikama, 1962)] and (4) *Prosipho*-clade (formed by 15 Antarctic and southern temperate water species currently assigned to nine genera within Buccinidae, including *Austrofusus* Kobelt, 1879 and, in part, *Antarctodomus* A.Adams, 1863). The remaining Buccinoidea form a

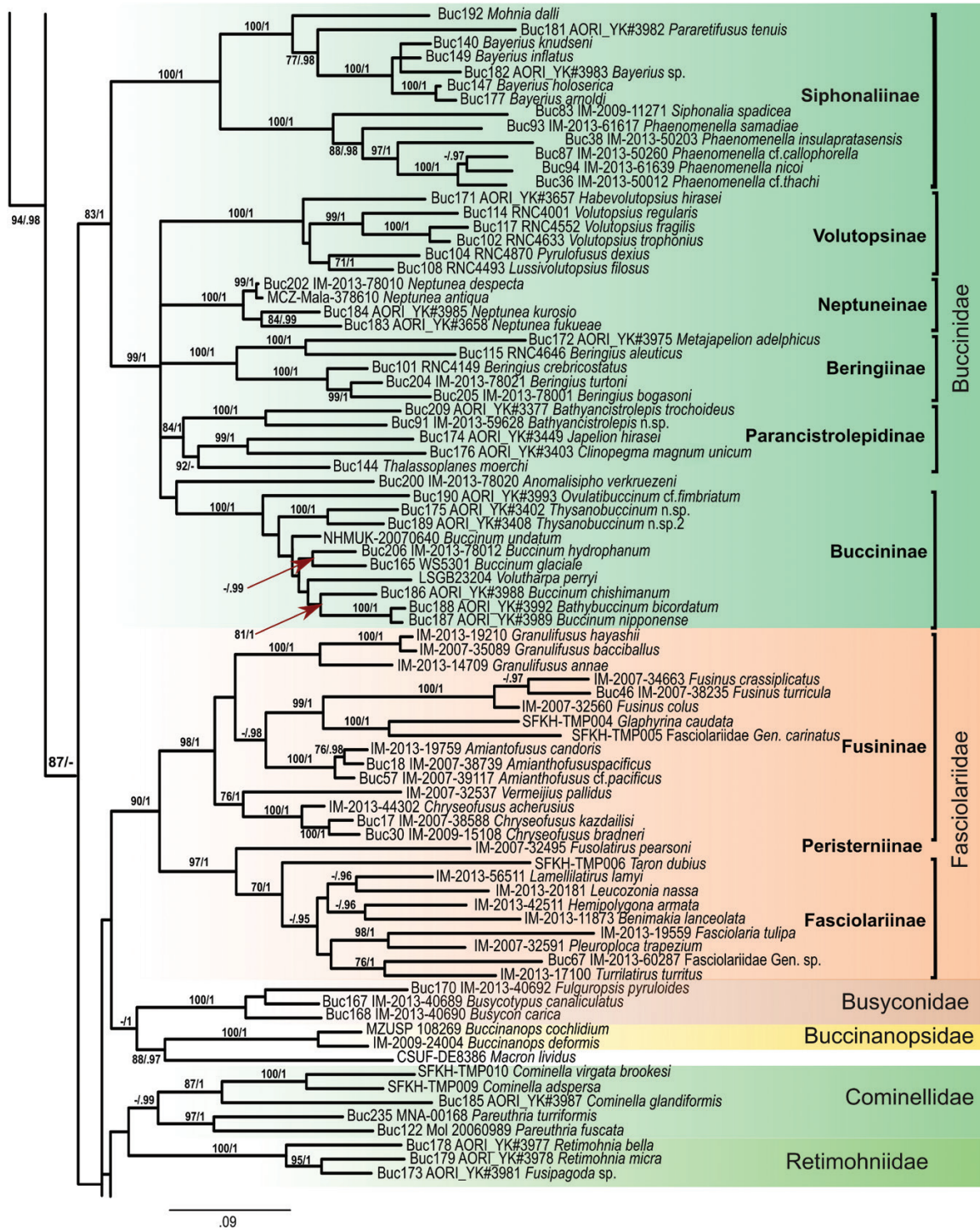
cluster, hereafter called core Buccinoidea, recovered in all analyses of multigene datasets, but with only moderate support in the ML analysis of the Buc5G dataset (B = 87). The first major division within the core Buccinoidea unites the *Siphonalia*-clade (with 13 species currently attributed to five buccinid genera) and a large, maximally supported clade referred to as the Bu-grouping. The Bu-grouping itself encompasses five

Downloaded from https://academic.oup.com/zool/advance-article/doi/10.1093/zool/194/3/789/6323346 by guest on 24 April 2024



**Figure 2.** (Three parts). Buccinoidea phylogenetic relationships obtained with maximum likelihood (ML) and 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.





Downloaded from https://academic.oup.com/zool/advance-article/doi/10.1093/zool/194/3/789/6323346 by guest on 24 April 2024

Figure 2. Continued.

clades, among them the *Volutopsius*-clade (six species), *Neptunea*-clade (four species), *Beringius*-clade (five species), *Bathyancistrolepis*-clade (five species) and *Buccinum*-clade (ten species). Relationships among

the clades of the Bu-grouping remain unresolved, as does the placement of *Anomalisipho verkruzei* (Kobelt, 1876) within it. The second well-supported major division of the core Buccinoidea, referred to



1927, *Buccinulum* Deshayes, 1830, *Euthria* Gray, 1850 and *Tasmeuthria* Iredale, 1925, mostly from the Southern Hemisphere).

Relationships among the other clades are either not consistently detected or lack support. Nevertheless, we mention here all divisions uniting two or more of the remaining 15 clades, and present in at least three multigene trees. The first such group, referred to as the BB-grouping, is well-supported in BI analyses of both the Buc5G\_GUI40 and Buc5G datasets, but absent in the ML analysis of the Buc5G\_GUI40 dataset. It unites the *Busycon*-clade (with three large species representing three genera from the tropical and temperate western Atlantic), *Buccinanops*-clade (comprising two species in the South American genus *Buccinanops* d'Orbigny, 1841) and the East-Pacific species *Macron lividus* (A. Adams, 1855) in a sister-relationship with the *Buccinanops*-clade. The complex grouping referred to as the NaCo-grouping (for Nassariidae–Columbellidae) is recovered in all multigene analyses but is never supported. It comprises the *Columbella*-clade (with seven species representing six genera of the family Columbellidae) and six terminal clades plus three species (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 *Caducifer* Dall, 1904, *Clivipolia* Iredale, 1929 and *Prodotia* Dall, 1924, previously attributed to the Pisaniidae); (3) large *Pisania*-clade (including 14 species currently classified in six further genera of the Pisaniidae: *Cancellopollia* Vermeij & Bouchet, 1998, *Cantharus* Röding, 1798, *Engina* Gray, 1839, *Hesperisternia* J. Gardner, 1944, *Pisania* Bivona-Bernardi, 1832 and *Pollia* Gray, 1834); 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* Gray, 1850 and *Pareuthria* Strebel, 1905) and (2) *Retimohnia*-clade (uniting three species of the deep-water, temperate North-Pacific genera *Fusipagoda* Habe & Ito, 1965 and *Retimohnia* McLean, 1995).

The phylogenetic position of particular taxa was checked in the extended *cox1* tree (Supporting Information, Fig. S1, specimens sequenced only for *cox1* gene are highlighted in red), but these are unfortunately missing in the multigene datasets. *Afer cumingi* (Reeve, 1848), *Africofusus africanus*

(G.B. Sowerby III, 1897) and *Tudicla spirillus* (Linnaeus, 1767) cluster with *Euthria cornea* (Linnaeus, 1758) and *E. japonica* (Shuto, 1978) in the *Buccinulum*-clade, with a moderate support (B = 78) for the grouping of *Tudicla*–*Euthria*–*Africofusus*. The two sequenced specimens of *Aulacofusus periscelidus* (Dall, 1891) formed a group sister to the *Neptunea*-clade in the Bu-grouping, although with weak support (B = 73). The sequenced specimen of *Ancistrolepis grammatus* (Dall, 1907) formed a well-supported clade with *Clinopegma magnum* (Dall, 1895) (B = 99), *Parancistrolepis fujitai* (Kuroda, 1931) clusters with high support (B = 100) with *Thalassoplanes moerchi* (Dall, 1908) and *Pseudoliomesus canaliculatus* (Dall, 1874) clusters with *Japelion hirasei* (Pilsbry, 1901) (B = 97), all in the *Bathyancistrolepis*-clade. *Metajapelion pericochlion* (Schrenk, 1863) clusters with high support with *Metajapelion adelphicus* (Dall, 1907) (B = 100). *Plicifusus rhyssus* (Dall, 1907) clusters with *Anomalisipho verkruezeni* and '*Colus*' *kujanus* Tiba, 1973 (B = 100). Four sequenced specimens of *Pisania striata* (Gmelin, 1791) resolve to the *Pisania*-clade, although not forming any supported grouping within it. The phylogenetic position of *Japeuthria ferrea* (Reeve, 1847), 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 the *Siphonalia*-clade with the maximal support (Supporting Information, 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 section below.

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

The *Colubraria*-clade comprises the type species of *Colubraria*, *C. muricata* (Lightfoot, 1786), as well as members of four other colubrariid genera, and therefore corresponds to the Colubrariidae, now globally accepted at the rank of family. The *Colus*- and *Eosipho*-clades of the CCBA grouping exclusively comprise taxa that are currently placed in Buccinidae, while being clearly not related to the *Buccinum*-clade (the latter recovered in the core Buccinoidea grouping, see below). Taking the family rank of the *Colubraria*-clade into account, we treat the *Colus*- and *Eosipho*-clades at the same rank. Because of differences in ecology (representatives of *Eosipho*-clade live in hydrothermal vents, methane seeps and sunken-wood habitats, while representatives of the *Colus*-clade dwell in ambient subtidal and bathyal benthic communities), distribution (only boreal and Arctic waters for *Colus*-clade, versus broad tropical and subtropical distribution for the *Eosipho*-clade) and morphology (radula), we cannot unite these two clades in a single family. The name Colusinae was established for *Colus* and some other genera and (despite nomenclatural problems discussed in the Taxonomy section) is herein applied at the rank of family to the *Colus*-clade. The *Eosipho*-clade was dealt with by Kantor *et al.* (2013), but no available name exists for it and we, therefore, propose a new family for it: Eosiphonidae. For the *Prosipho*-clade, the name Prosiphoninae, established at the rank of subfamily and currently (Bouchet *et al.*, 2017) accepted as a tribe within Buccinidae, is raised to family rank as Prosiphonidae.

The placement of the *Buccinum*-clade naturally defines the application of the name Buccinidae. Our analysis suggests that the family in its traditional scope is paraphyletic and several of its traditional constituent taxa are here split from it at family rank. Nevertheless, we demonstrate that four phylogenetic lineages (plus the genus *Anomalisipho*), namely the *Neptunea*-clade, *Beringius*-clade, *Voluptosius*-clade and *Bathyancistrolepis*-clade (the latter, based on *cox1*, also comprising the genera *Ancistrolepis* Dall, 1895, *Parancistrolepis* Azuma, 1965 and *Pseudoliomesus* Habe & Sato, 1973), are closely related to the *Buccinum*-clade. These five clades, together forming the well-supported Bu-grouping, correspond to the five subfamilies traditionally recognized

within the Buccinidae: Buccininae, Neptuneinae, Beringiinae, Voluptosiinae and Parancistrolepidinae (= Ancistrolepidinae). The *Siphonalia*-clade is recovered as the sister-group to the Bu-grouping in our multigene analyses, also with consistently high support. *Siphonalia* A. Adams, 1863 is the type genus of the subfamily Siphonaliinae and this name can naturally be applied to this clade. The taxonomic extension of the family Buccinidae can be restricted to the boundaries of the Bu-grouping, leading to a family Buccinidae with five subfamilies and a subfamily Siphonaliinae or, alternatively, it can be defined to include the Bu-grouping plus the *Siphonalia*-clade, leading to a single family Buccinidae. Here we favour the second option and include the *Siphonalia*-clade as a sixth subfamily. The rationale for this decision is that representatives of the *Siphonalia*-clade are morphologically heterogeneous and lack any morphological and anatomical characters that would allow them to be unambiguously distinguished from the Bu-grouping, itself highly morphologically heterogeneous.

All the members of the family Fascioliariidae included in our analysis, except the *Dolicholatirus*-clade, have clustered in the Fa-grouping. Therefore, we recognize the Fa-grouping as the family Fascioliariidae. Branching within the Fa-grouping is consistent with the division into three subfamilies, as was previously concluded by Couto *et al.* (2016).

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

The name Cominellinae (originally a subfamily within Buccinidae) is available for the *Cominella*-clade. As the *Cominella*-clade showed no affinity to Buccinidae, and is not included in any larger, supported cluster within the core Buccinoidea, we raise it to family rank as Cominellidae. Members of the *Cominella*-clade and the *Retimohnia*-clade are

morphologically highly dissimilar, and there is no family-group name available for the latter. Therefore, we introduce a new family Retimohniidae for the genera *Retimohnia* and *Fusipagoda*.

Australian and New Zealand species, as well as North Pacific *Kelletia* Bayle, 1884 spp. from the highly supported PB-grouping, were recently analysed by Vaux *et al.* (2017), who generated for these taxa most of the DNA sequence data that are included in our analysis. Although they used few buccinoidean outgroups in their analysis, Vaux *et al.* identified a close affinity of the genera *Aeneator* Finlay, 1926, *Antarctoneptunea* Dell, 1972, *Buccinulum*, *Kelletia* and *Penion* P.Fischer, 1884, and concluded that their placement in a single subfamily (Buccinulinae) is reasonable. However, our analysis reveals that the relationships of these genera are more complex, mainly because the genera *Aeneator* and *Buccinulum* are actually closer (in the multigene dataset) to the cosmopolitan genus *Euthria* and (in the expanded *cox1* dataset) to the tropical Indo-Pacific genera *Afer* and *Tudicla*, than to *Penion*, *Kelletia* and *Antarctoneptunea*. The members of the *Buccinulum*-clade share a synapomorphic feature in radular morphology: a distinct narrowing of the anterior edge of the central tooth, giving it a trapezoid, or sometimes nearly triangular, shape (see Discussion, taxonomic account). Such tooth shape has not been observed in species of the *Penion*-clade, nor in any other clades of the Buccinoidea. In light of these new results, we conclude that the two clades should be classified as two separate families. The family name Austrosiphonidae was proposed based on the fossil genus *Austrosipho*, currently considered a synonym of *Penion*. We apply it herein to the *Penion*-clade. Based on our results, the name Tudiclidae applies to the *Buccinulum*-clade, and has a priority over the junior (although widely used) name Buccinulidae. Thus, we here ascribe the name Tudiclidae to the *Buccinulum*-clade.

The *Melongena*-clade comprises species representing three genera currently included in the family Melongenidae, among them *Melongena melongena* (Linnaeus, 1758), the type species of *Melongena* Schumacher, 1817. Therefore, we identify this clade as the family Melongenidae. The genera currently included in Pisaniidae fall in two separate clades: the *Pisania*-clade and the *Prodotia*-clade (Fig. 1), and the tree suggests the polyphyly of the family as currently defined. All three species of the genus *Pisania* included in our multigene analyses were recovered in the former clade, as well as *Pisania striatula* Bivona-Bernardi, 1832 (the type of the genus), included in our expanded *cox1* dataset. Although the analysed species of *Pisania* do not form a monophyletic cluster and suggest the polyphyly of the genus, the position of *P. striatula* allows us to unequivocally apply the name Pisaniidae to the *Pisania*-clade. In most of our

reconstructions, the *Chauvetia*-clade forms a sister-group to the Pisaniidae, and species of *Chauvetia* possess a clearly divergent radula, with a unicuspid or acuspate central tooth and with the bases of the laterals extending to form a 'handle' unlike the radulae in the Pisaniidae examined. Despite several family-group names have been proposed for *Chauvetia*, none of them is nomenclaturally available (Gofas & Oliver, 2010) and, therefore, the new family Chauvetiidae is established herein for the *Chauvetia*-clade. As there is no family-group name available for the *Prodotia*-clade, we also introduce the new family Prodotiidae for it.

The application of names to the clades resulting from our phylogenetic analysis is most difficult in the NaCo-grouping, mainly because the distinctive families Nassariidae and Columbelloidae are not resolved as reciprocally monophyletic. All analysed members of Columbelloidae cluster in a monophyletic *Columbella*-clade, with the name Columbelloidae readily applicable to it. This clade occupies the most derived position in the NaCo-grouping, making the traditionally accepted Nassariidae (*sensu Galindo et al.*, 2016) paraphyletic. The *Phos*-clade, representing the subfamily Photinae, branches off first. The next offshoot is the large nassariid cluster combining the *Bullia*-clade (consistent with subfamily Bullinae), the *Anentome*-clade (consistent with subfamily Anentominae), the *Nassarius*-clade and three species related to it. The latter can either be entirely attributed to subfamily Nassariinae or subdivided into Nassariinae and Dorsaninae. The third offshoot is a distinctive clade combining species of the genera *Tomlinia* Peile, 1937 and *Nassaria* Link, 1807; no family-group name exists for this clade. Finally, the *Cyllene*-clade (consistent with the nassariid subfamily Cylleninae) forms a sister-group to the *Columbella*-clade. Thus, the topology of our tree supports six or seven distinctive phylogenetic clusters within what is now treated as Nassariidae, and these clusters generally align with the currently recognized subfamilies. The lack of nodal support and morphological criteria do not justify raising the nassariid subfamilies to full families. Additionally, the close relationship between Columbelloidae and Nassariidae was not recovered in previous molecular phylogenies. In the reconstructions of Galindo *et al.* (2016), Columbelloidae form one of the early offshoots of Buccinoidea with moderately high PP support (0.94), while in the phylogenetic reconstruction of Strong and DeMaintenon (in preparation, personal communication) Columbelloidae form a sister-group to Fascioliariidae. This diverging hypotheses cannot presently be resolved and, in order to minimize premature taxonomic changes, we do not make revisions to the contents of Nassariidae other than

the exclusion of Buccinanopsinae. The position of Columbellidae within Buccinoidea remains uncertain and deserves further studies with broader genomic sampling.

Our analysis provides a phylogenetic framework, which allows for the testing of the validity of the morphology-based family-group taxa previously proposed in Buccinoidea. The latest classification of the superfamily (Bouchet *et al.*, 2017) recognized eight families and 18 subfamilies (including four nominotypical ones). Most of the family-group taxa recognized in that work were here proven valid, although their composition has in many cases been changed. The present phylogeny-based classification recognizes 20 family level taxa and 22 subfamilies (including five nominotypical ones). Several taxa previously treated in Bouchet *et al.* (2017) as subfamilies or tribes are now raised to full families (Table 1): Colidae Gray, 1857, Prosiphonidae Powell, 1951, Cominellidae Gray, 1857, Tudicidae Cossman, 1901, Buccinanopsidae Galindo *et al.*, 2016 and Austrosiphonidae Cotton & Godfrey, 1938. Additionally, previously unrecognized lineages are revealed and are described below as new taxa: Retimohniidae fam. nov., Prodotiidae fam. nov., Eosiphonidae fam. nov. and Tomliniinae subfam. nov. (Nassariidae). We present below a revised classification of the superfamily with the description of new taxa, including the generic composition of every family-group taxon, based on molecular and, in some cases, morphological evidence. We did not consider in detail the composition and scope of the family Fasciolariidae, because it was the subject of a molecular phylogeny by Couto *et al.* (2016) and of Columbellidae, because it is being separately re-assessed by M. deMaitenon and E. Strong (personal communication).

CLASS GASTROPODA CUVIER, 1795

SUBCLASS CAENOGASTROPODA COX, 1960

ORDER NEOGASTROPODA WENZ, 1938

SUPERFAMILY BUCCINOIDEA RAFINESQUE, 1815

FAMILY DOLICHOлатIRIDAE FAM. NOV.

(FIGS 3A–E, 4A–C)

*Type genus:* *Dolicholatirus* Bellardi, 1884.

*Included genera:*

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

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

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

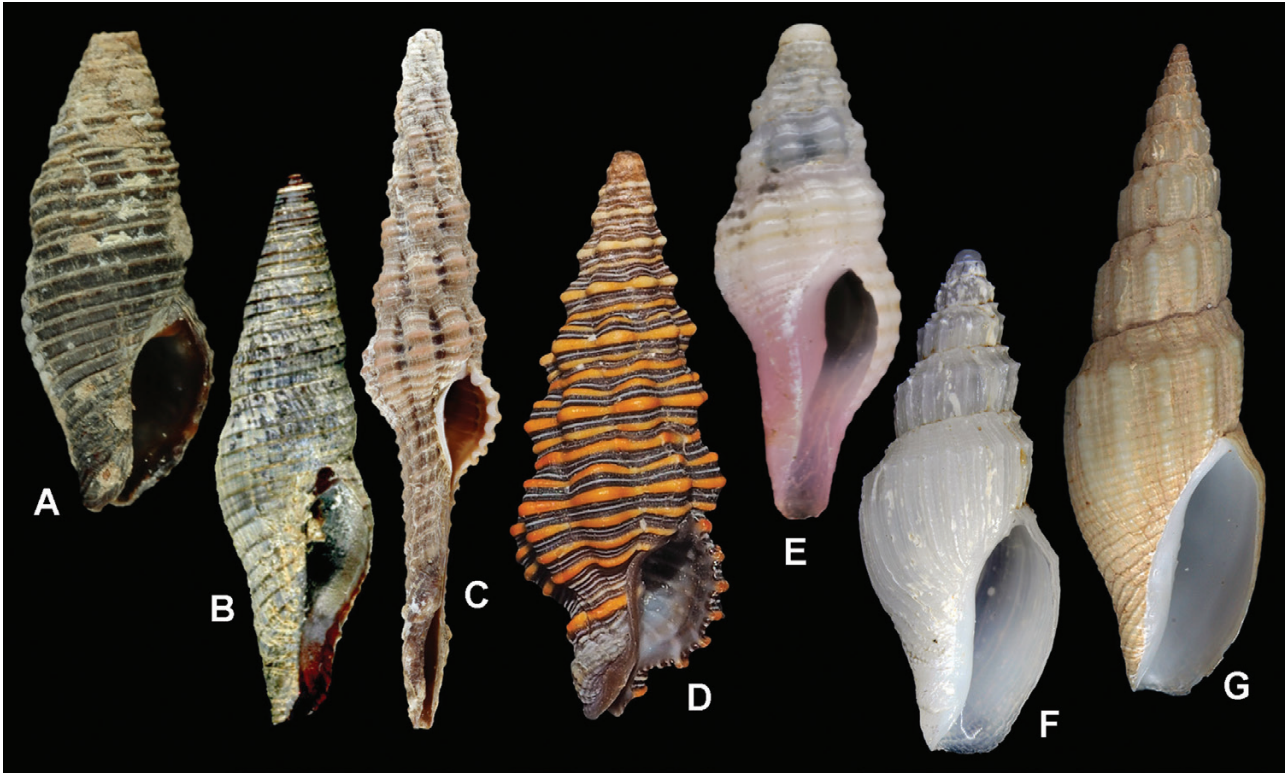
*Diagnosis:* Shell small to medium-large (60 mm), from broad to narrow fusiform or turritiform. Spire tall, siphonal canal from short to long, constituting nearly half of SL. Protoconch paucispiral, with smooth initial part and later whorls sometimes bearing axial ribs. Spiral sculpture of fine to strong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

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

Proboscis medium-long and narrow, single or paired ventral proboscis retractor, attached to anterior or medium part of rhynchodaeum. Salivary glands paired, large. Oesophagus narrow. Valve of Leiblein sphaerical, six or seven times wider than the narrow oesophagus, gland of Leiblein tubular or bulky, medium to large.

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

*Remarks:* The genera included in Dolicholatiridae have traditionally been classified in Fasciolariidae, but Ponder (1972) already noticed the uniqueness of the radula and protoconch morphology of *Crassicantharus*. That genus was later referred to Buccinoidea without definite family allocation (Fraussen & Stahlschmidt, 2015) and *Dolicholatirus* was also at some point tentatively attributed to 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 Fasciolariidae, but no formal taxonomic conclusion was then made. The radular morphology of Dolicholatiridae is characteristic and bears some resemblance to Belomitridae, their sister-taxon in our phylogeny, in having long and



**Figure 3.** Shells of Dolicholatiridae (A–D) and Belomitridae (E–G). 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* sp. nov., 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 *et al.*, 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).

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 *ET AL.*, 2012

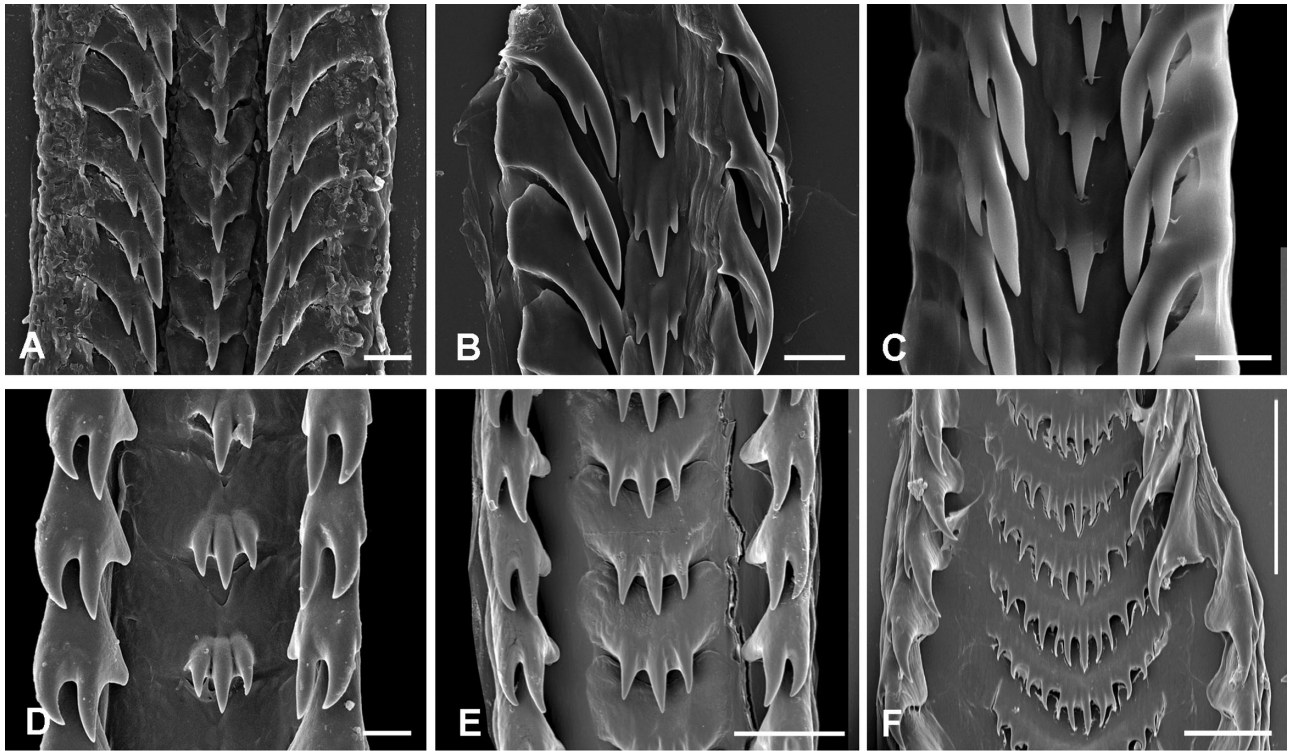
(FIGS 3F, G, 4D–F)

*Type genus:* *Belomitra* P.Fischer, 1883.

*Included genus:*

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

*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



**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 *et al.*, 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.

periostracum. Operculum present or absent; when present with terminal nucleus.

Radula (Fig. 4D–F) with central tooth with rectangular or trapeziform base and three to eight 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 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 limited dataset used in the original molecular phylogenetic analysis (Kantor *et al.*, 2012). The present

analysis shows a highly supported relationship with Dolicholatiridae, from which Belomitridae differs in having a relatively larger proboscis and a much thicker oesophagus, as well as a larger gland of Leiblein terminating in an ampulla.

#### FAMILY COLUBRARIIDAE DALL, 1904

(FIGS 5A–E, 6A–C)

*Type genus:* *Colubraria* Schumacher, 1817

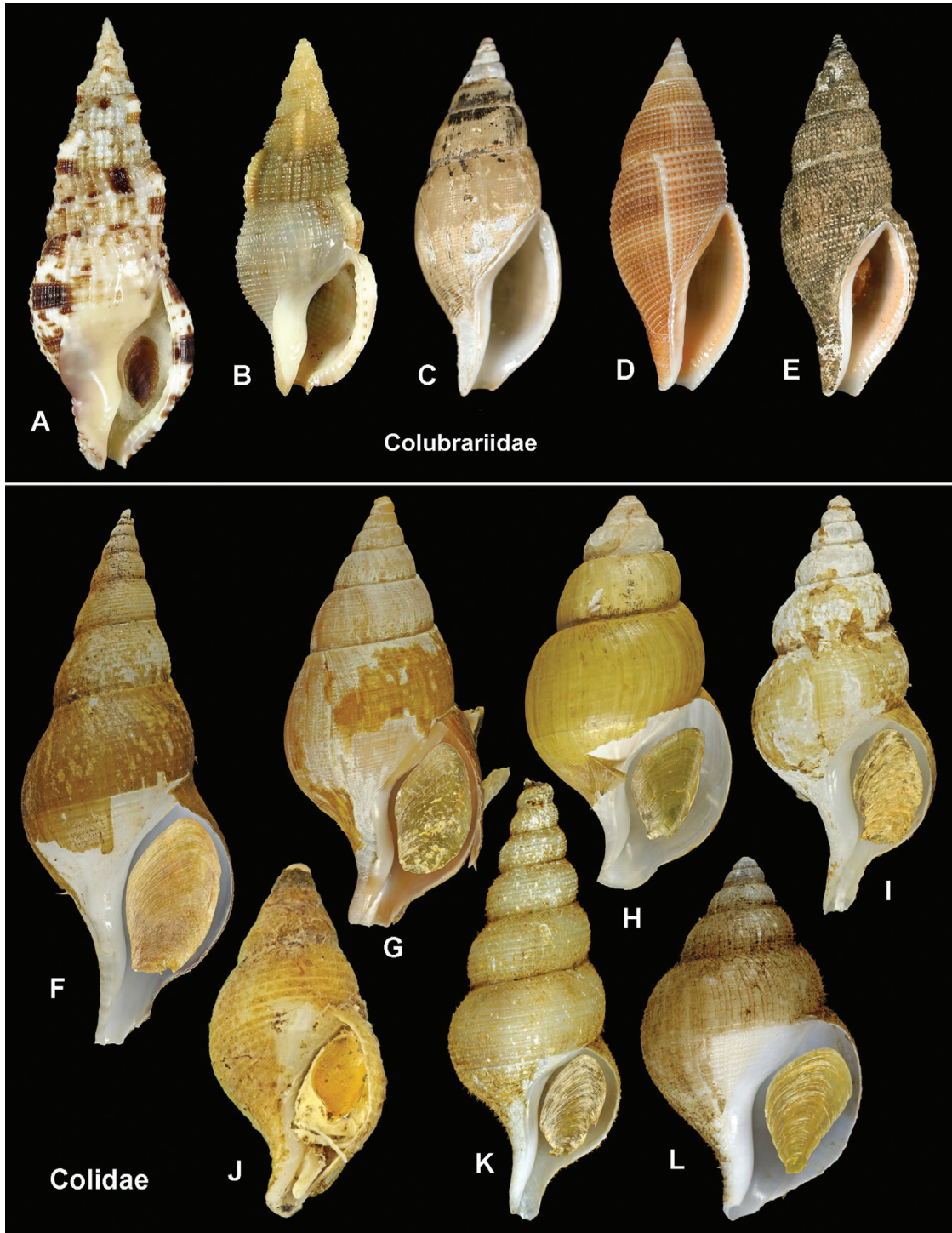
= Fusidae Iredale, 1915. Type genus: *Fusus* Helbling, 1779. Invalid name: type genus placed on the Official Index by ICZN Opinion 1765 (1994)

= Kanamaruidae Higo & Goto, 1993. Type genus: *Kanamarua* Kuroda, 1951

*Included genera:*

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





**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, *Kanamaria 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,

- Bartschia* Rehder, 1943 (TS *Bartschia significans* Rehder, 1943; OD) <sup>(3)</sup>
- Colubraria* Schumacher, 1817 [TS *Colubraria granulata* Schumacher, 1817 [= *Colubraria muricata* (Lightfoot, 1786)]; M] <sup>(1)</sup>
- Cumia* Bivona-Bernardi, 1838 [TS *Cumia decussata* Bivona-Bernardi, 1838 [= *Cumia reticulata* (Blainville, 1829)]; M]. Synonym: *Fusus* Helbling, 1779 (TS *Murex intertextus* Helbling, 1779; SD, [Dall, 1906](#)). Invalid: type genus placed on the Official Index by ICZN Opinion 1765 (1994) <sup>(1)</sup>
- Cyclimetula* S.-I.Huang & M.-H.Lin, 2019 (TS *Cyclimetula hsui* S.-I.Huang & M.-H.Lin, 2019; OD) <sup>(3)</sup>
- Iredalula* Finlay, 1926 (TS †*Bela striata* Hutton, 1873; OD) <sup>(3)</sup>
- Kanamarua* Kuroda, 1951 (TS *Colus adonis* Dall, 1919; OD) <sup>(1)</sup>
- Metula* H.Adams & A.Adams, 1853 [TS *Buccinum clathratum* A.Adams & Reeve, 1850 (= *Metula knudseni* Kilburn, 1975); SD, Kobelt, 1876] <sup>(1)</sup>
- Minibraria* Sarasúa, 1984 (TS *Colubraria monroei* McGinty, 1962; OD) <sup>(3)</sup>

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

Radula small, variable in teeth morphology. In *Colubraria*, central tooth broadly arcuate, with

about ten, subequal, relatively long cusps; lateral teeth broad, with ten or 11 subequal cusps, gradually diminishing towards inner side ([Fig. 6A](#)). In *Cumia*, *Iredalula* and *Metula*, teeth more narrow, central with three to seven relatively short and broadly spaced cusps; laterals with three or four cusps ([Fig. 6B, C](#)). Proboscis extremely long and narrow, multiple coiled within rhynchocoel. Proboscis retractors paired, attached to the base or middle part of rhynchodaeum. Valve of Leiblein either absent or poorly defined, gland of Leiblein absent, salivary glands medium-sized, not fused. Salivary ducts soon after leaving the glands enter the oesophagus wall, and follow within it. Middle oesophagus narrow when passing through nerve ring, posterior oesophagus greatly expanded, muscular. Stomach large, sac-like, thin-walled, straight, tapering posteriorly towards the narrow intestine.

**Distribution:** Temperate to tropical Indo-Pacific and Atlantic, from subtidal to several hundred metres.

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

#### FAMILY COLIDAE GRAY, 1857 (NEW RANK)

([FIGS 5F–L, 6D](#))

**Type genus:** *Colus* [Röding, 1798](#).

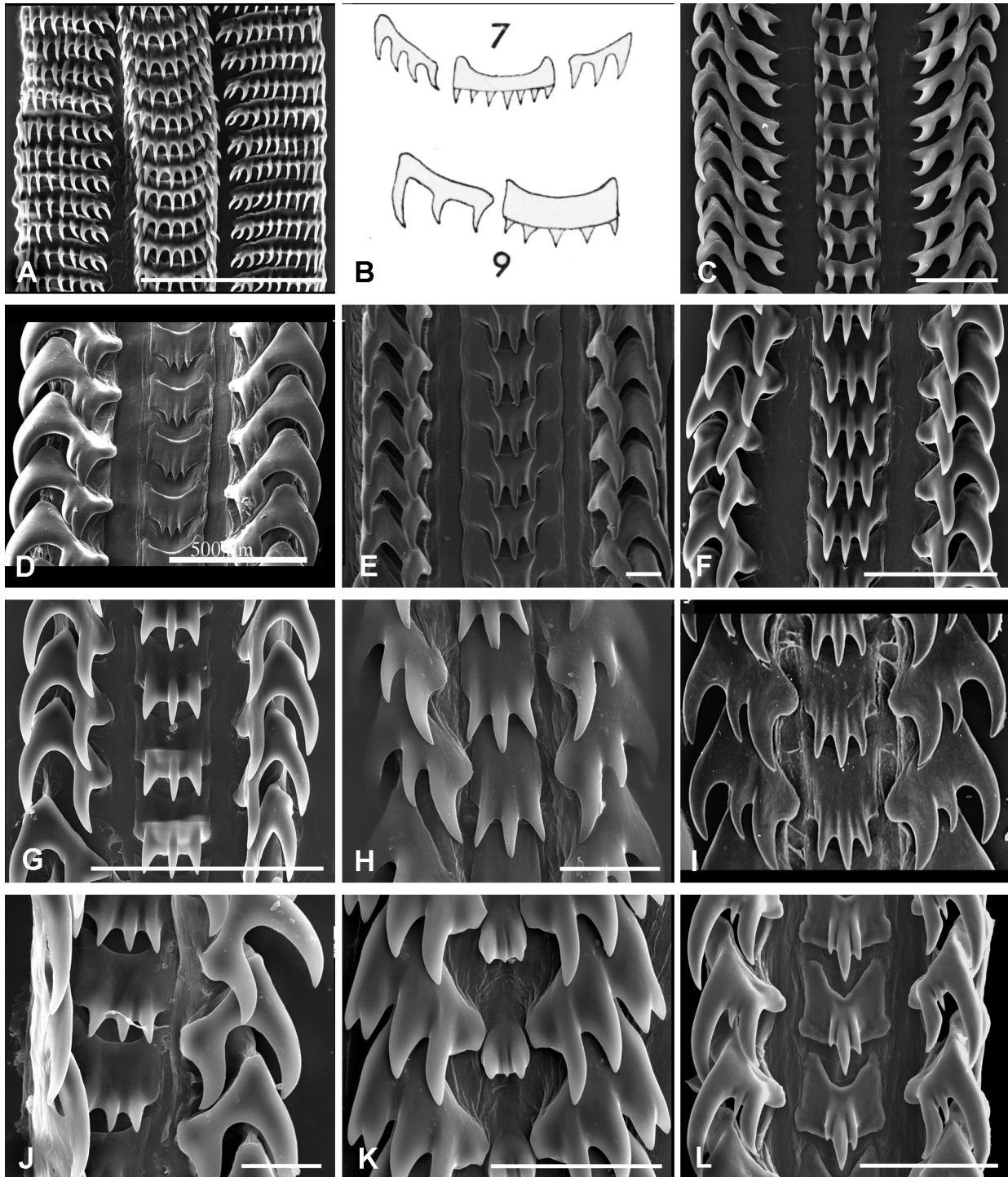
**Included genera:**

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

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

**Diagnosis:** Shell thin-walled, medium-large to large, reaching 200 mm, fusiform to broad fusiform or ovate, with moderately high to very high spire and distinct,

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 holboelli* (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, *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.



**Figure 6.** Radulae of Colubrariidae (A–C), Colidae (D) and Eosiphonidae (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 uncatalogued, 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,

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

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

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

*Remarks:* The use of the name Colidae for this clade is fraught with nomenclatural difficulty. The concept of the genus name *Colus* has differed significantly in the publications of various authors, due to the late fixation of the type species by Dall (1906). When he established the name *Colus*, Röding (1798) included in it species that are presently attributed to several families, including Fasciolaridae [e.g. *Murex tulipa* Linnaeus, 1758 (now *Fasciolaria tulipa*)] 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 Fasciolaridae, 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 fasciolariid. Ponder & Warén (1988) treated Colinae as a synonym of Buccinidae, not Fasciolaridae, 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 and *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.

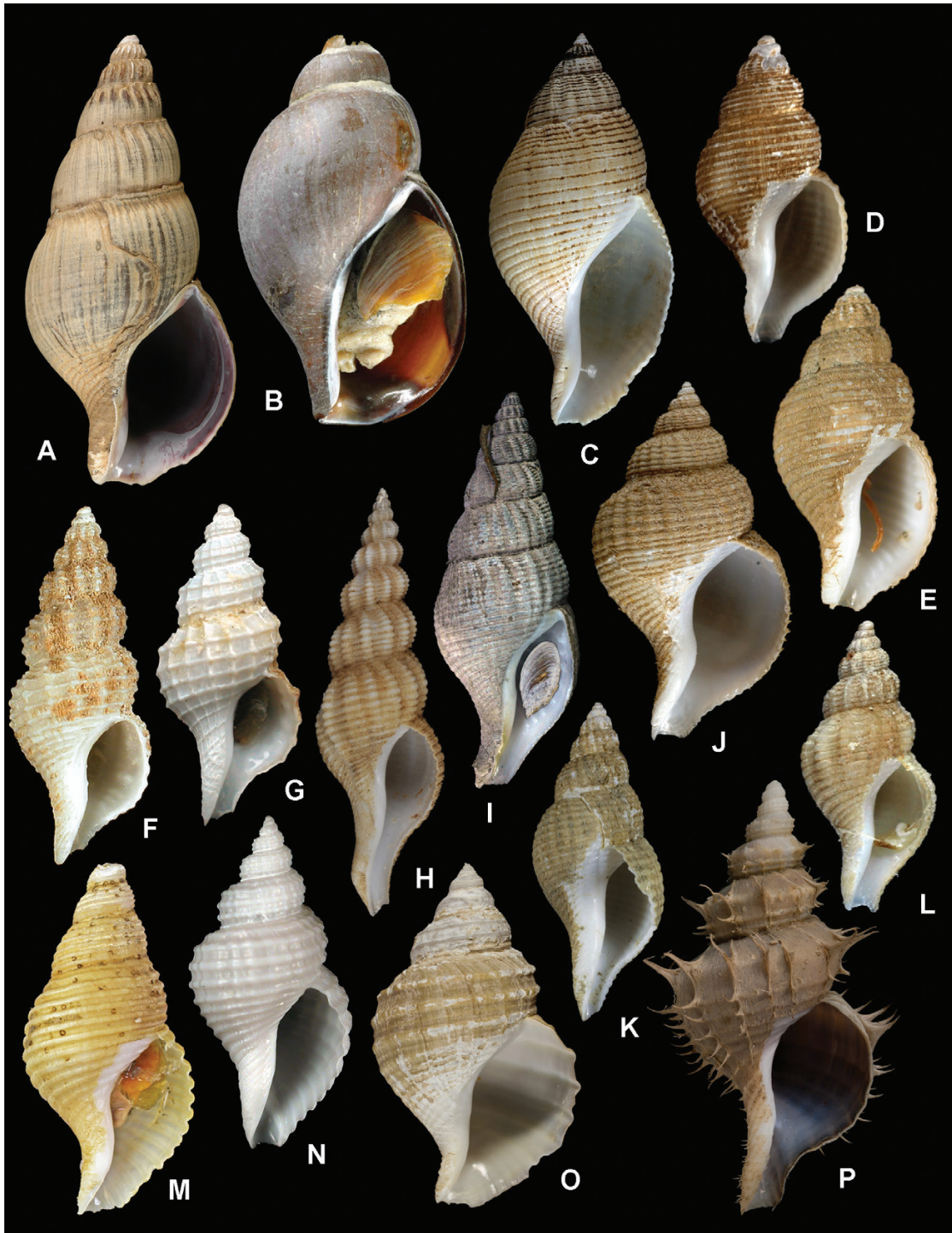
(FIGS 6E–L, 7)

*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)

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, *Eclectofusus* sp., Papua New Guinea, PAPUA NIUGINI st. CP3949, 5°12'S, 145°51'E, 380–407 m, MNHN IM-2013–4813 (sequenced specimen). I, *Eclectofusus 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, 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



**Figure 7.** Shells of Eosiphonidae. 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, Nautilé 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

- Calagrassor* Kantor *et al.*, 2013 (TS *Cantharus aldermenensis* Powell, 1971; OD) <sup>(1)</sup>
- Ecletofus* 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>
- Gaillia* Kantor *et al.*, 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 angsanana* K.Martin, 1921; OD) <sup>(2)</sup> – radula, see Bouchet & Warén [1986: *Preangeria dentata* (Schepman, 1911), as *Eosipho dentatus*]
- Thermosipho* Kantor *et al.*, 2013 (TS *Eosipho auzendei* Warén & Bouchet, 2001; OD) <sup>(1)</sup>
- Warenius* Kantor *et al.*, 2020b (TS *Costaria crosnieri* Bouchet & Warén, 1986; OD) <sup>(1)</sup>

**Diagnosis:** Shell medium-sized to large, from slightly over 10 mm to 100 mm, from ovate to narrowly fusiform. Siphonal canal from nearly absent (*Thermosipho*) to long (*Manaria*). Protoconch small, often eroded, paucispiral when known, with less than two whorls. Spire whorls usually evenly convex, rarely shouldered mainly due to axial sculpture. Axial sculpture either absent (*Thermosipho* and ‘*Aulacofusus*’ *hiranoi*) or represented by very weak to strong ribs or wide, rounded folds. Spiral sculpture (except *Thermosipho* with smooth shell) of distinct cords of uneven strength, breadth and density. In *Ecletofus* sculpture forms a reticulated pattern due to the intersection of narrow axial ribs and broadly spaced spiral cords. Aperture ovate or elongate, with smooth inner and outer lip, or bearing labral tooth (*Preangeria*) (Raven, 2016). Shell

covered with periostracum, from smooth to hirsute or forming spines (*Americominella*). Operculum leaf-shaped with terminal nucleus.

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

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

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

**Remarks:** This clade combining several genera from different biogenic substrates was first discovered and characterized by Kantor *et al.* (2013) and is herein expanded to include several additional genera (*Americominella*, *Ecletofus*, *Preangeria* and *Warenius*). The anatomy of *Enigmaticolus* and *Calagrassor* has been described by Kantor *et al.* (2013).

The first branch of the family to diverge from the others is ‘*Aulacofusus*’ *hiranoi* (Shikama, 1962), described as *Colus calameus hiranoi* and transferred to *Aulacofusus* by Higo *et al.* (1999: 229), a transfer later accepted (Hasegawa, 2009; Kosyan & Kantor, 2013). Hasegawa (2009) mentioned that ‘juvenile specimens smaller than *c.* 1.5 cm SL were found attached to pieces of sunken wood, and similar ecology has been

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

observed in *A. coerulescens* (Kuroda & Habe in Habe, 1961). However, its generic allocation is unconfirmed since it is conchologically somewhat different from other *Aulacofusus* and the radula and anatomy have not been examined. '*Aulacofusus*' *hiranoi* may belong to a new genus (see Discussion section of the subfamily Neptuneinae).

In our analysis, *Manaria* is found polyphyletic, as *Manaria fluentisona* Fraussen & Stahlschmidt, 2016 (Fig. 7F) clusters with species of *Electofusus*. Conchologically, it is particularly similar to *E. dedonderi* (Fraussen & Hadorn, 2001) (Fig. 7G) in the reticulated sculpture pattern and strong periostracum, and we thus transfer *Manaria fluentisona* to *Electofusus*.

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

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

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

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

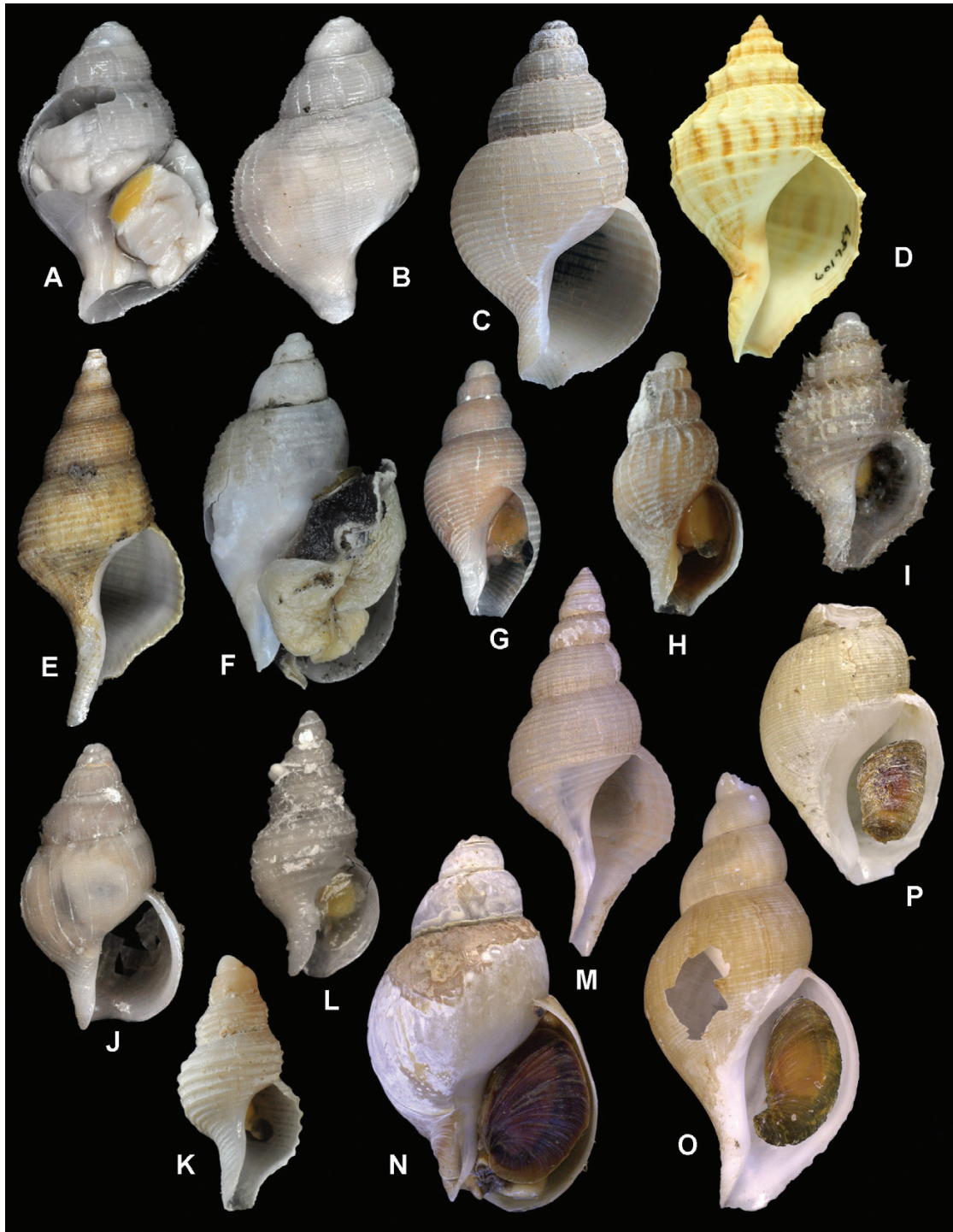
#### FAMILY PROSIPHONIDAE POWELL, 1951 (NEW RANK)

(FIGS 8, 9)

Type genus: *Prosipho* Thiele, 1912.

#### Included genera:

- Anomacme* Strebel, 1905 (TS *Anomacme smithi* Strebel, 1905; M)<sup>(2)</sup>; radula, see Powell (1951)
- Antarctodomus* Dell, 1972 (TS *Bathydromus thielei* Powell, 1958; OD)<sup>(1)</sup>
- Antistreptus* Dall, 1902 (TS *Antistreptus magellanicus* Dall, 1902; OD)<sup>(2)</sup>; radula, see Pastorino & Griffin (2019)
- Argeneuthria* Pastorino, 2016 (TS *Euthria cerealis* Rochebrune & Mabile, 1885; OD)<sup>(2)</sup>; radula, see Pastorino (2016)
- Austrofusus* Kobelt, 1879 [TS *Fusus nodosus* Gray, 1843 (= *Drupa glans* Röding, 1798); SD, Martens, 1882]<sup>(1)</sup>
- Bathydromus* Thiele, 1912 (TS *Bathydromus obtectus* Thiele, 1912; M)<sup>(2)</sup>; radula, see Thiele (1912)
- Cavineptunea* Powell, 1951 (TS *Cavineptunea monstrosa* Powell, 1951; OD)<sup>(1)</sup>
- Chlanidota* Martens, 1878 (TS *Cominella vestita* Martens, 1878; M)<sup>(1)</sup>
- Chlanidotella* Thiele, 1929 (TS *Cominella modesta* Martens, 1885; OD)<sup>(2)</sup>; radula, see Powell (1951)
- Chlanificula* Powell, 1958 (TS *Chlanificula thielei* Powell, 1958; OD)<sup>(2)</sup>; radula, see Hain (1990)
- Crenatosipho* Linse, 2002 (TS *Crenatosipho beaglensis* Linse, 2002; OD)<sup>(2)</sup>; radula, see Linse (2002)
- Drepanodontus* Harasewych & Kantor, 2004 (TS *Drepanodontus tatyanae* Harasewych & Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)
- Falsimacme* Pastorino, 2016 (TS *Euthria kobelti* Strebel, 1905; OD)<sup>(2)</sup>; radula, see Pastorino (2016)
- Falsimohnia* Powell, 1951 (TS *Buccinum albozonatum* Watson, 1882; OD)<sup>(1)</sup>
- Fusinella* Thiele, 1917 [TS *Buccinella jucunda* Thiele, 1912; by typification of replaced name (*Buccinella* Thiele, 1912)]<sup>(2)</sup>; radula, see Thiele (1912)
- Germonea* Harasewych & Kantor, 2004 (TS *Germonea rachelae* Harasewych & Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)
- Meteuthria* Thiele, 1912 (TS *Euthria martensi* Strebel, 1905, M)<sup>(2)</sup>; radula, see Pastorino (2016)
- Muffinbuccinum* Harasewych & Kantor, 2004 (TS *Muffinbuccinum catherinae* Harasewych & Kantor, 2004; OD)<sup>(2)</sup>; radula, see Harasewych & Kantor (2004)
- Neobuccinum* E.A.Smith, 1879 (TS *Buccinopsis eatoni* E.A.Smith, 1875; M)<sup>(1)</sup>
- Parabuccinum* Harasewych *et al.*, 2000 (TS *Chlanidota bisculpta* Dell, 1990; OD)<sup>(2)</sup>; radula, see Harasewych *et al.* (2000)



**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, *Austrofusus 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.



- Probuccinum* Thiele, 1912 (TS *Neobuccinum tenerum* E.A.Smith, 1907; SD, Wenz, 1943) <sup>(1)</sup>
- Proneptunea* Thiele, 1912 (TS *Proneptunea amabilis* Thiele, 1912; M) <sup>(1)</sup>
- Prosipho* Thiele, 1912 (TS *Prosipho gaussianus* Thiele, 1912; SD, Powell, 1951) <sup>(1)</sup>
- Savatieria* Rochebrune & Mabile, 1885 (TS *Savatieria frigida* Rochebrune & Mabile, 1885; M) <sup>(2)</sup>; radula, see Luca & Pastorino (2018)
- Spikebuccinum* Harasewych & Kantor, 2004 (TS *Spikebuccinum stephaniae* Harasewych & Kantor, 2004; OD) <sup>(2)</sup>; radula, see Harasewych & Kantor (2004)
- Strebelia* Kantor & Harasewych, 2013 (TS *Bela notophila* Strebel, 1908; OD) <sup>(2)</sup>; radula, see Kantor & Harasewych (2013)

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

Radula is variable and can be classified in six different types:

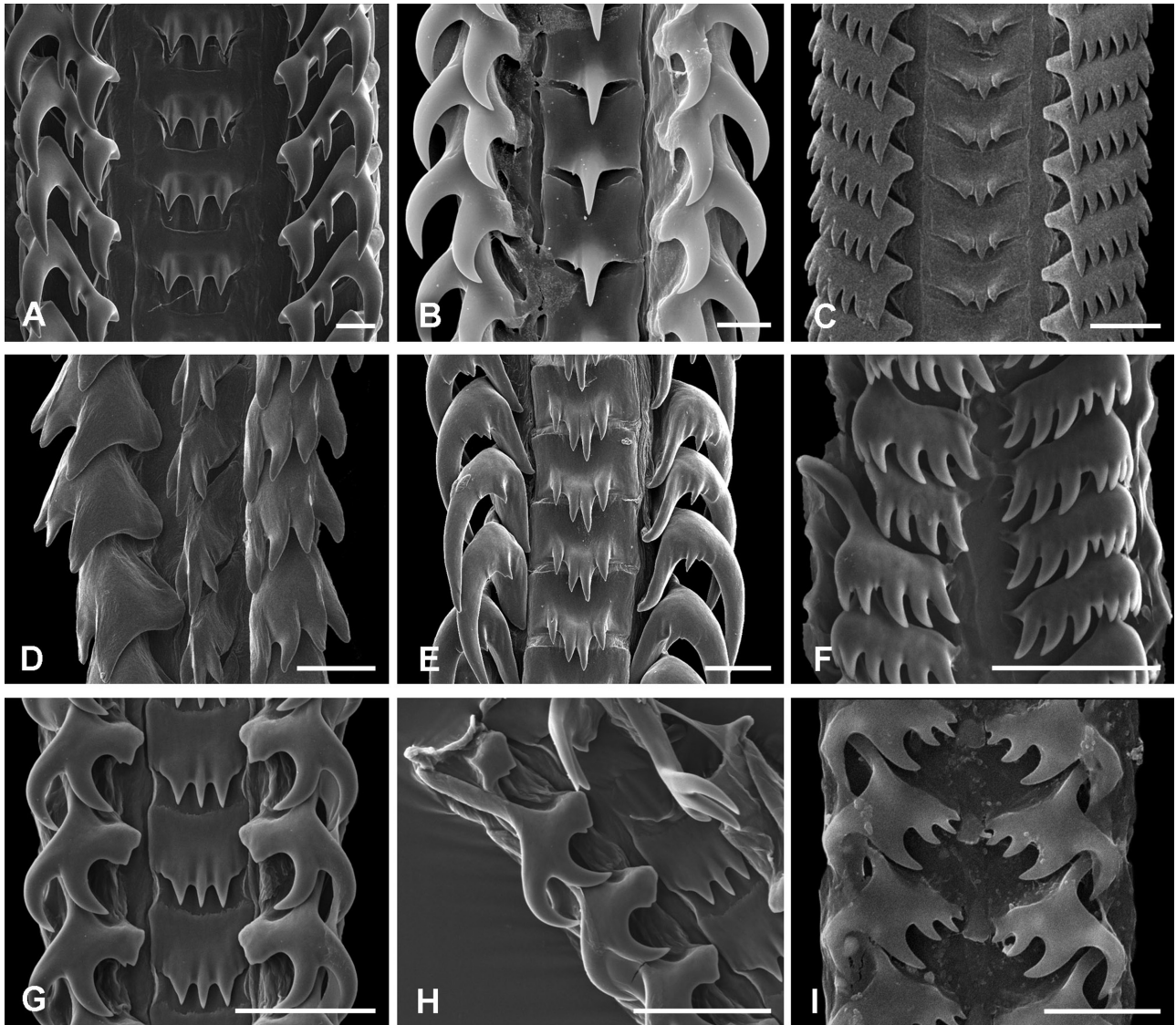
1. Lateral teeth with three to five cusps, outermost longest, inner one significantly shorter, central tooth with subsquare or subrectangular base and notched anterior edge and three to five sharp cusps (Fig. 9A) – found in *Austrofuscus*, *Bathydromus*,

*Cavineptunea*, *Chlanidota*, *Chlanificula*, *Neobuccinum*, *Parabuccinum*, *Probuccinum* and *Spikebuccinum*.

2. Lateral teeth bicuspid, with subequal cusps, and outer portion of basal plate attenuated, long. Central tooth with square base and single, large, pointed cusp (Fig. 9B) – found in *Falsimohnia* and *Strebelia*.
3. Lateral teeth multicuspoid, with four to seven subequal cusps, outermost shortest, sometimes with rows of denticles along the outer edge of outer cusp. Central tooth with subsquare or subrectangular base and notched anterior edge and three sharp cusps (Fig. 9C) – found in *Chlanidotella*, *Maffinbuccinum* and *Proneptunea*.
4. *Prosipho*-type. Lateral teeth varying in shape, but always with long and narrow attenuated outer portion of basal plate, forming ‘handle’, and with two to seven cusps. Central tooth sometimes absent, when present varying from small, acusate to well developed, bearing three cusps (Fig. 9D, F–I). Found in *Anomacne*, *Antistreptus*, *Argeneuthria*, *Crenatosipho*, *Falsimacme*, *Fusinella*, *Germonia*, *Metearthria*, *Prosipho* and *Savatieria*.
5. *Antarctodomus*-type. Lateral teeth with narrow base and two long, closely spaced cusps, outer one slightly longer. Central tooth broad with three blunt cusps (Numanami, 1996: fig. 96D).
6. *Drepanodontus*-type. Lateral teeth with a single large cusp (seems to be homologous to the outermost cusp in other genera) and small one to three cusplets on the inner side of the cusp (Fig. 9E).

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

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* (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, *Germonia 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.



**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 1, 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 & Mabilie, 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 µm; B, I, 10 µm; F, G, H, 30 µm.

**Distribution:** Antarctic and subantarctic waters, Magellan Province, from subtidal to abyssal depths.

**Remarks:** The concept and scope of this family is radically changed by the present study. Powell (1951) established the name Prosiphinae without providing any diagnosis or statement about the erection of this new family-group name. It was rather vaguely

circumscribed as a subfamily of Buccinulidae, to include several Antarctic and Magellanic genera (*Anomacme*, *Chlanidotella*, *Fusinella*, *Met euthria*, *Proneptunea* and *Prosipho*) with 'central tooth tricuspid, lateral teeth multicuspid'; Powell (1951: 132) added that 'typically, the laterals have a long basal projection, like a handle'. Other Antarctic and subantarctic buccinoid genera were attributed by Powell to the Buccinulidae

subfamilies Buccinulinae (central and lateral teeth tricuspid) and Cominellinae (central tooth tricuspid, lateral teeth bicuspid). Powell himself considered this classification provisional, having characterized it as 'probably more convenient than real'.

Our phylogeny demonstrates that the genera that Powell included in Buccinulinae (*Bathydomus*, *Cavineptunea*, *Chlanidota*, *Neobuccinum* and *Probuccinum*) and Cominellinae (*Falsimohnia*) are actually closely related to *Prosipho*, in spite of notable differences in radular morphology. Beside Antarctic and sub-Antarctic species, Prosiphonidae includes species from New Zealand (*Austrofusus glans*) and Tasmania (*Antarctodomus* cf. *powelli*). It should be 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* (Harasewych & Kantor, 2004) 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 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 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 four to eight cusps; lateral teeth with three to four 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 declivis* Habe & Ito, 1976); OD] and *Corneobuccinum* Golikov & Gulbin, 1977 [TS *Colus (Latisipho) lepidus* Dall, 1918; OD] remains uncertain.

##### SUBFAMILY BERINGIINAE GOLIKOV & STAROBOGATOV, 1975

(FIGS 10G–K, 11C)

Type genus: *Beringius* Dall, 1887

= Metajapelioninae Goryachev, 1987 (as subfamily of Beringiidae). Type genus: *Metajapelion* Goryachev, 1987

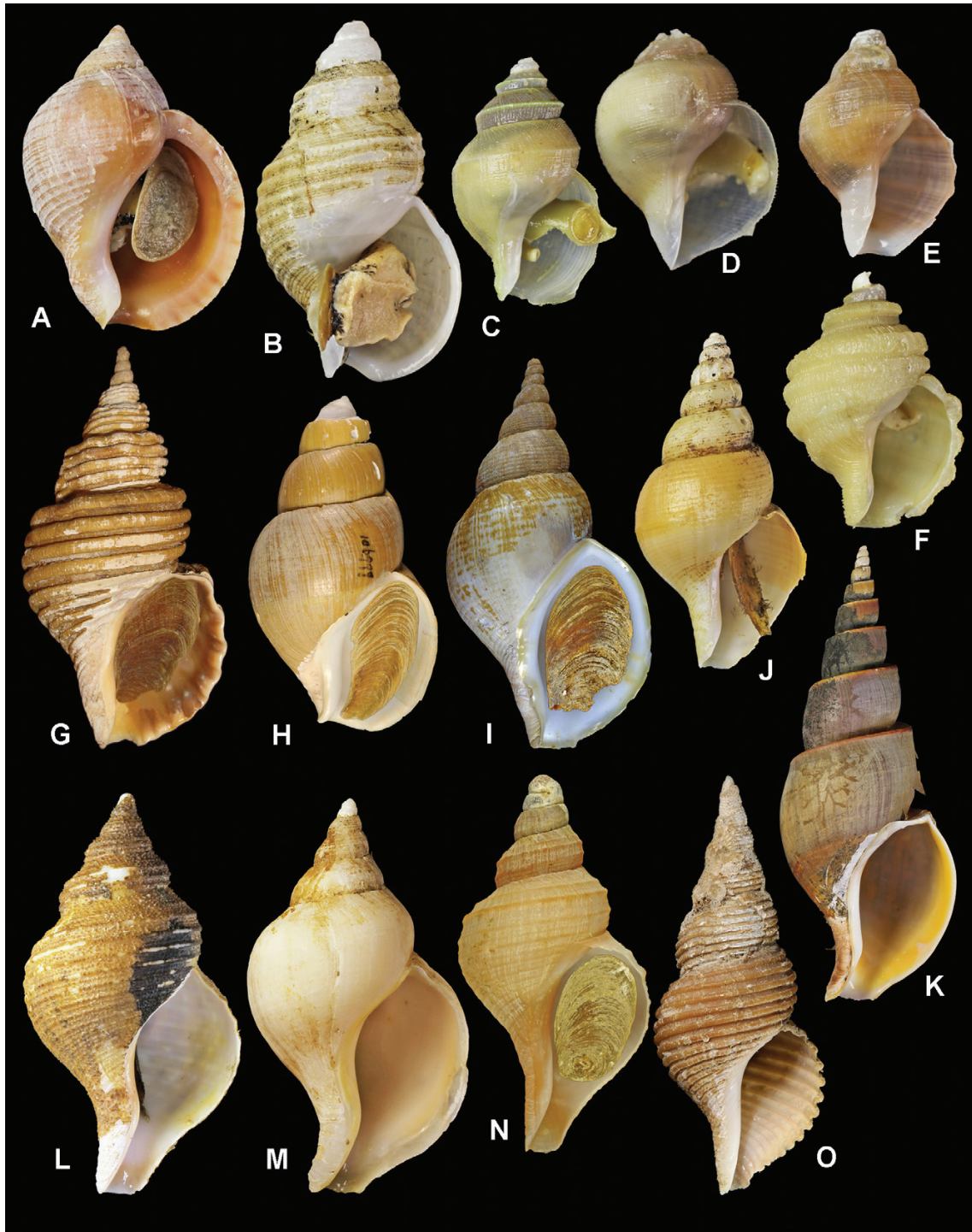
Included genera:

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

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

*Neoberingius* Habe & Ito, 1965 (TS *Beringius frielei* Dall, 1895, OD)<sup>(2)</sup>; radula, see (Habe & Sato, 1973)

**Diagnosis:** Shell large, reaching 140 mm, broadly fusiform, with high spire and very short to obsolete



**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* sp. nov., Japan, 38°16'N, 143°32'E, 3302–3311 m, AORI\_YK#3402, SL 20.3 mm, sequenced specimen. G,

siphonal canal. Protoconch paucispiral, of about 2.0–2.5 whorls, large, diameter similar to, or even exceeding, that of first teleoconch whorls. Whorl profile subcylindrical to evenly convex. Shell sculpture pronounced in most cases, spiral sculpture from microscopic threads to prominent keels; axial sculpture, when present, of distinct, broad, arcuated axial ribs. Aperture wide, ovate. Shell pale or brownish, covered with smooth periostracum. Operculum large, may exceed aperture length, detached from foot on large, oldest portion, with terminal nucleus.

Radula (Fig. 11C) with cusplless, subrectangular, plate-like central tooth; lateral teeth long, with narrow base of about one-third of tooth height, with three, rarely four, cusps, outermost one much longer. Proboscis long, thick, proboscis retractors multiple, attaching laterally to posterior portion of rhynchodaeum. Paired, medium-sized, salivary glands. Salivary ducts thick. Gland of Leiblein small, tubular, valve of Leiblein rounded, medium-sized.

Individual egg capsules large, rounded, with one convex and another concave surface, reaching more than 50 mm, with stalk, attached to substrate. Capsules aggregate in linear clusters. Capsule wall multilayered. Development direct, with nurse eggs, emerging molluscs large, reaching more than 15 mm in SL (Gulbin, 2018).

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

**Remarks:** In addition to three species of *Beringius*, ‘*Japelion*’ *adelphicus* (Dall, 1907) and ‘*Beringius*’ *aleuticus* Dall, 1895 cluster together in our multigene analysis. ‘*Japelion*’ *adelphicus* has a radula (Fig. 11C) morphologically similar to *Beringius* spp. (Bouchet & Warén, 1985: fig. 467, sic!; Habe & Sato, 1973: fig. 13). The radula of ‘*B.*’ *aleuticus* is unknown. ‘*Beringius*’ *aleuticus* is different in shell shape from other species of *Beringius*, particularly in having an ovoid, non-sculptured shell with short canal. The isolated position of this species in our tree suggests that it may represent a previously unrecognized lineage worthy of a separate genus status.

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 similar species, ‘*Japelion*’ *pericochlion* (included only in our *cox1* tree; radula, see Habe & Sato, 1973: fig. 14; shell see Fig. 10K herein), clusters together with ‘*Japelion*’ *adelphicus* and nests 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:*

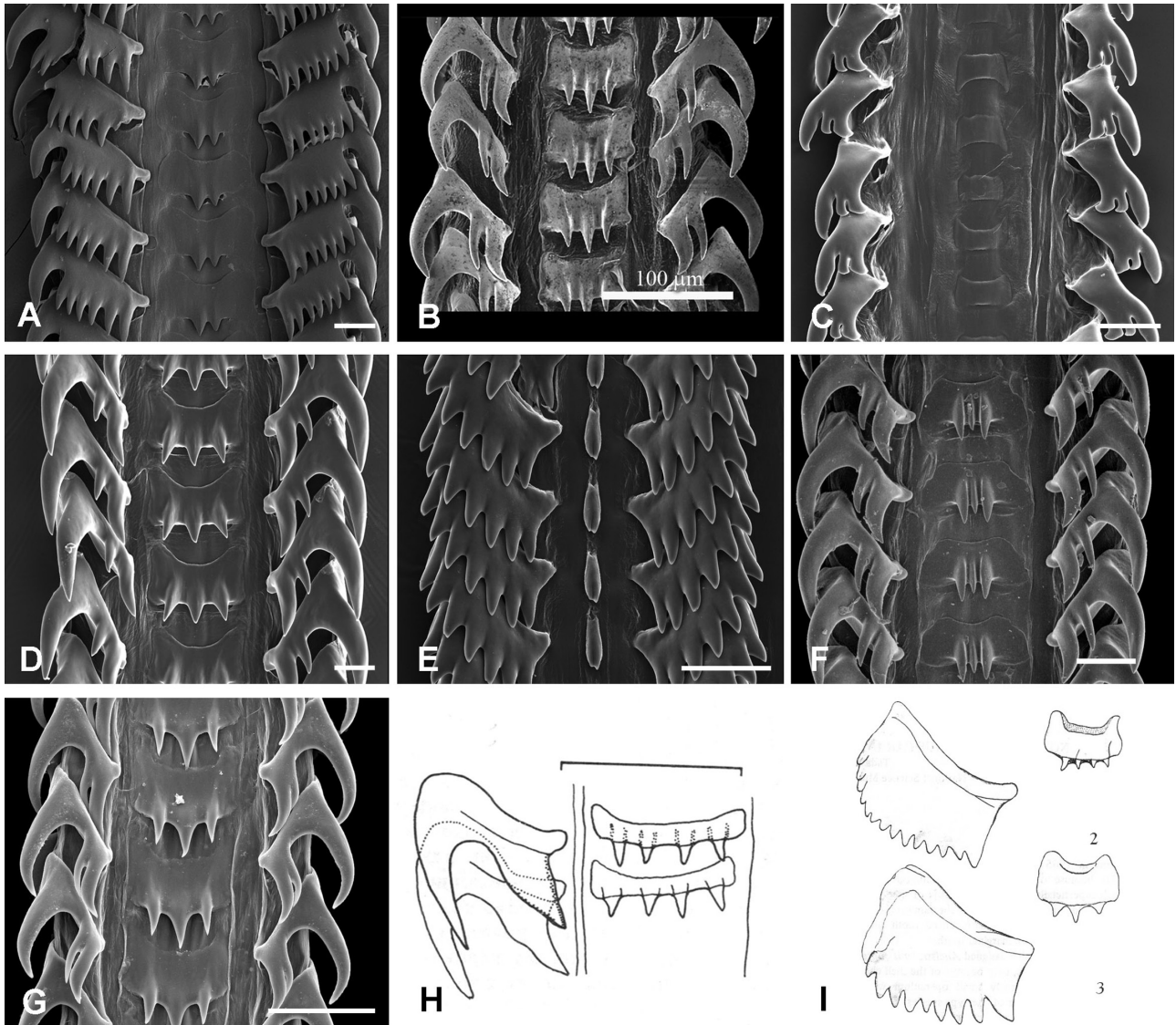
*Aulacofusus* Dall, 1918 [TS *Fusus spitzbergensis* Reeve, 1855 (= *Fusus brevicauda* Deshayes, 1832; OD)]<sup>(1)</sup>

*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 wide. Shell covered with smooth periostracum. Operculum large, spanning most of aperture, with terminal nucleus.

Radula with multicuspid (two to eight cusps) central tooth with rectangular and anteriorly arcuate base;

*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 pericochlion* (Schrenck, 1863), Japan, AORI\_YK#4142, SL 117.7 mm, specimen sequenced for *cox1*. L, *Neptunea kurosio* Oyama, 1959, Japan, Kyushu I., 32°10'N, 129°30'E, 470–487 m, AORI\_YK#3985, SL 86.4 mm, sequenced specimen. M, *Neptunea fukueae* Kira, 1959, Japan, Kyushu I., 32°10'N, 129°30'E, 470–487 m, AORI\_YK#3658, SL 61.7 mm, sequenced specimen. N, *Neptunea despecta* (Linnaeus, 1758), Iceland, 67°49'N, 21°44.5'W, 755–770 m, MNHN IM-2013–78010, SL 41.2 mm, sequenced specimen. O, *Aulacofusus periscelidus* (Dall, 1891), Kurile Is., Urup Is., 45°55.2'N, 150°15.8'E, 169–150 m, IEE BUC270, SL 58.5 mm, specimen sequenced for *cox1*.



**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. 5E). 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. 10I). 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 µm; F, 200 µm.

lateral teeth broad, with two to seven 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 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 (Pearce & 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). However, in addition to ‘*Aulacofusus*’ *hiranoi*, two specimens of a second species of the same genus, *A. periscelidus* (Dall, 1891), were included in the analysis based on *cox1* alone: whereas the placement of *A. hiranoi* remained the same as in the multigene tree, *A. periscelidus* was sister to *Neptunea* (B = 70). No data on radula or anatomy of ‘*Aulacofusus*’ *hiranoi* are available, but the conchological similarity with other members of the Eosiphonidae, particularly with *Eosipho*, was noted by Kosyan & Kantor (2013). Besides, *A. periscelidus* is similar in shell morphology and radula (see Fig. 13B) to *A. brevicauda*, the type species of the genus (Kosyan & Kantor, 2013). For this reason, we here include *Aulacofusus* in the subfamily Neptuneinae, whereas ‘*Aulacofusus*’ *hiranoi* should be excluded from *Aulacofusus* and reassigned to a new genus of Eosiphonidae.

#### SUBFAMILY VOLUTOPSIINAE HABE & SATO, 1973

(FIGS 11H, 12A–D)

*Type genus:* *Volutopsius* Mörch, 1857.

*Included genera:*

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

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

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

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

*Diagnosis:* Shell large, reaching 160 mm, from fusiform to broadly fusiform or ovate, with very short to medium-high spire and short to very short, nearly obsolete siphonal canal. Protoconch paucispiral, always retained in adults, of about two whorls, medium sized (3.5–5 mm in diameter) to very large

(up to 13 mm). Whorl profile convex to subcylindrical. Shell sculpture pronounced in most species, spiral sculpture from microscopic threads to prominent bulging keels; axial sculpture sometimes present, from knobs on shoulder and axial lamellae (some species of *Volutopsius*) to distinct axial ribs. Shell covered with smooth periostracum. Aperture ovate, wide, often with strongly calloused inner lip. Shell colour from ivory to orange or dark-brown, parietal callus and/or inside aperture often light- to dark-brown. Operculum small to medium-sized, spanning half of aperture or less, with terminal nucleus shifted leftwards.

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

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



**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 filusus* (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 *cox1*. 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



*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 *Tritonium ooides* Middendorff, 1848; OD) <sup>(1)</sup>

*Thalassoplanes* Dall, 1908 (TS: *Troschelia moerchii* 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 small (*Parancistrolepis* only), spanning about one-fifth 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 narrow and long, lateral teeth broad, with seven or eight 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.

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

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

**Remarks:** Our multigene dataset did not include any *Ancistrolepis* species, but in the *cox1*-based tree, *Ancistrolepis grammatus* (Dall, 1907) ([Fig. 12E](#)) clusters with other members of the subfamily, being sister with maximal support to *Clinopegma unicum*, the type species of *Clinopegma*. Similarly, *Parancistrolepis* was included only in the *cox1*-based tree and clustered with maximal support with *Thalassoplanes*. The radula of *Parancistrolepis* ([Fig. 13I](#)) shows some similarity to that of *Thalassoplanes* ([Fig. 13E](#)), but differs in the morphology of the central tooth. Therefore, the name Parancistrolepidinae [Habe, 1972](#) (original spelling Parancistrolepisinae) has priority over Ancistrolepidinae [Habe & Sato, 1973](#). The subfamily was raised to family level by [Goryachev \(1987\)](#), who included in it *Brevisiphonia*, *Parancistrolepis* and *Thalassoplanes*.

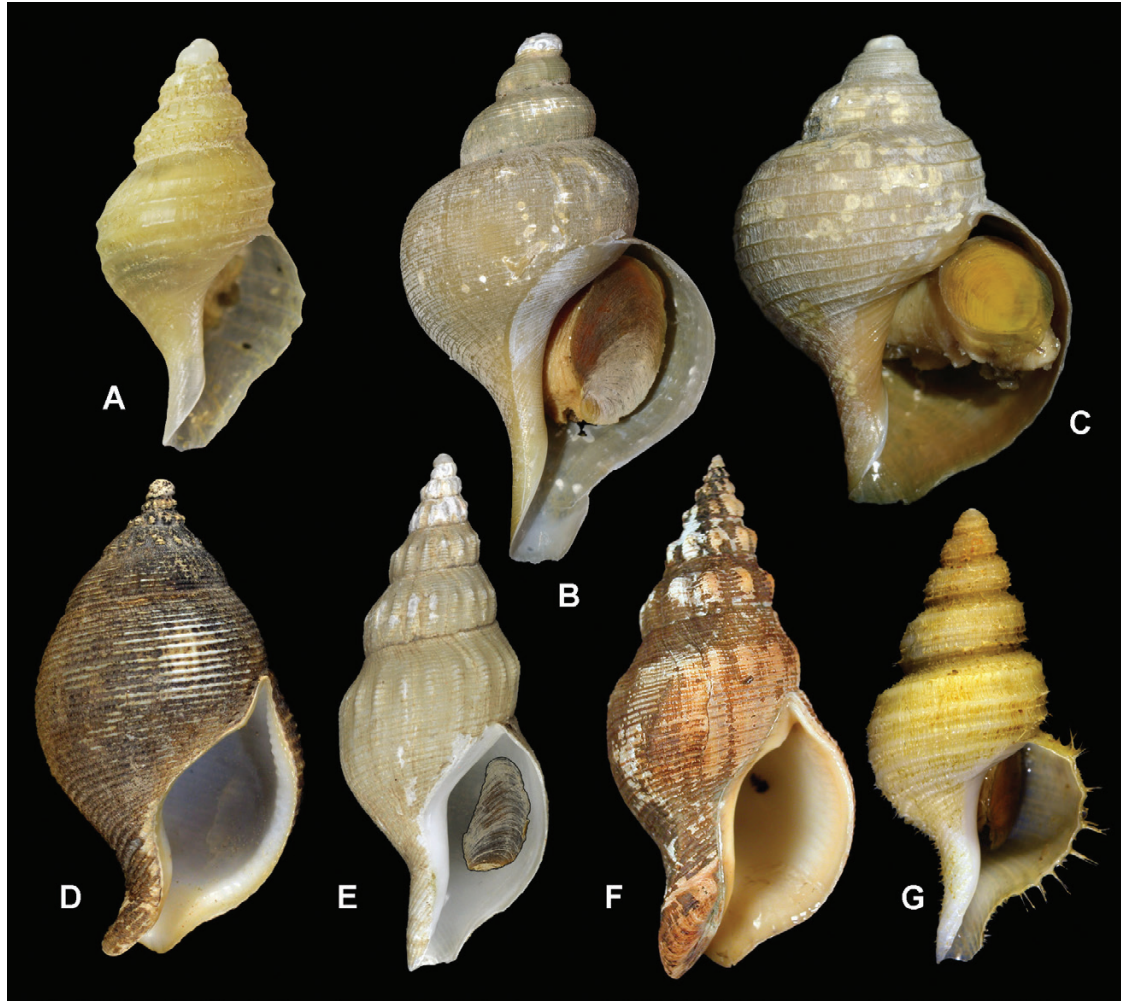
#### SUBFAMILY SIPHONALIINAE FINLAY, 1928 ([FIGS 13, 14](#))

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

**Included genera:**

*Bayerius* [Olsson, 1971](#) (TS *Fusinus fragillissimus* Dall, 1908; OD) <sup>(1)</sup>

[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, *Bathyancistrolepis 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 sequenced for *cox1*. K, *Parancistrolepis fujitai* (Kuroda, 1931), Japan, AORI\_YK#3401, SL 81.4 mm, specimen sequenced for *cox1*. L, *Anomalisiphon virgatus* (Friele, 1879), Spitzbergen, 80°57'N, 47°05'E, Icebraker *Litke st. 22*, 124 m, ZIN, uncatalogued, SL 40.3 mm (radula, see [Fig. 13G](#)). M, *Anomalisiphon verkruzeni* (Kobelt, 1876), Iceland, 67°06'N, 23°14'W, 246 m, MNHN IM-2013-78020, SL 61.5 mm, sequenced specimen. N, *Plicifusus rhyssus* (Dall, 1907), Japan, AORI\_YK#4211, SL 46.7 mm, specimen sequenced for *cox1*. O, '*Colus*' *kujianus* Tiba, 1973, Japan, AORI\_YK#4210, SL 57.7 mm, specimen sequenced for *cox1*. P, *Truncaria filosa* (A.Adams & Reeve, 1850) (holotype of *Cominella brunneocincta* Dall, 1896), Albatross st. 3390, Gulf of Panama, 102 m, USNM 123009, SL 31.5 mm (photo USNM). Q, *Liomesus ovum* (Turton, 1825), Scotland, SL 29.1 mm, Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be).



**Figure 13.** Shells of Siphonaliinae. A, *Pararetifusus tenuis* (Okutani, 1966), off Kesennuma, 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 *et al.*, 2020a, 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.

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

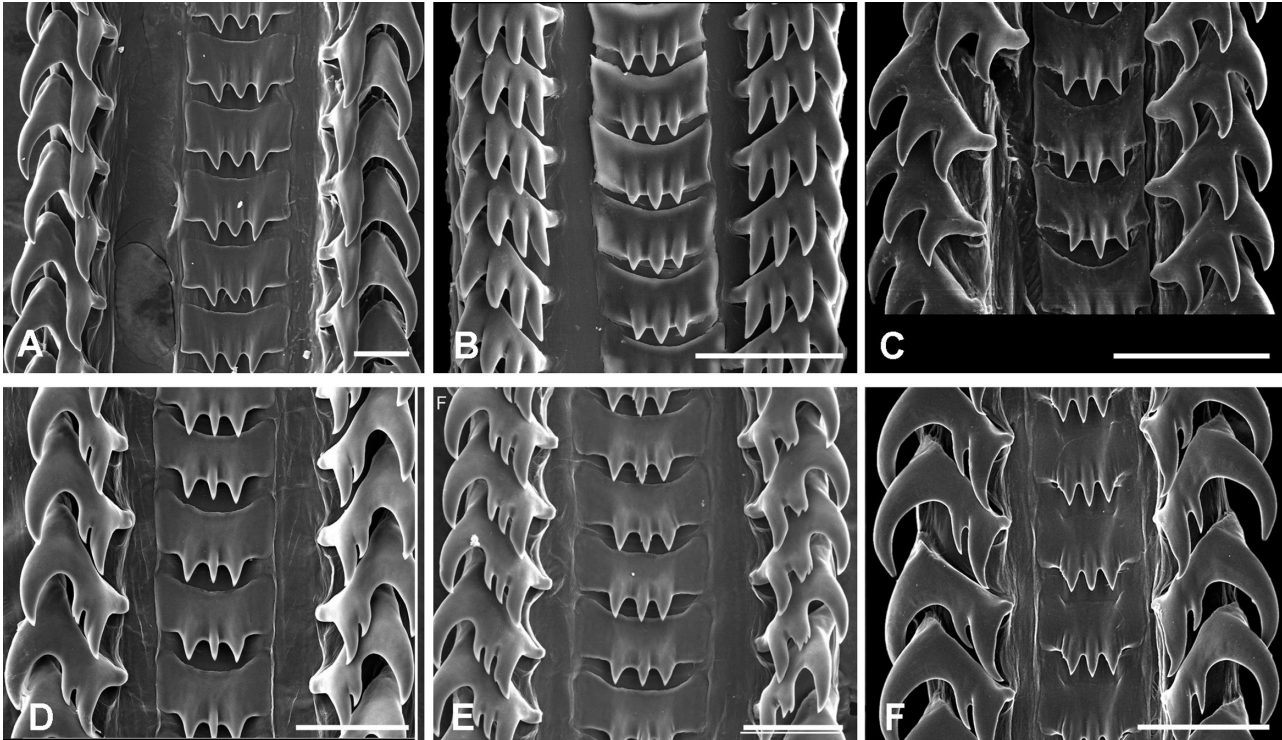
*Mohnia* Friele, 1878 (TS *Fusus mohni* Friele, 1877; M)<sup>(2)</sup>

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

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

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

**Diagnosis:** Shell small (10 mm) to medium-large (over 60 mm), very thin-walled and fragile to robust, oval to broadly fusiform. Protoconch paucispiral, sometimes large and bulbous (*Phaenomenella*), sometimes with small, smooth, initial part, followed by strong axial and spiral sculpture on the upper teleoconch whorls, forming a reticulated pattern (*Mohnia* and *Bayerius*). Whorl outline from evenly, gently or strongly convex, to distinctly shouldered. Spiral sculpture always present, of uniform or unequal spiral cords.



**Figure 14.** Radulae of Siphonaliinae. 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 *et al.*, 2020a: 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.

Axial sculpture present at least on upper whorls in *Phaenomenella* and *Siphonalia*, represented by low, rounded ribs, stronger on earlier whorls, on later whorls more pronounced at shoulder. Aperture wide to very wide. Siphonal canal short to moderately long, often bent abaxially. Operculum from oval paucispiral to elongate with terminal nucleus.

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

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

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

Based on the sequences of three genes (*cox1*, 16S, and *H3*) *Japeuthria ferrea* is here confidently placed in the subfamily (Supporting Information, Fig. S2), where it is recovered in a sister-position to all other taxa. These taxa, in turn, form two maximally supported clades: one uniting representatives of *Siphonalia* and *Phaenomenella*, and the other all remaining genera. The affinity of *Japeuthria* and *Siphonalia* has previously been proposed by Hayashi (2005) based on the analysis of a 1.3 Kb fragment of 16S rRNA, while the close relationship of *Mohnia dalli*,

*Pararetifusus* and *Bayerius* to the genera *Siphonalia* and *Phaenomenella* was shown and briefly discussed in Kantor *et al.* (2020b).

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

#### UNASSIGNED BUCCINIDAE

In our multigene analysis, type species of *Anomalisipho*, *A. verkruezeni*, constitutes its own branch, while in the *cox1*-based tree it clusters together with *Plicifusus rhyssus* (Dall, 1907) and '*Colus*' *kujianus* Tiba, 1973 with maximal support (Supporting Information, Fig. S1). Due to limited material we abstain from taking a taxonomic decision at the moment, but these genera may constitute a separate subfamily.

*ANOMALISIPHO* DAUTZENBERG & H. FISCHER, 1912  
(*TS SIPHO VERKRUEZENI* KOBELT, 1876; OD)<sup>(1)</sup>

(FIGS 11G, 12L, M)

*Remarks:* The type species of *Anomalisipho* from the subtidal depths of the northern Atlantic is included in the analysis and ends up isolated in the tree, forming a long branch sister to *Buccinum*, albeit without support. The radula of *Anomalisipho virgata* (Friele, 1879) (Fig. 11G), a morphologically similar species, is similar to the radulae encountered in different genera, e.g. *Ancistrolepis*, *Aulacofusus*, *Buccinum*, *Clinopegma* and others, and thus does not clarify the position of the genus. The operculum, with terminal nucleus, differs from the operculum of Buccininae with subcentral nucleus, and speaks against including *Anomalisipho* in that subfamily. In the expectation of additional data, we refrain from allocating *Anomalisipho* to any subfamily.

*PLICIFUSUS* DALL, 1902 (*TS FUSUS KROEYERI*  
MØLLER, 1842; OD)<sup>(1)</sup>

(FIG. 12N)

*Remarks:* The single species, *P. rhyssus* (Dall, 1907) was included in *cox1*-based analysis and clusters together with *Anomalisipho verkruezeni* and '*Colus*' *kujianus* Tiba, 1973. *Plicifusus* is a species-rich

and morphologically variable genus, including about dozen of species, and is distributed in the Arctic and North Pacific (Kosyan & Kantor, 2012). Its radula is similar to that of *Anomalisipho*. '*Colus*' *kujianus*, according to our tree, clearly does not belong to *Colus*. In shell characters (Fig. 12O) it resembles both *Plicifusus* (Fig. 12N) and *Anomalisipho*. Its generic placement is not defined yet pending the results of multigene analysis.

#### BUCCINIDAE INCERTAE SEDIS

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

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

SUBFAMILY LIOMESINAE P. FISCHER, 1884

(FIG. 12Q)

= 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 subrectangular central tooth and unicuspidate lateral ones. This morphology is 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*.

## SUBFAMILY TRUNCARIINAE COSSMANN, 1901

(FIG. 12P)

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

*Remarks:* The anatomy and radula of the type (and only included) genus remains unstudied (Olsson, 1971) and molecular data are lacking as well. The peculiar shell shape (Fig. 12P) does not provide any clue on the possible relationships of *Truncaria*, and even its position within Buccinidae remains to be confirmed.

## FAMILY FASCIOLARIIDAE GRAY, 1853

## SUBFAMILY FASCIOLARIINAE GRAY, 1853

*Type genus: Fasciolaria* Lamarck, 1799 (TS *Murex tulipa* Linnaeus, 1758; M)

= Latiridae Iredale, 1929. Type genus *Latirus* Montfort, 1810 (TS *Latirus aurantiacus* Montfort, 1810; OD).

## SUBFAMILY FUSININAE WRIGLEY, 1927

*Type genus: Fusinus* Rafinesque, 1815 [TS *Murex colus* Linnaeus, 1758; by typification of replaced name (*Fusus* Bruguière, 1789)]

= Fusinae Swainson, 1840 (inv.). Type genus: *Fusus* Bruguière, 1789 (inv.) (TS *Murex colus* Linnaeus, 1758; by subsequent monotypy, Lamarck, 1799)

= Cyrtulidae MacDonald, 1869. Type genus: *Cyrtulus* Hinds, 1843 (TS *Cyrtulus serotinus* Hinds, 1843; M)

## SUBFAMILY PERISTERIINAE TRYON, 1880

*Type genus: Peristernia* Mörch, 1852 (TS *Turbinella nassatula* Lamarck, 1822; SD, Martens, 1868).

*Remarks:* The five-gene molecular phylogeny of the Fasciolariidae of Couto *et al.* (2016) revealed four major lineages. Three of these cluster together and are generally consistent with the widely accepted subfamilies Peristerniinae, Fasciolariinae and Fusininae [the latter further analysed by Kantor *et al.* (2018)], but with a significantly altered content mostly due to the transfer of several genera from Peristerniinae to the other two subfamilies. The analysis is congruent with that of Couto *et al.* (2016), the results of which are followed here with additions and corrections based on Kantor *et al.* (2018).

Vaux *et al.* (2017) attributed *Pararetifusus* to the Fasciolariidae, based on the erroneous assignment of

*Microfulgur carinatus* Ponder, 1970 to *Pararetifusus*. Our analysis demonstrates that *M. carinatus* belongs to the Fasciolariidae (Fusininae), while *Pararetifusus*, represented in our dataset by its type species *P. tenuis*, belongs to the Buccinidae (Siphonaliinae). The morphology, anatomy and radula of a number of species of Fasciolariidae were recently described in detail by Couto & Simone (2019). For the genus-level taxonomy, see Snyder (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

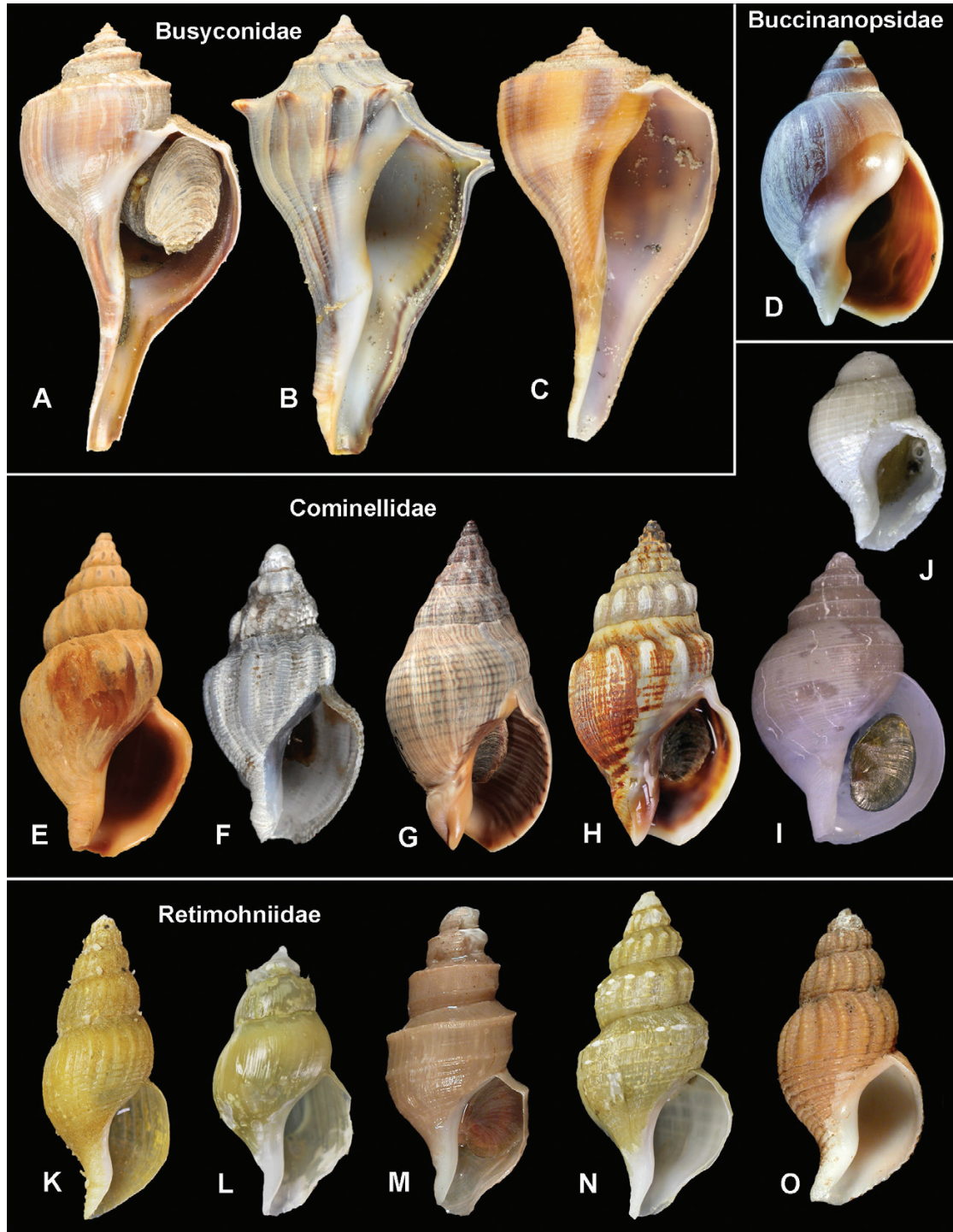
*Type genus: Busycotypus* Wenz, 1943.

*Included genera:*

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

*Fulguopsis* 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 canaliculated. 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



**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, *Fulguroopsis 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,

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 three to five subequal cusps on posterior edge; lateral teeth with three or four 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 the 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 *ET AL.*, 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 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 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 seven to nine cusps decreasing abaxially in size, one prominent cusp, not always the central one. Lateral teeth with three to five 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-planktrophic development.

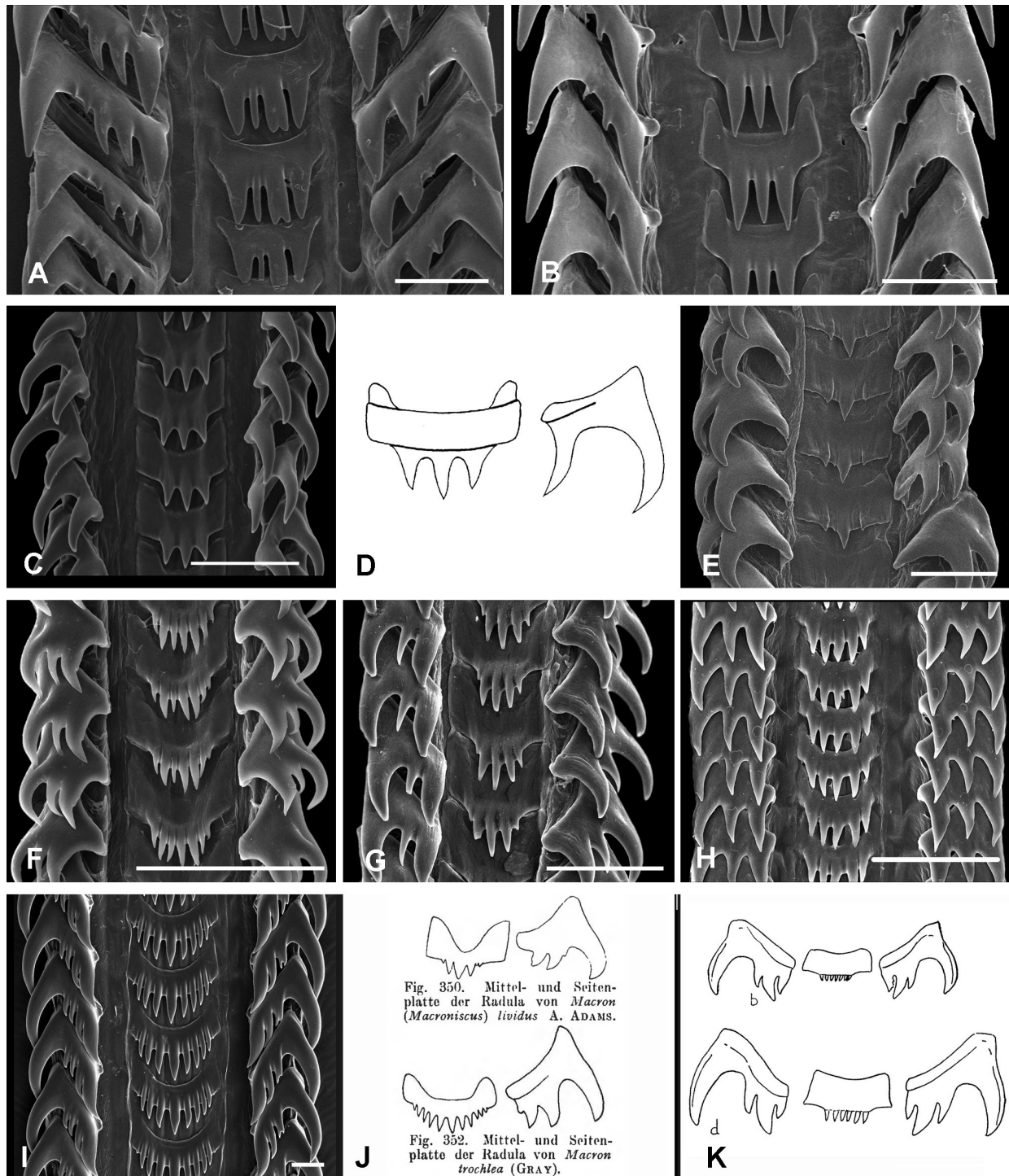
*Distribution:* Temperate waters of South America, intertidal.

*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. However, in our analysis it is sister to *Macron* and together they 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.

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* (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,



*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)

*Lusitromina* Harasewych & Kantor, 2004 (TS *Tromina abyssorum* Lus, 1993, OD) <sup>(2)</sup>; radula, see Harasewych & Kantor (2004)

*Pareuthria* Strebel, 1905 [TS *Fusus plumbeus* Philippi, 1844 [= *Pareuthria fuscata* (Bruguière, 1789)]; SD, Tomlin, 1932] <sup>(1)</sup>

*Parficulina* Powell, 1958 (TS *Notoficula problematica* Powell, 1951, OD) <sup>(2)</sup>; radula, see Powell (1951)

**Diagnosis:** Shell from small (5 mm) to medium-sized (to 75 mm), from broadly ovate to elongate-oval or nearly biconical, with short siphonal canal and often distinct siphonal notch. Protoconch paucispiral. Shoulder from weakly defined to distinct, with concave subsutural ramp. Axial sculpture absent or represented by rounded ribs, strongest on shoulder and whorl periphery. Spiral sculpture absent or composed of cords or striae varying in strength and number per whorl; cancellate sculpture rarely present. Operculum with terminal nucleus or paucispiral.

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

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

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

Only two genera (*Cominella* and *Pareuthria*) were included in our analysis, while three others are included in the family merely based on radular characters. However,

similar radulae with bicuspid lateral teeth and tricuspid central ones are also found in unrelated Buccinoidea (e.g. in *Phos*, Photinae) and the aforementioned genera may in fact belong to other family(-ies).

Kantor & Harasewych (2013) argued that most Antarctic species attributed to *Pareuthria* (Dell, 1990; Numanami, 1996) in fact belong to *Falsimohnia* (confirmed herein to be a Prosiphonidae) and *Strebelia* (suggested herein to be a Prosiphonidae), both restricted to the area of the Antarctic convergence. The position of *Pareuthria turiformis* Egorova, 1982 from the Ross Sea was considered doubtful since its anatomy was not studied and its shell does not resemble any other species of *Pareuthria*. Nevertheless, our molecular analysis confirmed that this species is closely related to *P. fuscata*, the type species of the genus, and thus we confirm the inclusion of *P. turiformis* in *Pareuthria*.

## FAMILY RETIMOHNIIDAE FAM. NOV.

(FIGS 15K–O, 16F–H)

*Type genus:* *Retimohnia* McLean, 1995.

*Included genera:*

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

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

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

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

Radula (Fig. 16F–H). Central tooth with three to six cusps and deeply anteriorly notched basal plate. Lateral teeth with three to five (typically three) cusps. Proboscis short, gland of Leiblein large, valve

*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 1862–1863), 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). Scale bars: A, B, 500 µm; C, 80 µm; E–I, 100 µm.

of Leiblein well developed. Salivary glands moderately developed or large, sometimes fused. Stomach large, with small or moderately large posterior mixing area.

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

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

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

The anatomy of *Retimohnia* and *Retifusus* was recently described by [Kosyan & Kantor \(2014, 2016\)](#).

#### 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 four 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 three cusps. Lateral teeth with three to seven (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:*

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

*Afer* Conrad, 1858 (TS *Murex afer* Gmelin, 1791; by tautonymy) <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)



**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, *Buccinulum*

- 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, 1991b (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, temperate Australasia, 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 *Afer*, *Euthria*, *Euthriostoma* and *Tudicla*.

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 similar to those of *Euthria* and *Buccinulum* ([Fraussen & Hadorn, 2000](#); [Li et al., 2013](#); [Harasewych, 2018](#)), having a characteristic and unique central tooth, leaving no doubt that *Afer*, *Buccinulum* and *Tudicla* belong to the same family. The name Tudicidae Cossmann, 1901 has priority over Buccinulidae [Finlay, 1928](#).

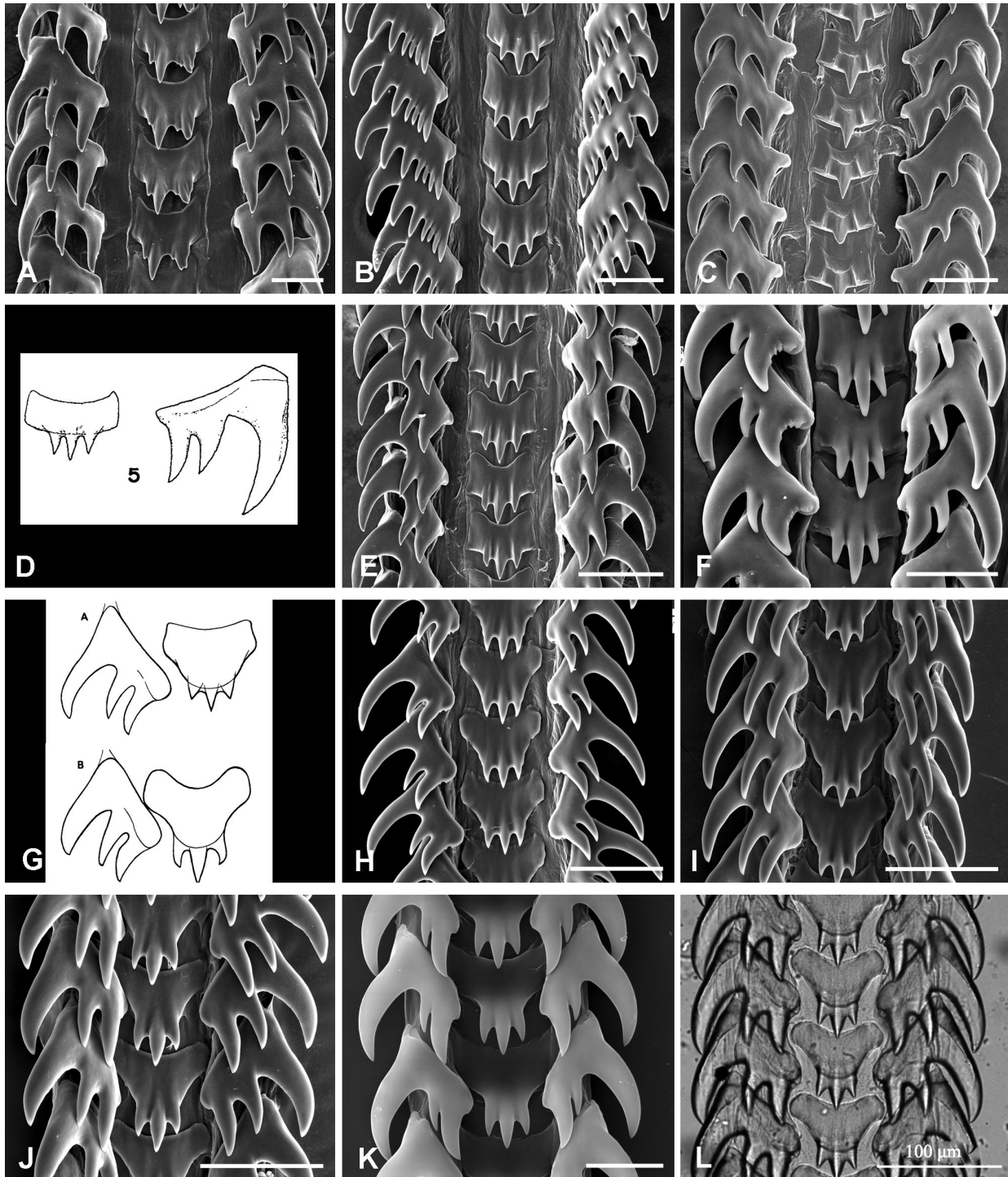
The position of *Africofusus* (TS *Fusus ocellifer* Lamarck, 1816; OD) remains doubtful due to the lack of molecular data and radula description for the type species, which is conchologically rather different from the sequenced *A. africanus* and may be not congeneric. [Vermeij & Snyder \(2018\)](#)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

The extension of the family Tudicidae (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. Tudicidae, as circumscribed herein, includes species from both the Southern and Northern Hemispheres.

The genus *Euthria* in its current scope is conchologically heterogeneous and our analysis did not recover it

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



**Figure 18.** Radulae of Austrosiphonidae (A–F) and Tudicidae (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, MNMZ 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* Harasevych, 1991, northern New Caledonia, 18°59'S, 163°24'E, 320–335 m, MNHN IM-2007–34666 (sequenced

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

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

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

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

*Type genus:* *Melongena* Schumacher, 1817.

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

= Galeodidae Thiele, 1925 (inv.). *Type genus:* *Galeodes* Röding, 1798  
 = Volemidae Winckworth, 1945. *Type genus:* *Volema* Röding, 1798  
 = †Heligmotomidae Adegoke, 1977. *Type genus:* †*Heligmotoma* Mayer-Eymar, 1896.

#### *Included genera:*

*Brunneifusus* Dekkers, 2018 (TS *Murex ternatanus* Gmelin, 1791; OD)<sup>(3)</sup>  
*Hemifusus* Swainson, 1840 (TS *Fusus colosseus* Lamarck, 1822; SD, Gray, 1847)<sup>(1)</sup>  
*Lenifusus* Dekkers, 2018 (TS *Pyrula elongata* Lamarck, 1822; OD)<sup>(3)</sup>  
*Melongena* Schumacher, 1817 [TS *Melongena fasciata* Schumacher, 1817 (= *Murex melongena* Linnaeus, 1758); M]. Synonym: *Galeodes* Röding, 1798 (TS *Murex melongena* Linnaeus, 1758; SD, Dall, 1906)<sup>(1)</sup>  
*Pugilina* Schumacher, 1817 (TS *Murex morio* Linnaeus, 1758; SD, Herrmannsen, 1848). Objective synonym: *Cassidulus* Gray, 1854 (TS *Murex morio* Linnaeus, 1758; M)<sup>(1)</sup>  
*Saginafus* Wenz, 1943 (TS *Fusus pricei* E.A. Smith, 1887; OD)<sup>(3)</sup>  
*Taphon* H. Adams & A. Adams, 1853 (TS *Fusus striatus* G.B. Sowerby I, 1833; M)<sup>(3)</sup>  
*Volegalea* Iredale, 1938 (TS *Volegalea wardiana* Iredale, 1938; OD)<sup>(3)</sup>  
*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 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

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, *Buccinulum linea* (Martyn, 1784), New Zealand, NMNZ. I, *Euthria cornea* (Linnaeus, 1758), Mediterranean, Capri I., IEE uncatalogued. 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.

axial lamellae and cilia. Operculum thick, large, spanning entire aperture, with terminal nucleus.

Radula (Fig. 20A) 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 four 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 lirate, 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 five to nine cusps, sometimes with additional cusplets. Lateral teeth narrow, with long outer cusp, bicuspid or with additional 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 rhynchodaemum. 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 the 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.

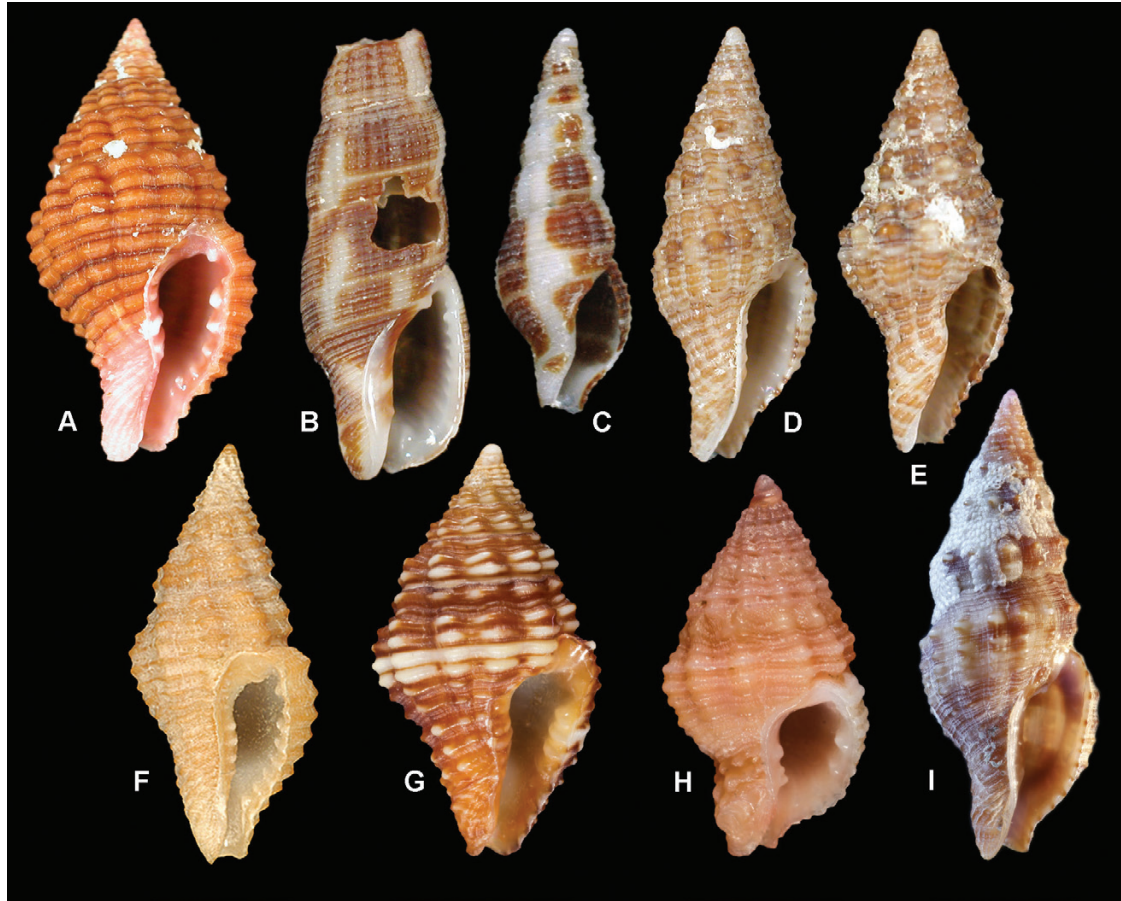
Four additional genera are attributed to Prodotiidae based on their conchological similarity to *Clivipollia* (Ponder, 1972; Fraussen & Stahlschmidt, 2016). It is possible that broader taxonomic sampling of the Pisaniidae will result in the transfer of some other genera and species to the Prodotiidae.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



**Figure 19.** Shells of Prodotiidae (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).

= Donovaniiidae T.L. Casey, 1904. Type genus: *Donovania* Bucquoy *et al.*, 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).

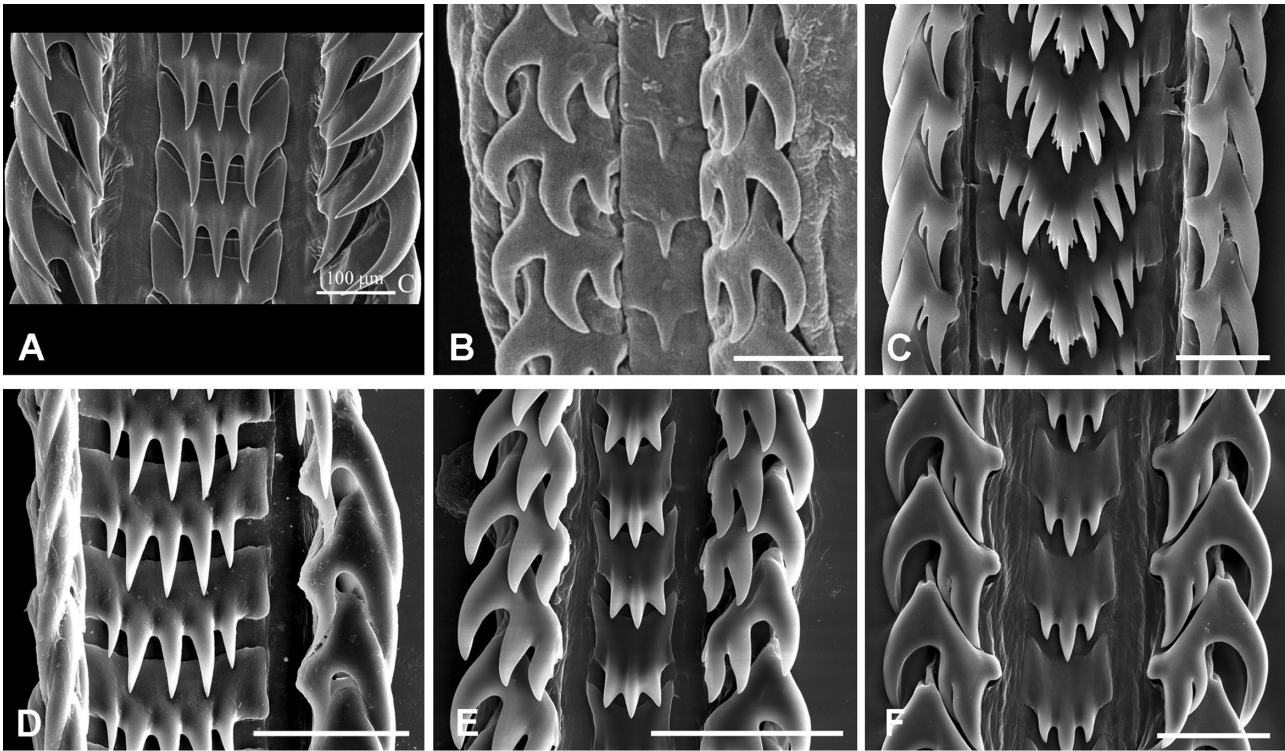
*Included genus:*

*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 *et al.* (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)]<sup>(1)</sup>

*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





**Figure 20.** Radulae of Melongenidae (A), Chauvetiidae (B) and Prodotiidae (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–F, 50 µm.

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 three cusps, inner one shorter.

**Distribution:** Mediterranean and adjacent north-eastern 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.

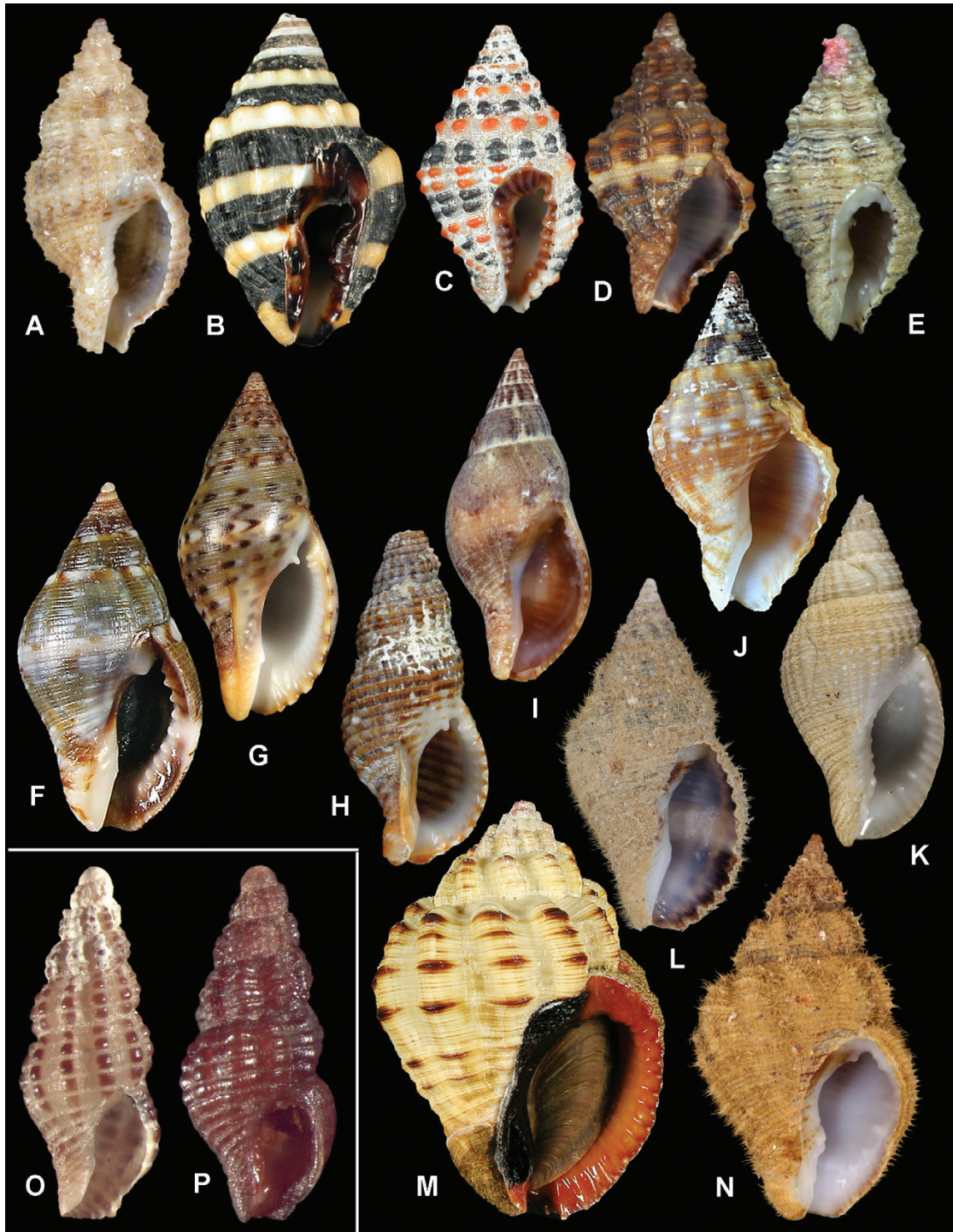
At least one species, *Chauvetia tenuisculpta* (Dautzenberg, 1891), was found parasitizing the sea star *Oreaster clavatus* Müller & Troschel, 1842 (Oliver & Rolán, 2008).

#### 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)]



**Figure 21.** Shells of Pisaniidae (A–N) and Chauvetiidae (O–P). A, *Sinetectula 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

*Included genera:*

- Aplus* De Gregorio, 1885 (TS †*Murex plicatus* Brocchi, 1814; SD, Vokes, 1971)<sup>(1,2)</sup>; see [Aissaoui et al. \(2016\)](#)
- Cancellopolia* [Vermeij & Bouchet, 1998](#) (TS *Cancellopolia 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>
- Polia* Gray, 1834 (TS *Buccinum undosum* Linnaeus, 1758; M)<sup>(1)</sup>
- Sinetectula* [Fraussen & Vermeij, 2021](#) (TS *Buccinum (Polia) farinosum* Gould, 1850; OD)<sup>(1)</sup>

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

spanning entire aperture, assymetrical, drop-shaped, thick, with terminal nucleus.

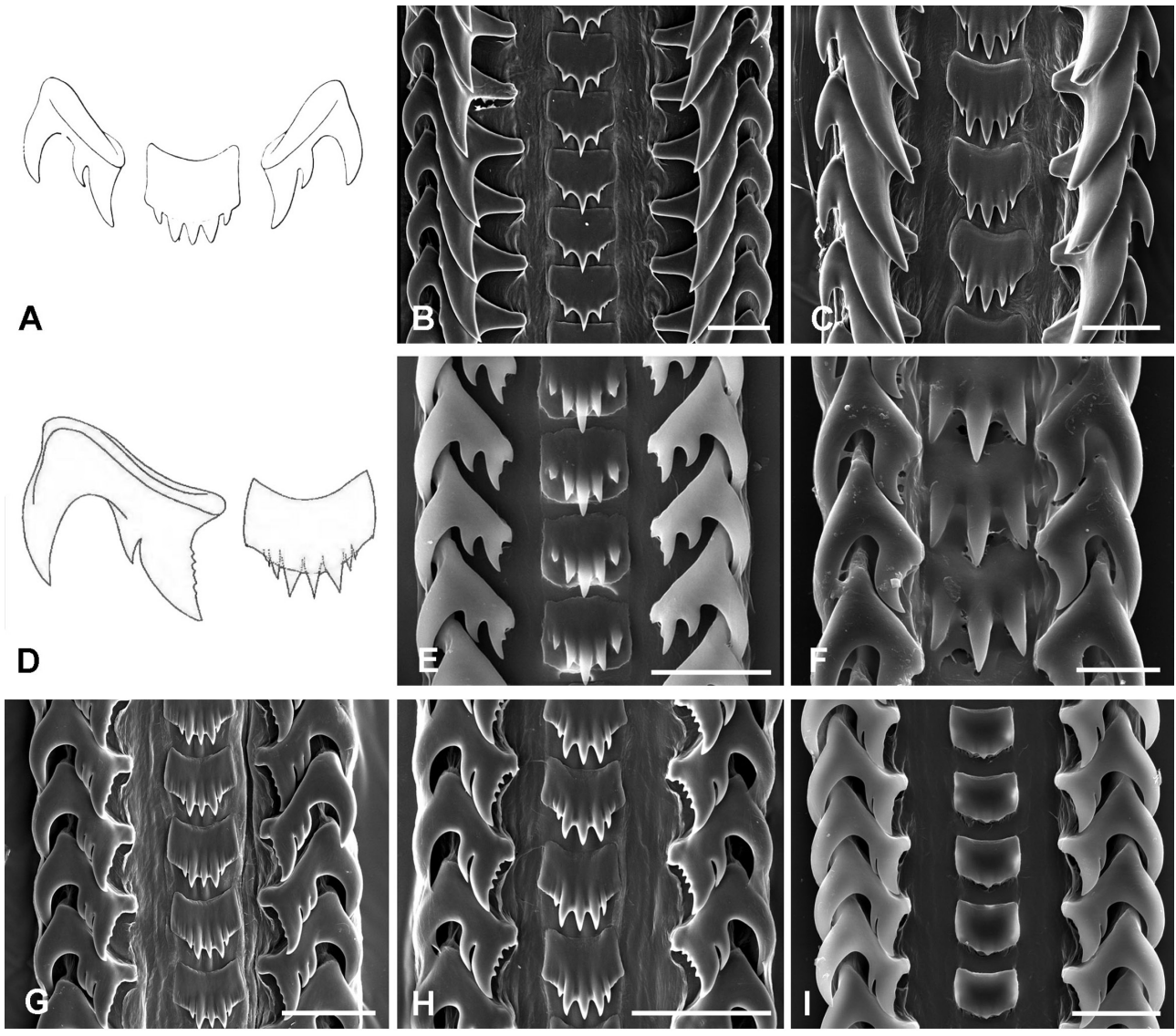
Radula ([Fig. 22](#)) central tooth with relatively narrow, rectangular or trapeziform base, bearing five cusps, outer pair weak, sometimes obsolete ([Fig. 20B](#)). Lateral teeth with two, three (usually) or four cusps, intermediate cusps always smaller, sometimes inner cusp longer ([Fig. 20B, C](#)),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

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

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

Eight of the genera traditionally included in the family were represented in our multigene analysis. The genus-level taxonomy was reviewed by

& Philippe Poppe – [www.conchology.be](http://www.conchology.be). G, '*Pisania pusio* (Linnaeus, 1758), Guadeloupe, SL 34.2 mm, Guido & Philippe Poppe – [www.conchology.be](http://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, *Cancellopolia gracilis* Vermeij & Bouchet, 1998, holotype, New Caledonia, Norfolk Ridge, 435 m, MNHN IM-2000-6329, SL 29.8 mm. L, *Polia fumosa* (Dillwyn, 1817), South Madagascar, 25°28.1'S, 44°56.4'E, 12–14 m, MNHN IM-2009-14575. M, *Cantharus melanostoma* (G.B.Sowerby I, 1825), Philippines, SL 59.2 mm, Guido & Philippe Poppe – [www.conchology.be](http://www.conchology.be). N, *Polia imprimelata* Fraussen & Rosado, 2011, South Madagascar, 24°23'S, 47°32'E, 154–168 m, IM-2009-14603, sequenced specimen. O, *Chauvetia mamillata* (Risso, 1826), Spain, Malaga, 0–5 m, IEE BUC 193, SL 5.5 mm, sequenced specimen. P, *Chauvetia procerula* (Monterosato, 1889), Spain, Malaga, 0–5 m, IEE BUC 210, SL 4.2 mm, sequenced specimen



**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, *Sinetectula 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.

Vermeij (2001) and is mostly followed here, with the exception of several genera transferred to Prodotiidae. In total, 15 valid genera are attributed to the family (see also Table S2).

The family is in need of a revision based on molecular data, since our data reveal the polyphyly of at least *Pisania* and *Engina*; furthermore, some of the genera currently assigned to the family may

belong to Prodotiidae. Three species of '*Pisania*' were included in our multigene analyses, two of them [*Pisania*' *decollata* (G.B.Sowerby I, 1833) and '*P.*' *ignea* (Gmelin, 1791)] cluster together with maximal support, while '*P.*' *pusio* (Linnaeus, 1758) forms a separate branch. In the analysis of the extended *cox1* dataset, *P. striata* (Gmelin, 1791), the type 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. Nevertheless, we can state that the name *Pisania* cannot be applied to any of the species included into our multigene analyses. Instead, *Ecmanis* Gistel, 1848 (nom. nov. pro *Proboscidea* Möller, 1832, non Bruguière, 1791; type species *Buccinum igneum* Gmelin, 1791) is applicable to the clade uniting ‘*P.*’ *decollata* and ‘*P.*’ *igneum*. Based on the characteristic spiral sculpture of broadly spaced strong keels in *P. decollata* (Fig. 21H), Dall (1904) proposed the subgenus *Taeniola* [invalid, non *Taeniola* Pallas, 1760 (Cestoda) = *Taenia* Linnaeus, 1758]. Furthermore, the radula of ‘*P.*’ *decollata* (Fig. 22B) is rather similar to the radula of ‘*P.*’ *fasciculata* (Reeve, 1846) (= *P. montrouzieri* Crosse, 1862) (Fig. 22C), the type species of *Appisania* Thiele, 1929, a name that may be applicable to ‘*P.*’ *decollata*.

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

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

(FIGS 23, 24)

Type genus: *Nassarius* Duméril, 1805.

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

- = Nassinae Swainson, 1835. Type genus: *Nassa* Lamarck, 1799. Invalid: type genus a junior homonym of *Nassa* Röding, 1798 (Gastropoda)
- = Cyclopsidae Chenu, 1859. Type genus: *Cyclops* Montfort, 1810. Invalid: type genus a junior homonym of *Cyclops* O.F.Müller, 1776 (Crustacea)
- = Cyclonassinae Gill, 1871. Type genus: *Cyclonassa* Swainson, 1840
- = Alectrionidae Dall, 1908. Type genus: *Alectrion* Montfort, 1810
- = Arculariidae Iredale, 1915. Type genus: *Arcularia* Link, 1807.

#### Included genera:

- Caesia* H.Adams & A.Adams, 1853 (TS *Nassa perpinguis* Hinds, 1844; SD, Wenz, 1943)<sup>(3)</sup>
- Demoulia* Gray, 1838 (TS *Buccinum retusum* Lamarck, 1822; SD, Herrmannsen, 1847)<sup>(3)</sup>
- Nassarius* Duméril, 1805 (TS *Buccinum arcularia* Linnaeus, 1758; by subsequent monotypy, Froriep, 1806). Synonyms: *Alectrion* Montfort, 1810 (TS *Buccinum papillosum* Linnaeus, 1758; OD); *Arcularia* Link, 1807 (TS *Buccinum gibbosulum* Linnaeus, 1758; SD, Cossmann, 1901b: 215)<sup>(1)</sup>
- Nassodonta* H.Adams, 1867 (TS *Nassodonta insignis* H.Adams, 1867; M)<sup>(1)</sup>
- Naytia* H.Adams and A.Adams, 1853 (TS *Strombus glabratus* G.B.Sowerby II, 1842; SD, Cossmann, 1901)<sup>(1)</sup>
- Phrontis* H.Adams and A.Adams, 1853 (TS *Buccinum tiarula* Kiener, 1841; SD, Cossmann, 1901)<sup>(1)</sup>
- Reticunassa* Iredale, 1936 (TS *Nassa paupera* Gould, 1850; OD)<sup>(1)</sup>
- Tritia* Risso, 1826 (TS *Buccinum reticulatum* Linnaeus, 1758; SD, Gray, 1847). Synonyms: *Nassa* Lamarck, 1799 (non Röding, 1798) (TS *Buccinum mutabile* Linnaeus, 1758; M); *Cyclops* Montfort, 1810 (non O.F.Müller, 1776) (TS *Cyclops asterizans* Montfort, 1810; OD); *Cyclonassa* Swainson, 1840 (TS *Buccinum neriteum* Linnaeus, 1758; M)<sup>(1)</sup>

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

Radula (Fig. 24E) central tooth broadly arcuated, with numerous even-sized cusps. Lateral teeth in most representatives bicuspid, but irregularly multicuspoid in *Hebra* H.Adams & A.Adams, 1853 [considered a synonym of *Nassarius* by Galindo *et al.* (2016)] (Cernohorsky, 1984: figs 43–45). At the inner corner of the lateral teeth a cusplless, irregular, intermediate



**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 fraussenii* 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* (Bruguière, 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,

lateral accessory plate is present in some species (Cernohorsky, 1984: figs 27, 28). Proboscis long, not coiled within rhynchocoel, valve of Leiblein distinct, gland of Leiblein tubular, medium-large. Salivary glands small, not fused. In some species, stomach with a crystalline style [e.g. *Tritia obsoleta* (Say, 1822); see Brown, 1969]. Foot with paired metapodial tentacles.

**Distribution:** Cosmopolitan, except Arctic and Southern Ocean, from intertidal to about 2000 m (Cernohorsky, 1984).

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

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

#### SUBFAMILY BULLIINAE ALLMON, 1990

**Type genus:** *Bullia* Gray, 1833.

**Included genus:**

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

**Diagnosis:** Shell from medium-sized to medium-large,

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

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

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

#### SUBFAMILY ANENTOMINAE STRONG *ET AL.*, 2017

**Type genus:** *Anentome* Cossmann, 1901.

**Included genera:**

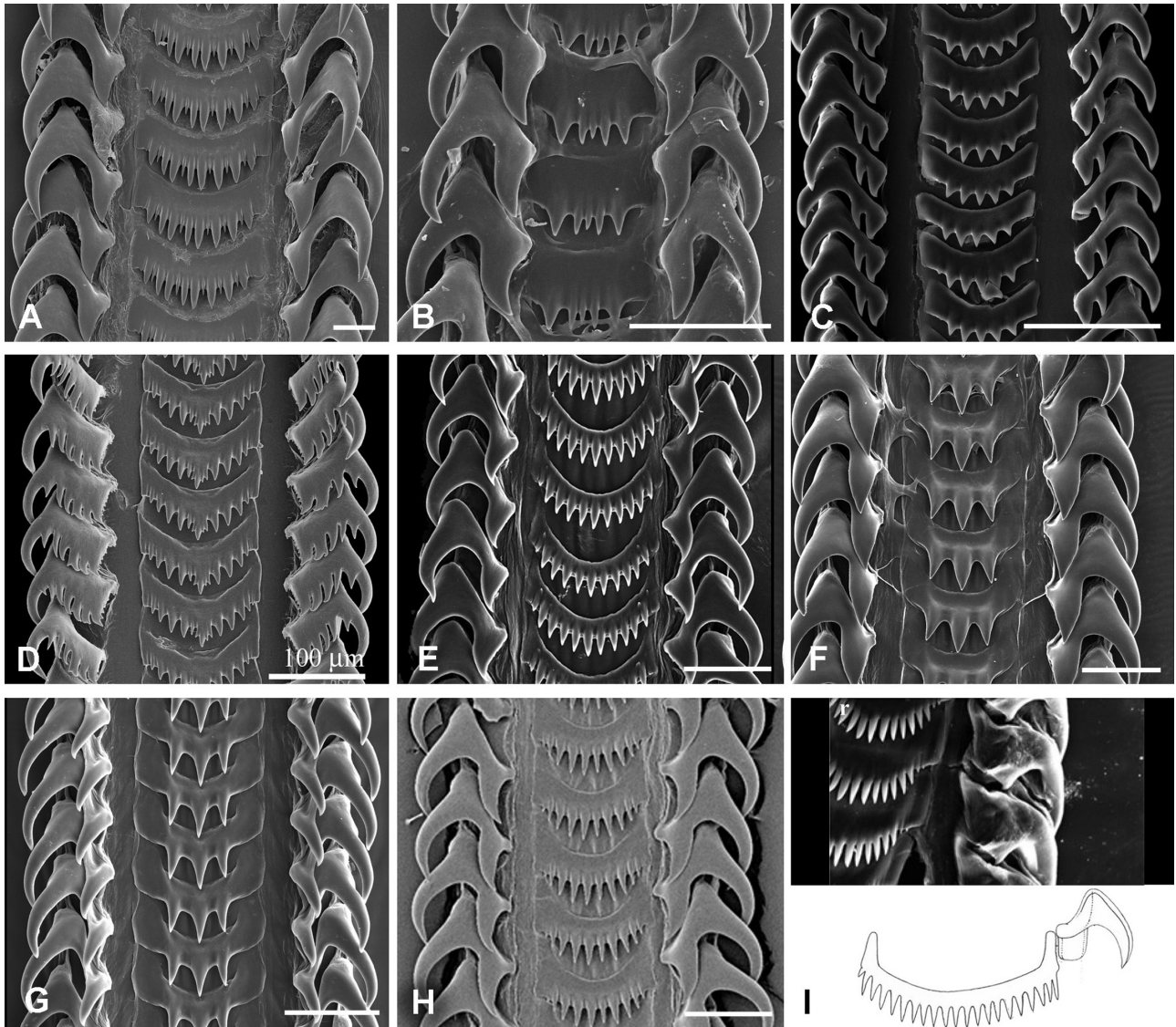
*Anentome* Cossmann, 1901 {TS *Melania helena* von dem Busch, 1847; by typification of replaced name [*Canidia* H. Adams, 1862 non J. Thomson, 1857 (Coleoptera)]<sup>(1)</sup>

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

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

**Diagnosis:** Shell medium-sized, variable in shape, from nearly oval to fusiform, without siphonal canal and with distinct siphonal notch. Spire from medium-high to high. Axial sculpture usually present, of distinct sigmoidal ribs, absent in *Clea*.

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



**Figure 24.** Radulae of Nassariidae. A, *Tomlinia frausseni* 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. E, *Oligohalinophila dorri* (Wattebled, 1886), Vietnam (after Kantor & Kilburn, 2001: fig. 18). F, *Tritia reticulata* (Linnaeus, 1758), Black Sea, Gelendzhik, IEE uncatologued. G, *Northia pristis* (Deshayes, 1844), Panama, Venado I., intertidal, IEE BUC YK1 (shell, see Fig. 21M). H, *Phos senticosus* (Linnaeus, 1758), Papua New Guinea, Laing Id., intertidal, IEE uncatologued, SL 33.5 mm (shell, see Fig. 21L). I, *Engoniophos unicinctus* (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.

Spiral sculpture of distinct, albeit low, cords, present at least on shell base, often on entire shell surface. Aperture smooth inside. Operculum large, with terminal nucleus, with simple edges, in *Anentome* with thickened, pointed, elevated process behind

nucleus.

Radula (Fig. 24C, D) variable, either with arcuated central tooth with five to seven medium-sized or small cusps (*Clea*, *Anentome*) and tricuspid lateral teeth, outer cusp largest; or with central tooth with about ten



cusps (*Oligohalinophila*, Fig. 24D) and multicuspid lateral teeth with six or seven cusps, innermost serrated along inner edge. Proboscis medium to long, numerous proboscis retractors forming bundles attached laterally to mid-rhynchodaeum, in *Anentome* with large additional paired retractors at base of rhynchodaeum. Valve of Leiblein distinct, gland of Leiblein absent. Stomach with long posterior mixing area and closely spaced ducts of digestive gland (anatomy after Strong *et al.*, 2017). Foot metapodial tentacles absent.

*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* (Bruguière, 1789)]; OD].  
Synonym: *Duplicata* Korobokov, 1955 (TS *Buccinum duplicatum* J.deC.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 about two whorls. Axial sculpture present on adapical spire whorls, vanishing on last whorls, of broad folds, rounded on top, spiral sculpture absent. Aperture weakly lirate 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* (Bruguière, 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, lirate 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 single tentacle. Head tentacles long with eyes situated at mid-length on poorly defined lobes. Proboscis long, usually not coiled within rhynchocoel, partially coiled in *Northia*. Proboscis retractors lateral, either a single pair or several on each side, detached from rhynchodaeum at mid-length. Valve of Leiblein distinct, gland of Leiblein tubular, not large, with long constricted duct. Salivary glands small, fused (*Phos*) or separate (*Engoniophos*, *Northia*), salivary ducts thin. Stomach (*Phos* and *Northia*) small, broadly U-shaped with small posterior mixing area.

*Distribution.* Tropical Atlantic and Indo Pacific, subtidal.

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

## SUBFAMILY TOMLININAE SUBFAM. NOV.

Type genus: *Tomlinia* Peile, 1937.

Included genera:

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

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

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

**Diagnosis:** Shell medium-large, reaching 50 mm, fusiform to broad-fusiform or nearly oval, with medium to high spire and from obsolete to short siphonal canal, with distinct siphonal notch, siphonal canal can be closed (*Trajana*). Protoconch small, paucispiral, off 1.5–3.0 whorls. Axial sculpture of strong and closely spaced, sometimes sharp, ribs, absent in *Tomlinia*. In addition to ribs periodical varices can be present. Spiral sculpture normally distinct on entire shell, but only on shell base in *Tomlinia*. Aperture medium to high, from narrow to broad. Outer lip lirate in *Nassaria* and *Trajana*, smooth in *Tomlinia*. Columella smooth or with low denticles. Operculum oval, with terminal nucleus, sometimes with serrated edge.

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

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

**Remarks:** This subfamily unites rather heterogeneous genera. While *Nassaria* lives subtidally to over 900 m throughout the Indo-Pacific, *Tomlinia* is one of a few genera of Buccinoidea that penetrate estuarine and fresh waters in South-East Asia. *Nassaria* and *Trajana* on one hand, and *Tomlinia* on the other, are conchologically markedly different. This clade with high support in our analysis was also recovered by Galindo *et al.* (2016) (albeit without support) as sister to *Cyllene* and included by them in the subfamily Cylleninae. In our analysis it is recovered, albeit without support, as a sister to the clade (*Cyllene*: Columbelloidea). We have chosen to form the name of the subfamily based on the genus *Tomlinia* to avoid the confusion of having two family group names based on the genera *Nassarius* and *Nassaria*.

## SUBFAMILY CYLLENINAE BELLARDI, 1882

Type genus: *Cyllene* Gray, 1834.

Included genera:

*Cyllene* Gray, 1834 (TS *Cyllene owenii* Gray, 1834; M) <sup>(1)</sup>  
*Neoterion* Pilsbry & Lowe, 1932 (TS *Hindsia ariel* Pilsbry & Lowe, 1932; M) <sup>(2)</sup>; radula, see D'Attilio (1981)

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

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

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

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

## FAMILY COLUMBELLIDAE SWAINSON, 1840

= Anachidae Golikov & Starobogatov, 1972. Type genus: *Anachis* H.Adams & A.Adams, 1853 (TS *Columbella scalarina* G.B. Sowerby I, 1832; SD, Tate, 1868)

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

## SUBFAMILY COLUMBELLINAE SWAINSON, 1840

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

## SUBFAMILY ATILIINAE COSSMANN, 1901

*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. (TS *Columbella scalarina* G.B.Sowerby I, 1832; SD, Tate, 1868).

*Remarks:* Columbelloidea is a species-rich 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 narrow base and three to five 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 ten small cusps ([Guralnick & deMaitenon, 1997](#)).

## UNNASSIGNED BUCCINOIDEA

*MACRON* H.ADAMS & A.ADAMS, 1853 (TS *BUCCINUM AETHIOPS* REEVE, 1847; M)

*Remarks:* The position of *Macron* has been debated for a 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* and *M. aethiops* (Reeve, 1847) [as *M. trochlea* (Gray, 1839)] (herein, [Fig. 16J](#)) and transferred it to Buccinidae. The placement proposed by Thiele was followed by some authors (e.g. Wenz, 1938–44; [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 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 different from *Buccinanops* and we thus 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

The soft body morphology of the Buccinoidea studied herein is rather uniform. Some families are characterized by specific characters, e.g. the 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 Buccininae) or a paucispiral one are present, the latter found in several unrelated groups (some Dolicholatiridae, some Cominellidae, some Siphonaliinae, Retimohniidae and some Prosiphonidae). Nevertheless, within Buccinidae the opercular morphology seems to be a reliable diagnostic character for subfamily-level taxa: in Beringiinae, the operculum closes entirely the aperture with a terminal nucleus strongly shifted adaxially; in Buccininae, the operculum is concentric, while in Volutopsiinae the operculum, with a nucleus strongly shifted adaxially, is small in comparison to the large aperture; in Neptuneinae, the operculum is large, drop-shaped, closing nearly entirely the aperture, with terminal nucleus shifted adaxially.

The digestive tract is rather uniform with regard to its main components: anterior foregut, containing proboscis, salivary glands, valve and gland of Leiblein and mid-gut (stomach). Accessory salivary glands are absent in all Buccinoidea. The proboscis is long to very long, the valve of Leiblein is usually present (absent in some Colubrariidae, all Melongenidae, and in the buccinid subfamily Volutopsiinae). The presence of the gland of Leiblein is usually correlated with the presence of the valve of Leiblein, although the gland can be absent even when the valve is still recognizable, although reduced (some Colubrariidae, Neptuneinae of Buccinidae and Anentominae of Nassariidae). The salivary glands are paired (and can be fused), acinous and the salivary ducts usually follow freely along the oesophagus, but they can enter the walls of the oesophagus shortly after leaving the glands (Belomitridae, Colubrariidae and Tudicliidae). Beyond these shared traits, some families have a

distinctive digestive system, e.g. Colubrariidae with an extremely long and thin proboscis coiled within the rhynchodaeum, an extended mid-oesophagus without traces of gland and valve of Leiblein, and, finally, a uniquely shaped stomach in which the intestine is opening posterior to the oesophagus.

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

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

In the most common radula type of Buccinoidea, found in many unrelated lineages, the central tooth with a rectangular base bears three to six cusps, and the lateral teeth are moderately multicuspid (three to six cusps), with the outer cusp longest. Such radulae are recorded in Austrosiphonidae, Buccinidae (Buccininae, Neptuninae, some Parancistrolepidinae), Busyconidae, Retimohniidae, some Nassariidae, Prodottiidae and some Prosiphonidae (e.g. *Neobuccinum* and *Chlanidota*). A peculiar shape of the lateral teeth is found in some genera of Prosiphonidae and in the unrelated Chauvetiidae. There, the outer portion of the basal plate is long, narrow and attenuated, forming a 'handle' (Figs 9F–I, 20B). In many cases, the rows of teeth are strongly overlapping and this attenuated portion is seen only in oblique view. The number of cusps on the lateral teeth is not correlated with the presence of the handle, nor is the central tooth morphology. The latter can be well developed, with squarish base and well-developed cusp(s) (e.g. some *Prosipho*, see: Numanami, 1996; *Argeneuthria*, Fig. 9G, H herein, both Prosiphonidae; or *Chauvetia*, Fig. 20B, Chauvetiidae), it can be reduced to a single obtuse cusp (e.g. *Antistreptus*, Prosiphonidae, Fig. 9I) or it can altogether be absent [*Meteuthria martensi* (Strebel, 1905); *Pastorino*, 2016].

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

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

Opposite examples are also numerous. The family Prosiphonidae exhibits the most diverse array of radulae of any buccinoideans (Fig. 9). Our tree includes sequenced representatives possessing at least three different radula types, which Powell (1951) thought were characterizing families/subfamilies. However, our data demonstrate that radula morphology of Prosiphonidae is not correlated with the evolutionary history of the group. Likewise, in Buccinidae the disparity of radula morphology is high, with some

subfamilies characterized by a rather specific morphology, e.g. Beringiinae with strongly modified lateral teeth and acuspate central teeth (Fig. 11C) and Volutopsiinae with always bicuspid lateral teeth (Fig. 11H) (Kantor, 1990). Nassariidae also exhibit a high disparity of radular morphology (Fig. 24) with multicupid vs. tricuspid central tooth found in the same subfamily Photinae (Fig. 24F–H).

Summing up, we conclude that, with the exception of some families, the rather uniform radular morphology alone does not allow the allocation of genera to a particular family without additional molecular data. The radula remains a valuable taxonomic character in 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 comment 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, 1991a; 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.*, 2011). Then, starting 3.5 Mya, when the Bering Strait opened, not only the northern Pacific fauna migrated to 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, 1991a).

Two buccinoidean families reached the Arctic: Colidae and Buccinidae, the latter represented in the Arctic by members of four subfamilies: Beringiinae, Buccininae, Neptuneinae 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. Despite none of these species

was included in the multigene phylogeny, '*Colus kujianus*' was present in the extended COI dataset, and showed no affinity to the true *Colus*, but instead fell in the *Anomalisipho* subclade of Buccinidae. Based on the examination of Miocene and Pliocene fossil material, Vermeij (1991) concluded that *Colus* is a genus that originated in the Atlantic. In the light of our results, it is doubtful that there are any species of *Colus*, descending from the cross-Arctic invasion and at present specific to North Pacific. Likewise, conspecificity of the Pacific and Atlantic populations of *Colus islandicus* remains to be confirmed.

The situation is opposite in the Buccinidae. Among the 44 species of Buccinidae (as redefined herein) included in the multigene and extended *cox1* analyses, 35 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 the 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 & Crame (1989: 264) have 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 the Paleocene and Eocene time: Trochidae, Naticidae, Conoidea and, above all, Buccinoidea (*sensu lato*)'. However, as suggested by Beu (2009), composition of buccinid fauna of Antarctica as per Early Eocene was a result of an earlier faunal change. In this change, in particular, larger forms referred by Beu to Busyconidae and Melongenidae (Beu, 2009), which were worldwide distributed in the Mesozoic and Palaeocene gradually declined in abundance. Previous studies by Vaux & co-authors (2017, 2018) and our present results identify at least three lineages of Buccinoidea that have independently originated in, or colonized, the Antarctic: the Austrosiphonidae, Cominellidae and Prosiphonidae.

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

Cominellidae are represented in our dataset by *Pareuthria turriiformis* from the Antarctic and *P. fuscata* from Patagonia, whereas most species of *Cominella* inhabit the temperate Australasian region ([Donald et al., 2015](#)). [Vaux et al.](#) dated the diversification of the *Cominella* crown group at ~55 Mya, and [Beu \(2009\)](#) mentioned that *Pareuthria* (representing another subclade of Cominellidae in our tree) was among the genera present in the Antarctic fauna by the Eocene. This suggests that Cominellidae, as circumscribed herein, originated in the Cretaceous–Palaeocene, and the distribution of recent members of the family, as in Prosiphonidae, does not reject an origin on continental shelves and slopes bordering the Southern Ocean.

The family Austrosiphonidae is mainly represented by Australasian taxa but, based on the analysis of [Vaux et al. \(2018\)](#), it includes the Antarctic *Antarctoneptunea aurora* and, based on our data, also *Serratifusus lineatus* from the Norfolk Ridge off New Caledonia. The evolutionary history of this group is discussed in detail by [Vaux et al. \(2017\)](#), and the inferred origin of its temperate water subclade (~78 Mya) predates the Cretaceous–Palaeogene boundary. The distribution of the recent members of this clade (including the species of *Serratifusus* reaching subtropical latitudes) is also consistent with an origin of this lineage in the Southern Ocean.

The hypothesis of a Southern Hemisphere origin of the entire Austrosiphonidae–Tudicidae clade needs to be revisited in the light of the new phylogenetic hypotheses obtained in the present study. [Vaux et al. \(2017\)](#) recovered the genera *Aeneator*, *Antarctoneptunea*, *Buccinulum*, *Kelletia* and *Penion* as a single clade, with an estimated origin at ~116 Mya in the Aptian–Albian. The recent species of the former three genera inhabit southern temperate or polar waters, whereas *Kelletia* by the Early Miocene had extended its distribution to the Northern Hemisphere ([Hayashi, 2005](#)) and its living species occur in the north-eastern and north-western Pacific. Nevertheless, [Vaux et al. \(2017\)](#) noted the possible

paraphyly of this group in relation to some Northern Hemisphere buccinoidean lineage(s). Our results confirm this suspicion and change the concept of Buccinulidae, in particular by demonstrating a close affinity of the *Buccinulum*–*Aeneator* subclade of the former Buccinulidae to the East African *Afer*, Indian *Tudicla* and widely distributed *Euthria*. However, the taxa from temperate Australia (*Tasmeuthria clarkei*) and the Norfolk Ridge (three species formerly placed in *Euthria*) are sister to the rest of the Tudicidae. Thus, if we accept an origin of the Austrosiphonidae–Tudicidae clade in the Southern Ocean, in the most parsimonious scenario, one northward dispersal event for the *Afer*–*Tudicla*–*Euthria* lineage (see the *cox1* tree in the [Supporting Information, Fig. S1](#)) is required to explain the current distribution of the Tudicidae. If we hypothesize that the family has originated elsewhere, three independent southward dispersals are required: for the ancestral Austrosiphonidae, for *Tasmeuthria* and for the *Aeneator*–*Buccinulum* subclade of the Tudicidae. The first scenario certainly seems more plausible. The northwards dispersal of *Afer*–*Tudicla*–*Euthria* might have been a ‘hitchhike’ with the concurrent drift of the Indian plate, with subsequent spread of taxa to the Tethys, temperate Pacific and East Africa, or could have proceeded along the eastern continental shelf of Africa. As remarked by [Vaux et al. \(2017\)](#), also based on previous conclusions ([Donald et al., 2015](#)), the Southern Hemisphere whelk lineages have non-planktotrophic larval development (except probably *Austrofusus*), thus implying limited dispersal abilities in timeframes of one or few generations, but range shifts happen over millions of years.

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

#### FUTURE WORK

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

## ACKNOWLEDGEMENTS

A large part of the molecular material in this paper originates from various shore-based expeditions and deep-sea cruises, conducted, respectively, by MNHN and Pro-Natura International (PNI) as part of the *Our Planet Reviewed* programme, and by MNHN and Institut de Recherche pour le Développement (IRD) as part of the *Tropical Deep-Sea Benthos* programme (in alphabetic order): ATIMO VATAE, AURORA 2007, BIOPAPUA, BOA1, CONCALIS, CORSICABENTHOS1, DongSha 2014, EBISCO, GUYANE 2014, ILES DU SALUT, INHACA 2011, KANACONO, KARUBENTHOS 2012, KARUBENTHOS 2, KAVALAN 2018, KOUMAC 2.1, MADIBENTHOS, MAINBAZA, MIRIKY, NanHai 2014, NORFOLK 2, PANGLAO 2004, PANGLAO 2005, PAPUA NIUGINI, SALOMON 2, SALOMONBOA 3, SANTO 2006, TAIWAN 2004, TARASOC, TERRASSES, Tuhaa Pae 2013, ZhongSha 2015. Funders, sponsors and partners include the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, Richard Lounsbery Foundation, and the Philippines Bureau of Fisheries and Aquatic Resources (BFAR). We thank, among others, Virginie Héros, Philippe Maestrati, Barbara Buge and Ellen Strong for their role in specimen processing during the expeditions and in MNHN.

We are thankful to our colleagues who collected or made available to us key material from different parts of the world, particularly Stefano Schiaparelli (Italian National Antarctic Museum, Genova, Italy), Enrico Schwabe (Bavarian State Collection of Zoology, Munich, Germany), Serge Gofas (Universidad de Málaga, Spain), Christiane Delongueville and Roland Scaillet (Brussels, Belgium), Jónbjörn Pálsson and Steinunn Hilma Ólafsdóttir (Marine and Freshwater Research Institute, Hafnarfjörður, Iceland), Marco Oliverio (Sapienza University, Rome, Italy), Douglas Eernisse (California State University, Fullerton, USA), Francesco Criscione (Australian Museum, Sydney, Australia), Ivan Nekhaev (Saint Petersburg University, Russia). Felix Vaux shared with us molecular data on New Zealand and Australian species, Bruce Marshall assisted with the specimens and photographs from NMNZ. S. Zvonareva and E. Mekhova (IEEE) assisted in collection of material in Vietnam and helped with photography.

Material from Japanese waters were collected during cruises with the research vessels *Shinsei-maru*, *Tansei-maru* and *Nagasaki-maru*; our special thanks go to Kazuhiro Kogure, Shigeaki Kojima, Toshi Nagata (AORI) and Jun Hashimoto (Nagasaki University) for organizing the cruises, and to Hiroaki Fukumori, Genki Ishiyama (AORI) and Tsuyoshi Takano (Meguro Parasitological Museum, Japan) for sorting and processing the specimens. Material from the abyssal depth in Kuril-Kamchatka Trench was collected

mostly during the Joint German-Russian research cruise KuramBio I on R/V *Sonne* in 2012 (cruise leaders Angelika Brandt and Marina V. Malyutina).

We thank Guido Pastorino, M. G. Harasewych, Daniel Abbate and Scott Johnson who kindly provided photos of radulae and shells; Guido and Philippe Poppe for photographs of shells; Koen Fraussen and Martin A. Snyder for help in identification; and Alan Beu for his valuable comments on the manuscript. Dr E. G. Zavarzina-Memmi assisted in handling the specimens.

The study was conducted using Joint Usage Center ‘Instrumental methods in ecology’ at the IEE RAS. We thank A. Neretina and A. Nekrasov for their friendly and helpful assistance with the SEM facilities.

The contributions of Yu. Kantor, A. Kosyan, P. Sorokin and A. Fedosov were financially supported by Russian Science Foundation (grant No. 16-14-10118-Π, PI Yu. Kantor). This project has received funding from the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement No. 865101). Financial support was also provided by JSPS KAKENHI grants to Y. Kano (Nos 18H02494 and 19H00999). The authors declare no conflict of interests.

## REFERENCES

- Abbate D, Simone LRL. 2015.** Review of *Pugilina* from the Atlantic, with description of a new species from Brazil (Neogastropoda, Melongenidae). *African Invertebrates* **56**: 559–577.
- Abbate D, Simone LRL. 2016.** Anatomy of *Bullia laevis* from Cape Town, South Africa (Mollusca, Caenogastropoda, Nassariidae). *Spixiana* **39**: 1–10.
- Abbate D, Simone LRL, Cavallari DC. 2018.** Anatomy of *Engoniophos uncinatus* from Isla Margarita, Venezuela (Gastropoda:Caenogastropoda: Nassariidae), with a discussion of buccinid–nassariid relationship. *The Nautilus* **132**: 101–112.
- Aissaoui C, Puillandre N, Bouchet P, Fassio G, Modica MV, Oliverio M. 2016.** Cryptic diversity in Mediterranean gastropods of the genus *Aplus* (Neogastropoda: Buccinidae). *Scientia Marina* **80**: 521–533.
- Bandel K. 1984.** The radula of Caribbean and other Mesogastropoda and Neogastropoda. *Zoologische Verhandlungen* **214**: 1–188.
- Beu AG. 1979.** Bathyal Nukumaruan Mollusca from Oaro, southern Marlborough, New Zealand. *New Zealand Journal of Geology and Geophysics* **22**: 87–103.
- Beu AG. 2009.** Before the ice: biogeography of Antarctic Paleogene molluscan faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* **284**: 191–226.
- Bouchet P, Perrine D. 1996.** More gastropods feeding at night on parrotfishes. *Bulletin of Marine Science* **59**: 224–228.

- Bouchet P, Rocroi J-P. 2005.** Classification and nomenclator of gastropod families. *Malacologia* **47**: 1–397.
- Bouchet P, Warén A. 1985.** Revision of the north-east Atlantic bathyal and abyssal Neogastropoda, excluding Turridae. *Bolletino Malacologico Supplement* **1**: 121–296.
- Bouchet P, Warén A. 1986.** Taxonomical notes on tropical deep water Buccinidae with descriptions of new taxa. Résultats des campagnes Musorstom, volume 4. *Mémoires du Muséum National d'Histoire Naturelle, ser. A* **133**: 457–517.
- Bouchet P, Heros V, Lozouet P, Maestrati P. 2008.** A quarter-century of deep-sea malacological exploration in the south and west Pacific: where do we stand? How far to go? Tropical deep-sea benthos, volume 25. *Mémoires du Muséum National d'Histoire Naturelle* **196**: 9–40.
- Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE. 2017.** Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* **61**: 1–526.
- Brown SC. 1969.** The structure and function of the digestive system of the mud snail *Nassarius obsoletus* (Say). *Malacologia* **9**: 447–500.
- Callomon P, Lawless AS. 2013.** On the recent members of the genus *Lirabuccinum* Vermeij, 1991 in the northern Pacific, with description of a new species (Gastropoda: Buccinidae). *Venus* **71**: 13–27.
- Cernohorsky WO. 1971.** Indo-Pacific Pisaniinae (Mollusca: Gastropoda) and related buccinid genera. *Records of the Auckland Institute and Museum* **8**: 137–167.
- Cernohorsky WO. 1981.** The family Buccinidae. Part 1. The genera *Nassaria*, *Trajana* and *Neoterion*. *Monographs of Marine Mollusca* **2**: 201–284.
- Cernohorsky WO. 1984.** Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum* **14**: 1–356.
- Clarke A, Crame JA. 1989.** The origin of the Southern Ocean marine fauna. In: Crame JA, ed. *Origins and evolution of the Antarctic biota*. *Geological Society Special Publication* **47**: 253–268.
- Cooke AH. 1917.** The radula of the genus *Euthria* Gray. *Proceedings of the Malacological Society of London* **12**: 232–235.
- Cotton BC, Godfrey FK. 1932.** South Australian shells (including descriptions of new genera and species) part III. *The South Australian Naturalist* **13**: 35–86, pls 1–4.
- Couto DR, Simone LRL. 2019.** A morphology-based phylogenetic analysis of Fasciolaridae (Gastropoda: Buccinoidea). *Zootaxa* **4684**: 1–65.
- Couto DR, Bouchet P, Kantor YI, Simone LRL, Giribet G. 2016.** A multilocus molecular phylogeny of Fasciolaridae (Neogastropoda: Buccinoidea). *Molecular Phylogenetics and Evolution* **99**: 309–322.
- Cowan MT. 1965.** The egg capsule and young of the gastropod *Pyrulofusus harpa*. *The Veliger* **8**: 1–2.
- D'Attilio A. 1981.** The radula of *Neoterion ariel* (Pilsbry and Lowe, 1932) (Gastropoda: Buccinidae). *The Festivus* **13**: 104–105.
- Dall WH. 1904.** An historical and systematic review of the frog-shells and tritons. *Smithsonian Miscellaneous Collections* **47**: 114–144.
- Dall WH. 1906.** Early history of the generic name *Fusus*. *Journal of Conchology* **11**: 289–297.
- Dell RK. 1990.** Antarctic Mollusca with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand* **27**: 1–311.
- Donald KM, Winter DJ, Ashcroft AL, Spencer HG. 2015.** Phylogeography of the whelk genus *Cominella* (Gastropoda: Buccinidae) suggests long-distance counter-current dispersal of a direct developer. *Biological Journal of the Linnean Society* **115**: 315–332.
- Durham JW, MacNeil FS. 1967.** Cenozoic migrations of marine invertebrates through the Bering Strait region. In: Hopkins DM, ed. *The Bering land bridge*. Stanford: Stanford University Press, 326–349.
- Fedosov AE, Puillandre P, Kantor YI, Bouchet P. 2015.** Phylogeny and systematics of mitriform gastropods (Mollusca: Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society* **175**: 336–359.
- Fedosov AE, Caballer M, Buge B, Sorokin PV, Puillandre N, Bouchet P. 2020.** Mapping the missing branch on the Neogastropoda tree of life: molecular phylogeny of marginelliform gastropods. *Journal of Molluscan Studies* **85**: 440–452.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.
- Finlay HJ. 1928.** The recent mollusca of the Chatham Islands. *Transactions and Proceedings of the Royal Society of New Zealand* **59**: 232–286, pls 38–43.
- Fraussen K, Hadorn R. 2000.** Transfer of *Afer* Conrad, 1858 to Buccinidae (Neogastropoda) with description of a new species from western Africa. *Gloria Maris* **38**: 28–42.
- Fraussen K, Hadorn R. 2001.** A new species of Buccinidae from the Philippine Islands. *Novapex* **2**: 93–96.
- Fraussen K, Stahlschmidt P. 2015.** An extensive radiation of the genus *Crassicantharus* Ponder, 1972 (Gastropoda: Buccinoidea) in French Polynesia, with description of nine new species. *Novapex* **16**: 65–80.
- Fraussen K, Stahlschmidt P. 2016.** Revision of the *Clivipollia* group (Gastropoda: Buccinidae: Pisaniinae) with description of two new genera and three new species. *Novapex* **17**: 29–46.
- Fraussen K, Vermeij G.J. 2021.** *Sinetectula* gen. nov., a new genus of Pisaniidae (Gastropoda: Buccinoidea) from the tropical Indian and Pacific Oceans. *European Journal of Taxonomy* **748**: 155–176.
- Fretter V, Graham A. 1962.** *British prosobranch molluscs. Their functional anatomy and ecology*. London: Ray Society.
- Galindo LA, Puillandre N, Strong EE, Bouchet P. 2014.** Using microwaves to prepare gastropods for DNA barcoding. *Molecular Ecology Resources* **14**: 700–705.
- Galindo LA, Puillandre N, Utge J, Lozouet P, Bouchet P. 2016.** The phylogeny and systematics of the Nassariidae revisited (Gastropoda, Buccinoidea). *Molecular Phylogenetics and Evolution* **99**: 337–353.



- Gladenkov YB, Sinelnikova VN, Titova LV. 1988.** Stages of development of the fauna of the shelf basins of the Neogene of Kamchatka (on the example of buccinids). In: Timofeev PP, Gladenkov YB, eds. *Lithology and stratigraphy of the Mesozoic and Cenozoic of the eastern regions of the USSR*. Moscow: Nauka, 58–135.
- Gofas S, Oliver JD. 2010.** Las especies del género *Chauvetia* (Gastropoda, Neogastropoda, Buccinidae) del área ibero-marroquí, con descripción de cuatro especies nuevas. *Iberus* **28**: 23–60.
- Golikov AN. 1963.** *Gastropod molluscs of the genus Neptunea* Bolten. *Fauna of the USSR, Molluscs 5(1)*. Leningrad: Nauka, 1–217.
- Golikov AN. 1980.** *Molluscs Buccininae of the world ocean*. *Fauna of the USSR, Molluscs 5(2)*. Leningrad: Nauka, 1–466.
- Golikov AN, Starobogatov YI. 1975.** Systematics of prosobranch gastropods. *Malacologia* **15**: 185–232.
- Golikov AN, Starobogatov YI. [1989 (“1988”)].** Problems of phylogeny and system of the prosobranchiate gastropods. *Trudy Zoologicheskogo Instituta AN SSSR* **187**: 4–77 (In Russian).
- Goryachev VN. 1987.** On the revision of the gastropod superfamily Buccinoidea (Mollusca, Gastropoda, Hamiglossa). The nontropical zones of the Northern Hemisphere. In: Starobogatov YI, Golikov AN, Likharev IM, eds. *Vsesoiuznoe soveshchanie po izucheniiu molliuskov* [Leningrad] **8**: 31–35 [in Russian].
- Gray JE. 1857.** *Guide to the systematic distribution of Mollusca in the British Museum. Part I*. London: Taylor & Francis.
- Gulbin VV. 2018.** The egg cases and capsules of the gastropod *Beringius marshalli* (Dall, 1919) (Gastropoda: Buccinidae: Beringiinae). *Ruthenica, Russian Malacological Journal* **28**: 83–86.
- Guralnick R, deMaitenon M. 1997.** Formation and homology of radular teeth: a case study using columbellid gastropods (Neogastropoda: Columbellidae). *Journal of Molluscan Studies* **63**: 65–77.
- Habe T. 1972.** Notes on the genus *Parancistrolepis* Azuma (Buccinidae). *The Nautilus* **86**: 51–52.
- Habe T, Sato J. 1973 [‘1972’].** [A classification of the family Buccinidae from the North Pacific]. *Proceedings of the Japanese Society of Systematic Zoology* **8**: 1–8, pls 1–2 [in Japanese].
- Hain SG. 1990.** Beiträge zur Biologie der beschalten Mollusken (Kl. Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Berichte zur Polarforschung* **70**: 1–181.
- Harasewych MG. 1991.** Mollusca Gastropoda: Columbariform gastropods of New Caledonia. In: Crosnier A, Bouchet P, eds. *Résultats des Campagnes Musorstom, volume 7. Mémoires du Muséum National d’Histoire Naturelle, ser. A* **150**: 243–259.
- Harasewych MG. 2018.** The anatomy of *Tudicla spirillus* (Linnaeus, 1767) and the relationships of the Tudicliidae (Gastropoda: Neogastropoda). *The Nautilus* **132**: 35–44.
- Harasewych MG, Kantor YI. 1999.** A revision of the Antarctic genus *Chlanidota* (Gastropoda: Neogastropoda: Buccinulidae). *Proceedings of the Biological Society of Washington* **112**: 253–302.
- Harasewych MG, Kantor YI. 2004.** The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches. *Nautilus* **118**: 1–42.
- Harasewych MG, Kantor YI, Linse K. 2000.** *Parabuccinum*, a new genus of Magellanic buccinulid (Gastropoda: Neogastropoda), with a description of a new species. *Proceedings of the Biological Society of Washington* **113**: 542–560.
- Hardy SM, Carr CM, Hardman M, Steinke D, Corstorphine E, Mah C. 2011.** Biodiversity and phylogeography of Arctic marine fauna: insights from molecular tools. *Marine Biodiversity* **41**: 195–210.
- Hasegawa K. 2009.** Upper bathyal gastropods of the Pacific coast of northern Honshu, Japan, chiefly collected by R/V Wakataka-maru. In: Fujita T, ed. *Deep-sea fauna and pollutants off Pacific coast of northern Japan. National Museum of Nature and Science Monographs* **39**: 225–383.
- Hayashi S. 2005.** The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the complete mitochondrial 16S rRNA gene sequences of selected representatives. *Molluscan Research* **25**: 85–98.
- Higo S, Callomon P, Goto Y. 1999.** *Catalogue and bibliography of the marine shell-bearing Mollusca of Japan*. Osaka: Elle Scientific Publications.
- Huelsenbeck JP, Ronquist F. 2001.** MrBayes: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755.
- International Commission on Zoological Nomenclature (ICZN). 1999.** *International Code of Zoological Nomenclature, 4th edn*. London: The International Trust for Zoological Nomenclature.
- Iredale T, McMichael DF. 1962.** A reference list of the marine Mollusca of New South Wales. *Australian Museum Memoir* **11**: 1–185.
- Jovelin R, Justine J-L. 2001.** Phylogenetic relationships within the polyopisthocotylean monogeneans (Platyhelminthes) inferred from partial 28S rDNA sequences. *International Journal for Parasitology* **31**: 393–401.
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermin LS. 2017.** ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**: 587–589.
- Kang PA. 1976.** Study on the radula of Korean marine gastropods. *Bulletin of the Korean Fishery Society* **9**: 25–34.
- Kantor YI. 1988.** Gastropods of the subgenus *Ancistrolepis* (*Clinopegma*) (Gastropoda, Buccinidae) of the Okhotsk Sea. *Zoologicheskii Zhurnal* **67**: 1126–1140.
- Kantor YI. 1990.** *Gastropods of the subfamily Volutopsiinae (Buccinidae) of the World Ocean*. Moscow: Nauka Publ.
- Kantor YI. 2003.** Comparative anatomy of the stomach of Buccinoidea (Neogastropoda). *Journal of Molluscan Studies* **69**: 203–220.
- Kantor YI, Harasewych MG. 2013.** Antarctica, where turrids and whelks converge: a revision of *Falsimohnia* Powell, 1951 (Neogastropoda: Buccinoidea) and a description of a new genus. *The Nautilus* **127**: 43–56.
- Kantor YI, Kilburn RN. 2001.** Rediscovery of *Canidia dorri* Wattlebed, 1886, with a discussion of its systematic position (Gastropoda: Neogastropoda: Nassariidae: *Nassodonta*). *The Nautilus* **115**: 99–104.

- Kantor YI, Puillandre N, Rivasseau A, Bouchet P. 2012.** Neither a buccinid nor a turrid: a new family of deep-sea snails for *Belomitra* P. Fischer, 1883 (Mollusca, Neogastropoda), with a review of Recent Indo-Pacific species. *Zootaxa* **3496**: 1–64.
- Kantor YI, Puillandre N, Fraussen K, Fedosov AE, Bouchet P. 2013.** Deep-water Buccinidae (Gastropoda: Neogastropoda) from sunken wood, vents and seeps: molecular phylogeny and taxonomy. *Journal of the Marine Biological Association of the UK* **93**: 2177–2195.
- Kantor YI, Fedosov AE, Puillandre N, Bonillo C, Bouchet P. 2017.** Returning to the roots: morphology, molecular phylogeny and classification of the Olivoidea (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society* **180**: 493–541.
- Kantor YI, Fedosov AE, Snyder MA, Bouchet P. 2018.** *Pseudolatirus* Bellardi, 1884 revisited, with the description of two new genera and five new species (Neogastropoda: Fasciolaridae). *European Journal of Taxonomy* **433**: 1–57.
- Kantor Y, Kosyan A, Sorokin P, Fedosov A. 2020a.** On the taxonomic position of *Phaenomenella* Fraussen & Hadorn, 2006 (Neogastropoda: Buccinoidea) with description of two new species. *Zoosystema* **42**: 33–55.
- Kantor YI, Kosyan A, Sorokin P, Herbert DG, Fedosov A. 2020b.** Review of the abyssal-hadal genus *Bayerius* (Gastropoda: Neogastropoda: Buccinidae) from the north-west Pacific, with description of two new species. *Deep-Sea Research Part I* **160**: 1–25.
- Katoh K, Rozewicki J, Yamada KD. 2019.** MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166.
- Keen AM. 1971.** *Seashells of tropical West America*. Palo Alto: Stanford University Press.
- Kosyan AR. 2006.** Two new species of the genus *Pararetifusus* Kosuge, 1967 (Buccinidae: Colinae), with notes on the morphology of *Pararetifusus tenuis* (Okutani, 1966), *Ruthenica*. *Russian Malacological Journal* **16**: 5–15.
- Kosyan AR. 2007.** Morphological features, ecology, and distribution of poorly studied molluscan genera of the Colinae subfamily (Bastropoda, Buccinidae) from the far eastern seas of Russia. *Oceanology* **47**: 531–536.
- Kosyan AR, Kantor YI. 2004.** Morphology, taxonomic status and relationships of Melongenidae (Gastropoda: Neogastropoda). *Ruthenica, Russian Malacological Journal* **14**: 9–36.
- Kosyan AR, Kantor YI. 2009.** Phylogenetic analysis of the subfamily Colinae (Neogastropoda: Buccinidae) based on morphological characters. *The Nautilus* **123**: 83–94.
- Kosyan AR, Kantor YI. 2012.** Revision of the genus *Plicifusus* Dall, 1902 (Gastropoda: Buccinidae). *Ruthenica, Russian Malacological Journal* **22**: 55–92.
- Kosyan AR, Kantor YI. 2013.** Revision of the genus *Aulacofusus* Dall, 1918 (Gastropoda: Buccinidae). *Ruthenica, Russian Malacological Journal* **23**: 1–33.
- Kosyan AR, Kantor YI. 2014.** Revision of the genus *Retifusus* Dall, 1916 (Gastropoda: Buccinidae). *Ruthenica, Russian Malacological Journal* **24**: 121–163.
- Kosyan AR, Kantor YI. 2015.** Notes on the abyssal genus *Fusipagoda* Habe & Ito, 1965 (Neogastropoda: Buccinidae) from the North Pacific. *Ruthenica, Russian Malacological Journal* **25**: 77–87.
- Kosyan AR, Kantor YI. 2016.** Revision of the genus *Retimohnia* McLean, 1995 (Gastropoda: Buccinidae). *Ruthenica, Russian Malacological Journal* **26**: 85–121.
- Landau BM, Harzhauser M, İslamoğlu Y, da Silva CM. 2013.** Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research* **11–13**: 1–584.
- Li H, Shi X, Zhou J, Zhou P, Lü X. 2013.** Study on the taxonomic status of *Afer cumingii* based on mitochondrial gene sequences and radular morphology. *Marine Sciences* **37**: 85–88.
- Linse K. 2002.** The shelled Magellanic Mollusca: with special reference to biogeography relations in the Southern Ocean. *Theses Zoologicae* **34**: 1–252.
- Luca JD, Pastorino G. 2018.** A revision of the genus *Savatieria* Rochebrune & Mabile, 1885: an endemic group of buccinid gastropods from the Magellanic region. *Journal of Molluscan Studies* **84**: 293–302.
- Macpherson JH, Chapple EH. 1951.** A systematic list of the marine and estuarine Mollusca of Victoria. *Memoirs of the National Museum of Victoria* **17**: 107–185.
- Marcus EB-R, Marcus E. 1962.** Studies on Columbidae. Faculdade de Filosofia, Ciências e Letras da Universidade de Sao Paulo, Boletim 261. *Zoologia* **24**: 335–384.
- Miller MA, Pfeiffer W, Schwartz T. 2010.** *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*. New Orleans: Gateway Computing Environments Workshop (GCE), 1–8.
- Numanami H. 1996.** Taxonomic study on Antarctic gastropods collected by Japanese Antarctic Research Expeditions. *Memoirs of National Institute of Polar Research, Series E (Biology and Medical Science)* **39**: 1–244.
- Okusu A, Schwabe E, Eernisse DJ, Giribet G. 2003.** Towards a phylogeny of chitons (Mollusca, Polyplacophora) based on combined analysis of five molecular loci. *Organisms Diversity & Evolution* **3**: 281–302.
- Okutani T, ed. 2017.** *Marine mollusks in Japan, 2nd edn (2 volumes)*. Tokyo: Tokai University Press.
- Okutani T, Iwasaki N. 2003.** Noteworthy abyssal mollusks (excluding vesicomid bivalves) collected from the Nankai Trough off Shikoku by the ROV Kaiko of the Japan Marine Science & Technology Center. *Venus* **62**: 1–10.
- Oliver JD, Rolan E. 2008.** Las especies del género *Chauvetia* del área de Dakar, Senegal, África occidental, con la descripción de diez especies nuevas. *Iberus* **26**: 133–175.
- Oliverio M, Modica MV. 2010.** Relationships of the haematophagous marine snail *Colubraria* (Rachiglossa: Colubrariidae), within the neogastropod phylogenetic framework. *Zoological Journal of the Linnean Society* **158**: 779–800.
- Olsson AA. 1971.** Mollusks from the Gulf of Panama collected by R/V *John Elliott Pillsbury*. *Bulletin of Marine Science* **21**: 35–92.

- Orr V. 1956.** The South African gastropod genus *Burnupena* (Buccinidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* **108**: 249–263.
- Palumbi SR. 1996.** *Nucleic acids 2: the polymerase chain reaction*. Sinauer Associates, Inc.
- Pastorino G. 2016.** Revision of the genera *Pareuthria* Strebel, 1905, *Glypteuthria* Strebel, 1905 and *Meteuthria* Thiele, 1912 (Gastropoda: Buccinulidae) with the description of three new genera and two new species from Southwestern Atlantic waters. *Zootaxa* **4179**: 301–344
- Pastorino G, Griffin M. 2019.** Gastropods of the genus *Antistreptus* as examples of persistent molluscan lineages in the Neogene of the southwestern Atlantic. *Journal of Paleontology* **93**: 916–924.
- Pearce JB, Thorson G. 1967.** The feeding and reproductive biology of the red whelk, *Neptunea antiqua* (L.) (Gastropoda, Prosobranchia). *Ophelia* **4**: 277–314.
- Penchaszadeh P, Pastorino G, Martinez MI, Miloslavich P. 2019.** Spawn and development of the gastropod *Americominella longisetosa* (Castellanos and Fernandez, 1972) (Mollusca: Buccinidae) from the Southwestern Atlantic deep sea. *Deep-Sea Research Part 1* **143**: 43–49.
- Petuch EJ, Myers RF, Berschauer DP. 2015.** *The living and fossil Busycon whelks: iconic mollusks of eastern North America*. San Diego: Special Publication of the San Diego Shell Club.
- Ponder WF. 1968.** Anatomical notes on two species of the Colubrariidae (Mollusca, Prosobranchia). *Transactions of the Royal Society of New Zealand, Zoology* **10**: 217–223.
- Ponder WF. 1971.** A review of the New Zealand recent and fossil species of *Buccinulum* Deshayes (Mollusca: Neogastropoda: Buccinidae). *Journal of the Royal Society of New Zealand* **1**: 231–283.
- Ponder WF. 1972.** Notes on some Australian species and genera of the family Buccinidae (Neogastropoda). *Journal of the Malacological Society of Australia* **2**: 249–265.
- Ponder WF. 1973.** A review of the Australian species of *Penion* Fischer (Neogastropoda: Buccinidae). *Journal of the Malacological Society of Australia* **2**: 401–428.
- Ponder WF, Warén A. 1988.** Classification of the Caenogastropoda and Heterostropha – a list of the family-group names and higher taxa. *Malacological Review, Supplement* **4**: 288–328.
- Powell AWB. 1929.** The recent and Tertiary species of the genus *Buccinulum* in New Zealand, with a review of related genera and families. *Transactions of the New Zealand Institute* **60**: 57–101.
- Powell AWB. 1951.** Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Reports* **26**: 47–196, pls 5–10.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018.** Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Systematic Biology* **67**: 901–904.
- Raven JGM. 2016.** Notes on molluscs from NW Borneo. 3. A revision of *Taurasia* (Gastropoda, Muricidae) and *Preangeria* (Gastropoda, Buccinidae) with comments on *Semiricinula* from NW Borneo. *Vita Malacologica* **15**: 77–104.
- Röding PF. 1798.** *Museum Boltenianum..., Pars secunda continens conchylia sive testacea univalvia, bivalvia & multivalvia*. Hamburg: Christ.
- Rosenthal RJ. 1970.** Observations on the reproductive biology of the Kellet's Whelk, *Kelletia kelletii*. *The Veliger* **12**: 319–324.
- Sars GO. 1878.** *Mollusca Regionis Arcticae Norwegiae*. Oslo (Christiania): Brögger.
- Sela I, Ashkenazy H, Katoh K, Pupko T. 2015.** GUIDANCE2: accurate detection of unreliable alignment regions accounting for the uncertainty of multiple parameters. *Nucleic Acids Research* **43**: W7–W14.
- Shuto T. 1978.** On the genera *Siphonofusus* and *Euthria* of the Indo-West Pacific. *Transactions and Proceedings of the Palaeontological Society of Japan* **111**: 358–369.
- Simon C, Franke A, Martin A. 1991.** The polymerase chain reaction: DNA extraction and amplification. *NATO ASI Series Series H Cell Biology* **57**: 329–355.
- Simone LRL. 1996.** Anatomy and systematics of *Buccinanops gradatus* (Deshayes, 1844) and *Buccinanops moniliferus* (Kiener, 1834) (Neogastropoda, Muricoidea) from the southeastern coast of Brazil. *Malacologia* **38**: 87–102.
- Simone LRL, Pastorino G. 2014.** Comparative morphology of *Dorsanum miran* and *Bullia granulosa* from Morocco (Mollusca: Caenogastropoda: Nassariidae). *African Invertebrates* **55**: 125–142.
- Simone LRL, Cavallari D, Abbate D. 2013.** Revision of the genus *Teralatirus* Coomans 1965 in the western Atlantic, with an anatomical description of *T. roboreus* (Reeve 1845) (Gastropoda: Neogastropoda: Fascioliariidae). *Archiv für Molluskenkunde* **142**: 215–226.
- Smith KE, Thatje S. 2013.** The subtle intracapsular survival of the fittest: maternal investment, sibling conflict, or environmental effects? *Ecology* **94**: 2263–2274.
- Snyder MA. 2021.** *Catalogue of the marine gastropod family Fascioliariidae. Second Edition*. Academy of Natural Sciences of Philadelphia.
- Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J. 2007.** Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* **57**: 573–583.
- Stamatakis A. 2006.** RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.
- Stamatakis A, Hoover P, Rougemont J. 2008.** A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology* **57**: 758–771.
- Strong EE, Galindo LA, Kantor YI. 2017.** Quid est *Clea helena*? Evidence for a previously unrecognized radiation of assassin snails (Gastropoda: Buccinoidea: Nassariidae). *PeerJ* **5**: e3638.
- Strong EE, Puillandre N, Beu AG, Castelin M, Bouchet P. 2019.** Frogs and tuns and tritons – a molecular phylogeny and revised family classification of the predatory gastropod superfamily Tonnoidea (Caenogastropoda). *Molecular Phylogenetics and Evolution* **130**: 18–34.

- Taylor JD, Morris NJ, Taylor CN. 1980.** Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology* **23**: 375–409.
- Thiele J. 1912.** Die antarktischen Schnecken und Muscheln. *Deutschen Sudpolar-Expedition 1901–1903* **13**: 183–285, pls 11–19.
- Thiele H. 1929.** *Handbuch der systematischen Weichtierkunde*. Vol. 1, part 1. Fischer, Jena.
- Tiba R, Kosuge S. 1980.** Genus *Japelion*. *North Pacific Shells, Part 6*: 14.
- UNESCO. 2009.** *Global open oceans and deep seabed (GOODS): biogeographic classification*. IOC Technical Series, No. 84. Paris: UNESCO-IOC.
- Vaux F, Hills SFK, Marshall BA, Trewick SA, Morgan-Richards M. 2017.** A phylogeny of Southern Hemisphere whelks (Gastropoda: Buccinulidae) and concordance with the fossil record. *Molecular Phylogenetics and Evolution* **114**: 367–381.
- Vaux F, Trewick SA, Crampton JS, Marshall BA, Beu AG, Hills SFK, Morgan-Richards M. 2018.** Evolutionary lineages of marine snails identified using molecular phylogenetics and geometric morphometric analysis of shells. *Molecular Phylogenetics and Evolution* **127**: 626–637.
- Vermeij GJ. 1991a.** Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology* **17**: 281–307.
- Vermeij GJ. 1991b.** Generic identity and relationships of the northeastern Pacific buccinid gastropod *Searlesia dira* (Reeve, 1846). *The Veliger* **34**: 264–271.
- Vermeij GJ. 1998.** Generic revision of the neogastropod family Pseudolividae. *The Nautilus* **111**: 53–84.
- Vermeij GJ. 2001.** Taxonomy, distribution, and characters of pre-Oligocene members of the *Cantharus* group of Pisaniinae (Neogastropoda: Buccinoidea). *Journal of Paleontology* **75**: 295–309.
- Vermeij GJ, Bouchet P. 1998.** New Pisaniinae (Mollusca, Gastropoda, Buccinidae) from New Caledonia, with remarks on *Cantharus* and related genera. *Zoosystema* **20**: 471–485.
- Vermeij GJ, Snyder MA. 2006.** Shell characters and taxonomy of *Latirus* and related fascioliariid groups. *Journal of Molluscan Studies* **72**: 413–424.
- Vermeij GJ, Snyder MA. 2018.** Proposed genus-level classification of large species of Fusiniinae (Gastropoda, Fascioliariidae). *Bacteria* **82**: 57–82.
- Vermeij GJ, Banker R, Capece LR, Hernandez ES, Salley SO, Padilla Vriesman V, Wortham BE. 2019.** The coastal North Pacific: origins and history of a dominant marine biota. *Journal of Biogeography* **46**: 1–18.
- Watters GT, Finlay CJ. 1989.** A revision of the western Atlantic recent species of the genus *Monostiolum* Dall, 1904, and *Bailya* (*Parabailya*) new subgenus (Gastropoda: Buccinidae). *The Veliger* **32**: 47–59.
- Wenz W. 1938–1944.** Gastropoda. Teil 1: Allgemeiner und Prosobranchia. *Handbuch der Paläozoologie* 6. Berlin: Borntraeger.
- Yang J, Zhang S. 2011.** The radular morphology of Nassariidae (Gastropoda: Caenogastropoda) from China. *Chinese Journal of Oceanology and Limnology* **29**: 1023–1032.
- Zou S, Li Q, Kong L. 2011.** Additional gene data and increased sampling give new insights into the phylogenetic relationships of Neogastropoda, within the caenogastropod phylogenetic framework. *Molecular Phylogenetics and Evolution* **61**: 425–435.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Fig. S1.** Buccinoidea phylogenetic relationships obtained with 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 maximum likelihood (ML) of the multigene dataset (concatenated alignment *cox1*, 12S, 16S, 28S and *H3* genes). For *Japeuthria ferrea* (highlighted in red) concatenated alignment of three genes (*cox1*, 16S, and *H3*) was used.

**Table S1.** List of sequenced species included in the molecular analysis with collecting details and not-aligned sequences.

**Table S2.** List of genera of Buccinoidea with uncertain familiar allocation.

*Cox1* dataset:

**File S1.** *Cox1* alignment used to reconstruct a phylogenetic tree on [Figure S1](#).

**File S2.** IQtree output consensus tree ([Fig. S1](#)).

Five-gene dataset:

**File S3.** Concatenated alignment of five genes (*cox1*–16S–12S–*H3*–28S) after removal of the columns with confidence values below 0.4 from 16S and 12S.

**File S4.** Concatenated alignment of five genes (*cox1*–16S–12S–*H3*–28S) after removal of the columns with confidence values below 0.9 from 16S and 12S.

**File S5.** Concatenated alignment of five genes (*cox1*–16S–12S–*H3*–28S) used for final Bayesian and RaxML analyses on the five-gene dataset ([Figs 1, 2](#)) (Buc5G\_231\_final.fas).

**File S6.** Output of the Model finder as implemented in the IQtree for the final five-gene dataset (Buc5G\_231\_final\_best\_models.txt).

**File S7.** Output tree file produced by RaxML for the dataset in File S5 (Buc5G\_231\_final.fas) with partitions as specified in File 6 (Buc5G\_231\_final\_best\_models.txt).

**File S8.** Consensus tree file generated after summing two \*.t files from the Bayesian analysis of the dataset in File S5 (Buc5G\_231\_final.fas) with partitions as specified in File S6 (Buc5G\_231\_final\_best\_models.txt) and discarding 25% trees from first generations of MCMC.

**File S9.** Alignment in File S5 (Buc5G\_231\_final.fas), with additional hymeric entry for *Japeuthria ferrea*, represented by three genes, *cox1*, 16S and *H3*, all obtained from GenBank. Used for analysis to generate the tree on Figure S2 (Buc5G\_232\_final\_Japeuthria.fas).

**File S10.** IQtree consensus tree resulting from the analysis of File S9 (Buc5G\_232\_final\_Japeuthria.fas) with partitions as specified in File S6 (Buc5G\_231\_final\_best\_models.txt).