A NEW OPERATIONAL CLASSIFICATION OF THE CONOIDEA (GASTROPODA)

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ABSTRACT

A new genus-level classification of the Conoidea is presented, based on the molecular phylogeny of Puillandre *et al*. in the accompanying paper. Fifteen lineages are recognized and ranked as families to facilitate continuity in the treatment of the names Conidae (for 'cones') and Terebridae in their traditional usage. The hitherto polyphyletic 'Turridae' is now resolved as 13 monophyletic families, in which the 358 currently recognized genera and subgenera are placed, or tentatively allocated: Conorbidae (2 (sub)genera), Borsoniidae (34), Clathurellidae (21), Mitromorphidae (8), Mangeliidae (60), Raphitomidae (71), Cochlespiridae (9), Drilliidae (34), Pseudomelatomidae (=Crassispiridae) (59), Clavatulidae (14), Horaiclavidae new family (28), Turridae *s. s.* (16) and Strictispiridae (2). A diagnosis with description of the shell and radulae is provided for each of these families.

INTRODUCTION

The history of classification of the Conoidea can be divided in two mains periods. During the first period, from Adams & Adams (1853), Bellardi (1875), Fischer (1887) and Cossmann (1896) to the 1980s (e.g. Powell, 1942, 1966; Morrison, 1965; McLean, 1971), classifications were based solely on the morphology of the 'hard parts' (shell and radula). Contradictions were commonplace and none of these classifications satisfied the malacological community, even if some of them were adopted by other authors (e.g. Kilburn, 1983, 1985, 1986, 1988, 1991, 1992, 1993, 1994, 1995; Chang, 1995, 2001). Actually, only the Conidae (cone snails) and Terebridae (auger snails) were confidently recognized as well-defined groups, all the other constituents being lumped in the artificial group 'turrids', more or less separated into different subfamilies. Indeed, numerous cases of homoplasy for the morpho-anatomical characters used in these pre-1990s classifications are known (Taylor, 1994; Kantor, Medinskaya & Taylor, 1997; Fedosov & Kantor, 2008; Holford *et al*., 2009), thus rendering earlier classifications questionable. Protoconch characters, in particular, have been much used and much misunderstood (Bouchet, 1990). Inevitably, different authors emphasized different types of characters (radula, foregut anatomy, shape of the shell, protoconch): when one taxonomist recognized a group based on protoconch similarities and ignored the radula morphology, another one stated that the similarity of the protoconch was the result of convergence, and split the group into as many groups as there were radula types. This contributed to the conoideans earning their reputation of 'taxonomic nightmare'.

In 1993, based on anatomical characters (and not just the radula), Taylor, Kantor and Sysoev proposed a completely revised classification that recognized six families. One of their major results was that *Conus*, hitherto a genus in its own monotypic family Conidae, became one of many genera in an expanded family Conidae, which also now contained genera formerly placed in 'Turridae', thus confirming Thiele's (1929) intuitive classification. The Taylor, Kantor & Sysoev (1993) classification formed the basis of the system published by Bouchet & Rocroi (2005; Fig. 1A). Most recently, a new shell-and-radula classification of the Toxoglossa, with emphasis on *Conus* and other 'cone-like' genera, has been proposed by Tucker & Tenorio (2009; Fig. 1C), who recognized two superfamilies: the Turroidea, grouping together the Turridae of Taylor *et al*. (1993), plus the Terebridae, Drilliidae, Pseudomelatomidae and Strictispiridae, and the Conoidea, corresponding to the Conidae of Taylor *et al*. (1993) except for several of their constituents having been raised to family level.

Based on a dataset of 57 genera and molecular sequences of fragments of one mitochondrial (COI) and three nuclear (28S, 18S and H3) genes, Puillandre *et al*. (2008) published the first molecular phylogeny of Conoidea. Even though ranks differed, most of the lineages defined by Taylor *et al*. (1993) were also retrieved in this molecular approach. The new molecular phylogeny of Puillandre *et al*. (2011) is based on a dataset of 102 conoidean genera (87 'turrids', 5 cones and 10 terebrids) and sequences of three gene fragments (COI, 12S rRNA and 16S rRNA). Because of the high congruency between the classification based on anatomical characters and the molecular tree obtained, we are inclined to think that our understanding of the phylogeny of the Conoidea has now reached a stable position, and that a new classification is warranted. The classification presented below (Fig. 1B) aims to transform the molecular phylogeny into an operational classification by: (1) presenting revised morphological diagnoses for the now redefined families of Conoidea; (2) allocating (sometimes tentatively) all Recent genera recognized or used in current literature to the corresponding family.

MATERIAL AND METHODS

Genus-group names have been allocated to the newly defined families based on the following critera:

(1) 224 genera were assigned to a family based on shell characters, and phenetic resemblance to those genera with radula and/or molecular characters available; those are marked [1].
(2) 103 genera were classified on the basis of radula morphology (both our own and published data), and congruence between radula and molecular characters for those genera that were sequenced; these are marked [2].

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(3) 98 genera were classified in a family on the basis of the molecular data; these are marked [3].
(4) 63 genera and subgenera do not fall easily into the morphological groups resulting from the preceding steps, but they have tentatively been assigned to a family as a working hypothesis; these genera are preceded by a question mark.
(5) 173 subgenera and/or synonyms are also listed; subgenera are in parentheses, synonyms in square brackets.

Our aim was to provide an exhaustive list of conoidean genus-group names based on Recent type species or reasonably recognized as Recent in the literature. Genera present exclusively in the fossil record are not included. In very few cases, obviously erroneous attribution of Recent species to entirely fossil genera also excluded these genera from our listing. Junior homonyms and *nomina nuda* are also not included because they are unavailable for nomenclatural purposes. When the status of a nominal

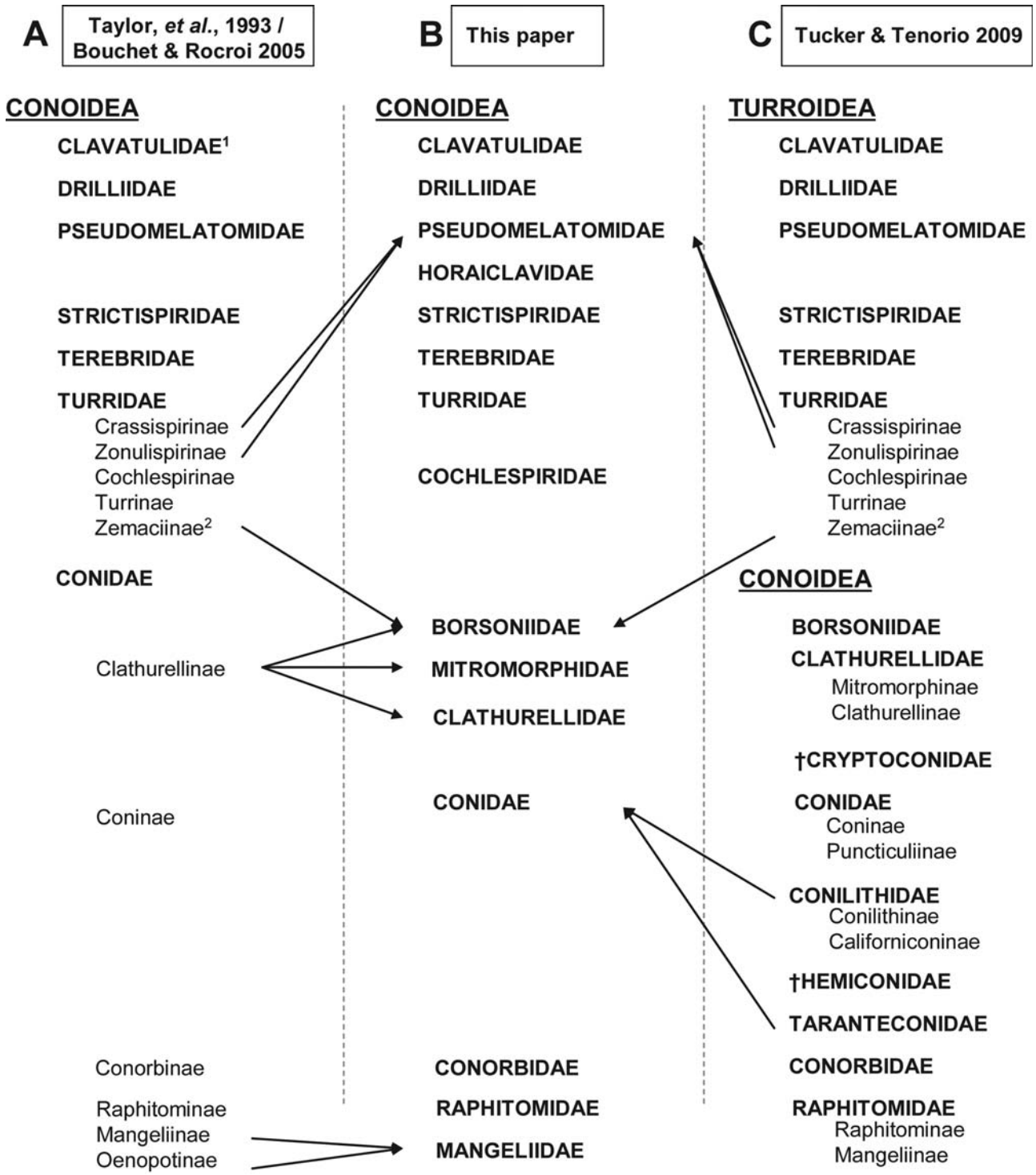

Figure 1. Comparison of the last two conoidean classifications with the new classification proposed in this article. **A.** Taylor *et al.* (1993) and Bouchet & Rocroi (2005). [1]Elevated to familial rank by Bouchet & Rocroi (2005). [2]Absent in Taylor *et al.* (1993). **B.** Proposed classification. **C.** Tucker & Tenorio (2009). †Fossil taxa.

genus is uncertain, we adopted a 'valid until synonymized' approach; that is, a name is regarded valid (irrespective of our opinion) if it has not been synonymized in literature. The names of synonyms are placed after corresponding valid names (the synonyms applied to the valid subgenus name are positioned after the subgenus name). All the genus and subgenus names are also listed in alphabetic order in Appendix 1.

Radulae

To illustrate the range of radular types in the molecularly defined clades, the radulae were extracted as far as possible from the specimens used for the molecular analyses or from conspecific specimens (after rehydration when soft parts had been dried), cleaned with diluted bleach, rinsed in distilled water, mounted on stubs, air dried, coated with gold-palladium, and investigated with a JEOL JSM 840A scanning electron microscope. Some of the previously photographed radulae (examined by YuIK and/or J.D. Taylor) were additionally illustrated.

For radular descriptions we mostly followed the terminology accepted and discussed by Kantor & Taylor (2000). In radular formulae, the parentheses indicate partial or complete fusion of lateral and rachidian teeth (for more details, see Kantor, 2006).

Ranking and nomenclature

Although the names Conoidea and Toxoglossa are used interchangeably in the taxonomic literature, we have avoided the name Toxoglossa because (i) it is not typified and cannot be used for a family–group name, and (ii) many of the included taxa do not have a toxoglossate radula. Within the Conoidea, ranking of the clades was determined by a conservative approach, thus retaining the names Terebridae and Conidae *s. s.* (the latter including the cone snails *Profundiconus*, *Californiconus*, *Conasprella*, *Conus* and *Taranteconus*) in their accustomed usage at family rank. An alternative would have been to recognize only two families, Conidae *sensu* Taylor *et al.* (1993) and Turridae (including the Turridae, Terebridae, Drilliidae and Pseudomelatomidae), with the resulting inconvenience that Conidae *s. s.* and Terebridae, although monophyletic, would lose their traditional usage and the vast associated literature dealing with these names that largely ignores the Taylor *et al.* (1993) and Bouchet & Rocroi (2005) classifications.

Fourteen clades of rank equivalent to Conidae *s. s.* and Terebridae are recognizable from the molecular phylogenetic tree (Puillandre *et al.*, 2011). Forty-three family–group names within Conoidea are nomenclaturally available (Appendix 2), of which five are based on a genus with a fossil type species (Andoniinae Vera-Pelaez, 2002; Cryptoconinae Cossmann, 1896; Hemiconidae Tucker & Tenorio, 2009; Johnwyattidae Serna, 1979; Siphopsinae Le Renard, 1995). These five cannot be applied to a molecular clade and will not be used in our classification. Names were applied to clades based on the position of their type genus in the tree. If more than one family–group name was applicable, the valid name was determined by priority. If the type genus of a nominal family name was not sequenced, application of the name was determined by reference to the morphologically most similar genus used in the analysis.

Because the molecular taxon sampling is still too patchy for such levels, we have abstained from extending the classification below family level (i.e. subfamilies, tribes), even when some molecular clades obviously match previously recognized 'subfamilies' (e.g. Californiconinae, Oenopotinae, Zemaciinae, Zonulispirinae). They are all included in a family (Appendix 2), without precluding their usefulness and potential taxonomic validity.

Illustration of voucher material

Each family (except the Conidae and Terebridae, already extensively covered and illustrated in other recent works, e.g. Röckel, Korn & Kohn, 1995; Terryn, 2007; Tucker & Tenorio, 2009) is illustrated by one or several shells, radulae and protoconchs, covering the morphological variability of the group. As far as possible, specimens used for the molecular analyses were used for illustration. However, since a substantial part of the morphological variability was not covered by our dataset, shells and radulae of other specimens are also illustrated.

SYSTEMATICS

Superfamily CONOIDEA Fleming, 1822

Family Conidae Fleming, 1822

[=Conilithidae Tucker & Tenorio, 2009, **new synonym**; =Taranteconidae Tucker & Tenorio, 2009, **new synonym**]

Diagnosis: Shell medium-sized to large or very large, normally 20–50 mm, up to 170 mm high, conical or biconical, with narrow aperture and short siphonal canal. Shell with considerable internal remodelling due to inner wall resorption. Spiral sculpture usually developed, axial sculpture absent or in form of shoulder tuberculation. Anal sinus on subsutural ramp, shallow to moderately deep. Operculum present, small, with terminal nucleus. Radula of marginal hypodermic teeth, generally harpoon-shaped, barbed at tip, often with complex inner structure of folds and serration, base small and swollen, tooth canal opening (sub)terminally, rarely laterally. Subradular membrane vestigial. Teeth can be attached to the membrane by long or very long flexible ligament. Tooth wall forms several overlapping layers.

Remarks: in Conidae and the other families that are included in this major clade (family Conidae *sensu* Taylor *et al.*, 1993), the radula consists only of marginal teeth that are usually enrolled with completely overlapping edges (hypodermic). Teeth at their formation in the radular sac are already enrolled and they are attached to the radular membrane only by their bases, sometimes through a long flexible ligament. In the 'turrids' with enrolled teeth, these are attached to the membrane along most of its length (Kantor & Taylor, 2000). A molecular phylogeny of the Conidae is currently in preparation (C. Meyer, personal communication).

Included genera:
Africonus Petuch, 1975[1]
Asprella Schaufuss, 1869[1]
[= *Embrikena* Iredale, 1937]
[= *Fumiconus* da Motta, 1991]
[= *Graphiconus* da Motta, 1991]
Austroconus Tucker & Tenorio, 2009[1]
Bathyconus Tucker & Tenorio, 2009[1]
Calamiconus Tucker & Tenorio, 2009[1]
Calibanus da Motta, 1991[1]
Californiconus Tucker & Tenorio, 2009[3]
Chelyconus Mörch, 1852[1]
Conasprella Thiele, 1929[3]
Conasprelloides Tucker & Tenorio, 2009[1]
Conus Linnaeus, 1758[3]
[= *Coronaxis* Swainson, 1840]
[= *Cucullites* Herrmannsen, 1847]
[= *Cucullus* Röding, 1798]
Cylindrus Batsch, 1789[1] (For authorship of *Cylindrus*, see Dubois & Bour (2010))
[= *Cylinder* Montfort, 1810]
[= *Cylindrella* Swainson, 1840]
Dalliconus Tucker & Tenorio, 2009[1]

Darioconus Iredale, 1930[1]
[= *Erythroconus* da Motta, 1991]
[= *Regiconus* Iredale, 1930]
Dauciconus Cotton, 1945[1]
[= *Cariboconus* Petuch, 1991]
Dendroconus Swainson, 1840[1]
[= *Clebula* Iredale, 1930]
Ductoconus da Motta, 1991[1]
Dyraspis Iredale, 1949[1]
Endemoconus Iredale, 1931[1]
[= *Kermasprella* Powell, 1958]
[= *Mamiconus* Cotton & Godfrey, 1932]
Eremiconus Tucker & Tenorio, 2009[1]
Eugeniconus da Motta, 1991[1]
Floraconus Iredale, 1930[1]
Fulgiconus da Motta, 1991[1]
[= *Thoraconus* da Motta, 1991]
Fusiconus da Motta, 1991[1]
Gastridium Modeer, 1793[1]
[= *Rollus* Montfort, 1810]
[= *Tuliparia* Swainson, 1840]
Genuanoconus Tucker & Tenorio, 2009[1]
Gladioconus Tucker & Tenorio, 2009[1]
Globiconus Tucker & Tenorio, 2009[1]
Gradiconus da Motta, 1991[1]
Harmoniconus da Motta, 1991[1]
Hermes Montfort, 1810[1]
[= *Theliconus* Swainson, 1840]
Jaspidiconus Petuch, 2003[1]
Kalloconus da Motta, 1991[1]
Kenyonia Brazier, 1896[1]
Ketyconus da Motta, 1991[1]
Kioconus da Motta, 1991[1]
[= *Ongoconus* da Motta, 1991]
Kohniconus Tucker & Tenorio, 2009[1]
Kuradoconus Shikama & Habe, 1968[1]
Lamniconus da Motta, 1991[1]
Lautoconus Monterosato, 1923[1]
Leporiconus Iredale, 1930[1]
Leptoconus Swainson, 1840[1]
Lilliconus Raybaudi Massilia, 1994[1]
Lindaconus Petuch, 2002[1]
[= *Calusaconus* Petuch, 2003]
[= *Spuriconus* Petuch, 2003]
[= *Utriculus* Schumacher, 1817]
Lithoconus Mörch, 1852[1]
[= *Tesselliconus* da Motta, 1991]
Lividoconus Wils, 1970[1]
[= *Splinoconus* da Motta, 1991]
Miliariconus Tucker & Tenorio, 2009[1]
Monteiroconus da Motta, 1991[1]
Nataliconus Tucker & Tenorio, 2009[1]
Parviconus Cotton & Godfrey, 1932[1]
Perplexiconus Tucker & Tenorio, 2009[1]
Phasmoconus Mörch, 1852[1]
Pionoconus Mörch, 1852[1]
[= *Heroconus* da Motta, 1991]
[= *Socioconus* da Motta, 1991]
[= *Strioconus* Thiele, 1929]
Plicaustraconus Moolenbeek 2008[1]
Profundiconus Kuroda, 1956[3]
[= *Lizaconus* da Motta, 1991]
Protoconus da Motta, 1991[1] [invalid name]
[= *Seminoleconus* Petuch, 2003]
Protostrioconus Tucker & Tenorio, 2009[1]
Pseudoconorbis Tucker & Tenorio, 2009[1]
Pseudolilliconus Tucker & Tenorio, 2009[1]
Pseudonoduloconus Tucker & Tenorio, 2009[1]
Puncticulis Swainson, 1840[1]
Purpuriconus da Motta, 1991[1]
[= *Magelliconus* da Motta, 1991]
Pyruconus Olsson, 1967[1]
Quasiconus Tucker & Tenorio, 2009[1]
Rhizoconus Mörch, 1852[1]
Rhombiconus Tucker & Tenorio, 2009[1]
[= *Rhombus* Montfort, 1810]
Rolaniconus Tucker & Tenorio, 2009[1]
Sciteconus da Motta, 1991[1]
Stellaconus Tucker & Tenorio, 2009[1]
Stephanoconus Mörch, 1852[1]
Strategoconus da Motta, 1991[1]
Taranteconus Azuma, 1972[3]
[= *Cornutoconus* Suzuki, 1972]
Textilia Swainson, 1840[1]
Trovaoconus Tucker & Tenorio, 2009[1]
Turriconus Shikama & Habe, 1968[1]
Varioconus da Motta, 1991[1]
Viminiconus Tucker & Tenorio, 2009[1]
Virgiconus Cotton, 1945[1]
Virroconus Iredale, 1930[1]
Vituliconus da Motta, 1991[1]
Ximeniconus Emerson & Old, 1962[1]
Yeddoconus Tucker & Tenorio, 2009[1]

Conorbidae de Gregorio, 1880
(Figs 2O, 22C)

Diagnosis (from Tucker & Tenorio, 2009): "Radular tooth: anterior fold is usually present; basal spur is directed toward the apex of the tooth or parallel with the tooth base; the waist, base and C-fold are absent; terminating cusps, serratins and accessory process are also absent. Shell characters: the interior of the shell is extensively remodelled including the columellar region; nodules are absent but cords may be present. Shells can be squatly conical to elongated or biconical."

Remarks: The type genus of the family is *Conorbis* Swainson, 1840, based on an Eocene type species. The only Recent species that was believed to belong to *Conorbis*, *Conus coromandelicus* E.A. Smith, 1894, was made the type of the new genus *Pseudoconorbis* Tucker & Tenorio, 2009, and included by them in their family Conilithidae (herein in Conidae). In the molecular phylogeny of Puillandre *et al.* (2011), what we have identified as '*Benthofascis*' constitutes an independent lineage (i.e. not included in any other family-ranked clade), characterized by a long branch. This certainly explains why its position is not the same in the Maximum Likelihood analyses (sister group of the Borsoniidae) and in the Bayesian analyses (included in the Borsoniidae). *Benthofascis lozoueti* (the sequenced species) differs from other species of the genus in the absence of inner shell wall resorption (N. Puillandre, personal observations), but the phylogenetic and taxonomic value of this character remains unverified. The problem could be resolved by sequencing other species of *Benthofascis*, which have inner wall resorption. Until then we prefer to keep *Benthofascis lozoueti* within this genus and to apply the name Conorbidae to this lineage.

Included genera:
Artemidiconus da Motta, 1991[1]
Benthofascis Iredale, 1936 [3]

Borsoniidae A. Bellardi, 1875
[=Zemaciinae Sysoev, 2003, **new synonym**]
(Figs 2A–N, 3)

Diagnosis: Shell small to large (5–80 mm), fusiform to biconic, sometimes with strong to obsolete columellar pleats. Sculpture

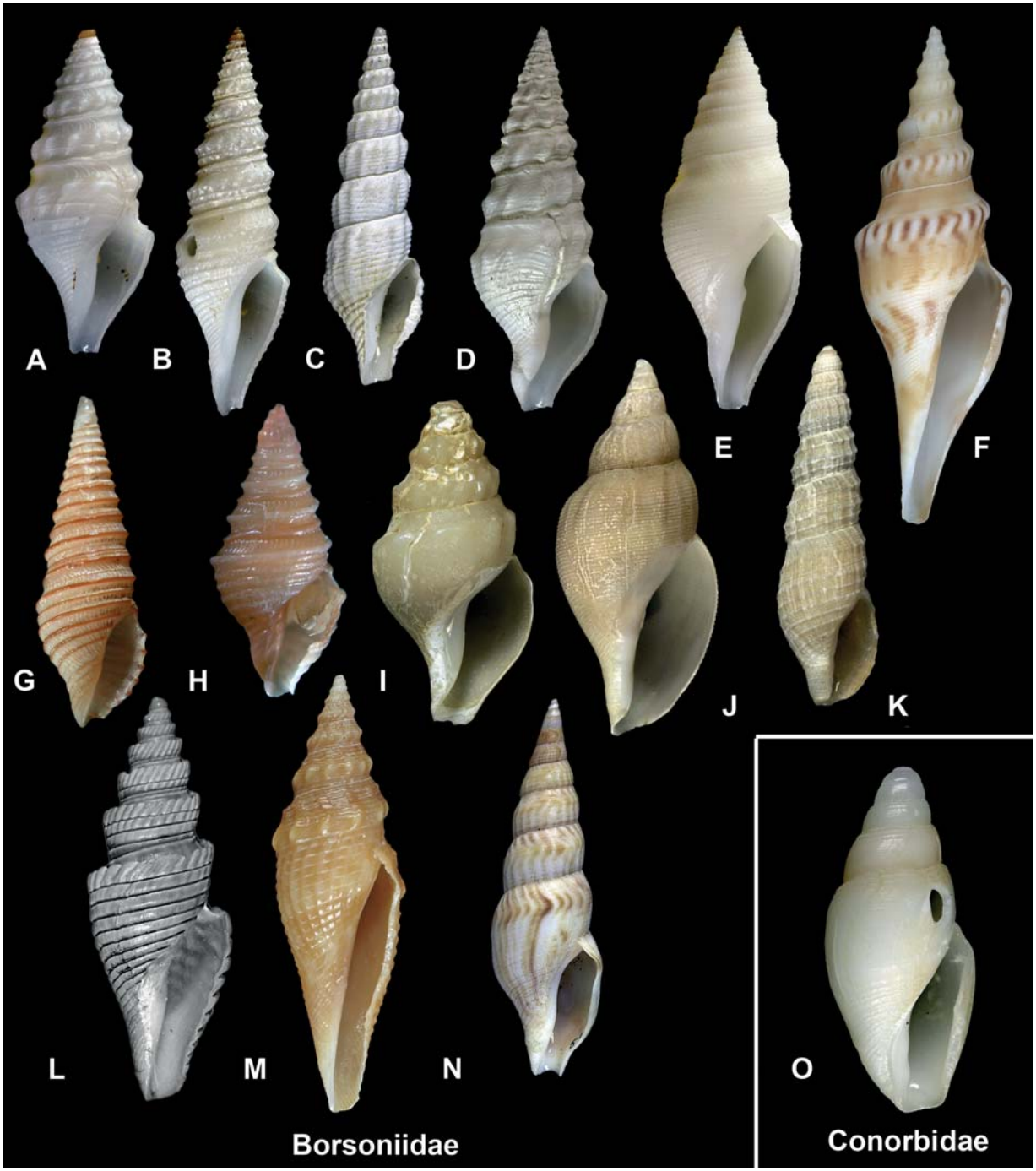

Figure 2. Shells. **A**–**N.** Borsoniidae. **A.** *Typhlomangelia* sp.**, MNHN IM200717931, Solomon Islands, SALOMON 2, st. CP2269, 07°45.1′S, 156°56.3′E, 768–890 m, SL 14.2 mm. **B.** Borsoniidae gen. 1**, MNHN IM200717911, Philippines, PANGLAO 2005, st. CP2333, 9°38.2′N, 123°43.5′E, 584–596 m, SL 17.1 mm (radula: Fig. 3D). **C.** *Darbya lira* Bartsch, 1934, USNM 810565, off Puerto Rico, SL 19.4 mm. **D.** *Borsonia* sp.**, MNHN IM200717932, Solomon Islands, SALOMON 2, st. CP2197, 08°24.4′S, 159°22.5′E, 897–1057 m, male, SL 24.6 mm (radula: Fig. 3B). **E.** *Bathytoma neocaledonica* Puillandre *et al*., 2010**, paratype, MNHN IM200717857, Coral Sea, EBISCO, st. CP2551, SL 44 mm (radula: Fig. 3C). **F.** *Zemacies excelsa* Sysoev & Bouchet, 2001**, MNHN IM200911056, New Caledonia, Musorstom 4, st. DW226, 22°47′S, 167°22′E, 395 m, SL 38 mm. **G.** *Tomopleura reevii* (C. B. Adams, 1850)**, MNHN IM200717875, Philippines, PANGLAO 2004, st. T26, 09°43.3′N, 123°48.8′E, 123–135 m, SL 7.7 mm. **H.** *Microdrillia* cf. *optima* (Thiele, 1925)**, MNHN IM200717887, Philippines, PANGLAO 2004, st. T36, 09°29.3′N, 123°51.5′E, 95–128 m, SL unknown (broken). **I.** *Borsonellopsis chrysothemis* (Dall, 1919), SIO (Scripps Institution of Oceanography) M2530, San Diego Trough, off San Diego Co., California, 1244 m, SL 19.3 mm. **J.** *Belaturricula turrita* (Strebel, 1908), USNM 897559, South Georgia Island, 54.3°S, 35.6°W, 238–247 m, SL 49.8 mm. **K.** *Glyptaesopus oldroydi* (Arnold, 1903). 10 m, off Punta Abreojos, Baja California, Mexico, SL 8.3 mm. **L.** *Tropidoturris fossata fossata* (Sowerby, 1903), holotype, SAMC A346, off Cape Vidal, Zululand, 146–182 m, SL 20.4 mm. **M.** *Genota mitriformis* (Wood, 1828)**, MNHN IM200742293, Angola, 30–50 m, SL 30 mm (radula: Fig. 3A). **N.** *Ophiodermella inermis* (Hinds, 1843), USNM 56092, W coast of North America, SL 40.7 mm. **O:** Conorbidae. **O.** *Benthofascis lozoueti* Sysoev & Bouchet, 2001**, MNHN IM200742331, New Caledonia, NORFOLK 2, st. DW2147, 22°50′S, 167°16′E, 496 m, SL 16.5 mm. Abbreviation and symbols: SL, shell length; * , sequenced species; **, sequenced specimen. Photo credits: B. Buge (A, B, D, E, G, H), M.G. Harasewych and D. Tippett (C, J, N), R.N. Kilburn (L), J. McLean (I, K).

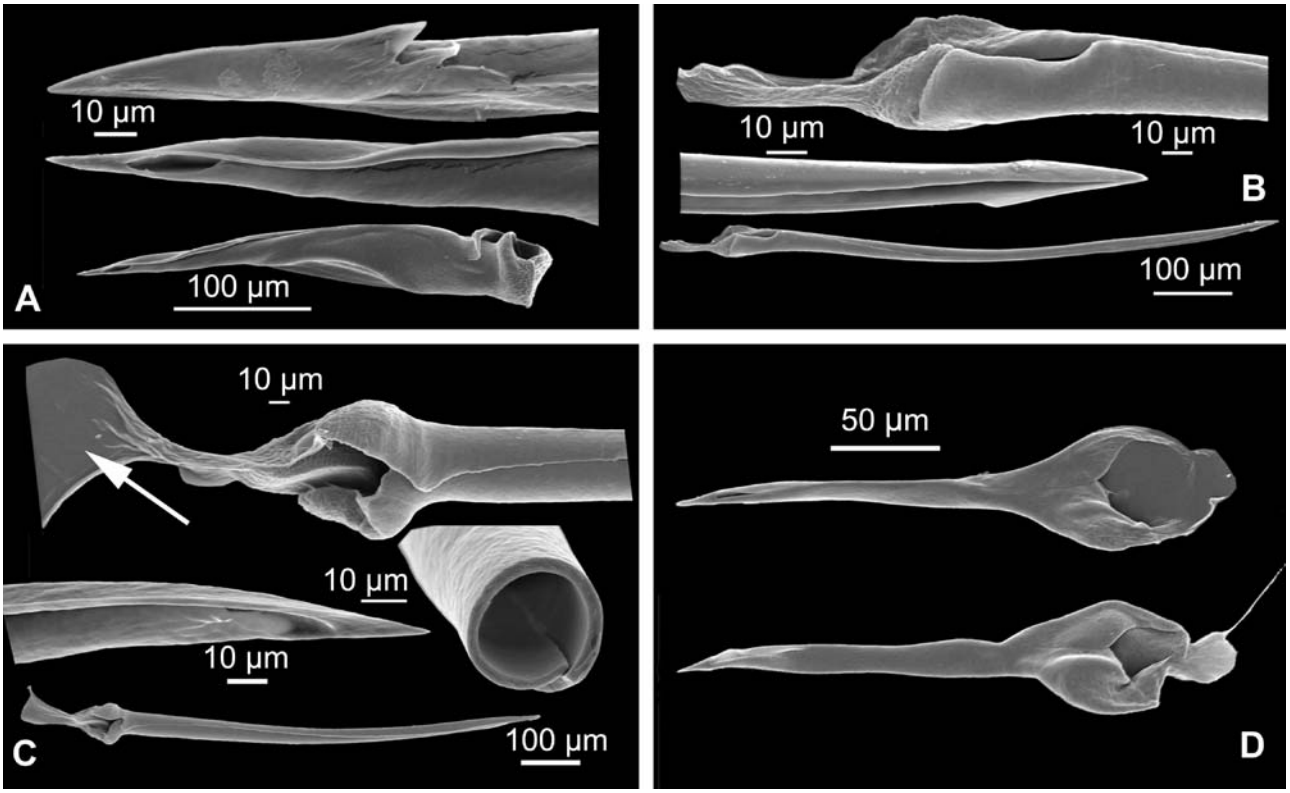

Figure 3. Radulae. Borsoniidae. **A.** *Genota mitriformis* (Wood, 1828)**, MNHN IM200742293 (shell: Fig. 2M). **B.** *Borsonia* sp.**, MNHN IM200717932 (shell: Fig. 2D). **C.** *Bathytoma neocaledonica* Puillandre *et al.*, 2010**, MNHN IM200717857 (shell: Fig. 2E). **D.** Borsoniidae gen. 1**, MNHN IM200717911 (shell: Fig. 2B). Symbol: **, sequenced specimen.

usually well developed, axial ribs sometimes obsolete to absent. Siphonal canal short to moderately long. Anal sinus on subsutural ramp, deep. Protoconch when multispiral with up to five whorls, initially smooth and then with arcuate axial riblets, when paucispiral up to two smooth whorls. Operculum with terminal nucleus, fully developed to missing. Radula of hypodermic marginal teeth that usually have a weakly developed solid basal part, often attached to the ligament (marked by an arrow on Fig. 3C). Tooth canal opening (sub)terminally or, sometimes, laterally. At their tip teeth can have weak to rather strong barb(s) (*Genota*, Fig. 3A). Overlapping of the tooth edges is weak (Fig. 3C). In *Zemacies*, the radula is completely absent.

Remarks: This is a rather heterogeneous group. Obviously, it is not fully resolved as it is based on molecular data and comprises rather conchologically different clades. This could be explained by the fact that many taxa of this group are among most ancient of conoideans, known since the Palaeocene (*Zemacies*, *Borsonia*, *Tomopleura*) or Eocene (*Bathytoma*, *Genota*, *Microdrillia*). The loss of apomorphies by mutation could be more important for old taxa (Puillandre *et al.*, 2011).

The names Borsoniinae Bellardi, 1875, and Pseudotominae Bellardi, 1875, were established simultaneously. As First Revisers, under Art. 24 of the ICZN Code, we here give precedence to the former over the latter.

Included genera:
?*Apaturris* Iredale, 1917[1]
Aphanitoma Bellardi, 1875[1]
Asthenotoma Harris & Burrows, 1891[1]
Austroturris Laseron, 1954[1]
Bathytoma Harris & Burrows, 1891[3]
(*Micantapex* Iredale, 1936)
(*Parabathytoma* Shuto, 1961)
(*Riuguhdrillia* Oyama, 1951)
?*Belaturricula* Powell, 1951[2]
Borsonella Dall, 1908[2]
Borsonellopsis McLean, 1971[1]
Borsonia Bellardi, 1839[3]
(*Boettgeriola* Wenz, 1943)
Cordieria Rouault, 1848[1]
Darbya Bartsch, 1944[1]
Diptychophlia Berry, 1964[1]
Drilliola Cossmann, 1903[2]
Filodrillia Hedley, 1922[1]
Genota H. Adams & A. Adams, 1853[3]
[= *Genotia* Fischer, 1883]
?*Glyptaesopus* Pilsbry & Olsson, 1941[2]
Heteroturris Powell, 1967[1]
Maoritomella Powell, 1942[2]
[= *Narraweena* Laseron, 1954]
Microdrillia Casey, 1903[3]
[= *Acropota* Nordsieck, 1977]
Ophiodermella Bartsch, 1944[2]
Paraborsonia Pilsbry, 1922[1]
Phenatoma Finlay, 1924[2]
Pulsarella Laseron, 1954[2]
Retidrillia McLean, 2000[1]
Suavodrillia Dall, 1908[2]
Tomopleura Casey, 1904[3]
Tropidoturris Kilburn, 1986[2]
?*Typhlodaphne* Powell, 1951[1]
Typhlomangelia G.O. Sars, 1878[3]
[= *Viridoturris* Powell, 1964]
[= *Vexithara* Finlay, 1926]
Zemacies Finlay, 1926[3]

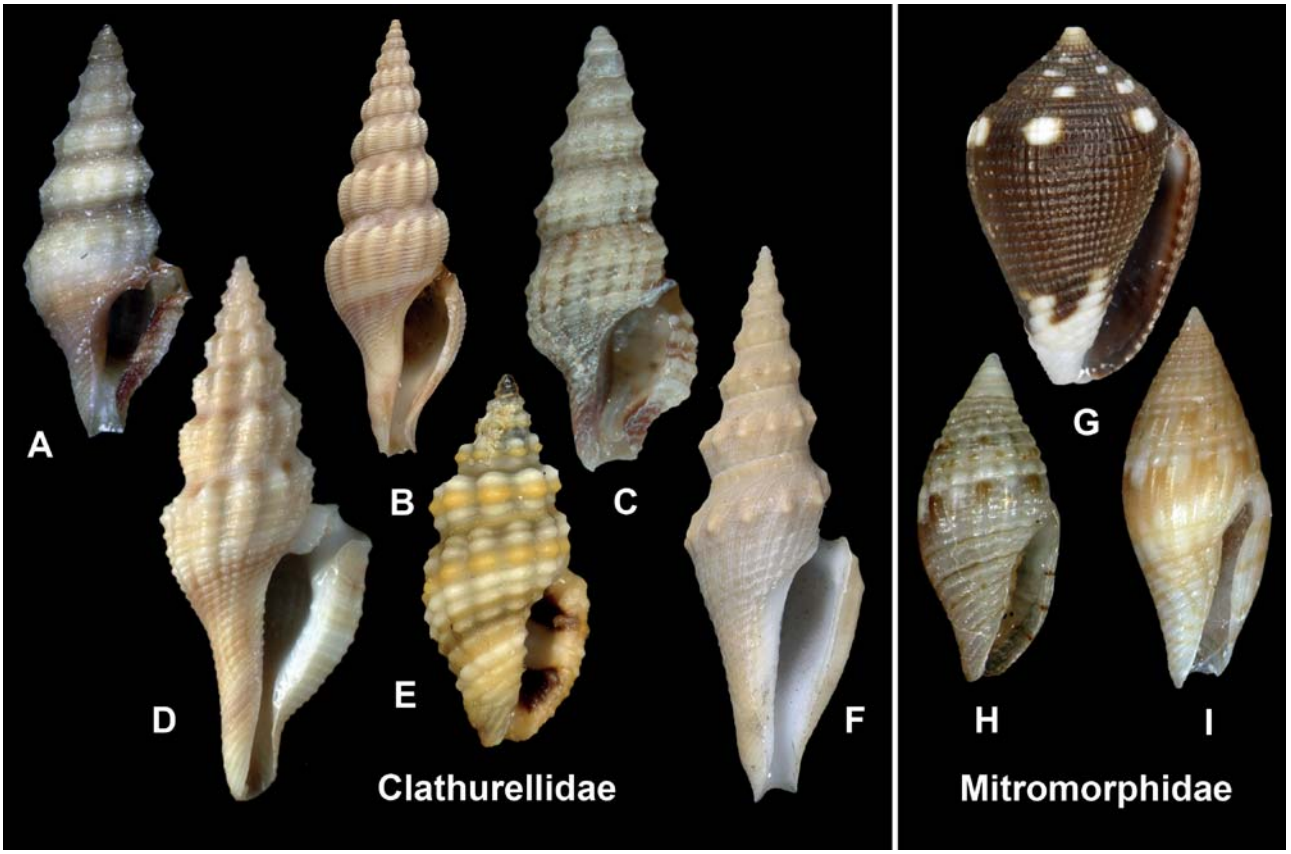

Figure 4. Shells. **A–F.** Clathurellidae. **A.** *Nannodiella ravella* (Hedley, 1922)*, MNHN IM200742350, Philippines, PANGLAO 2004, st. T9, 09°33.5′N, 123°49.5′E, 97–120 m, SL 5.8 mm (radula: Fig. 5A). **B.** *Comarmondia gracilis* (Montagu, 1803), MNHN, Le Brusc, Cap Sicié, Provence, France, 40–100 m, SL 23 mm. **C.** *Etrema* cf. *tenera* (Hedley, 1899)**, MNHN IM200717869, Philippines, PANGLAO 2004, st. S21, 09°41.7′N, 123°50.9′E, 4–12 m, SL unknown (broken). **D.** *Glyphostoma rostrata* Sysoev & Bouchet, 2001, MNHN, New Caledonia, BATHUS 4, st. DW896, 20°16′S, 163°52′E, 315–350 m, SL 21.5 mm. **E.** *Lienardia nigrotincta* (Montrouzier, 1872)*, MNHN, Touho, New Caledonia, 20°45.2′S, 165°16.3′E, intertidal, SL 6.9 mm (radula: Fig. 5B). **F.** *Strombinoturris crockeri* Hertlein & Strong, 1951, LACM 747–37, off Isabel Island, Mexico, 18–33 m, SL 47.5 mm. **G–I:** Mitromorphidae. **G.** *Lovellona atramentosa* (Reeve, 1849)*, MNHN, Philippines, PANGLAO 2004, st. M2, 09°32.8′N, 123°45.9′E, 0–2 m, SL 9.0 mm (radula: Fig. 6A). **H.** *Mitromorpha metula* (Hinds, 1843)*, MNHN IM200742339, Philippines, PANGLAO 2004, st. B8, 09°37.1′N, 123°46.1′E, 3 m, SL 3.1 mm (radula: Fig. 6B). **I.** *Anarithma* sp.*, MNHN, Philippines, PANGLAO 2004, st. S5, 09°37.1′N, 123°46.1′E, 2–4 m, SL 6.9 mm (radula: Fig. 6C). Abbreviation and symbols: SL, shell length; * , sequenced species; **, sequenced specimen. Photo credits: B. Buge (C), M.G. Harasewych and D. Tippett (F), P. Maestrati (D, E).

Clathurellidae H. Adams & A. Adams, 1858
(Figs 4A–F, 5)

Diagnosis: Shell small- to medium-sized (5–40, usually 10–20 mm), fusiform to broadly fusiform, subsutural ramp usually unclearly separated. Sculpture mostly strong, usually cancellate, subsutural fold lacking. Shell surface often microgranular. Apertural armature often well developed, in the form of pleats and denticles on both inner and outer lips; no true columellar pleats. Siphonal canal well expressed, moderately long. Anal sinus on subsutural ramp, deep, often (sub)tubular. Protoconch typically multispiral, up to six whorls, generally smooth with keeled last whorls; when paucispiral, protoconch usually smooth or spirally striated, sometimes with remaining carination in last portion. Operculum always absent. Radula of hypodermic marginal teeth that usually have relatively small solid basal part (Fig. 5). Distinct ligaments not found. At their tip, teeth can have a weak barb.

Included genera:
Acrista Hedley, 1922[1]
?*Adanaclava* Bartsch, 1950[1]
?*Clathromangelia* Monterosato, 1884[1]
Clathurella Carpenter, 1857[3]
Comarmondia Monterosato, 1844[1]
[= *Bellatula* Strand, 1929]
Corinnaeturris Bouchet & Warén, 1980[2]
Crockerella Hertlein & Strong, 1951[2]
Etrema Hedley, 1918[3]
[= *Iraquetrema* Dance & Eames, 1966]
(*Etremopa* Oyama, 1953)
(*Etremopsis* Powell, 1942)
Euclathurella Woodring, 1928[1]
Glyphostoma Gabb, 1872[2]
(*Euglyphostoma* Woodring, 1970)
(*Glyphostomops* Bartsch, 1934)
Lienardia Jousseaume, 1884[1]
(*Thetidos* Hedley, 1899)
Nannodiella Dall, 1919[3]
Paraclathurella Boettger, 1895[1]
Pseudoetrema Oyama, 1953[1]
Strombinoturris Hertlein & Strong, 1951[2]
Turrella Laseron, 1954[1]

Mitromorphidae Casey, 1904, **new rank**
(Figs 4F–H, 6)

Diagnosis: Shell small- to medium-sized, 3–30 mm, usually 5–10 mm high, biconic, of mitriform shape. Sculpture

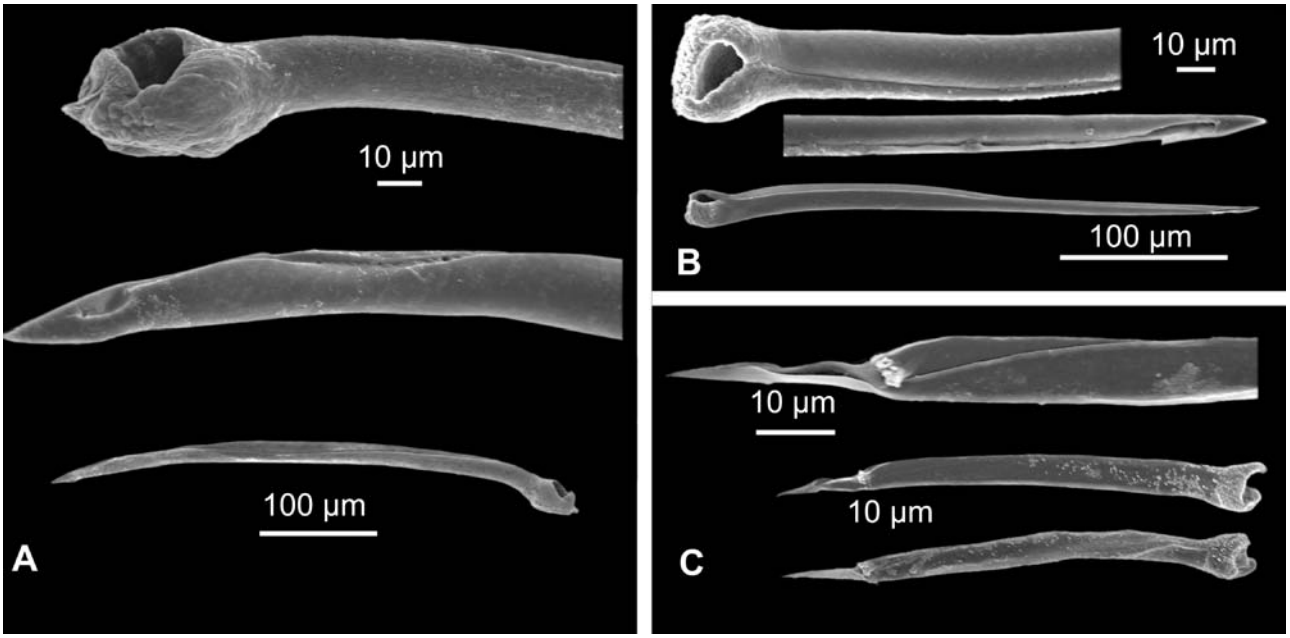

Figure 5. Radulae. Clathurellidae. **A.** *Nannodiella ravella* (Hedley, 1922)*, MNHN IM200742350 (shell: Fig. 4A). **B.** *Lienardia nigrotincta* (Montrouzier, 1872)*, MNHN (shell: Fig. 4E). **C.** *Lienardia jousseaumei* (Hervier, 1896), MNHN, Philippines, PANGLAO 2004, st. B7, 9°35.9′N, 123°51.8′E, 4–30 m. Symbol: *, sequenced species.

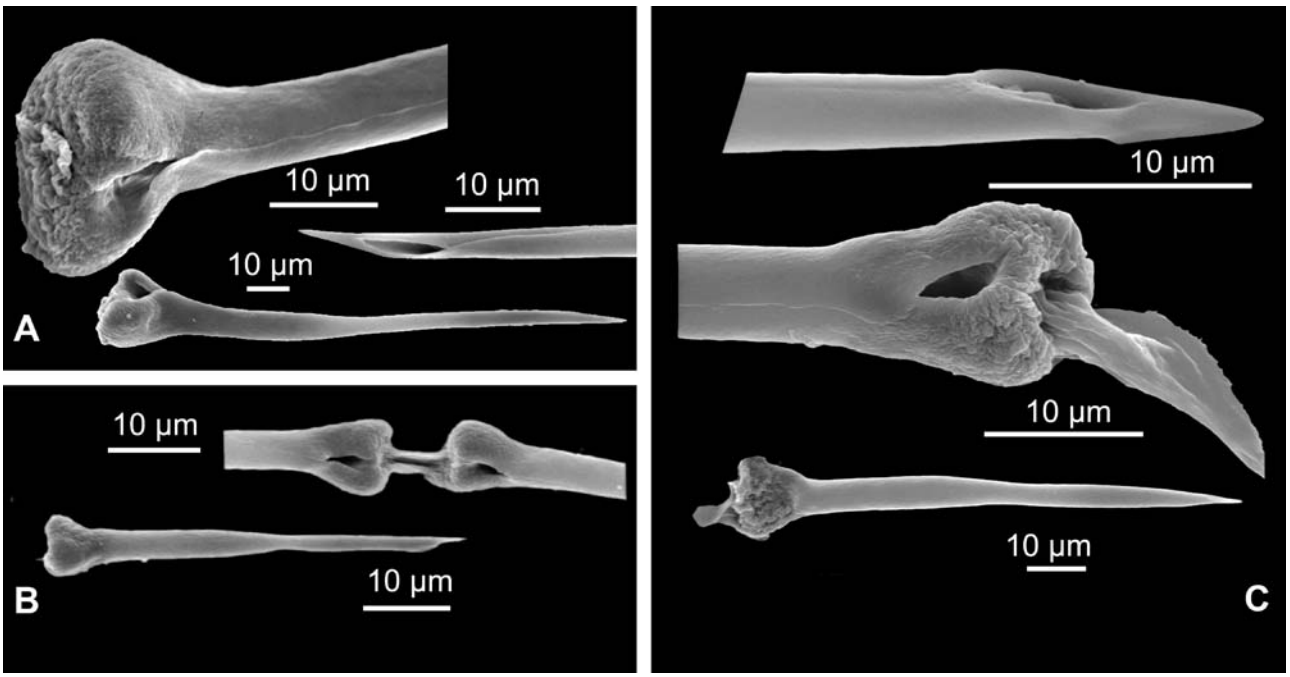

Figure 6. Radulae. Mitromorphidae. **A.** *Lovellona atramentosa* (Reeve, 1849)*, MNHN (shell: Fig. 4G). **B.** *Mitromorpha metula* (Hinds, 1843), MNHN IM200742339 (shell: Fig. 4H). **C.** *Anarithma* sp.*, MNHN (shell: Fig. 4 I). Symbol: *, sequenced species.

rather smooth, with dominant spiral elements. Aperture narrow, with or without 1–3 columellar pleats, sometimes with denticles within. Siphonal canal short or indistinct. Anal sinus from indistinct to rather shallow indentation on weakly pronounced subsutural ramp. Protoconch multispiral or paucispiral, up to 4.5 smooth whorls. No operculum. Radula of hypodermic, marginal, relatively short, awl-shaped teeth with large swollen solid basal part (Fig. 6). Distinct ligaments present, short. Tooth canal opening subterminally or laterally. At their tip, teeth can have a weak barb (Fig. 6C).

Remarks: Mitrolumninae was established as a substitute name for Diptychomitrinae. Mitromorphidae and Mitrolumninae were published the same year but Mitromorphidae (19 May 1904) has priority over Mitrolumninae (31 August 1904).

Included genera:
Anarithma Iredale, 1918[1]
Arielia Shasky, 1961[1]
(*Vexiariella* Shuto, 1983)
Lovellona Iredale, 1917[3]
Maorimorpha Powell, 1939[1]
Mitrellatoma Powell, 1942[1]
Mitromorpha Carpenter, 1865[3]
[= *Cymakra* Gardner, 1937]
[= *Helenella* Casey, 1904]
[= ?*Itia* Marwick, 1931]
[= *Mitrithara* Hedley, 1922]
[= *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883]
Scrinium Hedley, 1922[1]

Mangeliidae P. Fischer, 1883, **new rank**
[= Oenopotinae Bogdanov, 1987, **new synonym**]
(Figs 7, 8)

Diagnosis: Shell small to medium size, 3–30 mm, usually 6–12 mm, oval to low- or high-fusiform, usually with comparatively low spire, often with a shoulder angulation. Spiral and axial sculpture both well developed. Shell surface often bearing microsculpture of spirally aligned granules. Subsutural ramp usually not separated sculpturally. Anal sinus on subsutural ramp, shallow to rather deep, rarely tubular. Aperture normally not constrained with strong outgrowths or callus pads, rarely denticulate. Siphon rather short to moderately long. Protoconch typically multispiral, of up to five whorls, with axially ribbed protoconch II; spiral cords on protoconch II present or absent. When paucispiral, protoconch usually spirally lirate. Operculum present, with terminal nucleus (Oenopotinae), or normally absent. Radula of marginal teeth of very variable morphology. Teeth can be from semi-enrolled (Fig. 8F, G) to true hypodermic. Frequently side projections around the base are present and there is large irregularly shaped 'root' projecting from the base. Barbs may be present, from small to very large (Fig. 8C) or absent (Fig. 8B). Tooth canal opening laterally.

Included genera:
Acmaturris Woodring, 1928[1]
Agathotoma Cossmann, 1899[2]
Anticlinura Thile, 1934[3]
[= *Clinuromella* Beets, 1943]
Apispiralia Laseron, 1954[1]
Apitua Laseron, 1954[1]
Bactrocythara Woodring, 1928[1]
Bela Gray, 1847[2]
[= *Ginnania* Monterosato, 1884]
[= *Smithiella* Monterosato, 1890]
Bellacythara McLean, 1971[2]
Benthomangelia Thiele, 1925[3]
Brachycythara Woodring, 1928[1]
?*Cacodaphnella* Pilsbry & Lowe, 1932[1]
Citharomangelia Kilburn, 1992[2]
Cryoturris Woodring, 1828[1]
Curtitoma Bartsch, 1941[2]
[= *Nematoma* Bartsch, 1941]
[= *Widalli* Bogdanov, 1986]
Cytharopsis A. Adams, 1865[1]
Eucithara Fischer, 1883[3]
[= ?*Cythara* Schumacher, 1817]
?*Euryentmema* Woodring, 1928[1]
Fehria van Aartsen, 1988[1]
Genotina Vera-Peláez, 2004[1]
Gingicithara Kilburn, 1992[2]
Glyphoturris Woodring, 1928[1]
Granotoma Bartsch, 1941[2]
Granoturris Fargo, 1953[1]
Guraleus Hedley, 1918[2]
(*Euguraleus* Cotton, 1947)
Hemicythara Kuroda & Oyama in Kuroda, Habe & Oyama, 1971[1]
Heterocithara Hedley, 1922[3]
Ithycythara Woodring, 1928[2]
Kurtzia Bartsch, 1944[2]
Kurtziella Dall, 1918[2]
Kurtzina Bartsch, 1944[2]
Leiocithara Hedley, 1922[1]
Liracraea Odhner, 1924[2]
?*Macteola* Hedley, 1918[1]
Mangelia Risso, 1826[2]
[= *Cyrtocythara* Nordsieck, 1977]
[= *Cytharella* Monterosato, 1875]
[= *Lyromangelia* Nordsieck, 1977]
[= *Mangiliella* Bucqoy, Dautzenberg & Dollfus, 1883]
[= *Rissomangelia* Monterosato, 1917]
[= *Rugocythara* Nordsieck, 1977]
[= *Villiersiella* Monterosato, 1884]
Marita Hedley, 1922[1]
Mitraguraleus Laseron, 1954[1]
?*Neoguraleus* Powell, 1939[2]
?*Notocytharella* Hertlein & Strong, 1955[1]
Obesotoma Bartsch, 1941[2]
Oenopota Mörch, 1852[3]
(*Nodotoma* Bartsch, 1941)
Oenopotella Sysoev, 1988[1]
Papillocithara Kilburn, 1992[1]
?*Paraspirotropis* Sysoev & Kantor, 1984[2]
Perimangelia McLean, 2000[1]
Platycythara Woodring, 1928[1]
Propebela Iredale, 1918[2]
[= *Antiguraleus* Powell, 1942]
[= ?*Belalora* Powell, 1951]
[= *Cestoma* Bartsch, 1941]
[= *Funitoma* Bartsch, 1941]
[= ?*Lorabela* Powell, 1951]
[= *Turritomella* Bartsch, 1941]
(*Canetoma* Bartsch, 1941)
Pseudorhaphitoma Boettger, 1895[2]
Pyrgocythara Woodring, 1928[2]
Rubellatoma Bartsch & Rehder, 1939[1]
Saccharoturris Woodring, 1928[1]
Stellatoma Bartsch & Rehder, 1939[1]
Suturocythara García, 2008[1]
Tenaturris Woodring, 1928[2]
Toxicochlespira Sysoev & Kantor, 1990[3]
?*Venustoma* Bartsch, 1941[1]
Vitjazinella Sysoev, 1988[1]
?*Vitricythara* Fargo, 1953[1]

Raphitomidae A. Bellardi, 1875
(Figs 9, 10)

Diagnosis: Shell very variable in shape and size, from buccinoid to ovate or to elongate-fusiform or high-cylindrical and from about 2 to over 140 mm high. Sculpture variously developed: from nearly smooth shell to well-developed spiral and axial elements, subsutural ramp, when separated from rest of the whorl, usually smooth or with traces of anal sinus growth. Apertural armature rarely well expressed, inner lip usually smooth. Anal sinus either subsutural, shaped as a 'reversed-L', or on subsutural ramp, asymmetric, very shallow to rather deep, typically not constrained but sometimes even almost

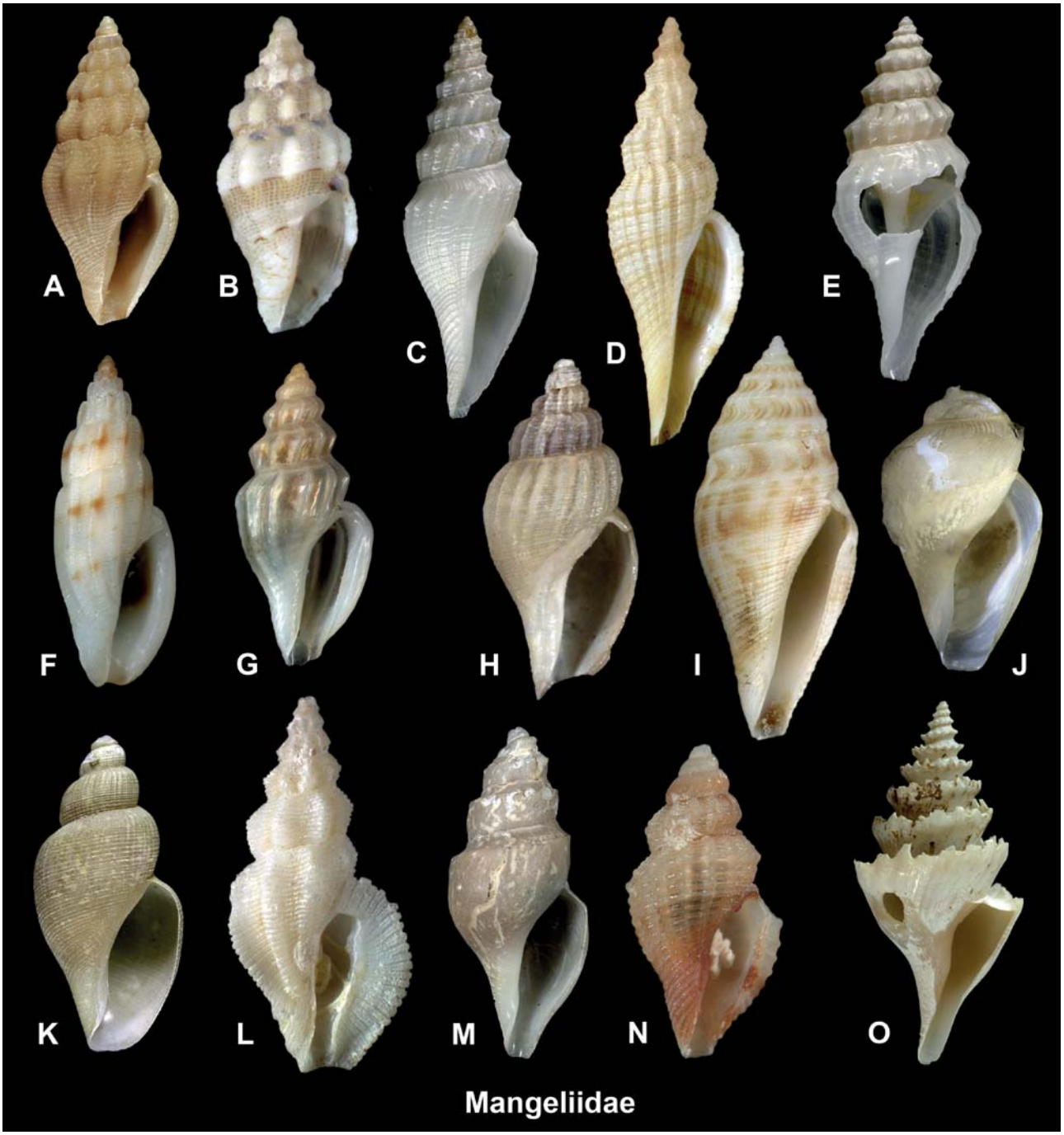

Figure 7. Shells. Mangeliidae. **A.** *Bela clarae* Peñas & Rolán, 2008, paratype, MNHN Moll 21396, Sitges, Vallcarca, Barcelona, Spain, 45–60 m, SL 7 mm. **B.** *Macteola segesta* (Duclos in Chenu, 1850), MNHN, LIFOU 2000, st. 1425, 20°46.8′S, 167°07.2′E, 4–5 m, SL 4.6 mm. **C.** *Benthomangelia* cf. *trophonoidea* (Schepman, 1913)**, MNHN IM200717835, Vanuatu, BOA1, st. CP2462, 16°38′S, 167°57′E, 618–641 m, SL 21 mm (radula: Fig. 8A). **D.** *Citharomangelia* sp., MNHN, Futuna Island, MUSORSTOM 7, st. DW504, 14°20′S, 178°04′E, 300–390 m, SL 15.4 mm. **E.** *Anticlinura* sp.**, MNHN IM200742513, Solomon Islands, SALOMON 2, st. CP2182, 08°47.0′S, 159°37.9′E, 762–1060 m, SL 17.3 mm (radula: Fig. 8E). **F.** *Eucithara* cf. *coronata* (Hinds, 1843)**, MNHN IM200717900, Philippines, PANGLAO 2004, st. B8, 09°37.1′N, 123°46.1′E, 3 m, SL 8.7 mm (radula: Fig. 8D). **G.** *Leiocithara* sp., MNHN, New Caledonia, BATHUS 2, st. DW719, 22°48′S, 167°16′E, 444–445 m, SL 5.4 mm. **H.** *Oenopota uschakovi* Bogdanov, 1985, holotype, ZIN 37974/1, Iturup Island, Kurile Islands, 44°24.2′N, 147°09′01″E. 160 m, SL 10.3 mm. **I.** *Genotina adamii* (Bozzetti, 1994), MNHN, LIFOU 2000, st. DW1650, 20°54.15′S, 167°01.7′E, 120–150 m, SL 20.0 mm. **J.** *Vitjazinella multicostata* Sysoev, 1988, Paratype, ZMMU 22356, Izu-Bonin Trench, 33°18′N, 149°46′E., 6096 m, SL 7.2 mm. **K.** *Oenopotella ultraabyssalis ultraabyssalis* Sysoev, 1988, holotype, ZMMU Lc-22681, Kurile-Kamchatka trench, 49°29′N, 158°41′E, 7210–7230 m, SL 12.8 mm. **L.** *Pseudorhaphitoma* sp., Coral Sea, Chestefield Plateau, 19 53′S, 158 40′E, 410 m, SL 9.7 mm. **M.** *Paraspirotropis simplicissima* (Dall, 1907), ZIN, off Shikotan I., S Kurile Islands, 1450–1530 m, SL 28.0 mm. **N.** *Heterocithara* sp.**, MNHN IM200717884, Philippines, PANGLAO 2004, st. L46, 09°30.9′N, 123°41.2′E, 90–110 m, SL 3.4 mm. **O.** *Toxicochlespira pagoda* Sysoev & Kantor, 1990**, MNHN IM200717925, Solomon Islands, SALOMON 2, st. CP2227, 6°37.2′N, 156°12.7′E, 508–522 m, SL 18.0 mm (radula: Fig. 8B)**.** Abbreviation and symbol: SL, shell length; **, sequenced specimen. Photo credits: B. Buge (F, O), P. Maestrati (B, D, G, I, L).

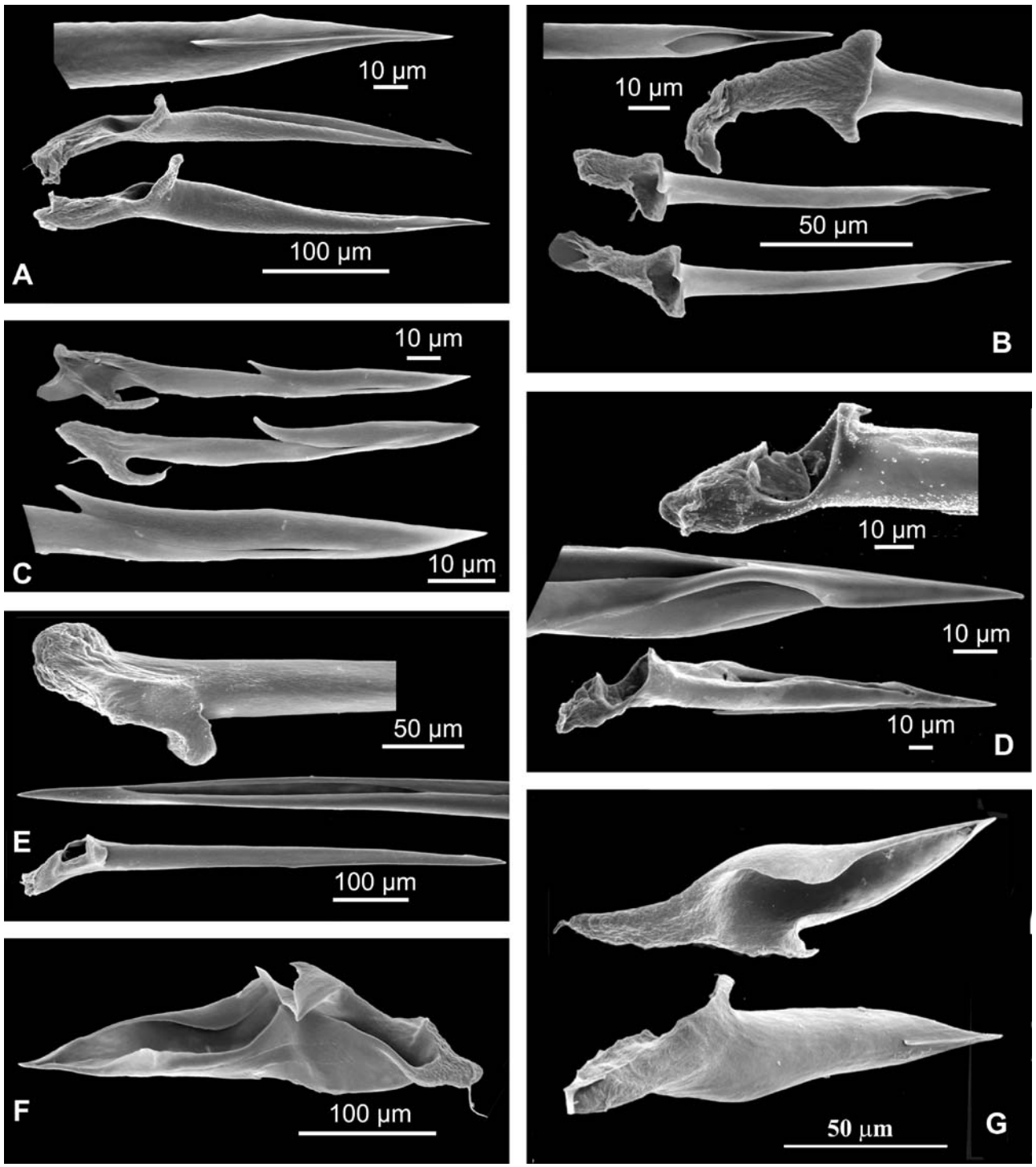

Figure 8. Radulae. Mangeliidae. **A.** *Benthomangelia trophonoidea* (Schepman, 1913), MNHN IM200717835 (shell: Fig. 7C). **B.** *Toxicochlespira pagoda* Sysoev & Kantor, 1990**, MNHN IM200717925 (shell: Fig. 7O). **C.** Mangeliinae gen. 2. MNHN IM200910331, Philippines, PANGLAO 2004, st. S26, 9°41.50′N, 123°51.00′E, 21 m, SL unknown (broken). **D.** *Eucithara* cf. *coronata* (Hinds, 1843)**, MNHN IM200717900 (shell: Fig. 7F). **E.** *Anticlinura* sp.**, MNHN IM200742513 (shell: Fig. 7E). **F.** Mangeliidae gen. sp., MNHN, Philippines, PANGLAO 2004, st. T26, 9°43.3′N, 123°48.8′E, 123–135 m. **G.** *Mangelia powisiana* (Dautzenberg, 1887). Plymouth, England, after Taylor *et al.* (1993). Symbol: **, sequenced specimen.

tubular. Siphon short to rather long. Protoconch typically planktotrophic, multispiral, of 2.5–6.5 whorls, protoconch I often spirally striated, protoconch II with diagonally cancellated sculpture. There are many variations of the basic pattern of the protoconch II sculpture, though a combination of spiral and axial elements is retained, with the latter usually more pronounced, but protoconchs with a spiral keel and axial pillars (Fig. 23) depart from this pattern. Paucispiral protoconch with predominantly spiral striation. No operculum. Radula of hypodermic marginal teeth of very variable

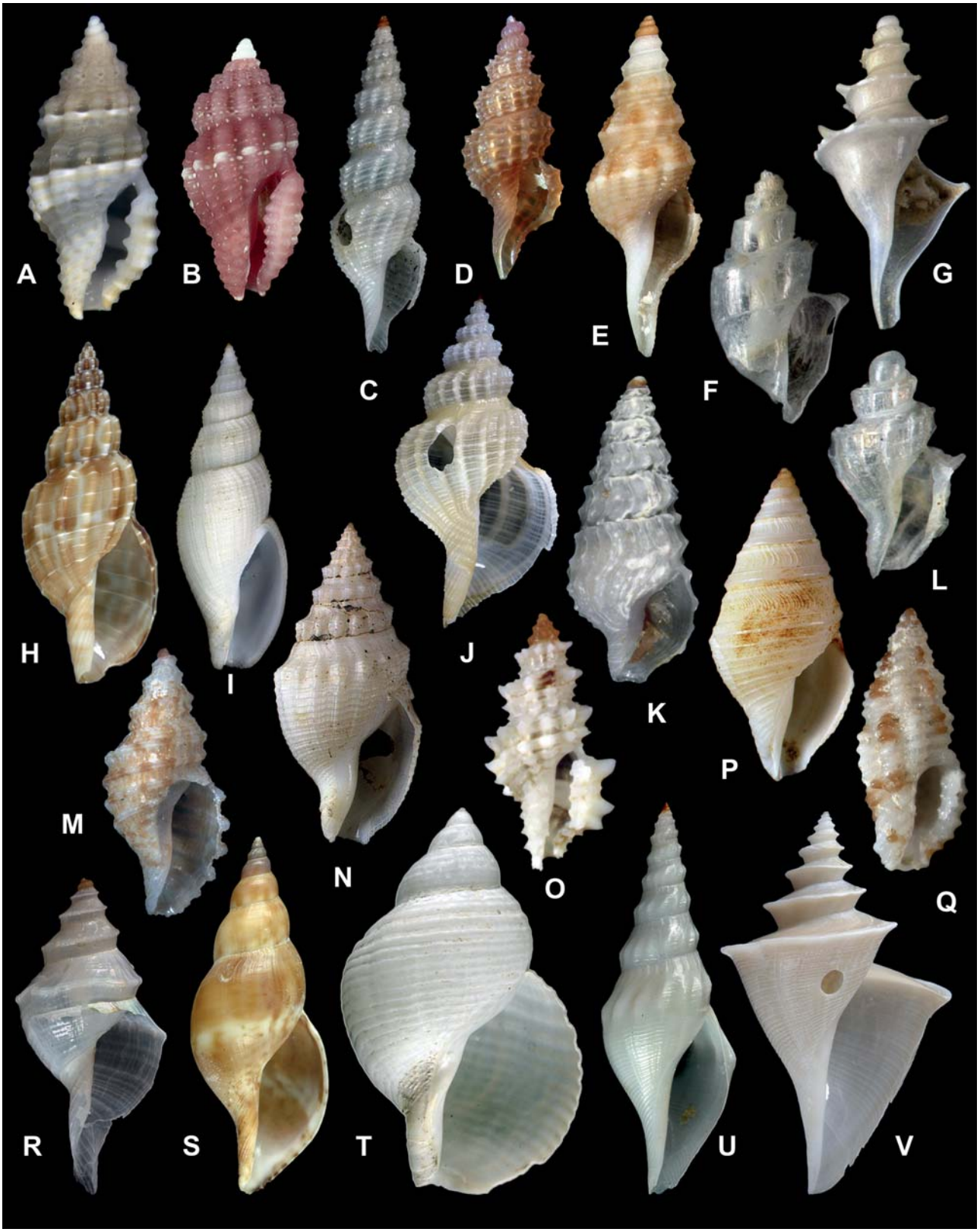

Figure 9. Shells. Raphitomidae. **A.** *Hemilienardia calcicincta* (Melvill & Standen, 1895)*, Philippines, PANGLAO 2004, st. B14, 09°38.5′N, 123°49.2′E, 2–4 m, SL 4.6 mm. **B.** *Hemilienardia malleti* (Recluz, 1852), MNHN, New Caledonia, MONTROUZIER, st. 1245, 20°45.2′S, 165°16.3′E, intertidal, SL 4.4 mm. **C.** *Rimosodaphnella* sp.**, MNHN IM200717836, Vanuatu, BOA1, st. CP2462, 16°37.5′S, 167°57.4′E, 618–641 m, SL 15.1 mm. **D.** *Veprecula* sp.**, MNHN IM200717883, Philippines, PANGLAO 2004, st. L46, 09°30.9′N, 123°41.2′E, 90–110 m, SL 3.4 mm. **E.** *Glyphostomoides* sp.**, MNHN IM200717892, Philippines, PANGLAO 2004, st. T39, 09°30′N, 123°50.4′E, 100–138 m, SL 7.0 mm. **F.** *Aliceia* sp., MNHN, Wallis Islands, MUSORSTOM 7, st. DW604, 13°21′S, 176°08′W, 415–420 m, SL 4.0 mm. **G.** *Thatcheriasyrinx orientis* (Melvill, 1904), MNHN, New Caledonia, 20°49′S, 165°19′E, 105–110 m, SL 3.6 mm. **H.** *Tritonoturris cumingii* (Powys in Powys & Sowerby, 1835), MNHN, New

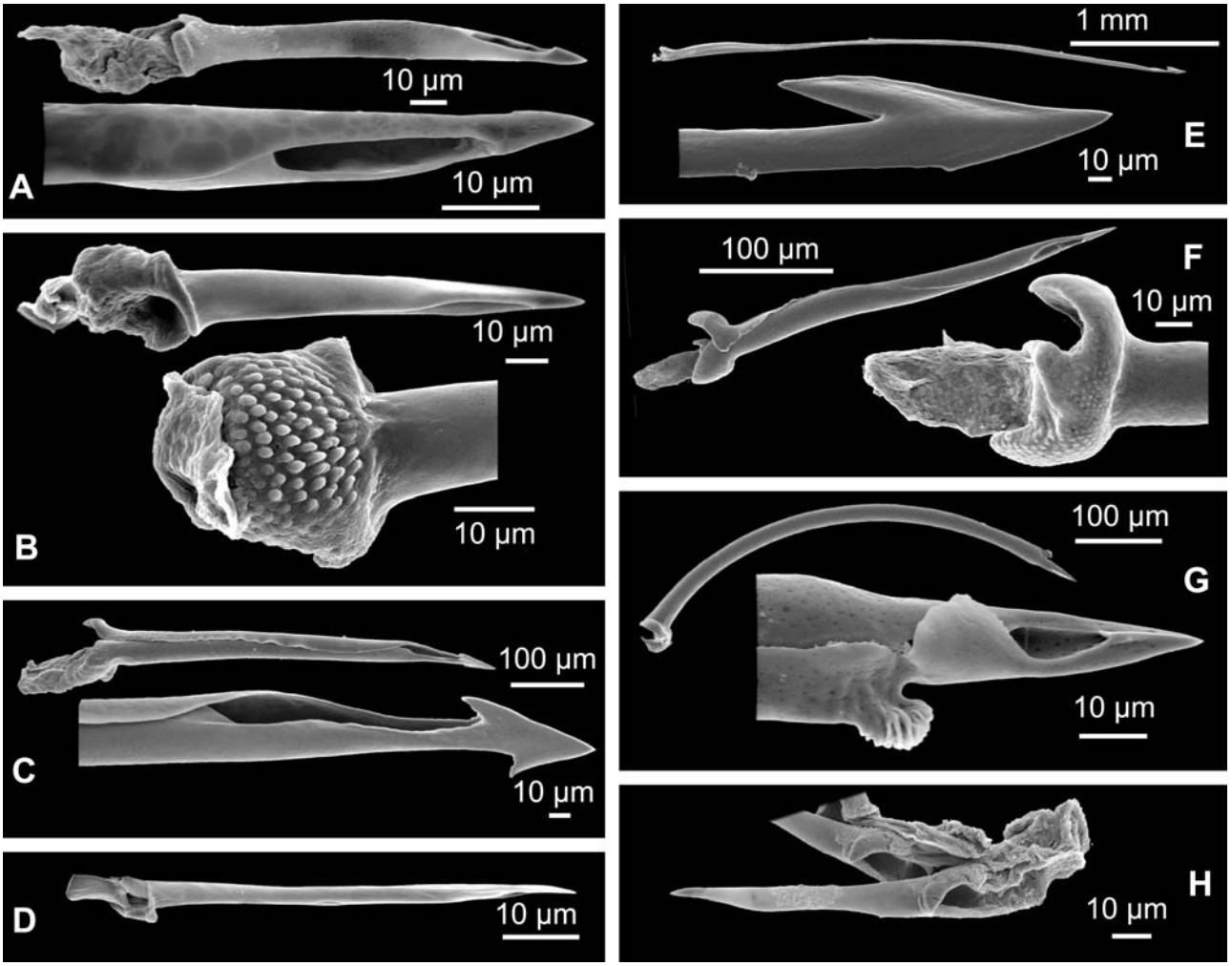

Figure 10. Radulae. Raphitomidae. **A.** *Buccinaria pendula* Bouchet & Sysoev, 1997, MNHN, New Caledonia, BATHUS 4, st. CP948, 20°33′S, 164°57′E, 533–610 m. **B.** *Daphnella pulvisculus* Chino, 2006, MNHN, New Caledonia, BATHUS 4, st. DW927, 18°56′S, 163°22′E, 444–452 m. **C.** *Gymnobela yoshidai* Kuroda & Habe in Habe, 1962, MNHN, Norfolk ridge, NORFOLK 2, st. DW2058, 24°40′S, 168°40′E, 591–1032 m. **D.** *Kermia irretita* (Hedley, 1899), MNHN, New Caledonia, LIFOU 2000, st. 1419, 20°55.6′S, 167°04.5′E, 0–5 m. **E.** *Daphnella cladara* Sysoev & Bouchet, 2001, MNHN, Norfolk Ridge, LITHIST, st. CP09, 24°53′S, 168°22′E, 518–540 m. **F.** *Daphnella mitrellaformis* (Nomura, 1940), MNHN, New Caledonia, LIFOU 2000, st. DW1649, 20°54′S, 167°01′E, 150–200 m. **G.** *Miowateria* sp., MNHN, Fidji, MUSORSTOM 10, st. CP1354, 17°43′S, 178°55′E, 959–963 m. **H.** *Spergo fusiformis* (Kuroda & Habe in Habe, 1962), MNHN, Tongatapu, Tonga, BORDAU 2, st. CP1566, 21°02′S, 175°18′W, 530–531 m.

morphology. Teeth can be relatively very long (to 12.8% of shell length in *Daphnella cladara*, Fig. 10E) to very short and reduced (0.13% of shell length in *Spergo fusiformis*, Fig. 10H). Solid base of the teeth from very small (Fig. 10E, G) to rather large (Fig. 10B, F), sometimes side projections around the base are present (Fig. 10F). Barb(s) present or absent. At least in one species cockscomb-shaped structure is present near the tooth tip (Fig. 10G). Tooth canal opening laterally or subapically. Reduction in radular apparatus and other structures of the anterior foregut is frequent, grading to complete absence.

Caledonia, SL 20 mm. **I.** *Rocroithys niveus* Sysoev & Bouchet, 2001, holotype, MNHN, Vanuatu, 15°08′S 167°12′E, 312–314 m, SL 25.5 mm. **J.** *Pleurotomella* sp.**, MNHN IM200717848, Coral Sea, EBISCO, st. DW2625, 20°05′S, 160°19′E, 627–741 m, SL 20.6 mm. **K.** *Taranis* sp.**, MNHN IM200742296, Philippines, AURORA 07, st. CP2749, 15°56.6′N, 121°50.2′E, 473 m, SL 6 mm. A07 1717. **L.** *Nepotilla* sp., MNHN, New Caledonia, SMIB8, st. DW146–147, 24°55′S, 168°22′, 508–532 m, SL 1.5 mm. **M.** *Eucyclotoma cymatodes* (Hervier, 1899)**, MNHN IM200717903, Philippines, PANGLAO 2004, st. S12, 09°29.4′N, 123°56.0′E, 6–8 m, SL 5.0 mm. **N.** *Buccinaria pendula* Bouchet & Sysoev, 1997, MNHN, New Caledonia, BATHUS 1, st. DE697, 20°34′S, 164°58′E, 570–650 m, SL 7.2 mm. **O.** *Microdaphne morrisoni* Rehder, 1980, MNHN, New Caledonia, SL 4.5 mm. **P.** *Cryptodaphne* sp., MNHN, New Caledonia, MUSORSTOM 4, st. DW150, 19°07′S, 163°22′E, 110 m, SL 11.2 mm. **Q.** *Kermia aureotincta* (Hervier, 1897)**, MNHN IM200717878, Philippines, PANGLAO 2004, st. B25, 09°29′N, 123°56.1′E, 16 m, SL 4.5 mm. **R.** *Teretiopsis* cf. *hyalina* Sysoev & Bouchet, 2001**, MNHN IM200717845, Coral Sea, EBISCO, st. CP2651, 21°29′S, 162°36′E, 883–957 m, SL 22.8 mm. **S.** *Daphnella itonis* Sysoev & Bouchet, 2001, holotype, MNHN, New Caledonia, 22°48′S 167°16′E, 444–445 m, SL 66.0 mm. **T.** *Phymorhynchus major* Warén & Bouchet, 2001, holotype, MNHN, Site Barbecue, East Pacific Rise, 09°50′N, 104°17′W, 2505 m, SL 72.0 mm. **U.** *Gymnobela* sp.**, MNHN IM200717841, Coral Sea, EBISCO, st. CP2648, 21°32′S, 162°30′E, 750–458 m, SL 25.7 mm. **V.** *Thatcheria mirabilis* Angas, 1877**, MNHN IM200717924, Solomon Islands, SALOMON 2, st. CP2184, 08°16.9′S, 159°59.7′E, 464–523 m, SL 32.5 mm. Abbreviation and symbols: SL, shell length; *, sequenced species; **, sequenced specimen. Photo credits: B. Buge (C–E, J, Q, R, U, V), P. Maestrati (F, G, L, P).

Remarks: This is the largest and most variable taxon in the Conoidea, as concerns the number of species, with the largest vertical range (intertidal to hadal depths).

Included genera:

Abyssobela Kantor & Sysoev, 1986[1]
?*Abyssothauma* Sysoev, 1996[1]
Acamptodaphne Shuto, 1971[1]
Acanthodaphne Bonfitto & Morassi, 2006[1]
Aliceia Dautzenberg & Fischer, 1897[1]
Asperdaphne Hedley, 1922[1]
(*Aspertilla* Powell, 1944)
Austrodaphnella Laseron, 1954[1]
?*Austropusilla* Laseron, 1954[1]
(*Metaclathurella* Shuto, 1983)
Bathybela Kobelt, 1905[2]
[= *Bathypota* Nordsieck, 1968]
Buccinaria Kittl, 1887[2]
[= *Ootomella* Bartsch, 1933]
[= *Pionotoma* Kuroda, 1952]
Cenodagreutes E.H. Smith, 1967[1]
Clathurina Melvill, 1917[1]
Clinura Bellardi, 1875[1]
Cryptodaphne Powell, 1942[1]
Daphnella Hinds, 1844[3]
[= *Eudaphnella* Bartsch, 1933]
[= *Paradaphne* Laseron, 1954]
(*Diaugasma* Melvill, 1917)
(*Hemidaphne* Hedley, 1918)
Eubela Dall, 1889[1]
Eucyclotoma Boettger, 1895[3]
[= *Turrhyssa* Dall, 1924]
?*Exomilus* Hedley, 1918[1]
Famelica Bouchet & Warén, 1980[1]
Favriella Hornung, 1920[1]
Glyphostomoides Shuto, 1983[3]
Gymnobela Verrill, 1884[3]
[= *Majox* Nordsieck, 1968]
[= *Watsonaria* Nordsieck, 1968]
(*Theta* Clarke, 1959)
Hemilienardia Boettger, 1895[3]
Isodaphne Laseron, 1954[1]
Kermia Olivier, 1915[3]
Kuroshiodaphne Shuto, 1965[1]
Leiosyrinx Bouchet & Sysoev, 2001[2]
Lusitanops Nordsieck, 1968[1]
Magnella Dittmer, 1960[1]
Microdaphne McLean, 1971[1]
Microgenia Laseron, 1954[1]
Mioawateria Vella, 1954[1]
Neopleurotomoides Shuto, 1971[1]
Nepotilla Hedley, 1918[2]
Pagodidaphne Shuto, 1983[1]
Paramontana Laseron, 1954[2]
Philbertia Monterosato, 1884[2]
[= *Leufroyia* Monterosato, 1884]
[= *Lineotoma* Nordsieck, 1977]
[= *Peratotoma* Harris & Burrows, 1891]
Phymorhynchus Dall, 1908[2]
Pleurotomella Verrill, 1873[3]
[= *Azorilla* Nordsieck, 1968]
[= *Azorita* Nordsieck, 1968]
[= *Anomalotomella* Powell, 1966]
[= *Fusidaphne* Laseron, 1954]
[= *Tasmadaphne* Laseron, 1954]
(*Cyrtoides* Nordsieck, 1968)
Pontiothauma E.A. Smith, 1895[2]
Pseudodaphnella Boettger, 1895[2]
(*Qii* Zhang, 1995)
Raphitoma Bellardi, 1848[3]
Rimosodaphnella Cossmann, 1915[3]
Rocroithys Sysoev & Bouchet, 2001[2]
Spergo Dall, 1895[2]
(*Speoides* Kuroda & Habe in Habe, 1962)
Stilla Finlay, 1926[1]
Taranidaphne Morassi & Bonfitto, 2001[1]
Taranis Jeffreys, 1867[3]
[= ?*Allo* Lamy, 1934]
[= ?*Feliciella* Lamy, 1934]
[= *Fenestrosyrinx* Finlay, 1926]
?*Teleochilus* Harris, 1897[1]
[= *Litachilus* Powell, 1944]
Teretia Norman, 1888[2]
Teretiopsis Kantor & Sysoev, 1989[3]
Thatcheria Angas, 1877[3]
[= *Cochlioconus* Yokoyama, 1928]
?*Thatcheriasyrinx* Powell, 1969[1]
Thatcherina Vera-Peláez, 1998[1]
?*Thesbia* Jeffreys, 1867[2]
Tritonoturris Dall, 1924[3]
Truncadaphne McLean, 1971[1]
Tuskaroria Sysoev, 1988[1]
Typhlosyrinx Thiele, 1925[2]
Veprecula Melvill, 1917[3]
[= *Mordica* Dall, 1924]
Vepridaphne Shuto, 1983[1]
Xanthodaphne Powell, 1942[2]
Zenepos Finlay, 1928[1]

Cochlespiridae Powell, 1942
(Figs 11A–D, 12)

Diagnosis: Shell of moderate size, about 20–30 mm, up to 100 mm high, high-pagodiform to fusiform, with a tall spire and usually a long siphonal canal. Axial sculpture poorly developed or absent, subsutural ramp usually smooth. Anal sinus deep, on subsutural ramp. Protoconch paucispiral, smooth. Operculum with terminal nucleus. Radula 1–0-R-0–1. Rachidian broad, subrectangular or arched, with a single rather large cusp (Fig. 12), rarely absent (some *Aforia*). Marginal teeth duplex, with well developed accessory limb.

Remarks: This is a clade with poor congruence between molecular and shell characters. The contents of most genera need revision and the family limits remain uncertain.

Sibogasyrinx was proposed as a subgenus of *Leucosyrinx* for two species characterized by a low position of the peripheral angle. During our examination of radulae of species provisionally attributed to *Leucosyrinx*, two distinct radulae types were found, differing in the presence of the rachidian, without apparent congruence with shell morphology. In *Sibogasyrinx pyramidalis*, the type species of *Sibogasyrinx*, as well as in the sequenced specimen (Fig. 11B), the radula is characterized by the presence of a well-developed rachidian. Although the sequenced specimen is conchologically closer to typical *Leucosyrinx*, the molecular sequence suggests affinities to *Cochlespira*.

Included genera:

?*Aforia* Dall, 1889[2]
[= *Irenosyrinx* Dall, 1908]
[= *Danilacarina* Bozzetti, 1997]
(?*Abyssaforia* Sysoev & Kantor, 1987)
(?*Dallaforia* Sysoev & Kantor, 1987)
(?*Steiraxis* Dall, 1896)
?*Apiotoma* Cossmann, 1889[1]
?*Clavosurcula* Schepman, 1913[1]

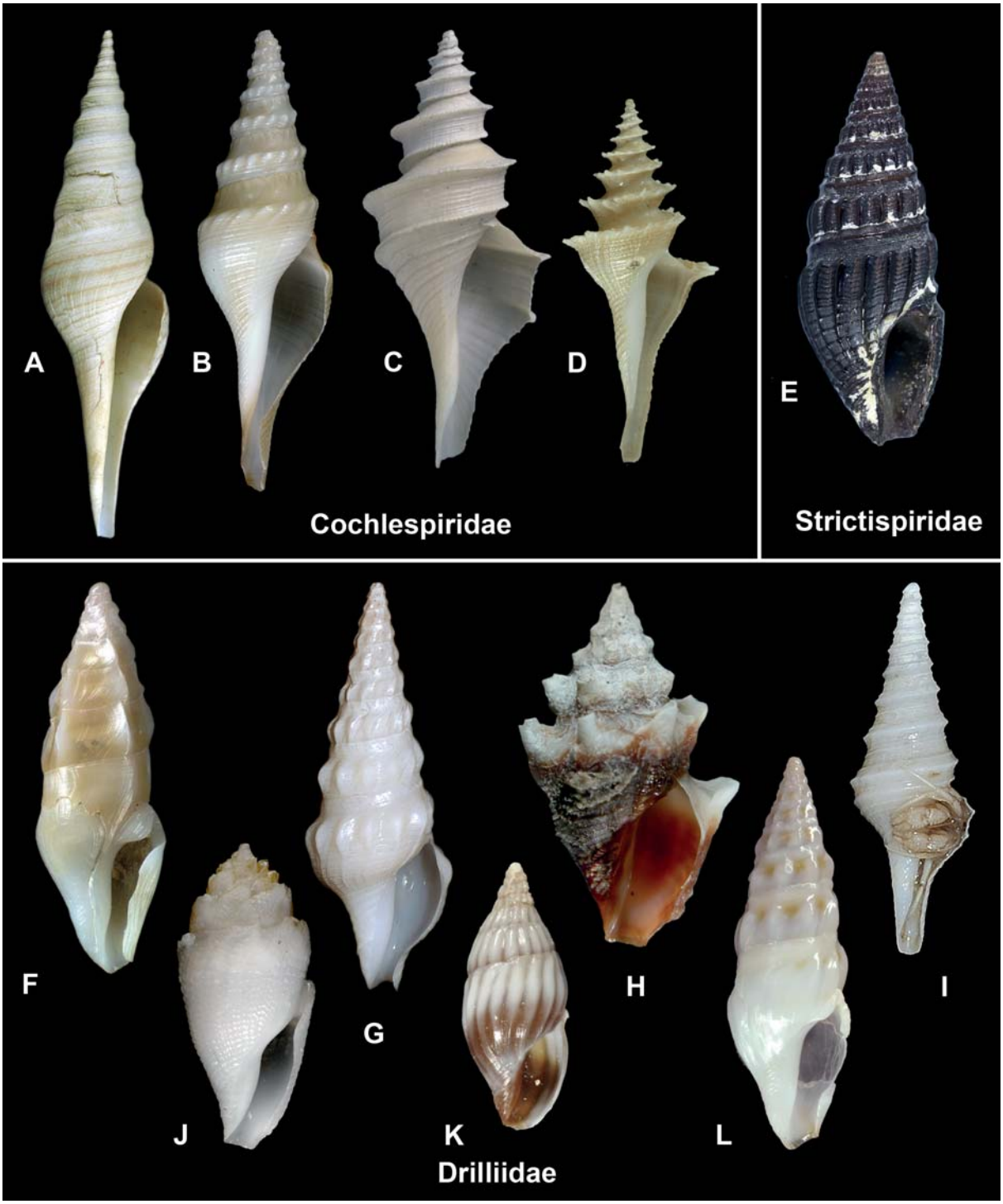

Figure 11. Shells. **A–D.** Cochlespiridae. **A.** *Nihonia maxima* Sysoev, 1997, holotype, MNHN, Indonesia, 09°23′S 131°09′E, 275–246 m, SL 128 mm. **B.** *Sibogasyrinx* sp.**, MNHN IM200717701, Vanuatu, BOA1, st. CP2432, 14°59.7′S, 166°55.0′E, SL 46.0 mm (radula: Fig. 12B, C). **C.** *Aforia multispiralis* Dell, 1990, USNM 870023, N of Livingston Island, South Shetland Islands, 62°S, 61.1°W, 1437 m, SL 45.6 mm. **D.** *Cochlespira pulchella* (Schepman, 1913)**, MNHN IM200717920, PANGLAO 2005, st. CP2340, 09°29.4′N, 123°44.4′E, SL 22.0 mm. **E.** Strictispiridae. **E.** *Strictispira solida* (C.B. Adams, 1850), USNM 900425, E side of Marquesas Keys, Florida Keys, SL 17.5 mm. **F–L.** Drilliidae. **F.** *Plagiostropha caledoniensis* Wells, 1995, S New Caledonia, SL 12.2 mm. **G.** *Imaclava unimaculata* (Sowerby I, 1834)* subadult, det. J.A. Todd, NHMUK MOEA 20100529, Gulf of Panama, JTD-00–46, 08°31.37′N, 79°05.79′W, 24–25 m, SL 25.5 mm. **H.** *Clavus canalicularis* (Röding, 1798)*, MNHN IM200742345, Philippines, PANGLAO 2004, st. B11, 09°29.4′N, 123°56.0′E, 2–4 m, SL 19 mm. **I.** *Cruziturricula arcuata* (Reeve, 1843)* subadult, det. J. A. Todd, YK; NHMUK 20100542, Gulf of Panama, JTD-00–34, 08°26.24′N, 79°09.14′W, 66–68 m, SL = 17.6 mm (radula: Fig. 13E). **J.** *Conopleura striata* Hinds, 1844*, New Caledonia, MONTROUZIER, st. 1311, 20°40.4′S, 164°14.9′E, 10–60 m, SL 15.6 mm. **K.** *Iredalea pupoidea* (H. Adams, 1872)*, MNHN, New Caledonia, MONTROUZIER, st. 1240, 20°46.5′S, 165°14′E-165°15′E, 2 m, SL 6.2 mm. **L.** *Splendrillia* sp.**, MNHN IM200717847, Coral Sea, EBISCO, st. DW2617, 20°06′S, 160°22′E, 427–505 m, SL 16.4 mm (radula: Fig. 13A, B). Abbreviation and symbols: SL, shell length; *, sequenced species; **, sequenced specimen. Photo credits: B. Buge (B, D, F), A. Fedosov (I, G), M.G. Harasewych and D. Tippett (C, E),

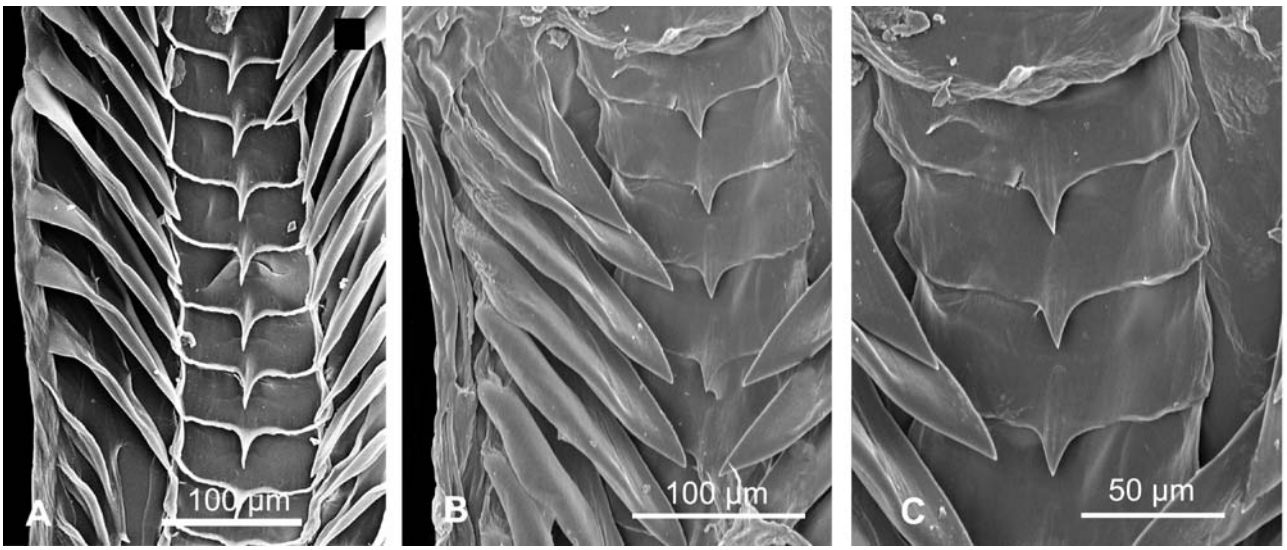

Figure 12. Radulae. Cochlespiridae. **A.** *Cochlespira radiata* (Dall, 1889), MNHN, SE Brazil, after Kantor & Taylor, 2000. **B–C.** *Sibogasyrinx* sp.**, MNHN IM200717701 (shell: Fig. 11B). Symbol: **, sequenced specimen.

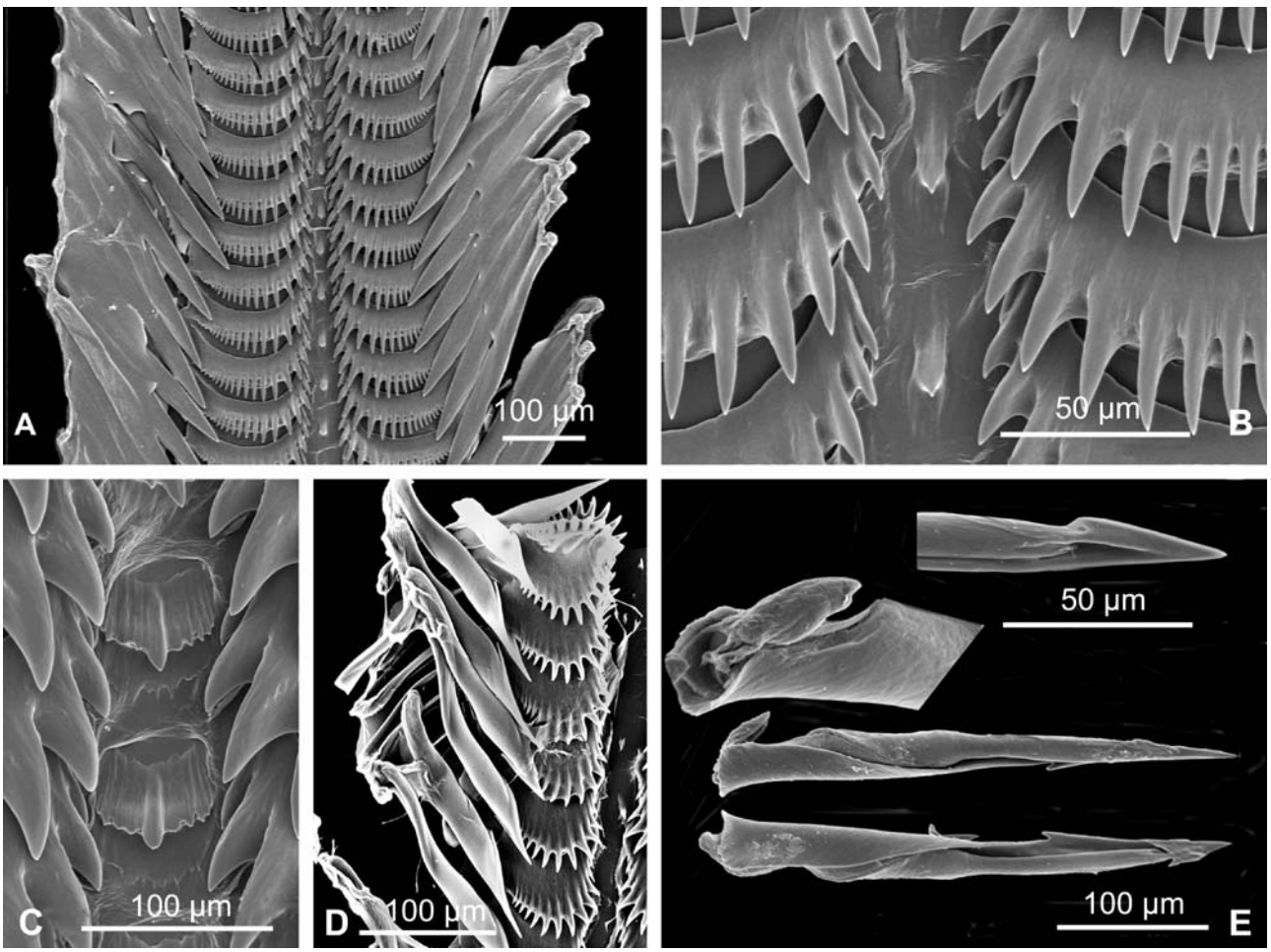

Figure 13. Radulae. Drilliidae. **A–B.** *Splendrillia* sp.**, MNHN IM200717847 (shell: Fig. 11L). **C.** *Clavus exasperatus* (Reeve, 1843), MNHN, New Caledonia, LIFOU 2000, st. 1420, 20°47.7′S, 167°09.35′E, 4–5 m. **D.** *Imaclava pilsbryi* (Bartsch, 1950), after Kantor & Taylor, 2000. **E.** *Cruziturricula arcuata* (Reeve, 1843)**, NHMUK MOEA 20100541, Gulf of Panama, JTD-00–34, 08°26.24′N, 79°09.14′W, 66–68 m (shell: Fig. 11I). Symbol: **, sequenced specimen.

Cochlespira Conrad, 1865[3]
[= *Ancistrosyrinx* Dall, 1881]
[= *Coronasyrinx* Powell, 1944]
[= *Pagodasyrinx* Shuto, 1969]
?*Nihonia* MacNeil, 1961[1]
Sibogasyrinx Powell, 1969[3]

Drilliidae Olsson, 1964
(Figs 11F–L, 13)

Diagnosis: Shell small- to medium-sized, usually 15–25 mm, up to 50 mm high, with a rather high spire and usually truncated base. Spiral sculpture often obsolete. Anal sinus on subsutural ramp, deep, (sub)symmetrical, sometimes tubular. Protoconch usually paucispiral (up to two whorls), smooth or abapically carinate. Operculum with terminal nucleus. Radular formula 1-1-R-1-1, rarely 1-1-0-1-1, central tooth small, from narrow unicuspid (Fig. 13B) to subrectangular with additional cusps (Fig. 13C), rarely reduced to completely absent. Lateral teeth broad, pectinate, and arched, marginal teeth from simple flat and sharply pointed (Fig. 13A) to duplex with slightly thickened edges and to loosely enrolled with the small barb near the tip (*Imaclava*, Fig. 13D).

Remarks: The genera *Cruziturricula* and *Fusiturricula* form an unsupported group that is sister to Drilliidae. In the studied *Cruziturricula arcuata* (Reeve, 1843), the very characteristic radula differs from the Drilliidae: 1-0-0-0-1. Marginal teeth are loosely enrolled with little overlap of the edges, with two barbs on the tip and a tongue-shape extension at the base (Fig. 13E). The type species of *Fusiturricula*, *Turris fusinella* Dall, 1908, is different from what is currently conceived as belonging to that genus (e.g. Williams, 2006), but those species are similar to *Cruziturricula sensu auctt*. The only data on the radula was provided by Powell (1966: 31), who stated (without mentioning the species): "Radula of marginals only, wishbone-type, but long and narrow". Although *Cruziturricula* and *Fusiturricula* definitely do not belong in Drilliidae and may represent a new family, they are here provisionally placed in Drilliidae for lack of a better alternative.

Included genera:
?*Acinodrillia* Kilburn, 1988[1]
Agladrillia Woodring, 1928[3]
Bellaspira Conrad, 1868[1]
Calliclava McLean, 1971[3]
Cerodrillia Bartsch & Rehder, 1939[3]
(*Lissodrillia* Barsch and Rehder, 1943)
Clavus Monfort, 1810[3]
[= *Clavicantha* Swainson, 1840]
[= *Eldridgea* Bartsch, 1934]
[= *Tylotia* Melvill, 1917]
Clathrodrillia Dall, 1918[3]
Conopleura Hinds, 1844[3]
Crassopleura Monterosato, 1884[1]
?*Cruziturricula* Marks, 1951[3]
Cymatosyrinx Dall, 1889[2]
Douglassia Bartsch, 1934[1]
Drillia Gray, 1838[3]
Elaeocyma Dall, 1918[2]
Eumetadrillia Woodring, 1928[1]
Fenimorea Bartsch, 1934[1]
?*Fusiturricula* Woodring, 1928[3]
(?*Fusisyrinx* Bartsch, 1934)
Globidrillia Woodring, 1928[2]
Imaclava Bartsch, 1944[3]
Iredalea Oliver, 1915[3]
[= *Brephodrillia* Pilsbry & Lowe, 1932]
Kylix Dall, 1919[2]
Leptadrillia Woodring, 1928[2]
Neodrillia Bartsch, 1943[2]
Orrmaesia Kilburn, 1988[2]
?*Paracuneus* Laseron, 1954[1]
Plagiostropha Melvill, 1927[2]
Splendrillia Hedley, 1922[3]
(*Hauturua* Powell, 1942)
Spirotropis G.O. Sars, 1878[2]
?*Stenodrillia* Korobkov, 1955[1]
Syntomodrillia Woodring, 1928[2]
Tylotiella Habe, 1964[2]

Pseudomelatomidae Morrison, 1965

(Figs 14–16)

Diagnosis: Shell small to rather large, 15–100 mm high, claviform to fusiform. Spiral and axial sculpture generally well developed, often strong. Subsutural fold often present. Anal sinus on subsutural ramp, usually moderately deep to very deep, often constrained by callus rendering anal sinus subtubular. Protoconch usually paucispiral, sometimes multispiral, with up to three whorls, smooth or sometimes axially or spirally sculptured on later whorls. Operculum with terminal nucleus.

Radula very variable; four types are recorded:

1-(1-R-1)-1 – *Comitas* type (includes also *Knefastia* and *Antiplanes*). The central formation is rather variable in degree of development of the rachidian tooth and fusion of three teeth. In some *Comitas* (Fig. 15C, D), the central formation looks like single well-defined tooth [as in *Comitas murrawolga* (Garrard, 1961)], while in *Comitas onokeana vivens* Dell, 1956, *Knefastia* and *Antiplanes*, the rachidian is totally reduced and the formation appears as two poorly developed paired plates (reduced laterals) (Fig. 15B). Marginal teeth in *Comitas* and *Knefastia* flat, broadly oval, with thickened edges and teeth tips and without pronounced accessory limb. In *Antiplanes* marginal teeth narrowly elongate, with well-developed accessory limb.

1-1-0-1-1 – *Crassiclava* type. Differs from the *Comitas* type by the better defined laterals (Fig. 15E, F) that are low, arcuate and sharply curved towards the midline of the ribbon.

1-0-R-0-1 – *Pseudomelatoma* type (also includes *Hormospira* and *Tiariturris*, Fig. 15A). Rachidian with strong cusp and subrectangular base (contrary to the other types with a central formation formed by fused lateral and rachidian). Despite neither ontogeny nor folding of the radula have been examined, we tentatively treat this structure as a true rachidian. Marginal teeth simple, solid and strongly curved, attached to the membrane by rather a narrow base and free along most of their length.

1-0-0-0-1 – Most genera of the family. Marginal teeth elongated, narrow, flat, with thickened edge (e.g. *Funa*, *Carinodrillia*, Fig. 16C), or trough-shaped in transverse section, sometimes with small barb near the tip (*Cheungbeia*, Fig. 16E), which may become semi-enrolled (e.g. *Pyrgospira*, *Pilsbryspira*, *Zonulispira*, Fig. 16B), to nearly hollow, where limbs overlap at significant length of the teeth (*Ptychobela*, Fig. 16D).

Remarks: Anatomically, Pseudomelatomidae is the most variable family of Conoidea. Most genera were formerly included in the subfamily Crassispirinae, but the nomenclaturally valid name for this clade is Pseudomelatomidae. Its constituents includes several taxa that were previously recognized as separate (sub)families: Zonulispirinae, characterized by semi-enrolled marginal radular teeth (a character found in several branches of the clade), and Pseudomelatominae, defined on the basis of the very characteristic solid marginal teeth and strongly developed rachidian.

The genus *Leucosyrinx* has long been a convenient genus for placement of turreted-fusiform species, mostly from deep water of the Atlantic and Indo-Pacific. Currently, it is a mixture of species of probably different taxonomic position, and the

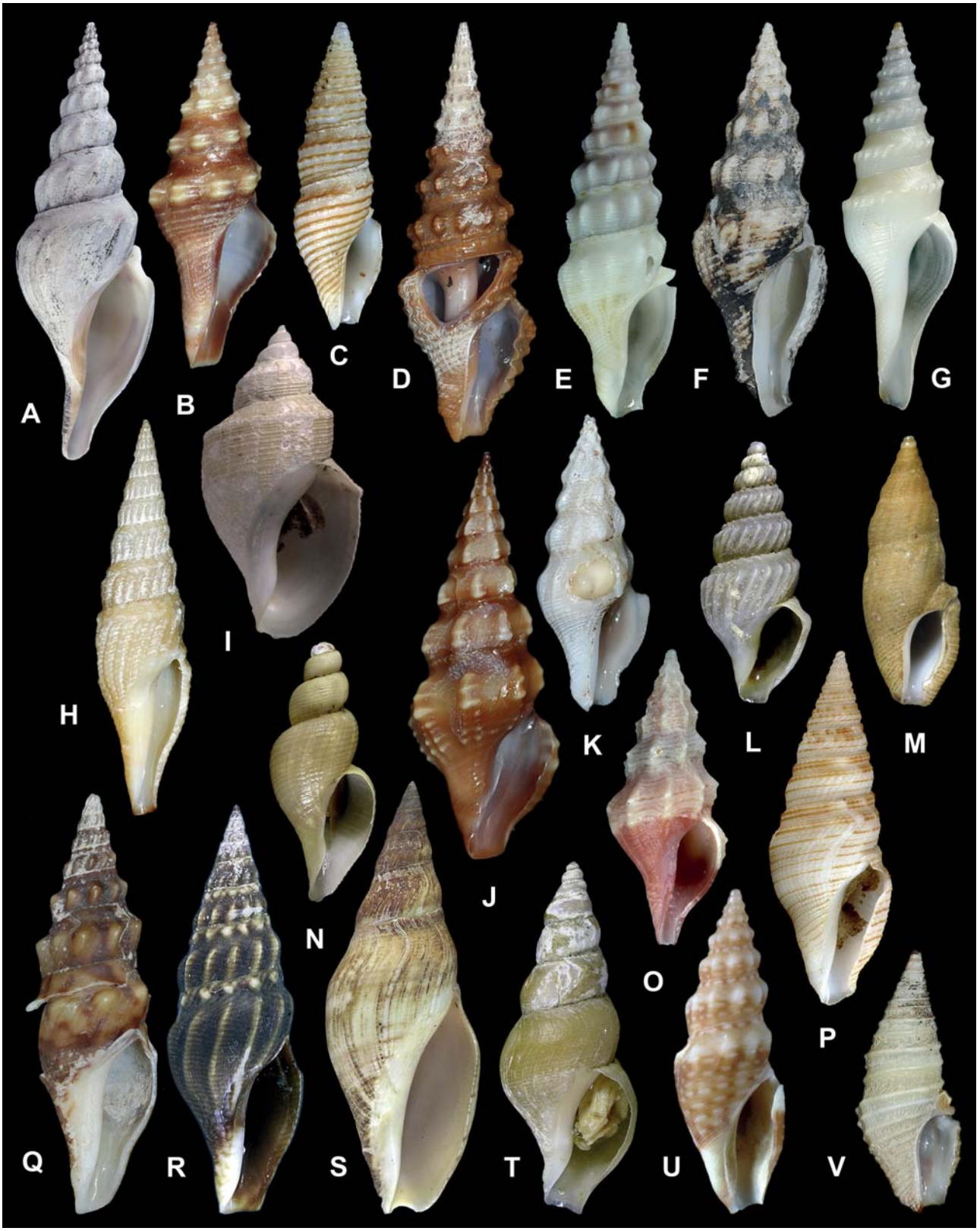

Figure 14. Shells. Pseudomelatomidae. **A.** *Comitas* sp.**, MNHN IM200717918, Philippines, PANGLAO 2005, st. CP2388, 09°26.9′N, 123°34.5′E, 762–786 m, SL 113.8 mm (radula: Fig. 15C, D). **B.** *Knefastia tuberculifera* (Broderip & Sowerby, 1829)*, NHMUK MOEA 20100534, Gulf of Panama, JTD-00-18, 08°19.50′N, 78°47.71′W, 25–32 m, SL 36.6 mm. **C.** *Otitoma* sp.**, MNHN IM200717905, Philippines, PANGLAO 2005, st. CP2348, 09°26.6′N, 123°52.5′E, 196–216 m, SL 17.2 mm. **D.** *Pyrgospira aenone* (Dall, 1919)**, det. J. A. Todd, YK, NHMUK MOEA 20100539, Gulf of Panama, JTD-00–18, 08°19.50′N, 78°47.71′W, 25–32 m. SL 36.2 mm. **E.** *Inquisitor* sp.**, MNHN IM200717851, Coral Sea, EBISCO, st. DW2625, 20°05′N, 160°19′E, 627–741 m, SL 32.2 mm (radula: Fig. 16F). **F.** *Funa incerta* (Smith, 1877)**, NHMUK MOEA 20100553, st. 70, off southern Hong Kong, SL 42.8 mm. **G.** *Leucosyrinx* sp.**, MNHN IM200717846, Coral Sea, EBISCO, st. CP2600, 19°38′S, 158°46′E, 603–630 m,

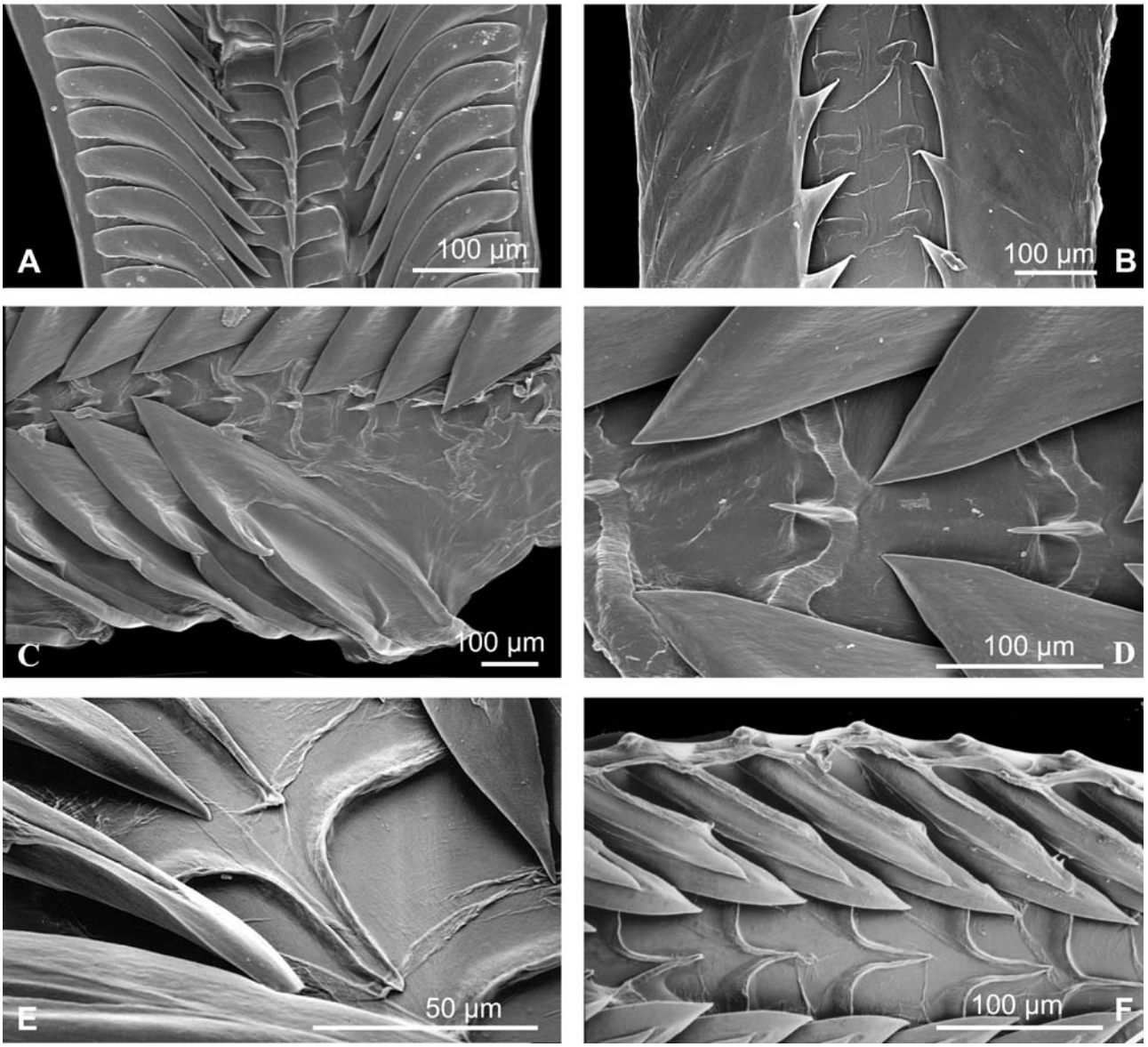

Figure 15. Radulae. Pseudomelatomidae. **A.** *Tiariturris spectabilis* Berry, 1958**, NHMUK MOEA 20100540, Gulf of Panama, JTD-00-34, 08°26.24′N, 79 09.14′W, 66–68 m (shell: Fig. 14Q). **B.** *Comitas onokeana vivens* Dell, 1956, MNHN, New Caledonia, MONTROUZIER, st. 1269, after Kantor & Taylor (2000). **C, D**. *Comitas* sp.**, MNHN IM200717918 (shell: Fig. 14A). **E, F.** *Crassiclava turricula* (Sowerby, 1834), Off Nacascola, West side of Bahia Culebra, Costa Rica, after Kantor *et al.* (1997). Symbol: **, sequenced specimen.

SL 27.1 mm (radula: Fig. 16A). **H.** *Hindsiclava alesidota* (Dall, 1889)**, det. J. A. Todd, NHMUK MOEA 20100524, Lower Florida Keys, JTD-01-15, 24°33.47′N, 81°07.72′W, 117–148 m SL 37.9 mm. **I.** *Conorbela antarctica* (Strebel, 1908) USNM 894465, Zavodovski Island, South Sandwich Islands, 56.27°S, 27.5°W, 208–375 m, SL 23.6 mm. **J.** *Carinodrillia dichroa* Pilsbry & Lowe, 1932*, det. J. A. Todd, NHMUK MOEA 20100531, Gulf of Panama, JTD-00-18, 08°19.50′N, 78°47.71′W, 25–32 m, SL 23.0 mm (radula: Fig. 16C). **K.** *Cheungbeia robusta* (Hinds, 1839)*, NHMUK MOEA 20100558, st. 70, off southern Hong Kong, South China Sea, SL 21.2 mm (radula: Fig. 16E). **L.** *Plicisyrinx vitjazi* Sysoev t Kantor, 1986, holotype, ZMMU Lc-22382, E of northern Honshu, Japan, 40°55.2′N, 144°53.3′E, 3880–4000 m, SL 13.9 mm. **M.** *Maesiella maesae* McLean & Poorman, 1971, LACM 1513, holotype, Guaymas, Sonora, Mexico, SL 9.2 mm. **N.** *Kurilohadalia elongata* Sysoev & Kantor, 1986, holotype, ZMMU Lc-22401, Kurile-Kamchatka Trench, 43°55′ N, 149°47′ E, 8080–8160 m, SL 12.5 mm. **O.** *Crassispira quadrilirata* (E.A. Smith, 1882)**, MNHN IM200717755, Philippines, PANGLAO 2004, st. L46, 09°30.9′N, 123°41.2′E, 90–110 m, SL 14.0 mm. **P.** *Epideira sibogae* (Schepman, 1913), MNHN, Vanuatu, MUSORSTOM 8, st. DW1097, 15°05′S, 167°11′E, 281–288 m, SL 24.1 mm. **Q.** *Tiariturris spectabilis* Berry, 1958**, det. J. A. Todd, NHMUK MOEA 20100540, Gulf of Panama, JTD-00-34, 08°26.24′N, 79 09.14′W, 66–68 m SL 48.7 mm (radula: Fig. 15A). **R.** *Pseudomelatoma penicillata* Carpenter, 1864, USNM 130590, California, SL 28.1 mm. **S.** *Megasurcula carpenteriana* (Gabb, 1865), USNM 523713, California, SL 84.1 mm. **T.** *Antiplanes sanctiioannis* (E.A. Smith, 1875), ZMMU Lc-17096, off northern Kurile Islands, 49°40.9′N, 154°41′E, 142 m, SL 37.2 mm. **U.** *Naudedrillia* sp., New Caledonia, VAUBAN, st. 3, 22°17′S, 167 °12′E, 390 m, SL 19.0 mm. **V.** *Zonulispira* sp.*, NHMUK MOEA 20100537, det. J. A. Todd, Gulf of Panama, JTD-00-18, 08°19.50′N, 78°47.71′W, 25–32 m, SL 21.2 mm (radula: Fig. 16B). Abbreviation and symbols: SL, shell length; *, sequenced species; **, sequenced specimen. Photo credits: B. Buge (A, G), A. Fedosov (B–F, H, J, K, Q), M.G. Harasewych and D. Tippett (R, S), P. Maestrati (U), J. McLean (M).

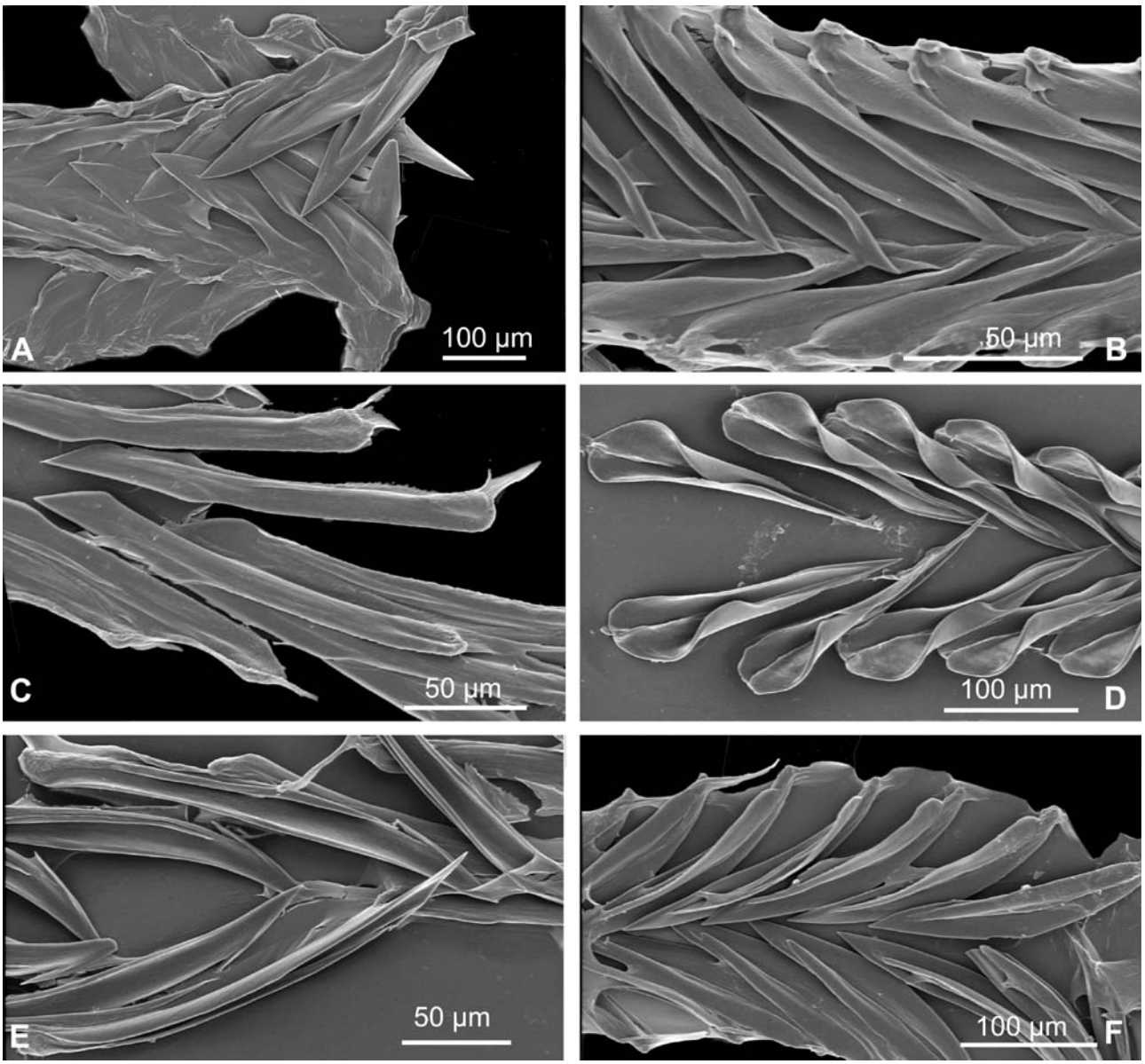

Figure 16. Radulae. Pseudomelatomidae. **A.** *Leucosyrinx* sp.**, MNHN IM200717846 (shell: Fig. 14G). **B.** *Zonulispira* sp.**, NHMUK MOEA 20100536, Gulf of Panama, JTD-00-18, 08°19.50′N, 78°47.71′W, 25–32 m (shell: Fig. 14V). **C.** *Carinodrillia dichroa* Pilsbry & Lowe, 1932**, NHMUK MOEA 20100530, Gulf of Panama, JTD-00-18, 08°19.50′N, 78°47.71′W, 25–32 m (shell: Fig. 1 J). **D.** *Ptychobela suturalis* (Gray, 1838)**, det. J.A. Todd, YK, NHMUK MOEA 20100560, off southern Hong Kong, Sta. 71. **E.** *Cheungbeia robusta* (Hinds, 1839)*, NHMUK MOEA 20100557, coll. B. Morton, off southern Hong Kong, Sta. 70 (shell: Fig. 14K). **F.** *Inquisitor* sp.**, MNHN IM200717851 (shell: Fig. 14E). Symbols: *, sequenced species; **, sequenced specimen.

membership of the genus needs revision. The type species from the northern Atlantic, *Leucosyrinx verrilli* (Dall, 1881), has a radula consisting of only duplex, rather robust marginal teeth (Powell, 1966: text fig. B12), a radula type also found by us in Indo-Pacific species (Fig. 16A). A second type of radula is found in *Sibogasyrinx*, originally described as a subgenus of *Leucosyrinx*, and which clusters in the molecular tree with the Cochlespiridae (see under that family). In our study, true *Leucosyrinx* appears to be sister to the Pseudomelatomidae, but this relationship has poor support. As a working hypothesis, we tentatively include *Leucosyrinx* in the Pseudomelatomidae.

Included genera:
?*Abyssocomitas* Sysoev & Kantor, 1986[2]
Aguilaria Taylor & Wells, 1994[2]
?*Anticomitas* Powell, 1942[1]
Antimelatoma Powell, 1942[1]
Antiplanes Dall, 1902[2]
[= *Rectiplanes* Bartsch, 1944]
[= *Rectisulcus* Habe, 1958]
Austrotoma Finlay, 1924[1]
?*Benthodaphne* Oyama, 1962[1]
Burchia Bartsch, 1944[2]
Buridrillia Olsson, 1942[2]
Calcatodrillia Kilburn, 1988[2]
Carinodrillia Dall, 1919[3]
?*Carinoturris* Bartsch, 1944[2]
Cheungbeia Taylor & Wells, 1994[3]
Comitas Finlay, 1926[3]
Compsodrillia Woodring, 1928[2]
(*Mammillaedrillia* Kuroda and Oyama in Kuroda, Habe & Oyama, 1971)

?*Conorbela* Powell, 1951[2]
Conticosta Laseron, 1954[1]
Crassiclava McLean, 1971[2]
Crassispira Swainson, 1840[3]
(*Crassispirella* Bartsch & Rehder, 1939)
Cretaspira Kuroda & Oyama in Kuroda, Habe & Oyama, 1971[1]
Dallspira Bartsch, 1950[2]
Doxospira McLean, 1971[2]
Epideira Hedley, 1918[2]
[= *Epidirona* Hedley, 1931]
Funa Kilburn, 1988[3]
Gibbaspira McLean, 1971[2]
Glossispira McLean, 1971[2]
Hindsiclava Hertlein & Strong, 1955[3]
[= *Turrigemma* Berry, 1958]
Hormospira Berry, 1958[2]
Inquisitor Hedley, 1918[3]
Knefastia Dall, 1919[3]
?*Kurilohadalia* Sysoev & Kantor, 1986[2]
Kurodadrillia Azuma, 1975[1]
?*Leucosyrinx* Dall 1889[3]
Lioglyphostoma Woodring, 1928[2]
Lioglyphostomella Shuto, 1970[1]
Maesiella McLean, 1971[2]
Megasurcula Casey, 1904[2]
?*Meggittia* Ray, 1977[1]
Miraclathurella Woodring, 1928[2]
Monilispira Bartsch & Rehder, 1939[2]
Naudedrillia Kilburn, 1988[2]
Otitoma Jousseaume, 1898[3]
[= *Thelecytharella* Shuto, 1969]
?*Paracomitas* Powell, 1942[1]
Pilsbryspira McLean, 1971[3]
(*Nymphispira* McLean, 1971)
Plicisyrinx Sysoev & Kantor, 1986[2]
Pseudomelatoma Dall, 1918[3]
?*Pseudotaranis* McLean, 1995[2]
Ptychobela Thiele, 1925[3]
[= ?*Brachytoma* Swainson, 1840]
Pyrgospira McLean, 1971[3]
?*Rhodopetoma* Bartsch, 1944[2]
Sediliopsis Petuch, 1988[1]
?*Shutonia* Van der Bijl, 1993[1]
Striospira Bartsch, 1950[2]
Tiariturris Berry, 1958[3]
Viridrillia Bartsch, 1943[1]
[= *Viridrillina* Bartsch, 1943]
Zonulispira Bartsch, 1950[3]

Clavatulidae Gray, 1853
(Figs 17A–F, 18)

Diagnosis: Shell medium-sized to rather large (usually 15–30 mm, up to 85 mm high), broad-fusiform to turreted-fusiform, with high spire and usually moderately long siphonal canal. Subsutural ramp usually well developed, with very shallow to rather deep anal sinus situated on its lower part or shifted abapically, with apex at almost a peripheral position. Sculpture variously developed, from almost smooth shell surface to well-developed axial ribs and spiral cords. Protoconch only known as paucispiral, up to *c.* 2.5 smooth whorls. Operculum with medio-lateral nucleus. Radular formula 1-(1-R-1)-1. The central formation is composed of very thin, broad, plate-like lateral teeth and a small, but sometimes strong, narrow rachidian. The central formation is variously developed, sometimes appearing as a pronounced tooth (Fig. 18B), sometimes clearly consisting of three elements (*Clionella sinuata*, see Taylor *et al.*, 1993; Fig. 18A, B), to its nearly complete reduction (Fig. 18C). Marginal teeth usually duplex, with sharp-edged major limb and a deep socket where an accessory limb is inserted, often with angulation distal to the socket (arrow in Fig. 18E). In *Toxiclionella* the marginal teeth are hypodermic, loosely enrolled, attached along their length to radular membrane, having two barbs at the tip and a tooth canal opening subterminally (Fig. 18D).

Remarks: The genus *Gemmuloborsonia* represents a sister group to the (Clavatulidae + Horaiclavidae) clade, but this node is not well supported. Because it resembles much more the Clavatulidae than the Horaiclavidae in terms of shell and radular characters (Fig. 18F), *Gemmuloborsonia* is provisionally included in the former family. If further studies support that hypothesis, then the diagnosis of the Clavatulidae should be amended to account for the presence of weak columellar pleats and multispiral Turridae-type protoconch present in *Gemmuloborsonia*.

Included genera:
Benthoclionella Kilburn, 1974[2]
Caliendrula Kilburn, 1985[1]
Clavatula Lamarck, 1801[3]
Clionella Gray, 1847[2]
?*Fusiturris* Thiele, 1929[1]
[= *Tyrrhenoturris* Coen, 1929]
?*Gemmuloborsonia* Shuto, 1989[3]
Makiyamaia Kuroda in MacNeil, 1961[1]
Perrona Schumacher, 1817[3]
(*Tomellana* Wenz, 1943)
Pusionella Gray, 1847[3]
[= *Netrum* Philippi, 1850]
Scaevatula Gofas, 1989[1]
Toxiclionella Powell, 1966[2]
Trachydrillida Nolf & Swinnen, 2010[1]
Turricula Schumacher, 1817[3]
[= *Surcula* H. & A. Adams, 1853]

Horaiclavidae new family
(Figs 17G–R, 19)

Type genus: *Horaiclavus* Oyama, 1954.

Diagnosis: Shell generally small, 5–25 mm, usually 7–15 mm high, shortly claviform, with relatively low spire and a short, truncated, poorly differentiated siphonal canal. Subsutural ramp usually poorly differentiated. Axial sculpture almost always present, usually as strong sinuate ribs. Spiral sculpture normally weak or obsolete, often with glossy shell surface. Anal sinus on subsutural slope, weak to moderately deep, often constrained by callus. Protoconch of up to 3.5 medially carinate but otherwise smooth whorls when multispiral, but usually paucispiral and smooth. Operculum with terminal nucleus. Radular formula: 1-0-0-0-1. Marginal teeth duplex, with lanceolate major limb and usually narrow accessory limb, which is inserted in a shallow socket. Major limb often with angulation lateral to the place of accessory limb insertion. Rarely (some *Paradrillia*, cf. Kilburn, 1988, Fig. 17; *Inkinga*, Fig. 19B) the additional limb is of similar size to the major limb and the teeth become trough-shaped in transverse section, with a collar near the base (arrows in Fig. 19B). In several species of *Horaiclavus* the radular apparatus is absent.

Remarks: This family shares many characters with Pseudomelatomidae, conchologically differing by a small stout shell with short siphonal canal and usually poorly developed spiral sculpture.

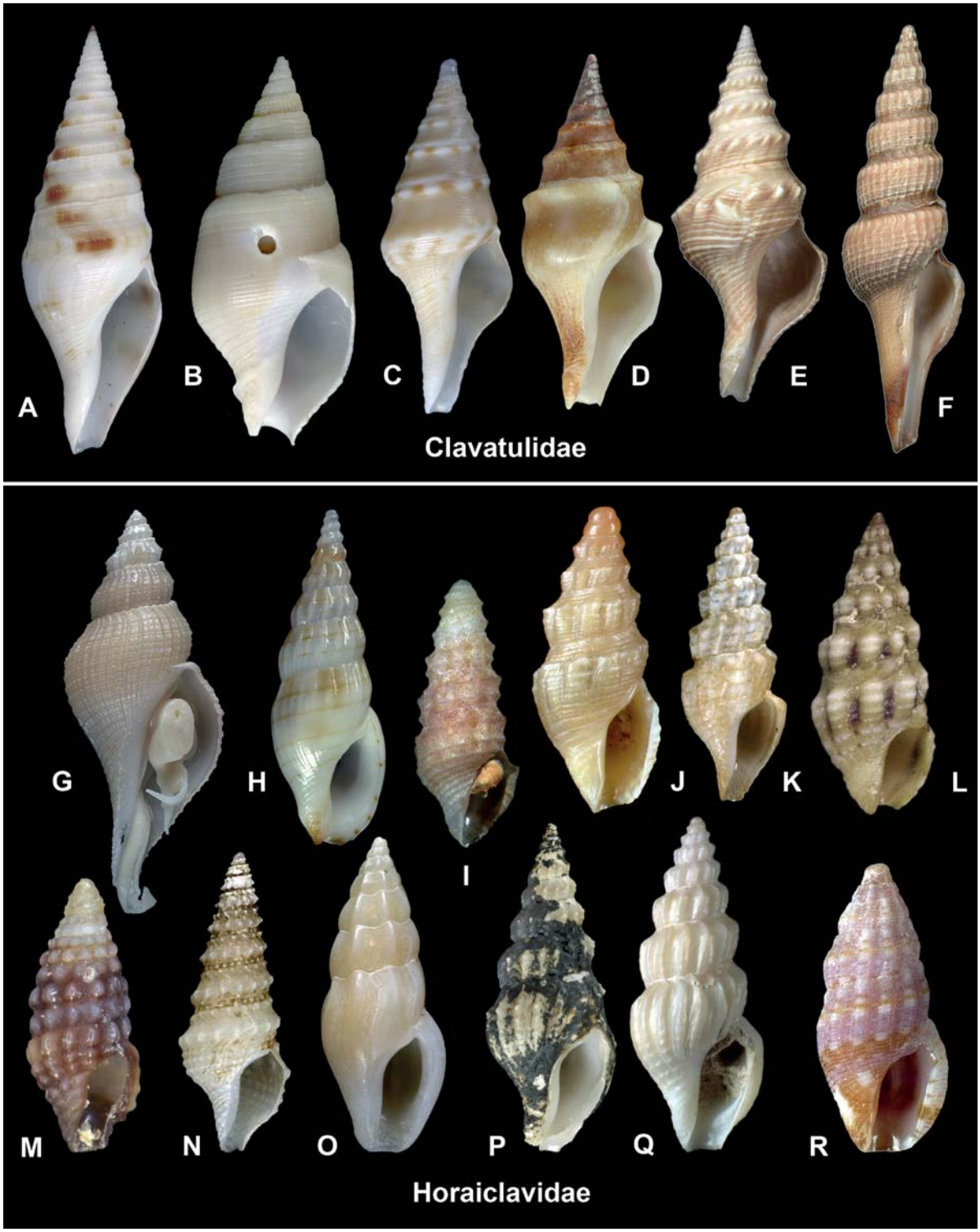

Figure 17. Shells. **A–F.** Clavatulidae**. A.** *Gemmuloborsonia colorata* (Sysoev & Bouchet, 2001)**, MNHN IM200717849, Coral Sea, EBISCO, st. DW2619, 20°06′S, 160 °23′E, 490–550 m, SL 45.5 mm (radula: Fig. 18F). **B.** *Pusionella compacta* Strebel, 1914**, MNHN IM200717830, Cacuaco, Bengo Prov., Angola, 5–10 m, SL 24.1 mm (radula: Fig. 18C). **C.** *Clavatula xanteni* Nolf & Verstraeten, 2006**, MNHN IM200717829, Ilha de Luanda, Luanda Prov., Angola, 40–60 m, SL 20.5 mm (radula: Fig. 18E). **D.** *Perrona subspirata* (von Martens, 1902)**, MNHN IM200717833, Moçâmedes, Namibe Prov., Angola, 5–10 m, SL 24.9 mm. **E.** *Turricula javana* (Linnaeus, 1767), S India, SL 63 mm. **F.** *Fusiturris undatiruga* (Bivona, 1838), Sierra Leone, 60–80 m, SL 43 mm. **G–R:** Horaiclavidae. **G.** *Marshallena philippinarum* (Watson, 1882), MNHN Philippines, PANGLAO 2005, st. CP2334, 09°37.5′N, 123°40.2′E, 606–631 m, SL 26 mm. **H.** *Horaiclavus splendidus* (A. Adams, 1867)**, MNHN IM200717840, Coral Sea, EBISCO, st. DW2631,21°03′S, 160°44′E, 372–404 m, SL 18.0 mm (radula: Fig. 19D). **I.** *Ceritoturris pupiformis* (Smith, 1884)**, MNHN IM200717888, Philippines, PANGLAO 2004, st. T36, 09°29.3′N, 123°51.5′E, 95–128 m, SL 3.4 mm (radula: Fig. 19C). **J.** *Inkinga* sp., New Caledonia, NORFOLK 1, st. DW1737, 22°52′S, 167°12′E, 343–400 m, SL 11.1 mm. (radula: Fig. 19B). **K.** Horaiclavidae gen. 1**, MNHN IM200742501, Solomon Islands, SALOMON 2, st. CP2219, 07°58.3′S, 157°34.4′E, 650–836 m, SL 10.1 mm. **L.** *Buchema interpleura* (Dall & Simpson, 1901), USNM 900896, Lemon Cay, San Blas Islands, Panama, Caribbean Sea, 2 m, SL 10.0 mm. **M.** *Carinapex minutissima* (Garrett, 1873), MNHN,

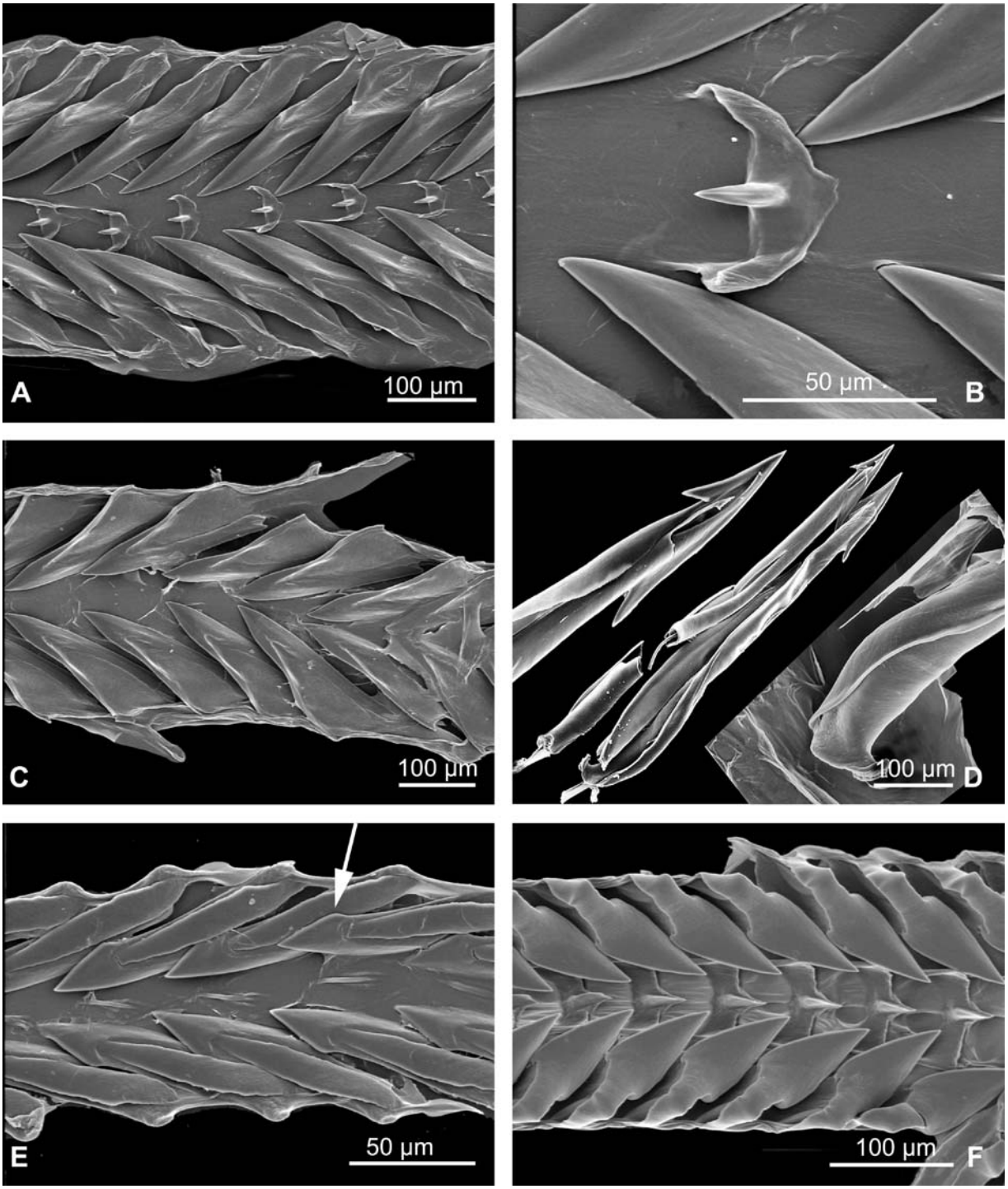

Figure 18. Radulae. Clavatulidae. **A, B.** *Turricula nelliae* (E.A. Smith, 1877)**, NHMUK MOEA 20100551, Danang, Vietnam. **C.** *Pusionella compacta* Strebel, 1914**, MNHN IM200717830 (shell: Fig. 17B). **D.** *Toxiclionella tumida* (Sowerby, 1870), South Africa, after Kantor & Taylor (2000). **E.** *Clavatula xanteni* Nolf & Verstraeten, 2006**, MNHN IM200717829 (shell: Fig. 17C). **F.** *Gemmuloborsonia colorata* (Sysoev & Bouchet, 2001)**, MNHN IM200717849 (shell: Fig. 17A). Symbol: **, sequenced specimen. Arrow, see text.

New Caledonia, LIFOU 2000, st. 1457, 20°46.8′S, 167°02.75′E, 5–10 m, SL 3.1 mm. **N.** *Paradrillia* sp.**, MNHN IM200742475, Philippines, PANGLAO 2005, st. CP2396 09°36.3′N, 123°42.0′E, 609–673 m, SL 11.5 mm (radula: Fig. 19A). **O.** *Haedropleura septangularis* MNHN, Finistère, France, 20–30 m, SL 11 mm. **P.** *Anguloclavus* sp.**, MNHN IM200717908, PANGLAO 2005, st. CP2332, 09°38.8′N, 123°45.9′E, SL 19.0 mm. **Q.** *Iwaoa* sp., New-Caledonia, MUSORSTOM6, st. DW489, 20°48′S, 167°06′E, 700 m, SL 13.5 mm. **R.** *Anacithara themeropsis* (Melvill & Standen, 1896), MNHN, LIFOU 2000, st. 1427, 20°47.6′S, 167°10.2′E, 10 m, SL 4.5 mm. Abbreviation and symbols: SL, shell length; * , sequenced species; **, sequenced specimen. Photo credits: B. Buge (B–D, H, I, P, O), M.G. Harasewych and D. Tippett (L), P. Maestrati (J, Q, R).

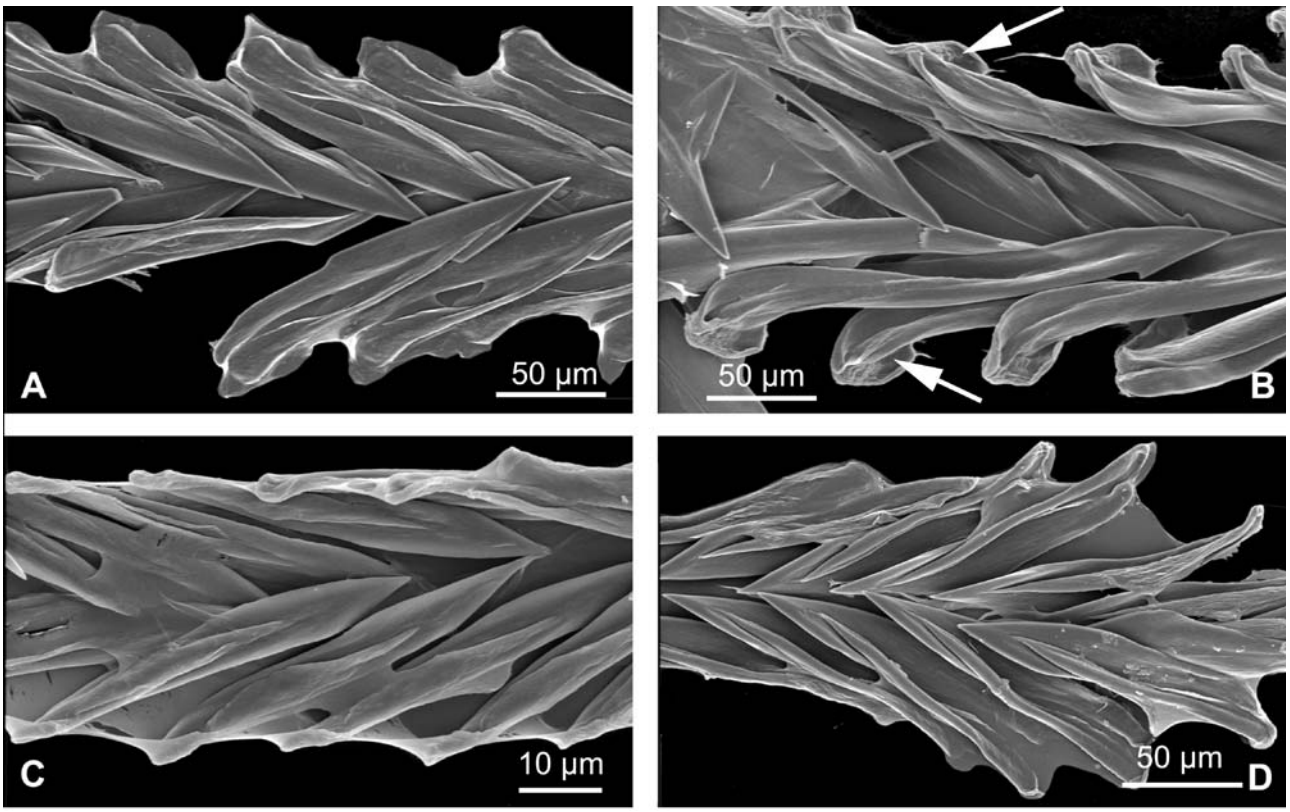

Figure 19. Radulae. Horaiclavidae. **A.** *Paradrillia* sp.**, MNHN IM200742475 (shell: Fig. 17N). **B.** *Inkinga* sp., MNHN (shell: Fig. 17 J). **C.** *Ceritoturris pupiformis* (E.A. Smith, 1884)**, MNHN IM200717888 (shell: Fig. 17I). **D.** *Horaiclavus splendidus* (A. Adams, 1867)**, MNHN IM200717840 (shell: Fig. 17H). Symbol: **, sequenced specimen. Arrows, see text.

Radulae also are rather similar to many representatives of Pseudomelatomidae and no clear cut distinctions were found. Genera currently included in Horaiclavidae have been usually included in the Crassispiridae (= Pseudomelatomidae), and the clear molecular-based division between the two clades seems to be not so clearly reflected in shell-based distinction. Therefore, the generic composition of the family is somewhat provisional and needs confirmation by further molecular data and/or a detailed analysis of conchological and radular characters.

Included genera:
Anacithara Hedley, 1922[3]
Anguloclavus Shuto, 1983[3]
?*Aoteadrillia* Powell, 1942[2]
?*Austrocarina* Laseron, 1954[1]
Austrodrillia Hedley, 1918[1]
(*Regidrillia* Powell, 1942)
Buchema Corea, 1934[2]
Carinapex Dall, 1924[3]
Ceritoturris Dall, 1924[3]
Coronacomitas Shuto, 1983[1]
Cytharoclavus Kuroda & Oyama in Kuroda, Habe & Oyama, 1971[1]
?*Darrylia* García, 2008[1]
Graciliclava Shuto, 1983[1]
Haedropleura Bucquoy, Dautzenberg & Dollfus, 1883[2]
Horaiclavus Oyama, 1954[3]
Inodrillia Bartsch, 1943[1]
[= *Inodrillara* Bartsch, 1943]
[= *Inodrillina* Bartsch, 1943]
Inkinga Kilburn, 1988[1]
Iwaoa Kuroda, 1940[1]
?*Marshallena* Allan, 1927[2]
[= *Sugitanitoma* Kuroda, 1959]
Mauidrillia Powell, 1942[2]
?*Micropleurotoma* Thiele, 1929[2]
Naskia Sysoev & Ivanov, 1985[1]
Nquma Kilburn, 1988[2]
Paradrillia Makiyama, 1940[3]
[= *Vexitomina* Powell, 1942]
[= *Alticlavatula* MacNeil, 1960]
?*Pseudexomilus* Powell, 1944[1]
Psittacodrillia Kilburn, 1988[1]
Striatoguraleus Kilburn, 1994[1]
?*Thelecythara* Woodring, 1928[1]

Turridae H. Adams & A. Adams, 1853
(Figs 20 and 21)

Diagnosis: shell of medium to large size (usually 20–30 mm, up to 110 mm high), short- to high-fusiform, usually with a high spire and a long (rarely short and truncated) siphonal canal. Axial sculpture weak or absent. Anal sinus on whorl periphery. Protoconch typically multispiral, up to six whorls, protoconch I smooth, protoconch II with arcuate axial riblets; reduced paucispiral protoconch usually smooth, may have arcuate axial riblets. Operculum fully developed, with terminal nucleus. Radular formula typically 1-(1:R:1)-1. Small and narrow rachidian and plate-like laterals are fused together, together constituting a central formation of different development (Kantor, 2006), varying from a well-defined broad central tooth (Fig. 21B) to a tooth clearly formed of three elements (Fig. 21A) through a gradual reduction of rachidian and/or laterals to complete absence (Fig. 21D). Marginals duplex, of variable morphology, from broadly oval and flattened (Fig. 21E, F) with nearly equally developed limbs to awl-

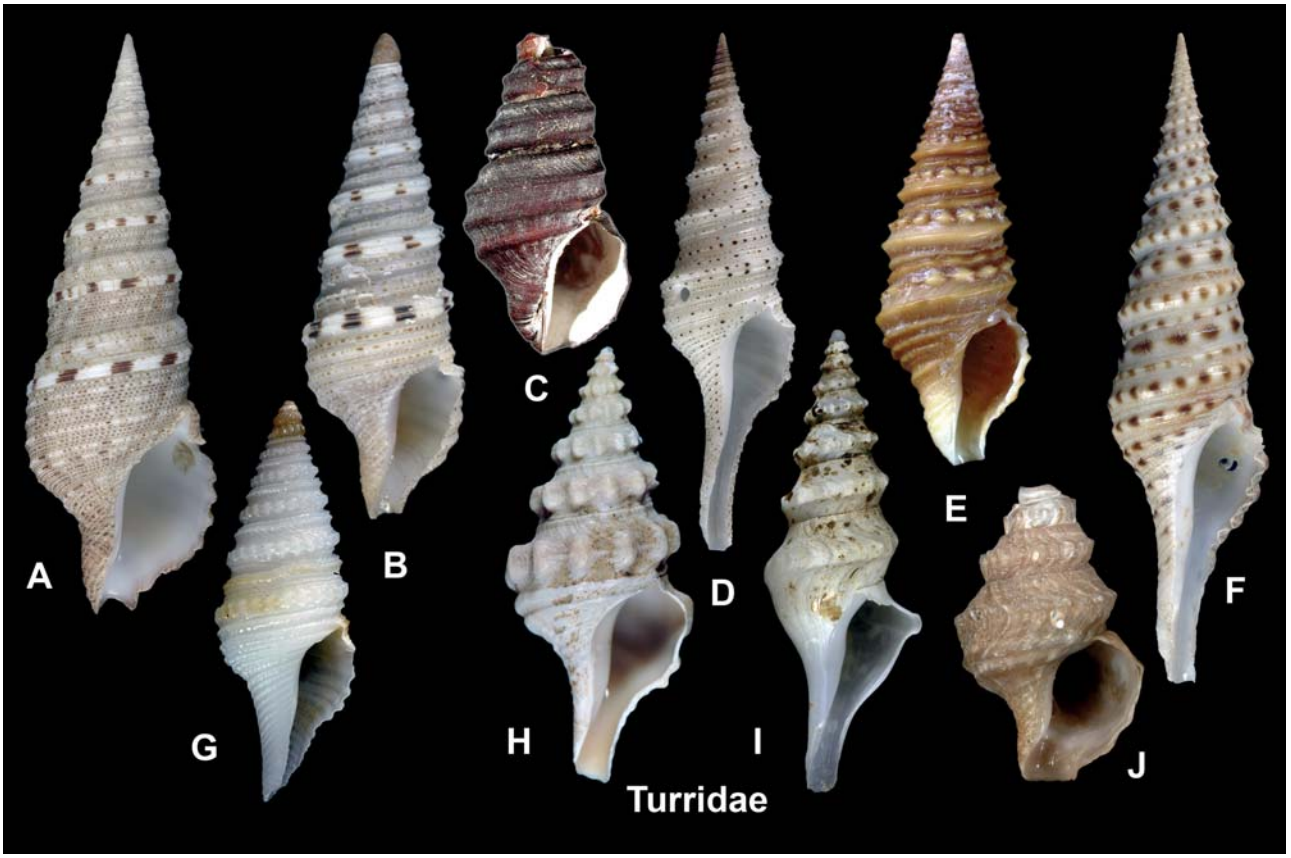

Figure 20. Shells. Turridae. **A.** *Xenuroturris legitima* Iredale, 1929**, MNHN IM200717684, Vanuatu, SANTO 2006, st. DR087, 15°38.5′S, 167°15.1′E, 13 m, SL 57.0 mm (radula: Fig. 21C). **B.** *Iotyrris cingulifera* (Lamarck, 1822)**, MNHN IM200717685, Vanuatu, SANTO 2006, st. FS84, 15°33.6′S, 167°16.6′E, 8–9 m, SL 15.5 mm (radula: Fig. 21D). **C.** *Decollidrillia nigra* Habe & Ito, 1965, ZMMU uncatalogued, southern Kurile Islands, SL 12.8 mm. **D.** *Lophiotoma acuta* (Perry, 1811)**, MNHN IM200717860, Philippines, PANGLAO 2004, st. R44, 09°33.3′N, 123°43.9′E, 2 m, SL 44.0 mm. **E.** *Turridrupa acutigemmata* (E.A. Smith, 1877), New Caledonia, 46 m, SL 26.5 mm. **F.** *Turris babylonia* (Linnaeus, 1758)**, MNHN IM200717754, Philippines, PANGLAO 2004, st. R42, 09°37.1′N, 123°52.6′E, 8–22 m, SL 79.4 mm. **G.** *Gemmula rarimaculata* (Kuroda & Oyama, 1971)**, MNHN IM200717838, Coral Sea, EBISCO, st. DW2533, 22°18′S, 159°28′E, 360–370 m, SL 13.7 mm. **H.** *Ptychosyrinx chilensis* Berry, 1968, USNM 870005, S of Coquimbo, Chile, 31.1° S, 71.8° W, 179–187 m, SL 21.1 mm. **I.** *Lucerapex* cf. *casearia* (Hedley & Petterd, 1906)**, MNHN IM200742448, Philippines, PANGLAO 2005, st. CP2363, 09°06.0′N, 123°25.0′E, 437–439 m, SL 21.0 mm (radula: Fig. 21 E). **J.** *Cryptogemma corneus* (Okutani, 1966), ZIN 58809/1, off Shikotan I., Kurile Islands, 1450–1530 m, 12.3 mm. Abbreviation and symbol: SL, shell length; **, sequenced specimen.

shaped and divided only in basal part (Fig. 21A). In most cases, the major limb is large and knife-shaped, while the accessory limb is dorsal and more weakly developed (Fig. 21). In *Iotyrris*, marginal teeth have equally developed limbs that form a shallow broad trough (Fig. 21D).

Remarks: This group is well defined by its usually narrowly fusiform shell with obsolete axial sculpture and peripheral anal sinus. However, the genus *Lucerapex*, although fully conforming conchologically, occupies a position on the tree (sister group to Turridae + Terebridae) that excludes it from the Turridae. It is nevertheless tentatively included here in Turridae.

Included genera:
Cryptogemma Dall, 1918[2]
Decollidrillia Habe & Ito, 1965[1]
Epidirella Iredale, 1913[1]
[= *Austrogemmula* Laseron, 1954]
Gemmula Weinkauff, 1875[3]
[= *Eugemmula* Iredale, 1931]
(*Pinguigemmula* MacNeil, 1960)
Iotyrris Medinskaya & Sysoev, 2001[3]
Kuroshioturris Shuto, 1961[1]
Lophiotoma Casey, 1904[3]
[= *Lophioturris* Powell, 1964]
?*Lucerapex* Iredale, 1936[3]
Polystira Woodring, 1928[3]
[= *Oxytropa* Glibert, 1955]
Ptychosyrinx Thiele, 1925[3]
[= *Bathybermudia* Haas, 1949]
Turridrupa Hedley, 1922[3]
Turris Batsch, 1789[3] (For authorship of Turris, see Dubois & Bour (2010))
[= *Pleurotoma* Lamarck, 1799]
[= *Pleurotomus* Blainville, 1810]
(*Annulaturris* Powell, 1966)
Unedogemmula MacNeil, 1961[2]
Xenuroturris Iredale, 1929[3]
[= *Clamturris* Iredale, 1931]

Strictispiridae McLean, 1971
(Figs 11E, 22A, B)

Diagnosis: Shell medium-sized, to 20 mm, claviform. Spiral and axial sculpture well developed, shoulder with a marked subsutural fold. Anal sinus deep, laterally directed. Parietal callus

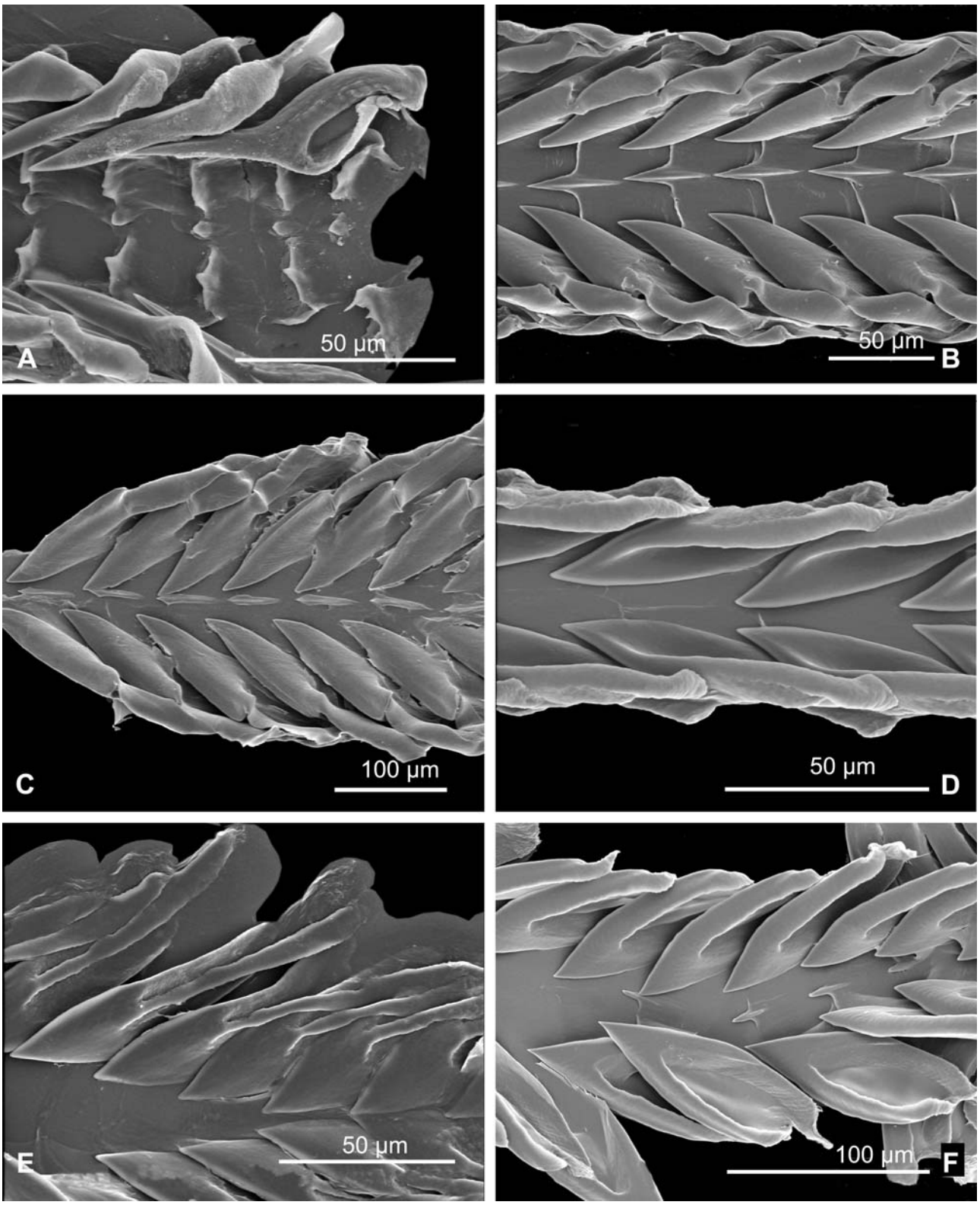

Figure 21. Radulae. Turridae. **A.** *Turridrupa* cf. *armillata* (Reeve, 1845), MNHN IM200740773, Coral Sea, EBISCO, st. DW2607, 19°33′S, 158°40′E, 400–413 m. **B.** *Gemmula kieneri* (Doumet, 1840), MNHN, Vanuatu, MUSORSTOM 8, st. CP1123, 15°07′S, 166°55′E, 262–352 m. **C.** *Xenuroturris legitima* Iredale, 1929, MNHN IM200717684 (shell: Fig. 20A). **D.** *Iotyrris cingulifera* (Lamarck, 1822)**, MNHN IM200717685 (shell: Fig. 20B). **E.** *Lucerapex* cf. *casearia* (Hedley & Petterd, 1906)**, MNHN IM200742448 (shell: Fig. 20I). **F.** *Turris crispa* (Lamarck, 1816), MNHN, Ile Ouen-Baie du Prony, st. 80, 22°31S, 166°28E, 33 m, SS 39 mm. Symbols: **, sequenced specimen.

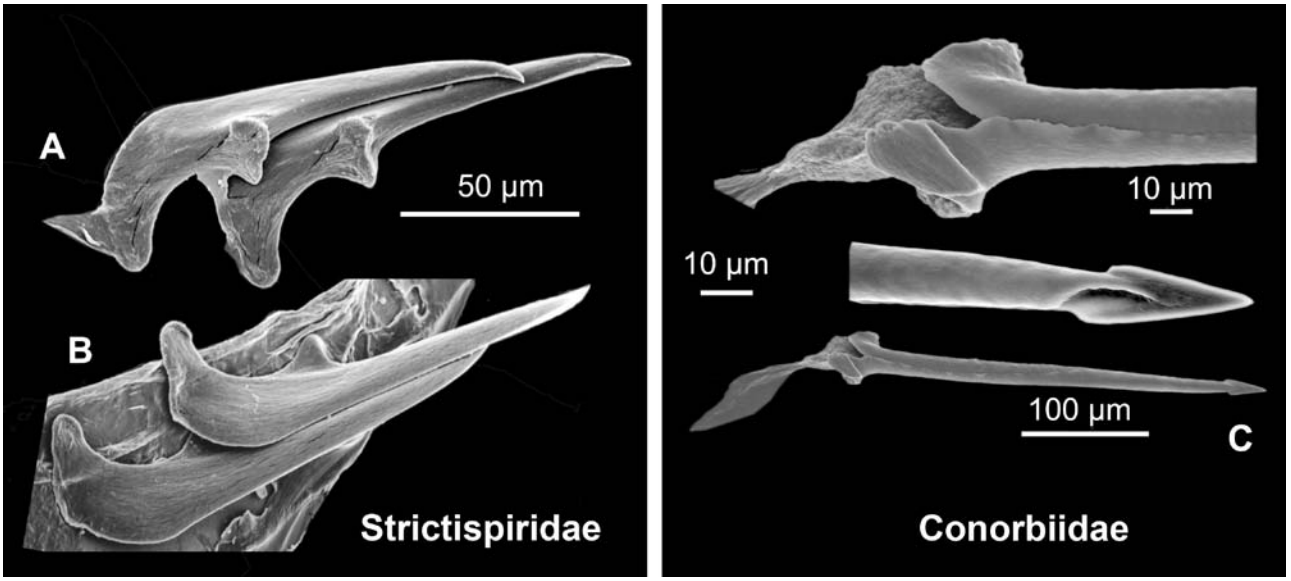

Figure 22. Radulae. **A, B.** Strictispiridae**.** *Strictispira paxillus* (Reeve, 1845), British Virgina Islands, ANSP. **A**. teeth detached from the membrane and showing the large median flange. **B**. Two teeth, showing the large median flange attached to the membrane. Photo submit: J.D. Taylor (A. B). **C.** Conorbidae**.** *Benthofascis lozoueti* Sysoev & Bouchet, 2001, MNHN IM200742331 (shell: Fig. 2O).

well developed. Protoconch paucispiral in all species examined, smooth. Operculum leaf-shaped, with terminal nucleus. Radula consisting of a pair of solid awl-shaped marginal teeth that have a prominent flange, located above the base of the tooth and firmly attached to the radular membrane.

Remarks: We did not obtain any material of Strictispiridae for molecular analysis and the position of the family group remains unclear. The shell resembles that of Pseudomelatomidae and the shape of the radular marginal teeth is also somewhat similar to *Pseudomelatoma*, *Hormospira* and *Tiariturris*, but it differs in the absence of the rachidian. Among the examined species of *Strictispira*, *S. paxillus* is characterised by rather unusual characters, such as the absence of the venom gland together with very large and powerful odontophore (Kantor & Taylor, 1994). Until molecular data are available, we conservatively treat this family as valid, following Taylor *et al.* (1993).

Included genera:

Strictispira McLean, 1971[2]
Cleospira McLean, 1971[2]

Terebridae Mörch, 1852

Diagnosis: Shell medium-sized to large, 8–270 mm, usually 30–100 mm high, auger-shaped, with high to very high multiwhorled spire and flattened shell profile, aperture relatively small. Siphonal canal short, anal sinus not pronounced. Protoconch with up to 5 smooth whorls when multispiral. Radular formula 1–0-0-0-1 but radular apparatus absent in many species. Marginal teeth range from solid and curved to hypodermic, with or without small barb at the tip. Hypodermic teeth without solid bases. In some species (e.g. *Impages hectica*) the walls of the teeth are penetrated by numerous holes.

Included genera (After Bratcher & Cernohorsky, 1987; Terryn, 2007; Terryn & Holford, 2008):

Cinguloterebra Oyama, 1961[3]
Clathroterebra Oyama, 1961[3]
Duplicaria Dall, 1908[1]
    [= *Diplomeriza* Dall, 1919]
    [= *Myurellisca* Bartsch, 1923]
    [= *Pervicacia* Iredale, 1924]
Euterebra Cotton & Godfrey, 1932[3]
    [= *Gradaterebra* Cotton & Godfrey, 1932]
    [= *Partecosta* Dance & Eames, 1966]
Granuliterebra Oyama, 1961[1]
Hastula H. & A. Adams, 1853[3]
    [= *Acuminia* Dall, 1908]
    [= *Egentelaria* Rehder, 1980]
    [= *Hastulina* Oyama, 1961]
Hastulopsis Oyama, 1961[3]
Impages E.A. Smith, 1873[1]
Microtrypetes Pilsbry & Lowe, 1932[1]
Myurella Hinds, 1845[3]
    [= *Decorihastula* Oyama, 1961]
Oxymeris Dall, 1903[3]
    [= *Acus* Gray, 1847 (non Müller, 1774)]
    [= *Nototerebra* Cotton, 1947]
Pellifronia Terryn & Holford, 2008[1]
Perirhoe Dall, 1908[1]
    [= *Abretiella* Bartsch, 1923]
    [= *Dimidacus* Iredale, 1929]
Pristiterebra Taki & Oyama, 1954[1]
    [= *Laeviacus* Oyama, 1961]
Strioterebrum Sacco, 1891[3]
    [= *Brevimyurella* Oyama, 1961]
    [= *Punctoterebra* Bartsch, 1923]
Terebra Bruguière, 1789[3]
    [= *Myurellina* Bartsch, 1923]
    [= *Panaterebra* Olsson, 1967]
    [= *Paraterebra* Woodring, 1928]
    [= *Subula* Schumacher, 1817]
    [= *Terebrum* Montfort, 1810]
Terenolla Iredale, 1929[3]
Triplostephanus Dall, 1908[1]

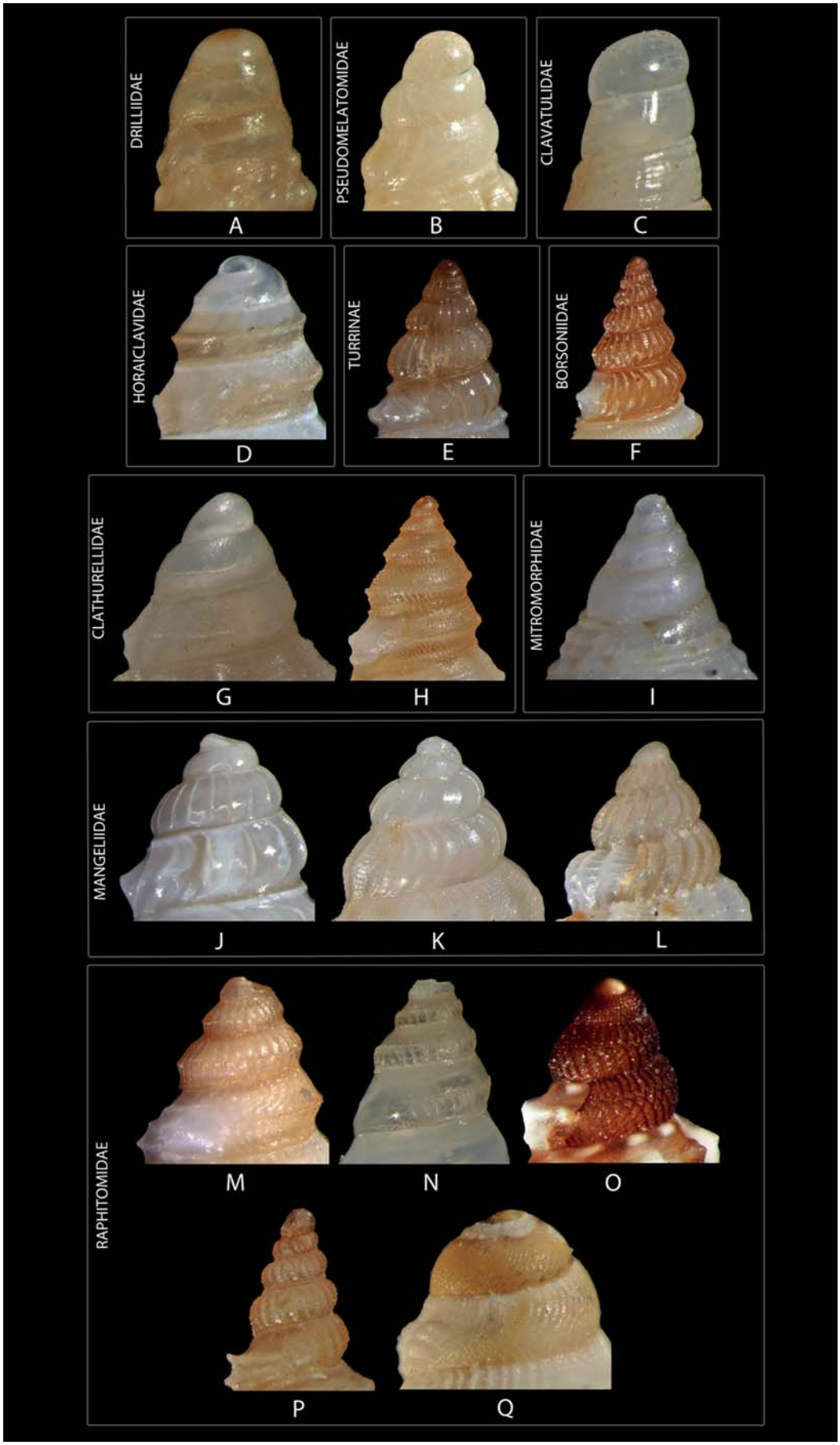

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Figure 23. Protoconchs. Only multispiral protonchs are illustrated. **A.** Drilliidae. *Iredalea* sp. (= *aureolinea*), MNHN, New Caledonia, LIFOU 2000, st. 1441, 20°46.4′S, 167°02.0′E, 20 m. **B.** Pseudomelatomiidae. *Inquisitor* cf. *nodicostatus* Kilburn, 1988, MNHN, New Caledonia, MUSORSTOM 6, st. DW391, 20°47′S, 167°06′E, 390 m. **C.** Clavatulidae. *Clavatula strebeli* Knudsen, 1952, MNHN, Ilha de Luanda, Angola, 40–60 m. **D.** Horaiclavidae. *Ceritoturris pupiformis* (E.A. Smith, 1884)*, MNHN, New Caledonia, MONTROUZIER, st.1249, 20°49′S, 165°19′E, 80–140 m. **E.** Turridae. *Gemmula* sp., MNHN IM200740766, Coral Sea, EBISCO, DW2625, 20°05′S, 160°20′E, 627–741 m. **F.** Borsoniidae. *Microdrillia fastosa* (Hedley, 1907), MNHN, New Caledonia, SMIB 8, st. DW146, 24°55′S, 168°22′E, 514–522 m. **G, H.** Clathurellidae. **G.** *Clathurella curtisiana* (Hedley, 1922), MNHN, New Caledonia, MONTROUZIER, st.1250, 20°46.7′S, 165°13.7′E, 3–6 m. **H.** *Nannodiella acricula* (Hedley, 1922), MNHN, New Caledonia, MONTROUZIER, st.1261, 20°46′S, 165°15′E, 45–56 m. **I.** Mitromorphidae. *Mitromorpha metula*** (Hinds, 1843), MNHN IM200717898, Philippines, PANGLAO 2004, st. B8, 9°37.1′N, 123°46.1′E, 3 m. **J–L.** Mangeliidae. **J.** *Benthomangelia* sp., MNHN, Fiji, BORDAU 1, st. CP1407, 16°40′S, 179°39′E, 499–529 m. **K.** *Neoguraleus* sp., MNHN, New Caledonia, CONCALIS, st. DW2982, 18°02′S, 163°04′E, 320–337 m. **L.** *Pyrgocythara notabilis* (E.A. Smith, 1888), MNHN, New Caledonia, LIFOU 2000, st. 1429, 20°47.5′S, 167°07.1′E, 8–18 m. **M–Q.** Raphitomidae. **M.** *Neopleurotomoides* sp., MNHN, New Caledonia, BIOCAL, st. CP75, 22°19′S, 167°23′E. **N.** *Famelica* sp., MNHN, New Caledonia, BATHUS 4, st. DW914, 18°49′S, 163°15′E, 600–616 m. **O.** *Tritonoturris cumingi* (Powys, 1835), MNHN, Touho, New Caledonia, st. 1357, 22°30.2′S, 166°26,4′E, 22–35 m. **P.** *Veprecula* sp., MNHN, New Caledonia, MONTROUZIER, st. 1306, 20°39.1′S, 164°12.4′E, 11–13 m. **Q.** *Pleurotomella packardi* Verrill, 1872, MNHN, INCAL, Porcupine abyssal plain, st. WS10, 47°27′N, 09°40′W, 4354 m. Symbol: *, sequenced species; **, sequenced specimen.

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APPENDIX 1: INDEX OF GENERA AND SUBGENERA

Genus-group taxa removed from Conoidea are preceded by an asterisk.

(Sub) genus	Family
Abretiella	Terebridae
Abyssaforia	?Cochlespiridae
Abyssobela	Raphitomidae
Abyssocomitas	?Pseudomelatomidae
Abyssothauma	?Raphitomidae
Acamptodaphne	Raphitomidae
Acanthodaphne	Raphitomidae
Acinodrillia	?Drilliidae
Acmaturris	Mangeliidae
Acrista	Clathurellidae
Acropota	Borsoniidae
Acuminia	Terebridae
Acus	Terebridae
Adanaclava	?Clathurellidae
Aforia	?Cochlespiridae
Africonus	Conidae
Agathotoma	Mangeliidae
Agladrillia	Drilliidae
Aguilaria	Pseudomelatomidae
Aliceia	Raphitomidae
Allo	?Raphitomidae
Alticlavatula	Horaiclavidae
Anacithara	Horaiclavidae
Anarithma	Mitromorphidae
Ancistrosyrinx	Cochlespiridae
Anguloclavus	Horaiclavidae
Annulaturris	Turridae
Anomalotomella	Raphitomidae
Anticlinura	Mangeliidae
Anticomitas	?Pseudomelatomidae
Antiguraleus	Mangeliidae
Antimelatoma	Pseudomelatomidae
**Antimitra*	Buccinidae
Antiplanes	Pseudomelatomidae
Aoteadrillia	?Horaiclavidae
Apaturris	?Borsoniidae
Aphanitoma	Borsoniidae
Apiotoma	?Cochlespiridae
Apispiralia	Mangeliidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Apitua	Mangeliidae
Arielia	Mitromorphidae
Artemidiconus	Conorbidae
Asperdaphne	Raphitomidae
Aspertilla	Raphitomidae
Asprella	Conidae
Asthenotoma	Borsoniidae
Austrocarina	?Horaiclavidae
Austroconus	Conidae
Austrodaphnella	Raphitomidae
Austrodrillia	Horaiclavidae
Austrogemmula	Turridae
Austropusilla	?Raphitomidae
Austrotoma	Raphitomidae
Austroturris	Borsoniidae
Azorilla	Raphitomidae
Azorita	Raphitomidae
Bactrocythara	Mangeliidae
Bathybela	Raphitomidae
Bathybermudia	Turridae
**Bathyclionella*	Buccinidae
Bathyconus	Conidae
Bathypota	Raphitomidae
Bathytoma	Borsoniidae
Bela	Mangeliidae
Belalora	?Mangeliidae
Belaturricula	?Borsoniidae
Bellacythara	Mangeliidae
Bellaspira	Drilliidae
Bellatula	Clathurellidae
**Belomitra*	Buccinidae
Benthoclionella	Clavatulidae
Benthodaphne	?Pseudomelatomidae
Benthofascis	Conorbidae
Benthomangelia	Mangeliidae
Boettgeriola	Borsoniidae
Borsonella	Borsoniidae
Borsonellopsis	Borsoniidae
Borsonia	Borsoniidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Brachycythara	Mangeliidae
Brachytoma	?Pseudomelatomidae
Brephodrillia	Drilliidae
Brevimyurella	Terebridae
Buccinaria	Raphitomidae
Buchema	Horaiclavidae
Burchia	Pseudomelatomidae
Buridrillia	Pseudomelatomidae
Cacodaphnella	?Mangeliidae
Calamiconus	Conidae
Calcatodrillia	Pseudomelatomidae
Calibanus	Conidae
Caliendrula	Clavatulidae
Californiconus	Conidae
Calliclava	Drilliidae
Calusaconus	Conidae
Canetoma	Mangeliidae
Cariboconus	Conidae
Carinapex	Horaiclavidae
Carinodrillia	Pseudomelatomidae
Carinoturris	?Pseudomelatomidae
Cenodagreutes	Raphitomidae
Ceritoturris	Horaiclavidae
Cerodrillia	Drilliidae
Cestoma	Mangeliidae
Chelyconus	Conidae
Cheungbeia	Pseudomelatomidae
Cinguloterebra	Terebridae
Citharomangelia	Mangeliidae
Clamturris	Turridae
Clathrodrillia	Drilliidae
Clathromangelia	?Clathurellidae
Clathroterebra	Terebridae
Clathurella	Clathurellidae
Clathurina	Raphitomidae
Clavatula	Clavatulidae
Clavicantha	Drilliidae
Clavosurcula	?Cochlespiridae
Clavus	Drilliidae
Clebula	Conidae
Cleospira	Strictispriridae
Clinura	Raphitomidae
Clinuromella	Mangeliidae
Clionella	Clavatulidae
Cochlespira	Cochlespiridae
Cochlioconus	Raphitomidae
Comarmondia	Clathurellidae
Comitas	Pseudomelatomidae
Compsodrillia	Pseudomelatomidae
Conasprella	Conidae
Conasprelloides	Conidae
Conopleura	Drilliidae
Conorbela	?Pseudomelatomidae
Conticosta	Pseudomelatomidae
Conus	Conidae
Cordieria	Borsoniidae
Corinnaeturris	Clathurellidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Cornutoconus	Conidae
Coronacomitas	Horaiclavidae
Coronasyrinx	Cochlespiridae
Coronaxis	Conidae
Crassiclava	Pseudomelatomidae
Crassispira	Pseudomelatomidae
Crassispirella	Pseudomelatomidae
Crassopleura	Drilliidae
Cretaspira	Pseudomelatomidae
Crockerella	Clathurellidae
Cruziturricula	?Drilliidae
Cryoturris	Mangeliidae
Cryptodaphne	Raphitomidae
Cryptogemma	Turridae
**Cryptomitra*	Buccinidae
Cucullites	Conidae
Cucullus	Conidae
Curtitoma	Mangeliidae
Cylinder	Conidae
Cylindrella	Conidae
Cylindrus	Conidae
Cymakra	Mitromorphidae
Cymatosyrinx	Drilliidae
Cyrtocythara	Mangeliidae
Cyrtoides	Raphitomidae
Cythara	?Mangeliidae
Cytharella	Mangeliidae
Cytharoclavus	Horaiclavidae
Cytharopsis	Mangeliidae
Dallaforia	?Cochlespiridae
Dalliconus	Conidae
Dallspira	Pseudomelatomidae
Danilacarina	Cochlespiridae
Daphnella	Raphitomidae
**Daphnellopsis*	Muricidae
Darbya	Borsoniidae
Darioconus	Conidae
Darrylia	?Horaiclavidae
Dauciconus	Conidae
Decollidrillia	Turridae
Decorihastula	Terebridae
Dendroconus	Conidae
Diaugasma	Raphitomidae
Dimidacus	Terebridae
Diplomeriza	Terebridae
Diptychophlia	Borsoniidae
Douglassia	Drilliidae
Doxospira	Pseudomelatomidae
Drillia	Drilliidae
Drilliola	Borsoniidae
Ductoconus	Conidae
Duplicaria	Terebridae
Dyraspis	Conidae
Egentelaria	Terebridae
Elaeocyma	Drilliidae
Eldridgea	Drilliidae
Embrikena	Conidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Endemoconus	Conidae
Epideira	Pseudomelatomidae
Epidirella	Turridae
Epidirona	Pseudomelatomidae
Eremiconus	Conidae
Erythroconus	Conidae
Etrema	Clathurellidae
Etremopa	Clathurellidae
Etremopsis	Clathurellidae
Eubela	Raphitomidae
Eucithara	Mangeliidae
Euclathurella	Clathurellidae
Eucyclotoma	Raphitomidae
Eudaphnella	Raphitomidae
Eugemmula	Turridae
Eugeniconus	Conidae
Euglyphostoma	Clathurellidae
Euguraleus	Mangeliidae
Eumetadrillia	Drilliidae
Euryentmema	?Mangeliidae
Euterebra	Terebridae
Exomilus	?Raphitomidae
Famelica	Raphitomidae
Favriella	Raphitomidae
Fehria	Mangeliidae
Feliciella	?Raphitomidae
Fenestrosyrinx	Raphitomidae
Fenimorea	Drilliidae
Filodrillia	Borsoniidae
Floraconus	Conidae
Fulgiconus	Conidae
Fumiconus	Conidae
Funa	Pseudomelatomidae
Funitoma	Mangeliidae
Fusiconus	Conidae
Fusidaphne	?Raphitomidae
Fusisyrinx	?Drilliidae
Fusiturricula	?Drilliidae
Fusiturris	?Clavatulidae
Gastridium	Conidae
Gemmula	Turridae
Gemmuloborsonia	?Clavatulidae
Genota	Borsoniidae
Genotia	Borsoniidae
Genotina	Mangeliidae
Genuanoconus	Conidae
Gibbaspira	Pseudomelatomidae
Gingicithara	Mangeliidae
Ginnania	Mangeliidae
Gladioconus	Conidae
Globiconus	Conidae
Globidrillia	Drilliidae
Glossispira	Pseudomelatomidae
Glyphostoma	Clathurellidae
Glyphostomoides	Raphitomidae
Glyphostomops	Clathurellidae
Glyphoturris	Mangeliidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Glyptaesopus	?Borsoniidae
Graciliclava	Horaiclavidae
Gradaterebra	Terebridae
Gradiconus	Conidae
Granotoma	Mangeliidae
Granoturris	Mangeliidae
Granuliterebra	Terebridae
Graphiconus	Conidae
Guraleus	Mangeliidae
Gymnobela	Raphitomidae
Haedropleura	Horaiclavidae
Harmoniconus	Conidae
Hastula	Terebridae
Hastulina	Terebridae
Hastulopsis	Terebridae
Hauturua	Drilliidae
Helenella	Mitromorphidae
Hemicythara	Mangeliidae
Hemidaphne	Raphitomidae
Hemilienardia	Raphitomidae
Hermes	Conidae
Heroconus	Conidae
Heterocithara	Mangeliidae
Heteroturris	Borsoniidae
Hindsiclava	Pseudomelatomidae
Horaiclavus	Horaiclavidae
Hormospira	Pseudomelatomidae
Imaclava	Drilliidae
Impages	Terebridae
Inkinga	Horaiclavidae
Inodrillara	Horaiclavidae
Inodrillia	Horaiclavidae
Inodrillina	Horaiclavidae
Inquisitor	Pseudomelatomidae
Iotyrris	Turridae
Iraquetrema	Clathurellidae
Iredalea	Drilliidae
Irenosyrinx	Cochlespiridae
Isodaphne	Raphitomidae
Ithycythara	Mangeliidae
Itia	?Mitromorphidae
Iwaoa	Horaiclavidae
Jaspidiconus	Conidae
**Jumala*	Buccinidae
Kalloconus	Conidae
Kenyonia	Conidae
Kermasprella	Conidae
Kermia	Raphitomidae
Ketyconus	Conidae
Kioconus	Conidae
Knefastia	Pseudomelatomidae
Kohniconus	Conidae
Kuradoconus	Conidae
Kurilohadalia	?Pseudomelatomidae
Kurodadrillia	Pseudomelatomidae
Kuroshiodaphne	Raphitomidae
Kuroshioturris	Turridae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Kurtzia	Mangeliidae
Kurtziella	Mangeliidae
Kurtzina	Mangeliidae
Kylix	Drilliidae
Laeviacus	Terebridae
Lamniconus	Conidae
Lautoconus	Conidae
Leiocithara	Mangeliidae
Leiosyrinx	Raphitomidae
Leporiconus	Conidae
Leptadrillia	Drilliidae
Leptoconus	Conidae
Leucosyrinx	?Pseudomelatomidae
Leufroyia	Raphitomidae
Lienardia	Clathurellidae
Lilliconus	Conidae
Lindaconus	Conidae
Lineotoma	Raphitomidae
Lioglyphostoma	Pseudomelatomidae
Lioglyphostomella	Pseudomelatomidae
Liracraea	Mangeliidae
Lissodrillia	Drilliidae
Litachilus	Raphitomidae
Lithoconus	Conidae
Lividoconus	Conidae
Lizaconus	Conidae
Lophiotoma	Turridae
Lophioturris	Turridae
Lorabela	?Mangeliidae
Lovellona	Mitromorphidae
Lucerapex	?Turridae
Lusitanops	Raphitomidae
Lyromangelia	Mangeliidae
Macteola	?Mangeliidae
Maesiella	Pseudomelatomidae
Magelliconus	Conidae
Magnella	Raphitomidae
Majox	Raphitomidae
Makiyamaia	Clavatulidae
Mamiconus	Conidae
Mammillaedrillia	Pseudomelatomidae
Mangelia	Mangeliidae
Mangiliella	Mangeliidae
Maorimorpha	Mitromorphidae
Maoritomella	Borsoniidae
Marita	Mangeliidae
Marshallena	?Horaiclavidae
Mauidrillia	Horaiclavidae
Megasurcula	Pseudomelatomidae
Meggittia	?Pseudomelatomidae
Metaclathurella	Raphitomidae
Micantapex	Borsoniidae
Microdaphne	Raphitomidae
Microdrillia	Borsoniidae
Microgenia	Raphitomidae
Micropleurotoma	?Horaiclavidae
Microtrypetes	Terebridae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Miliariconus	Conidae
Mioawateria	Raphitomidae
Miraclathurella	Pseudomelatomidae
Mitraguraleus	Mangeliidae
Mitrellatoma	Mitromorphidae
Mitrithara	Mitromorphidae
Mitrolumna	Mitromorphidae
Mitromorpha	Mitromorphidae
Monilispira	Pseudomelatomidae
Monteiroconus	Conidae
Mordica	Raphitomidae
Myurella	Terebridae
Myurellina	Terebridae
Myurellisca	Terebridae
Nannodiella	Clathurellidae
Narraweena	Borsoniidae
Naskia	Horaiclavidae
Nataliconus	Conidae
Naudedrillia	Pseudomelatomidae
Nematoma	Mangeliidae
Neodrillia	Drilliidae
Neoguraleus	?Mangeliidae
Neopleurotomoides	Raphitomidae
Nepotilla	Raphitomidae
Netrum	Clavatulidae
Nihonia	?Cochlespiridae
Nodotoma	Mangeliidae
Notocytharella	?Mangeliidae
Nototerebra	Terebridae
Nquma	Horaiclavidae
Nymphispira	Pseudomelatomidae
Obesotoma	Mangeliidae
Oenopota	Mangeliidae
Oenopotella	Mangeliidae
Ongoconus	Conidae
Ootomella	Raphitomidae
Ophiodermella	Borsoniidae
Orrmaesia	Drilliidae
Otitoma	Pseudomelatomidae
Oxymeris	Terebridae
Oxytropa	Turridae
Pagodasyrinx	Cochlespiridae
Pagodidaphne	Raphitomidae
Panaterebra	Terebridae
Papillocithara	Mangeliidae
Parabathytoma	Borsoniidae
Paraborsonia	Borsoniidae
Paraclathurella	Clathurellidae
Paracomitas	?Pseudomelatomidae
Paracuneus	?Drilliidae
Paradaphne	Raphitomidae
Paradrillia	Horaiclavidae
Paramontana	Raphitomidae
Paraspirotropis	?Mangeliidae
Paraterebra	Terebridae
Partecosta	Terebridae
Parviconus	Conidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Pellifronia	Terebridae
Peratotoma	Raphitomidae
Perimangelia	Mangeliidae
Perirhoe	Terebridae
Perplexiconus	Conidae
Perrona	Clavatulidae
Pervicacia	Terebridae
Phasmoconus	Conidae
Phenatoma	Borsoniidae
Philbertia	Raphitomidae
Phymorhynchus	Raphitomidae
Pilsbryspira	Pseudomelatomidae
Pinguigemmula	Turridae
Pionoconus	Conidae
Pionotoma	Raphitomidae
Plagiostropha	Drilliidae
Platycythara	Mangeliidae
Pleurotoma	Turridae
Pleurotomella	Raphitomidae
Pleurotomus	Turridae
Plicaustraconus	Conidae
Plicisyrinx	Pseudomelatomidae
Polystira	Turridae
Pontiothauma	Raphitomidae
Pristiterebra	Terebridae
Profundiconus	Conidae
Propebela	Mangeliidae
Protoconus	Conidae
Protostrioconus	Conidae
Pseudexomilus	?Horaiclavidae
Pseudoconorbis	Conidae
*Pseudodaphnell*a	Raphitomidae
Pseudoetrema	Clathurellidae
*Pseudolilliconu*s	Conidae
*Pseudomelatom*a	Pseudomelatomidae
*Pseudonodulo*conus	Conidae
*Pseudorhaphitom*a	Mangeliidae
Pseudotaranis	?Pseudomelatomidae
Psittacodrillia	Horaiclavidae
Ptychobela	Pseudomelatomidae
Ptychosyrinx	Turridae
Pulsarella	Borsoniidae
Puncticulis	Conidae
Punctoterebra	Terebridae
Purpuriconus	Conidae
Pusionella	Clavatulidae
Pyrgocythara	Mangeliidae
Pyrgospira	Pseudomelatomidae
Pyruconus	Conidae
Qii	Raphitomidae
Quasiconus	Conidae
Raphitoma	Raphitomidae
Rectiplanes	Pseudomelatomidae
Rectisulcus	Pseudomelatomidae
Regiconus	Conidae
Regidrillia	Horaiclavidae
Retidrillia	Borsoniidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Rhizoconus	Conidae
Rhodopetoma	?Pseudomelatomidae
Rhombiconus	Conidae
Rhombus	Conidae
Rimosodaphnella	Raphitomidae
Rissomangelia	Mangeliidae
Riuguhdrillia	Borsoniidae
Rocroithys	Raphitomidae
Rolaniconus	Conidae
Rollus	Conidae
Rubellatoma	Mangeliidae
Rugocythara	Mangeliidae
Saccharoturris	Mangeliidae
Scaevatula	Clavatulidae
Sciteconus	Conidae
Scrinium	Mitromorphidae
Sediliopsis	Pseudomelatomidae
Seminoleconus	Conidae
Shutonia	?Pseudomelatomidae
Sibogasyrinx	Cochlespiridae
Smithiella	Mangeliidae
Socioconus	Conidae
Speoides	Raphitomidae
Spergo	Raphitomidae
Spirotropis	Drilliidae
Splendrillia	Drilliidae
Splinoconus	Conidae
Spuriconus	Conidae
Steiraxis	?Cochlespiridae
**Steironepion*	Columbellidae
Stellaconus	Conidae
Stellatoma	Mangeliidae
Stenodrillia	?Drilliidae
Stephanoconus	Conidae
Stilla	Raphitomidae
Strategoconus	Conidae
Striatoguraleus	Horaiclavidae
Strictispira	Strictispriridae
Strioconus	Conidae
Striospira	Pseudomelatomidae
Strioterebrum	Terebridae
Strombinoturris	Clathurellidae
Suavodrillia	Borsoniidae
Subula	Terebridae
Sugitanitoma	Horaiclavidae
Surcula	Clavatulidae
**Surculina*	Turbinellidae
Suturocythara	Mangeliidae
Syntomodrillia	Drilliidae
Taranidaphne	Raphitomidae
Taranis	Raphitomidae
Taranteconus	Conidae
Tasmadaphne	Raphitomidae
Teleochilus	?Raphitomidae
Tenaturris	Mangeliidae
Terebra	Terebridae
Terebrum	Terebridae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Terenolla	Terebridae
Teretia	Raphitomidae
Teretiopsis	Raphitomidae
Tesselliconus	Conidae
Textilia	Conidae
Thatcheria	Raphitomidae
Thatcheriasyrinx	?Raphitomidae
Thatcherina	Raphitomidae
Thelecythara	Horaiclavidae
Thelecytharella	Pseudomelatomidae
Theliconus	Conidae
Thesbia	?Raphitomidae
Theta	Raphitomidae
Thetidos	Clathurellidae
Thoraconus	Conidae
Tiariturris	Pseudomelatomidae
Tomellana	Clavatulidae
Tomopleura	Borsoniidae
Toxiclionella	Clavatulidae
Toxicochlespira	Mangeliidae
Trachydrillida	Clavatulidae
Triplostephanus	Terebridae
Tritonoturris	Raphitomidae
Tropidoturris	Borsoniidae
Trovaoconus	Conidae
Truncadaphne	Raphitomidae
Tuliparia	Conidae
Turrella	Clathurellidae
Turrhyssa	Raphitomidae
Turriconus	Conidae
Turricula	Clavatulidae
Turridrupa	Turridae
Turrigemma	Pseudomelatomidae
**Turrijaumelia*	Columbellidae
Turris	Turridae
Turritomella	Mangeliidae
Tuskaroria	Raphitomidae
Tylotia	Drilliidae
Tylotiella	Drilliidae
Typhlodaphne	?Borsoniidae
Typhlomangelia	Borsoniidae
Typhlosyrinx	Raphitomidae
Tyrrhenoturris	Clavatulidae
Unedogemmula	Turridae
Utriculus	Conidae
Varioconus	Conidae
Venustoma	?Mangeliidae
Veprecula	Raphitomidae
Vepridaphne	Raphitomidae
Vexiariella	Mitromorphidae
Vexithara	Borsoniidae
Vexitomina	Horaiclavidae
Villiersiella	Mangeliidae
Viminiconus	Conidae
Virgiconus	Conidae
Viridoturris	Borsoniidae

Continued

Appendix 1. *Continued*

(Sub) genus	Family
Viridrillia	Pseudomelatomidae
Viridrillina	Pseudomelatomidae
Virroconus	Conidae
Vitjazinella	Mangeliidae
Vitricythara	Mangeliidae
Vituliconus	Conidae
Watsonaria	Raphitomidae
Widalli	Mangeliidae
Xanthodaphne	Raphitomidae
Xenuroturris	Turridae
Ximeniconus	Conidae
Yeddoconus	Conidae
Zemacies	Borsoniidae
Zenepos	Raphitomidae
**Zetekia*	Columbellidae
Zonulispira	Pseudomelatomidae

APPENDIX 2: LIST OF ALL THE FAMILY AND SUBFAMILY NAMES AVAILABLE FOR THE CONOIDEA.

(see Bouchet and Rocroi, 2005 for details). The status of names including only fossil genera is not discussed

Acidae Gray, 1853 (nomenclaturally invalid)
Andoniinae Vera-Pelaez, 2002 (fossil)
Belinae Bellardi, 1875 (synonym of Mangeliidae)
Borsoniidae Bellardi, 1875
Brachytominae Thiele, 1929 (nomen dubium)
Californiconinae Tucker & Tenorio, 2009 (synonym of Conidae)
Clathurellidae H. Adams & A. Adams, 1858
Clavatulidae Gray, 1853
Clavinae Casey 1904 (nomenclaturally invalid)
Clionellidae Stimpson, 1865 (synonym of Clavatulidae)
Cochlespiridae Powell, 1942
Conidae Fleming, 1822
Conilithidae Tucker & Tenorio, 2009 (synonym of Conidae)
Conorbidae de Gregorio 1880
Conulinae Rafinesque, 1815 (nomenclaturally invalid)
Crassispirinae McLean, 1971 (synonym of Pseudomelatomidae)
Cryptoconinae Cossmann, 1896 (fossil)
Cytharinae Thiele, 1929 (synonym of Mangeliidae)
Daphnellinae Casey, 1904 (synonym of Raphitomidae)
Defranciinae Gray, 1853 (nomenclaturally invalid)
Diptychomitrinae Bellardi, 1888 (synonym of Mitromorphidae)
Drilliidae Olsson, 1964
Hemiconidae Tucker & Tenorio, 2009 (fossil)
Horaiclavidae fam. nov.
Johnwyattidae Serna, 1979 (fossil)
Lorinae Thiele, 1925 *sensu* Opinion 666 (synonym of Clathurellidae)
Lorinae Thiele, 1925 *sensu* Thiele (synonym of Mangeliidae)
Mangeliidae Fischer, 1883
Melatomidae Gill, 1871 (synonym of Clavatulidae)
Mitrolumnidae Sacco, 1904 (synonym of Mitromorphidae)
Mitromorphidae Casey, 1904
Oenopotinae Bogdanov, 1987 (synonym of Mangeliidae)
Pervicaciinae Rudman, 1969 (synonym of Terebridae)
Pleurotominae Gray, 1838 (synonym of Turridae)
Pleurotomellinae Nordsieck, 1968 (synonym of Raphitomidae)
Pseudomelatomidae Morrison, 1965
Pseudotominae Bellardi, 1875 (synonym of Borsoniidae)
Puncticuliinae Tucker & Tenorio, 2009 (synonym of Conidae)
Pusionellinae Gray, 1853 (synonym of Clavatulidae)
Raphitomidae Bellardi, 1875
Siphopsinae Le Renard, 1995 (fossil)
Speightiidae Powell, 1942 (fossil; doubtfully Conoidea)
Strictispiridae McLean, 1971
Taraninae Casey, 1904 (synonym of Raphitomidae)
Taranteconidae Tucker & Tenorio, 2009 (synonym of Conidae)
Terebridae Mörch, 1852
Thatcheriidae Powell, 1942 (synonym of Raphitomidae)
Turriculinae Powell, 1942 (synonym of Clavatulidae)
Turridae H. Adams & A. Adams, 1853
Zemaciinae Sysoev, 2003 (synonym of Borsoniidae)
Zonulispirinae McLean, 1971 (synonym of Pseudomelatomidae)