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An assessment of *Raphitoma* and allied genera (Neogastropoda: Raphitomidae)

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Running head: Systematics of *Raphitoma*

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ABSTRACT

The systematics of several Eastern Atlantic conoidean species, traditionally ascribed to the genus *Raphitoma* Bellardi, 1847, are revised on the basis of DNA sequence data from three gene regions (cytochrome *c* oxidase subunit I, 16S rRNA and 12S rRNA). We assign genus ranking to three major lineages (*Raphitoma*, *Cyrellia* Kobelt, 1905 and *Leufroyia* Monterosato, 1884), and suggest that two West African species belong in the subgenus *Daphnella* (*Paradaphne*) Laseron, 1954. A new classification, based on molecular systematics and critical study of morphology, is provided for of all Eastern Atlantic and Mediterranean species that are currently ascribed to *Raphitoma s. l.* The genus *Clathromangelia* Monterosato, 1884 is confirmed as belonging to Raphitomidae. Phylogenetic relationships and genetic distances suggest that *R. maculosa* Høisæter, 2016 and *R. obesa* Høisæter, 2016 may be deviating morphotypes of *R. bicolor* (Risso, 1826) and *Cyrellia aequalis* (Jeffreys, 1867), respectively.

INTRODUCTION

The Raphitomidae are probably the most diverse family of Conoidea, in terms of species richness, ecological range and anatomy (Kantor & Taylor, 2002; Bouchet *et al.*, 2011). The name Raphitomidae Bellardi, 1875 is based on the genus *Raphitoma* Bellardi, 1847. At the time of its introduction, this genus comprised 34 fossil and Recent species (Bellardi, 1847: 85) that had previously been classified in various genera, such as *Pleurotoma* and *Clathurella*. The genus *Raphitoma* has been particularly well studied in the northeastern Atlantic and Mediterranean, where a recent estimate (Giannuzzi-Savelli *et al.*, 2018) suggested that over 50 extant species occur. These snails, which are usually active at night, live mostly in marine soft-bottom environments at depths ranging from 0–100 m (*R. pseudohystrix* has been collected at 700 m). While they inhabit a wide variety of habitats ranging from coastal bioclastic coarse sands to muddy bioclastic coarse sands, they also occur in sandy pockets, between rocks and in seagrass meadows, with individuals hiding buried under sand or concealed under stones and in crevices during the day. The limits of the genus are still under debate and *Raphitoma s. l.*, as currently conceived, comprises species with the following shell characters: turreted to biconic-pupoidal shape; small to medium size (5–25 mm) in relation to the family Raphitomidae as whole; a frequently keeled last whorl; protoconch consisting of 3–4.5 whorls when multispiral, with the typical raphitomid diagonally cancellate sculpture (Giannuzzi-Savelli *et al.*, 2018; Manousis *et al.*, 2019; Fig. 1). While available data on the morphology of the soft parts are scarce, they nonetheless suggest that there is substantial variation in the anatomy of the foregut. Some species, such as *R. villaria* and *R. linearis*, have neither a radula nor a venom gland. Others, such as *R. purpurea* and *R. leufroyi*, do have a radula, a venom gland or both (Sheridan *et al.*, 1973: 177; Pusateri & Giannuzzi-Savelli, 2008: 124). The arrangement of the foregut has been described for *R. purpurea* (Miller, 1989: 173; Sheridan *et al.*, 1973: 177), but there is a different arrangement in *R. linearis* and *R. leufroyi*, where a rhynchodeal introvert or pseudoproboscis is present (Taylor *et al.*, 1993: 128; Sheridan *et al.*, 1973: 178). The systematic implications of this variability are still unknown, and the problem is further complicated by the lack of a comprehensive phylogenetic framework for the family Raphitomidae.

The type species of *Raphitoma* is *R. hystrix* Bellardi, 1847 [ex *Pleurotoma hystrix* Cristofori & Jan, 1832, *nomen nudum*] by subsequent designation (Monterosato, 1872: 54). *Raphitoma hystrix* as almost always conceived is a fossil species (Miocene–Pleistocene) and has a complex nomenclatural history that has been summarized by Giannuzzi-Savelli *et al.* (2018: 9; see also Dall, 1918: 316; van Aartsen *et al.*, 1984: 89–90; Rolán *et al.*, 1998: 105). *Raphitoma pseudohystrix* (Sykes, 1906) appears to be the extant closest relative of *R. hystrix*; while the teleoconch of the former is almost identical to that of the latter, the protoconch in the extant species is paucispiral whereas in *R. hystrix* it is multispiral.

According to current taxonomy, at least eight nominal genera are included in the synonymy of *Raphitoma s. l.* (see Systematic Descriptions below).

Høisæter (2016) argued that DNA-sequence-based phylogenetic studies would most likely show that *Raphitoma s. l.* consists of several genus-level taxa, for which available names could be employed. By carrying out a molecular phylogenetic study of the raphitomids, we seek to explore this issue. Our dataset consists of representatives of at least 13 recognized genera of Raphitomidae (18% of the *c.* 70 genera known for this family; MolluscaBase, 2018), as well as two species of *Clathromangelia*, a genus that has been considered to be a raphitomid (Oliverio, 1995) or a clathurellid (Bouchet *et al.*, 2011). The dataset also includes 14 species which, on the basis of morphology, have been ascribed to *Raphitoma s. l.*; these include the type species of *Cenodagreutes*, *Cyrellia*, *Leufroyia*, *Lineotoma* and *Philbertia*, the apparent closest relatives of the type species of *Cordieria* and *Cyrtoides*, and the closest extant relative of the (fossil) type species of *Raphitoma*.

Table 1. List of material used in the study along with voucher registration numbers, collection localities, GenBank accession numbers for sequences and relevant references.

Taxon	Voucher ID	Locality	GenBank accession numbers			References
			COI	16S rRNA	12S rRNA	
Raphitomidae						
<i>Cyrrillia aequalis</i> (Jeffreys, 1867)	ZMBN-020209-O	Norway, 60°13'48"N 5°12'E	JF834219	JF834214		Høisæter (2016)
<i>Cyrrillia aequalis</i> (Jeffreys, 1867)	ZMBN-E-345-66a	Norway, 60°18'N 5°10'48"E	JF834221			Høisæter (2016)
<i>Cyrrillia aequalis</i> (Jeffreys, 1867)	ZMBN-E-345-66b	Norway, 60°18'N 5°10'48"E	JF834225			Høisæter (2016)
<i>Cyrrillia aequalis</i> (Jeffreys, 1867)	MT09383	North Sea, 57°53'56.4"N 0°54'57.6"W	KR084567			Barco <i>et al.</i> (2016)
<i>Cyrrillia aequalis</i> (Jeffreys, 1867)	MT09222	North Sea, 55°22'15.6"N 0°12'25.2"W	KR084390			Barco <i>et al.</i> , 2016
<i>Cyrrillia linearis</i> (Montagu, 1803)	BAU-2234	Italy, Giannutri Is., loc. Le Cerniette, 42°15'10"N 011°05'32"E	MK410632	MK410605	MK410585	This study
<i>Cyrrillia linearis</i> (Montagu, 1803)	BAU-2912.1	Italy, Giglio Is., Cala Cupa, 42°22'06"N 10°55'12"E, 10-20 m	MK410623	MK410599		This study
<i>Cyrrillia obesa</i> (Høisæter, 2016)	ZMBN-E-37-68	Norway, 60°18'N 5°07'48"E	JF834220	MK410610		Høisæter (2016); this study
<i>Clathromangelia granum</i> (Philippi, 1844)	BAU-3082.1	Italy, Scilla, 38°15'23"N 15°42'45"E, 35-37 m	MK410624	MK410600		This study
<i>Clathromangelia loiselierii</i> Oberling, 1970	BAU-1545	Greece, Astypalea Is., VYLLAS, 36°35'02"N 026°25'24"E, 1-7 m, under rocks	MK410627	MK410601		This study
<i>Daphnella</i> sp.	MNHN-IM-2007-17927	Salomon Is., Vella Gulf, SALOMON 2, 8°3'32.4' S 156°54'32.4"E	EU015740	HQ401674	HQ401607	Puillandre <i>et al.</i> (2008)
<i>Daphnella (Paradaphne) corimbensis</i> Rolán, Otero-Schmitt & Fernandes, 1998	BAU-2989	Canary Islands, Tenerife, Radazul, 28°24'08"N 16°19'5"W, 20 m	MK410635	MK410608	MK410587	This study
<i>Eucyclotoma cymatodes</i> (Hervier, 1897)	MNHN-IM-2007-17903	Philippines, Pamilacan Is., PANGLAO 2004, 9°29'24"N 123°56'0"E	EU015678	HQ401676	HQ401610	Puillandre <i>et al.</i> (2008)
<i>Hemilienardia acinonyx</i> Fedosov, Stahlschmidt, Puillandre, Aznar-Cormano & Bouchet, 2017	MNHN-IM-2009-33593	Philippines, Panglao Is., Momo beach	KX233238	KX233249		Fedosov <i>et al.</i> (2017)
<i>Hemilienardia calcicincta</i> (Melvill & Standen, 1895)	MNHN-IM-2007-17861	Philippines, Panglao Is., Sungcolan Bay, PANGLAO 2004, 9°38'30"N 123°49'12"E	EU015683	HQ401684	HQ401618	Puillandre <i>et al.</i> (2008)
<i>Leufroyia concinna</i> (Scacchi, 1836)	ZMBN-H-3-69a	Norway, 60°33'N 4°52'12"E	JF834222			Høisæter (2016)
<i>Leufroyia concinna</i> (Scacchi, 1836)	ZMBN-E-23-67	Norway, 60°18'N 5°10'48"E	JF834223			Høisæter (2016)
<i>Leufroyia concinna</i> (Scacchi, 1836)	ZMBN-020209-F	Norway, 60°13'48"N 5°12'E	JF834224	JF834218		Høisæter (2016)
<i>Leufroyia concinna</i> (Scacchi, 1836)	BAU-2254.1	Croatia, Biograd, 43°55'51"N 15°26'42"E	MK410616	MK410593	MK410580	This study
<i>Leufroyia concinna</i> (Scacchi, 1836)	BAU-2237	France, La Ciotat, Figuerolles, 43°09'53"N 5°35'45"E, 15 m	MK410633	MK410606		This study
<i>Leufroyia leufroyi</i> (Michaud, 1828)	BAU-2240.1	Croatia, Sevid, 43°28'46"N 16°02'08"E, 2-4 m	MK410613			This study

<i>Leufroyia leufroyi</i> (Michaud, 1828)	BAU-1742	Sardinia, Villasimius, 39°07'43"N 9°32'17"E	MK410628		MK410584	This study
' <i>Phymorhynchus</i> ' sp.	MCR-1256	Mid-Cayman Spreading Centre, Beebe vent chimneys	KJ566952	KM979537		Plouviez <i>et al.</i> (2015)
<i>Pleurotomella</i> sp.	MNHN-IM-2007-17848	New Caledonia, Lansdowne, EBISCO, 20°4'52.32"S 160°20'2.34"E	EU015657	HQ401701	HQ401640	Puillandre <i>et al.</i> (2008)
<i>Pseudodaphnella aureotincta</i> (Hervier, 1897)	MNHN-IM-2007-17878	Philippines, Pamilacan Is., PANGLAO 2004, 9°29'24"N 123°56'6"E	EU015700	HQ401688	HQ401624	Puillandre <i>et al.</i> (2008)
<i>Raphitoma bicolor</i> (Risso, 1826)	BAU-1897	France, St. Maxime, 43°18'49"N 6°40'22"E, intertidal	MK410630	MK410603		This study
<i>Raphitoma cordieri</i> (Payraudeau, 1826)	BAU-2262.1	Croatia, Sukosan, 44°02'04"N 15°18'57"E	MK410619	MK410595	MK410582	This study
<i>Raphitoma cordieri</i> (Payraudeau, 1826)	BAU-2262.2	Croatia, Sukosan, 44°02'04"N 15°18'57"E	MK410625			This study
<i>Raphitoma densa</i> (Monterosato, 1884)	BAU-2257.1	Croatia, Sukosan, 44°02'10"N 15°18'55"E	MK410617	MK410594	MK410581	This study
<i>Raphitoma densa</i> (Monterosato, 1884)	BAU-1895	Italy, Torre Colimena, 40°17'39"N 17°45'17"E, 3 m	MK410629	MK410602		This study
<i>Raphitoma horrida</i> (Monterosato, 1884)	BAU-2264.1	Croatia, Dugi Otok, 43°59'N 15°05'34"E	MK410620	MK410596	MK410583	This study
<i>Raphitoma horrida</i> (Monterosato, 1884)	BAU-1900	Corsica, Tour d'Ancone, 42°02'36"N 8°43'20"E, 10 m	MK410631	MK410604		This study
<i>Raphitoma horrida</i> (Monterosato, 1884)	BAU-1906.1	France, St. Maxime, 43°18'49"N 6°40'22"E, intertidal	MK410612	MK410590	MK410577	This study
<i>Raphitoma laviae</i> (Philippi, 1844)	BAU-2253.1	Croatia, Telascjca, 43°53'30"N 15°09'33"E	MK410615	MK410592	MK410579	This study
<i>Raphitoma laviae</i> (Philippi, 1844)	BAU-2246.1	Croatia, Zaton, 44°13'07"N 15°09'41"E	MK410614	MK410591	MK410578	This study
<i>Raphitoma maculosa</i> Høisæter, 2016	ZMBN-040809_X	Norway, 60°18'N 5°07'48"E	MK410638			Høisæter (2016); this study
<i>Raphitoma philberti</i> (Michaud, 1829)	BAU-2365.1	Croatia, Biograd, 43°55'51"N 15°26'42"E	MK410622	MK410598		This study
<i>Raphitoma philberti</i> (Michaud, 1829)	BAU-2258.1	Croatia, Vrsi, 44°16'56"N 15°12'35"E	MK410618			This study
<i>Raphitoma philberti</i> (Michaud, 1829)	BAU-1893.1	Greece, Limnos, Koukonisi Bay, 39°53'07"N 25°16'16"E	MK410611			This study
<i>Raphitoma philiberti</i> (Michaud, 1829)	BAU-3046	Greece: Astypalea Is., Vai, VYLLAS 2017, 36°35'13"N 026°24'10"E, 1-6 m, under rocks	MK410636		MK410588	This study
<i>Raphitoma pseudohystrix</i> (Sykes, 1906)	BAU-3205	Malta, SW, off Gnejna Bay, 35°49'54.3"N 14°17'15.2"E, 220 m, fine sand and mud	MK410637	MK410609	MK410589	This study
<i>Raphitoma purpurea</i> (Montagu, 1803)	BAU-2337.1	France, Ploubazlanec, 48°48'5"N 3°00'10"W, intertidal	MK410621	MK410597		This study
<i>Raphitoma purpurea</i> (Montagu, 1803)	BAU-2337.3	France, Ploubazlanec, 48°48'5"N 3°00'10"W, intertidal	MK410626			This study
<i>Raphitoma purpurea</i> (Montagu, 1803)	BAU-2338	France, Ploubazlanec, 48°48'5"N 3°00'10"W, intertidal	MK410634	MK410607	MK410586	This study
' <i>Raphitoma</i> ' <i>rubroapicata</i> (E. A. Smith, 1885)	MNHN-IM-2007-17890	Philippines, Panglao Is., off Momo beach, PANGLAO 2004, 9°36'30"N 123°45'18"E	EU015713	HQ401703	HQ401642	Puillandre <i>et al.</i> (2008)
' <i>Raphitoma</i> ' sp.	MNHN-IM-2007-17882	Philippines, Balicasag Is., PANGLAO 2004, 9°30'54"N 123°41'12"E	EU015704			Puillandre <i>et al.</i> (2008)
<i>Rimosodaphnella</i> sp.	MNHN-IM-2007-17836	New Caledonia, Koumac Sector, around Ouaco, BOA1, 20°48'42"S 164°24'12"E	EU015645	HQ401704		Puillandre <i>et al.</i> (2008)
<i>Spergo</i> sp.	MNHN-IM-2007-17841	New Caledonia, SE Fairway, EBISCO, 21°32'36"S 162°28'36"E	EU015650	HQ401682	HQ401616	Puillandre <i>et al.</i> (2008)
<i>Taranis</i> sp.	MNHN-IM-2007-42296	Philippines, AURORA 2007, 15°56'34.2"N 121°50'11.4"E	HQ401584	HQ401707	HQ401645	Puillandre <i>et al.</i> (2011)

<i>Taranis</i> sp.	MNHN-IM-2013-52046	Papua New Guinea, Bismarck Archipelago, W Kairiru I., 3°19'26.4"S 143°27'14.4"E	KR087296	KR088045	KR087382	Fedosov <i>et al.</i> (2015)
<i>Teretiopsis</i> cf. <i>hyalina</i> Sysoev & Bouchet, 2001	MNHN-IM-2007-17845	New Caledonia, SE Fairway, EBISCO, 21°28'8"S 162°33'54"E	EU015654	HQ401708	HQ401646	Puillandre <i>et al.</i> (2008)
<i>Thatcheria mirabilis</i> Angas, 1877	MNHN-IM-2007-17924	Salomon Is., SE Isabel, SALOMON 2, 8°16'54"S 159°59'42"E	EU015736	FJ868138	FJ868124	Puillandre <i>et al.</i> (2008)
<i>Vepracula</i> cf. <i>spanionema</i> (Melvill, 1917)	MNHN-IM-2007-17883	Philippines, Balicasag Is., PANGLAO 2004, 9°30'54"N 123°41'12"E	EU015705	HQ401717	HQ401654	Puillandre <i>et al.</i> (2008)
Clathurellidae						
<i>Lienardia crassicosata</i> (Pease, 1860)	NA	NA	JF823629	JF823611	JF823590	Cabang <i>et al.</i> (2011)
<i>Lienardia nigrotincta</i> (Montrouzier in Souverbie & Montrouzier, 1873)	MNHN-IM-2007-42607	Vanuatu, E Luganville, Segond Channel, SANTO 2006, 15°30'58"S 167°11'52"E	HQ401575	HQ401666	HQ401599	Puillandre <i>et al.</i> (2011)
<i>Nannodiella ravella</i> (Hedley, 1922)	MNHN-IM-2007-17904	Philippines, Panglao Is., off San Isidro, PANGLAO 2004, 9°33'54"N 123°50'30"E	EU015679	HQ401698	HQ401634	Puillandre <i>et al.</i> (2008)
Mangeliidae						
<i>Anticlinura</i> sp. Thiele, 1934	MNHN-IM-2007-42513	Salomon Is., Sta Isabel, SALOMON 2, 8°47'0"S 159°37'54"E	HQ401572	HQ401660	HQ401590	Puillandre <i>et al.</i> (2011)
<i>Propebela</i> cf. <i>scalaris</i> (Møller, 1842)	MNHN-IM-2007-42325	Norway, Hornsund, Svalbard	HQ401582	HQ401699	HQ401635	Puillandre <i>et al.</i> (2011)
<i>Toxicochlespira pagoda</i> Sysoev & Kantor, 1990	MNHN-IM-2007-17925	Salomon Is., Choiseul, SALOMON 2, 6°37'12.6"S 156°12'44.4"E	EU015738	HQ401711	HQ401649	Puillandre <i>et al.</i> (2008)
Conidae						
<i>Conus radiatus</i> Gmelin, 1791	MNHN-IM-2007-30883	Philippines, Bohol Is., Ubajan, PANGLAO 2004, 9°41'30"N 123°50'60"E	KJ550437	KJ550900	KJ551133	Puillandre <i>et al.</i> (2014)
<i>Conus textile</i> Linnaeus, 1758	MNHN-IM-2007-30900	Vanuatu, NW Aésé Is., SANTO 2006, 15°25'7"S 167°14'10"E	KJ550497	KJ550930	KJ551134	Puillandre <i>et al.</i> (2014)
<i>Conus ventricosus</i> Gmelin, 1791	NA	Djerba, Tunisia	KJ550006	KJ550745	KJ551370	Puillandre <i>et al.</i> (2014)

Institutional abbreviations are as follows: BAU, Department of Biology and Biotechnologies, 'Sapienza' University, Rome; MNHN, Muséum national d'Histoire naturelle, Paris; MT, German Centre for Marine Biodiversity Research, Senckenberg Institute, Wilhelmshaven; ZMBN, University Museum of Bergen Natural History Collections. NA indicates that specimen registration data were not available.

MATERIAL AND METHODS

The dataset is composed of 62 specimens representing 14 raphitomid genera from the Mediterranean Sea, North Sea and Indo–Pacific region. DNA sequence data were generated by us for 28 of these specimens; sequence data for the remaining individuals were obtained from GenBank (Table 1). The specimens sampled included 17 species ascribed to the genus *Raphitoma* s. l.: *Raphitoma aequalis*, *R. bicolor*, *R. concinna*, *R. cordieri*, *R. corimbensis*, *R. densa*, *R. horrida*, *R. laviae*, *R. leufroyi*, *R. linearis*, *R. maculosa*, *R. obesa*, *R. philberti*, *R. pseudohystrix*, *R. purpurea*, *R. rubroapicata*, an unidentified *Raphitoma* sp. The dataset also included 13 other raphitomid or putative raphitomid genera: *Clathromangelia* Monterosato, 1884; *Hemilienardia* Boettger, 1895; *Eucyclotoma* Boettger, 1895; *Rimosodaphnella* Cossmann, 1916; *Vepracula* Melvill, 1917; *Pleurotomella* Verrill, 1872; *Phymorhynchus* Dall, 1908; *Pseudodaphnella* Boettger, 1895; *Spergo* Dall, 1895; *Taranis* Jeffreys, 1870; *Thatcheria* Angas, 1877; *Daphnella* Hinds, 1844; and *Teretiopsis* Kantor & Sysoev, 1989. Specimens from two other conoidean families were also included. These groups are the Clathurellidae (the putative sister group of the raphitomids) and the Mangeliidae (considered to be sister to the clade comprising the Raphitomidae and Clathurellidae) (Abdelkrim *et al.*, 2018). The outgroup comprised three species of Conidae.

DNA was isolated from a piece of foot tissue following a standard proteinase K/phenol–chloroform extraction protocol (Oliverio & Mariottini, 2001). Three mitochondrial gene fragments were amplified: the 658-bp barcode region of cytochrome *c* oxidase subunit I (COI), with universal primers LCO1490 and HC02198 (Folmer *et al.*, 1994); a c. 500-bp region of the 16S rRNA gene, with primers 16SA (Palumbi, 1996), and CGLeuR (Hayashi, 2003) or 16SH (Espiritu *et al.*, 2001); and a c. 600 bp region of the 12S rRNA, with primers 12SI and 12SIII (Oliverio & Mariottini, 2001). The following PCR conditions were used: initial denaturation (94 °C for 4 min); 35 cycles of denaturation (94 °C for 30 s); annealing (48–51 °C for COI, 52 °C for 16S rRNA, 58–60 °C for 12S rRNA for 40 s) and extension (94 °C for 60"); final extension (72 °C for 10 min). Amplicons were purified using Exosap-IT (USB Corporation) and sequenced by Macrogen Inc. (The Netherlands).

COI sequences were aligned using Geneious v. 11 (Kearse *et al.*, 2012). Sequences for 16S rRNA and 12S rRNA were aligned with the online version of MAFFT v. 7 (Katoh *et al.*, 2017, Kuraku *et al.*, 2013), using the Q-INS-I algorithm. Ambiguous regions in the 16S rRNA and 12S rRNA alignments were discarded using Gblocks v. 0.91b (Castresana, 2000) with respectively 76% and 64% of the original positions being retained; we used default options.

In our phylogenetic analyses we used the three single-gene datasets as well as a combined dataset (COI+12S rRNA+16S rRNA). The Bayesian information criterion (BIC) implemented in jModelTest v. 2.1.7 (Posada, 2008) was used to identify the best substitution models and parameters for each gene partition; the substitution model selected for all datasets was GTR+I+G. Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian approaches; all analyses were run on the CIPRES Science Gateway (Miller Pfeiffer & Schwartz, 2010). ML analyses were done using RAxML v. 8 (Stamatakis, 2014). Branch support estimates were based on 1000 bootstrap replicates. Bayesian analyses were performed using MrBayes v. 3.2.3 (Huelsenbeck & Ronquist, 2001); analyses were run for 10⁷ generations, with trees sampled every 1000 generations and 25% burn-in (for all other parameters we used default settings). Convergence of MCMC was assumed to have occurred when the effective sample size was >200 and the potential scale reduction factor was ~1, as calculated with Tracer v. 1.6. Branches with bootstrap values (BS) ≥70% and posterior probabilities (PP) ≥0.95 were considered to be strongly supported.

RESULTS

The final datasets consisted of 62 COI sequences, 47 16S rRNA sequences and 34 12S rRNA sequences. Single-gene and combined analyses yielded topologically similar trees. The trees

obtained from the concatenated dataset tended to show higher branch support values, and this was especially so in the case of the Bayesian analysis (Fig. 2, Supplementary Material Figs S1–S7). The three families Raphitomidae, Clathurellidae and Mangeliidae together formed a strongly supported monophyletic group. Our Bayesian analyses recovered the Clathurellidae as sister to the raphitomid clade, but this relationship was not strongly supported (e.g. PP = 0.71 for combined dataset, Fig. 2). We found consistently strong support for the monophyly of the Raphitomidae.

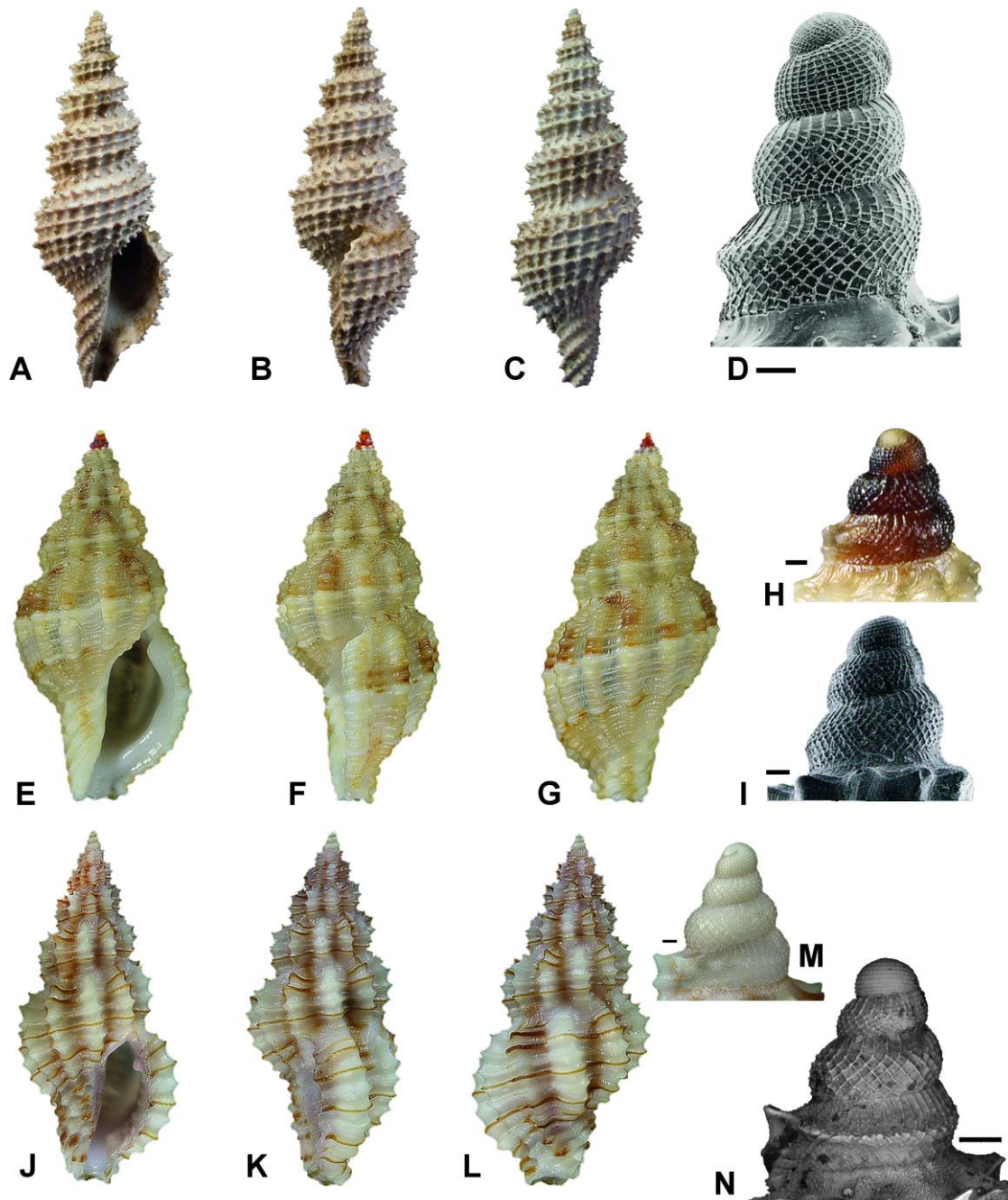


Figure 1. Type species of Raphitomidae illustrated by representative shell material. **A–D.** *Raphitoma hystrix* Bellardi, 1847, the type species of the genus *Raphitoma* Bellardi, 1847. Neotype (MRSN n. cat. 011.16.008) from Colli Astesi (Italy; Pliocene, Piacentian); shell height is 17.6 mm. **E–I.** *Leufroyia leufroyi* (Michaud, 1828), the type species of the genus *Leufroyia* Monterosato, 1884. Shell from a depth of 40 m, Ile Rousse (Corsica); shell height is 11 mm. **J–M.** *Cyrellia linearis* (Jeffreys, 1867), the type species of the genus *Cyrellia* Kobelt, 1905. Shell from a depth of 1 m, Lastovo (Croatia); shell height is 7 mm. All scale bars are 100 μ m in length.

Within the Raphitomidae, specimens of the genus *Raphitoma* s. l. were distributed across five clades. *Raphitoma leufroyi* and *R. concinna* were strongly supported as sister species (BS = 99%, PP = 1); these two species together with *R. rubroapicata* and the genus *Hemilienardia* formed a clade that was strongly supported in the ML analysis (BS = 85%), but not in the Bayesian analysis (PP = 0.94). The Bayesian analysis showed strong support for the clade comprising *R. corimbensis*, *Rimosodaphnella* and *Vepracula* (PP = 0.95), and the clade comprising the ‘*Raphitoma*’ sp. from the Philippines (MNHN-IM-2007-17882) and *Eucyclotoma cymatodes* (PP = 0.99). Relationships between these two clades and other raphitomids were unresolved. The two species of *Clathromangelia*, which were strongly supported as sister taxa (BS = 99%, PP = 1), formed a clade with *Pseudodaphnella*, *Eucyclotoma* and a ‘*Raphitoma*’ sp. (MNHN-IM-2007-17882) in the Bayesian analysis (PP = 1). This clade was nested within the raphitomid clade.

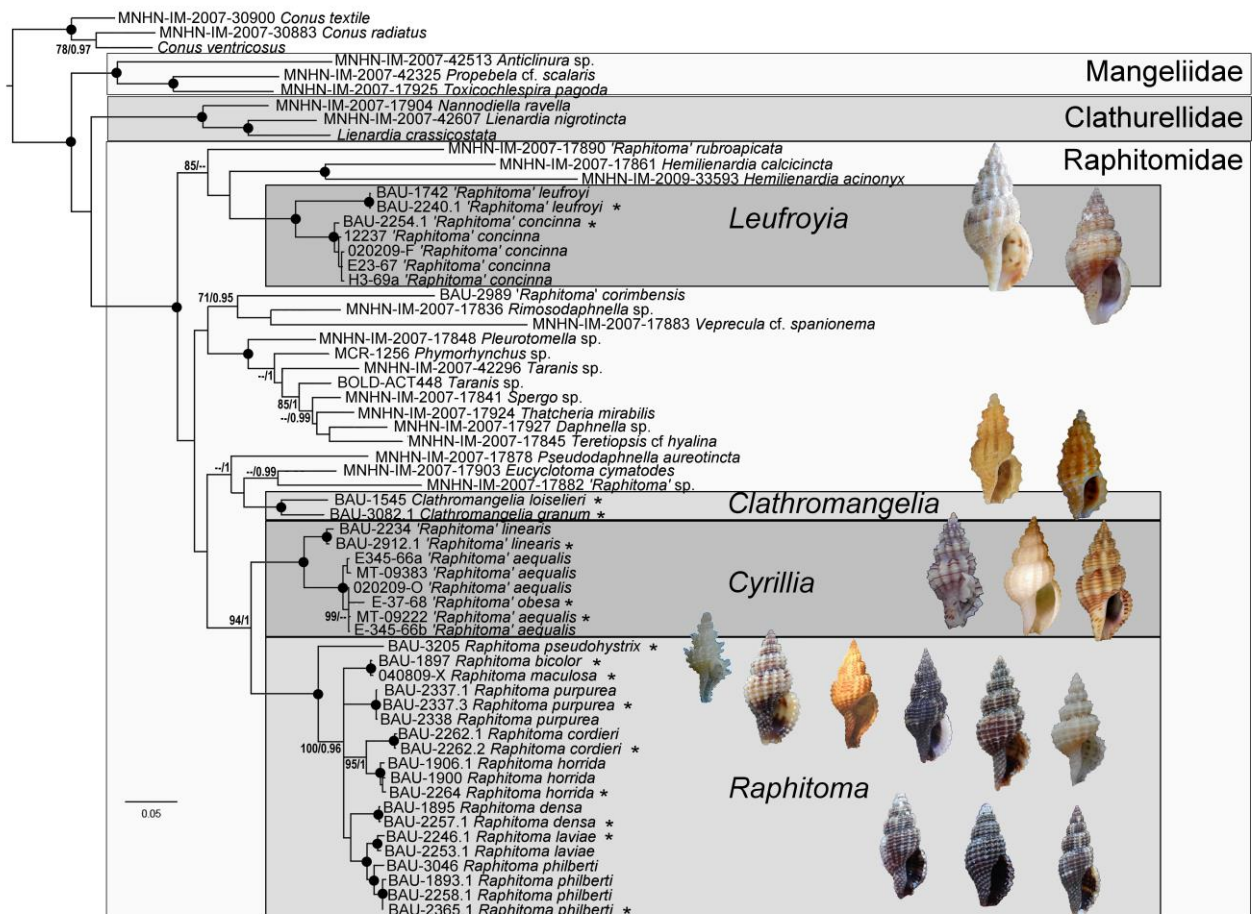


Figure 2. Phylogenetic relationships among conoideans, as illustrated by the Bayesian majority consensus tree of the combined dataset (COI+12S rRNA+16S rRNA). The tree is rooted on a composite outgroup comprising three species of *Conus*. Support values are given as posterior probabilities for the Bayesian analysis (only values ≥ 0.95 are shown) and as bootstrap percentages for the ML analysis (only values $\geq 70\%$ are shown). Closed circles indicate branches with bootstrap support $> 95\%$ and posterior probabilities > 0.98 . Shells of vouchers are indicated by asterisks and are not to scale. Scale bar indicates substitutions per site.

Most of the specimens ascribed to *Raphitoma s. l.* formed a strongly supported clade only in the Bayesian analyses of the 12S rRNA, 16S rRNA and combined datasets (PP = 1 in Fig. 1; see also Supplementary Material Figs S1, S3, S5); this large clade was not strongly supported in most of the remaining analyses (Supplementary Material Figs S2, S4, S6, S7). However we consistently found strong support for two lineages within this clade. The first sublineage comprised *Raphitoma linearis*, *R. aequalis* and *R. obesa* (BS = 100%, PP = 1). The second sublineage consisted of *R. pseudohystrix*, *R. bicolor*, *R. cordieri*, *R. densa*, *R. horrida*, *R. laviae*, *R. maculosa*, *R. philberti* and *R. purpurea* (BS = 100%, PP = 1); in this sublineage, *R. pseudohystrix* was sometimes strongly supported as sister to the clade containing the other members of the sublineage.

DISCUSSION

The Bayesian analyses showed a sister-group relationship between the Raphitomidae and Clathurellidae; this agrees with the most recent phylogenetic hypotheses on the Conoidea, which are based on the most extensive taxon sampling achieved to date (Puillandre *et al.*, 2011, Abdelkrim *et al.*, 2018), but was not strongly supported. The genus *Clathromangelia* was confirmed as belonging to the Raphitomidae, as has previously been suggested on the basis of anatomical and protoconch data (Oliverio, 1995). Our finding that *Clathromangelia* is a member of a clade containing *Pseudodaphnella* and *Eucyclotoma*, is not surprising given the similarity in shell morphology between these three taxa, and particularly between *Clathromangelia* and *Pseudodaphnella*. This study shows that most of the species ascribed to *Raphitoma s. l.* fall into three clades, and we propose that these distinct lineages should be ranked as genera.

We propose to use the name *Raphitoma* for the clade containing *R. pseudohystrix* (believed to be the closest extant relative of the type species of *Raphitoma*), *R. bicolor*, *R. cordieri*, *R. densa*, *R. horrida*, *R. laviae*, *R. maculosa*, *R. philberti* and *R. purpurea*. We note that a strongly supported sister-group relationship of *R. pseudohystrix* to the other species in the sublineage was recovered in some analyses. We also note that *R. pseudohystrix* never formed a clade with other morphologically similar spiny-shelled raphitomids, such as *R. cordieri* and *R. horrida*.

The clade comprising *R. linearis*, *R. aequalis* and *R. obesa* may be the sister group of *Raphitoma s. s.*, but this relationship was strongly supported in only three of the eight analyses we carried out. We propose, therefore, to treat the clade of *R. linearis*, *R. aequalis* and *R. obesa* as a distinct genus for which the name *Cyrillia* Kobelt, 1905 is available (see Systematic Descriptions, below). Our results show that the *R. leufroyi* + *R. concinna* lineage is not nested within the clade that contains most of the *Raphitoma* species or the clade of *R. linearis* + *R. aequalis* + *R. obesa*. We use the generic name *Leufroyia* Monterosato, 1884 for the *R. leufroyi* + *R. concinna* lineage.

Raphitoma corimbensis was not related to any of these lineages (*Raphitoma*, *Cyrillia* or *Leufroyia*) and, as suggested by its shell morphology (and by that of its certainly close relative, *R. bedoyai* Rolán, Otero-Schmitt & Fernandes, 1998), further studies on its systematic position should explore the relationship between this species and lineages currently placed in the genus *Daphnella* Hinds, 1844 (which may prove to be polyphyletic). We suggest a provisional classification of *R. corimbensis* and *R. bedoyai* in *Paradaphne* Laseyron, 1954 (type species: *Daphnella botanica* Hedley, 1922 by original designation), which is currently ranked as a subgenus of *Daphnella* Hinds, 1844. The rationale for this classification is that the shell features of the type species of *Paradaphne* is strikingly similar to *R. bedoyai* and *R. corimbensis*.

Our findings suggest that *Raphitoma rubroapicata* (E.A. Smith, 1885), and the '*Raphitoma*' sp. (IM-2007-17882) do not belong in the genus *Raphitoma*, but further work involving broader taxon sampling is needed to clarify their relationships.

On the basis of the phylogenetic results presented here and shell morphological data, we propose the following new classification for the bulk of Mediterranean/East Atlantic species currently ascribed to *Raphitoma s. l.*, as previously conceived.

Table 2. List of Recent species of the genus *Raphitoma* with their geographic range (NEA, North East Atlantic; WA, West Africa; Mac, Macaronesia; Med, Mediterranean) and the type of protoconch (m, multispiral; p, paucispiral).

Species	NEA	WA	Mac	Med	P
<i>R. alida</i> Pusateri & Giannuzzi-Savelli, 2016				+	p
<i>R. alleryana</i> (Sullioti, 1889)				+	p
<i>R. alternans</i> (Monterosato, 1884)				+	p
<i>R. arnoldi</i> (Pallary, 1906)				+	p
<i>R. atropurpurea</i> (Locard & Caziot, 1900)	+		+	+	m
<i>R. bartolinorum</i> Pusateri & Giannuzzi-Savelli, 2018				+	p
<i>R. bernardo</i> Rolán, Otero-Schmitt & Fernandes, 1998		+			m
* <i>R. bicolor</i> (Risso, 1826) = <i>R. maculosa</i> Høisæter, 2016	+		+	+	m
<i>R. bourguignati</i> (Locard, 1891)	+			+	m
<i>R. bracteata</i> (Pallary, 1904)				+	p
<i>R. brunneofasciata</i> Pusateri, Giannuzzi-Savelli & Oliverio, 2013				+	m
<i>R. christfriedi</i> Rolán, Otero-Schmitt & Fernandes, 1998		+		+	m
<i>R. contigua</i> (Monterosato, 1884)	+			+	m
<i>R. corbis</i> (Potiez & Michaud, 1838)				+	m
* <i>R. cordieri</i> (Payraudeau, 1826)	+	+	+	+	m
* <i>R. densa</i> (Monterosato, 1884)			+	+	m
<i>R. digiulioi</i> Pusateri & Giannuzzi Savelli, 2017				+	m
<i>R. ebreorum</i> Pusateri & Giannuzzi-Savelli, 2018				+	m
<i>R. echinata</i> (Brocchi, 1814) sensu Auctores	+		+	+	m
<i>R. farolita</i> F. Nordsieck, 1977				+	p
<i>R. formosa</i> (Jeffreys, 1867)	+				m
<i>R. griseomaculata</i> Pusateri & Giannuzzi-Savelli 2018				+	p
<i>R. hispida</i> (Monterosato, 1890)	+			+	m
* <i>R. horrida</i> (Monterosato, 1884)				+	p
<i>R. kharybdis</i> Pusateri & Giannuzzi-Savelli, 2018				+	p
* <i>R. laviae</i> (Philippi, 1844)				+	m
<i>R. lineolata</i> (Bucquoy, Dautzenberg & Dollfus, 1883)	+			+	m
<i>R. locardi</i> Pusateri, Giannuzzi-Savelli & Oliverio, 2013				+	m
* <i>R. maculosa</i> Høisæter, 2016 [=? <i>R. bicolor</i>]	+				m
<i>R. mirabilis</i> (Pallary, 1904)				+	p
<i>R. nivea</i> (J. T. Marshall in Sykes, 1906)				+	p
<i>R. oblonga</i> (Jeffreys, 1867)	+				m
<i>R. papillosa</i> (Pallary, 1904)				+	p
* <i>R. philberti</i> (Michaud, 1829)			+	+	p
<i>R. pruinosa</i> (Pallary, 1906)				+	p
* <i>R. pseudohystrix</i> (Sykes, 1906)			+	+	p
<i>R. pumila</i> (Monterosato, 1890)				+	m
<i>R. pupoides</i> (Monterosato, 1884)				+	m
* <i>R. purpurea</i> (Montagu, 1803)	+	+	+	+	m
<i>R. radula</i> (Monterosato, 1884)				+	m
<i>R. skylla</i> Pusateri & Giannuzzi-Savelli, 2018				+	m
<i>R. smriglioi</i> Pusateri & Giannuzzi-Savelli, 2013				+	p
<i>R. spadiana</i> Pusateri & Giannuzzi-Savelli, 2012				+	p
<i>R. strucki</i> (Maltzan, 1883)		+			?
<i>R. syrtensis</i> F. Nordsieck, 1977				+	p
<i>R. zelotypa</i> Rolán, Otero-Schmitt & Fernandes, 1998		+			m

Species included in our molecular systematic analyses are indicated by an asterisk.

SYSTEMATIC DESCRIPTIONS

Family RAPHITOMIDAE Bellardi, 1875

Genus *Raphitoma* Bellardi, 1847

(Fig. 1A–D; Table 2)

Raphitoma Bellardi, 1847: 612. [type species *Raphitoma histrix* Bellardi, 1847 (ex *Pleurotoma histrix* Cristofori & Jan, 1832, *nomen nudum*) SD, Monterosato, 1872: 54].

Homotoma Bellardi, 1875: 22 (type species *Murex reticulatus* Renier, 1804; SD, Powell, 1966). *Cordieria* Monterosato, 1884: 131 (type species *Murex reticulatus* Renier, 1804.; SD, Crosse, 1885; erroneously credited to Brocchi, 1814, ICZN, 1999, Art. 67.7; not Rouault, 1848). *Philbertia* Monterosato, 1884: 132 (type species *Pleurotoma bicolor* Risso, 1826; SD, Crosse, 1885). *Peratotoma* Harris & Burrows, 1891: 113 (replacement name for *Homotoma* Bellardi, 1875, not Guérin-Ménéville, 1844). *Cyrtoides* F. Nordsieck, 1968: 176 [type species *Pleurotoma rudis* Scacchi, 1836 (not G.B. Sowerby I, 1834; renamed *Cordieria pupoides* Monterosato, 1884 and *Raphitoma neapolitana* F. Nordsieck, 1977) OD].

Diagnosis: Shell small to medium size for family, ranging in height from 5 mm (*R. laviae*) to 25 mm (*R. cordieri*, *R. bourguignati*); shape turreted to biconic-pupoidal; suture impressed.

Protoconch: if multispiral, then 3–4.5 whorls, with protoconch I (embryonic shell) of 0.5–0.7 whorls, with reticulate sculpture of spirals and orthocline axial striae, and protoconch II (larval shell) of 2.3–3.5 whorls, with diagonally cancellate sculpture and often keeled last whorl; if paucispiral, then of 2 whorls, with large nucleus and reticulate sculpture. Teleoconch with slender spire of 5 (*R. brunneofasciata*) to 9 (*R. cordieri*) uniformly convex whorls; reticulate-cancellate sculpture, axials broader than spirals. Fine granular microsculpture occasionally present on whole teleoconch (*R. papillosa*) or on first whorl only (*R. philberti*). Outer lip thickened, with 7–13 inner denticles. Columella simple, slightly sinuous anteriorly. Siphonal canal very short (*R. contigua*) to moderately long (*R. cordieri*). Siphonal notch wide, plain or intorted.

Remarks: As type species of *Cordieria*, Crosse (1885) designated ‘*Murex reticulatus* Brocchi, 1814’ (following the indication by Monterosato: 1884: 131 “*C. reticulata*, (Ren.) Brocc. / = *Murex reticulatus* ed *echinatus*, Brocc. - 1814, p. 423, t. 8, f. 3”). However, *Murex reticulatus* Brocchi (1814: 435, pl. 9, fig. 12) is not a raphitomid, but a species of *Genota* Gray, 1847 (Borsoniidae). It is clear that Monterosato (1884: 131) confused *Murex reticulatus* Brocchi with *M. reticulatus* Renier (which is also invalid: ICZN, 1999: Op. 316); the latter is probably the same as *Murex echinatus* Brocchi, 1814 (= *Raphitoma echinata*) and it was this species that Monterosato (1884) was indicating. Therefore, we retain Crosse’s (1885) designation but as an incorrect citation (ICZN, 1999: Art. 67.7) and use Renier’s name which, even if unavailable, can be designated as the type species for *Cordieria* and *Homotoma*; see ICZN, 1999: Art 67.1.2).

The phylogenetic results presented here do not support any further splitting of this genus. In this respect it is important to note that the species traditionally ascribed to the ‘genera’ *Philbertia* and *Cordieria* (= *Peratotoma*) are distributed across the tree. Similarly, the grouping of species in the phylogeny does not correspond to differences in larval development (as indicated by their multispiral or paucispiral protoconch), and this is consistent with the currently accepted view that larval development is not a reliable taxonomic character at the genus level (Bouchet, 1990). The genetic distance between *Raphitoma maculosa* and *R. bicolor* is small (<1%), and this level of variation could well fall within the variation of the latter species when a denser sampling of *R. bicolor* is carried out. In contrast, our phylogenetic data indicate that a DNA-barcode-based approach could potentially be used to discriminate between closely related species of *Raphitoma* (e.g. *R. philberti* and *R. densa* in the COI phylogeny; see Supplementary Material Figs S1, S2).

DNA barcodes should be used in combination with shell morphology to define species limits in this difficult group of neogastropods.

Table 3. List of Recent species of the genus *Cyrillia* with their geographic range (NEA, North East Atlantic; WA, West Africa; Mac, Macaronesia; Med, Mediterranean) and the type of protoconch (m, multispiral; p, paucispiral).

Species	NEA	WA	Mac	Med	P
* <i>C. aequalis</i> (Jeffreys, 1867)	+		+	+	m
<i>C. ephesina</i> (Pusateri, Giannuzzi-Savelli & Stahlschmidt, 2017)				+	m
<i>C. kabuli</i> (Rolán, Otero-Schmitt & Fernandes, 1998)		+			m
* <i>C. linearis</i> (Montagu, 1803)	+		+	+	m
* <i>C. obesa</i> (Høisæter, 2016) [=? <i>C. aequalis</i>]	+				m
<i>C. zamponorum</i> (Horro, Gori & Rolán, 2019)		+			m

Species included in our molecular systematic analyses are indicated by an asterisk.

Genus *Cyrillia* Kobelt, 1905

(Fig. 1J–M; Table 3)

Cirillia Monterosato, 1884: 133 [type species *Murex linearis* Montagu, 1803, SD Crosse, 1885; not Rondani, 1856 (Diptera)].

Cyrillia Kobelt, 1905: 367 (unjustified emendation of *Cirillia* Monterosato, 1884).

Cenodagreutes E. H. Smith, 1967: 1 (type species *Cenodagreutes aethus* E. H. Smith, 1967 = *Defranciaaequalis* Jeffreys, 1867; OD). *Lineotoma* F. Nordsieck, 1977 (replacement name for *Cirillia* Monterosato, 1884, not Rondani, 1856).

Diagnosis: Shell small in size for family, from 5 mm (*C. linearis*) to 10 mm (*C. ephesina*); biconic, suture impressed. Protoconch 3.5–4 whorls, multispiral, with protoconch I (embryonic shell) of 0.5–0.7 whorls, with reticulate sculpture of spirals and orthocline axial striae, and protoconch II (larval shell) of 3.3–3.5 whorls, with diagonally cancellate sculpture and weakly keeled last whorl. Teleoconch with slender spire of 5 (*C. linearis*) to 7 (*C. ephesina*) convex whorls, with reticulate-cancellate sculpture; axials broader than spirals. Microsculpture of granules or pustules; growth lines seldom obvious. Outer lip thickened, with 7–13 inner denticles, the 2 anterior-most stronger. Columella simple, slightly sinuous anteriorly. Siphonal canal short; siphonal notch plain.

Remarks: *Cirillia* Monterosato, 1884 is preoccupied by *Cirillia* Rondani, 1856, but the emended name *Cyrillia* Kobelt, 1905 is available, and has already been used (e.g. Ceulemans *et al.*, 2018). This is a clear case of a demonstrably intentional emendation (ICZN, 1999: Art. 33.2), since the prescriptions of the Code are met: “there is an explicit statement of intention” ... and “both the original and the changed spelling are cited and the latter is adopted in place of the former” (ICZN, 1999: Art. 33.2.1). As an intentional, yet unjustified emendation, the name that should be used is *Cyrillia* Kobelt, 1905 (ICZN, 1999: Art. 33.2.3).

Cirillia aequalis and *C. linearis* lack radula and venom gland. Our phylogenetic results suggest that denser sampling may show *C. obesa* to be simply a colour variant of *C. aequalis*. *Cyrillia zamponorum* from São Tomé Island and another probably undescribed species from Madagascar (N. Puillandre & M. Oliverio, unpubl.) indicate that this lineage has a wide geographical distribution.

Table 4. List of Recent species of the genus *Leufroyia* with their geographic range (NEA, North East Atlantic; WA,

West Africa; Mac, Macaronesia; Med, Mediterranean) and the type of protoconch (m, multispiral; p, paucispiral).

Species	NEA	WA	Mac	Med	P
* <i>L. concinna</i> (Scacchi, 1836)	+		+	+	m
<i>L. erronea</i> Monterosato, 1884				+	m
* <i>L. leufroyi</i> (Michaud, 1828)	+	+	+	+	m
<i>L. villaria</i> (Pusateri & Giannuzzi-Savelli, 2008)		+		+	m

Species included in our molecular systematic analyses are indicated by an asterisk.

Genus *Leufroyia* Monterosato, 1884

(Fig. 1E–I; Table 4)

Leufroyia Monterosato, 1884: 134 (type species *Pleurotoma leufroyi* Michaud, 1828; SD Crosse, 1885).

Diagnosis: Shell medium to large size for family, from 15 mm (*L. concinna*) to 24 mm (*L. villaria*); shape suboval (*L. erronea*) to fusiform (*L. leufroyi*). Protoconch of 3–3.5 whorls with protoconch I (embryonic shell) of 0.5–0.7 whorls, with reticulate sculpture of spirals and orthocline axial striae, and protoconch II (larval shell) of 2.5–3 whorls, with diagonally cancellate sculpture, sometimes lightly keeled last whorl. Teleoconch with slender spire of 5 (*L. concinna*) to 7 (*L. villaria*) uniformly convex whorls; sculpture of thin, numerous low spiral cords and broader, wavy axial ribs. Microsculpture of dense, rather conspicuous growth lines, or rugae; no granules or pustules. Inner lip smooth with no denticles. Columella simple, slightly sinuous anteriorly. Siphonal canal short (*L. erronea*) to moderately long (*L. leufroyi*); siphonal notch wide, plain.

Remarks: The protoconch is wider (diameter = *c.* 220–250 µm) and lower than in the ‘multispiral’ propoconch of species of *Raphitoma* and *Cyrrillia*.

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