

The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 16: Raphitomidae (Gastropoda, Conoidea)

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In this paper we review the Raphitomidae of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. Sixty-two species are recorded representing 21 genera and subgenera, of which 12 species are described as new: *Clathromangelia acuticostata* nov. sp., *Clathromangelia mulderi* sp. nov., *Clathromangelia oliverioi* sp. nov., *Cyrellia clathrataeformis* nov. sp., *Cyrellia saldubensis* nov. sp., *Diagasma mediterranea* nov. sp., *Microandonia minutissima* nov. sp., *Pleurotomella turrata* nov. sp., *Pleurotomella obesula* nov. sp., *Pseudodaphnella iberica* nov. sp., *Pseudodaphnella velerinensis* nov. sp., *Teretia inflatissima* nov. sp., and one genus *Microandonia* nov. gen.

Mangelia (*Mangeliella*) *marcellinae* Hornung, 1920 is considered a subjective junior synonym of *Andonia bonellii* (Bellardi & Michelotti, 1841). *Homotoma raynevali* Bellardi, 1877 is considered a subjective junior synonym of *Cyrellia linearis* (Montagu, 1803). *Pleurotoma rochettae* Bellardi, 1847, *Pleurotoma subasperum* Brugnone, 1862 and *Gymnobela pelagia* Vera-Peláez, 2002 are considered subjective junior synonyms of *Gymnobela galerita* (Philippi, 1844). *Raphitoma* (*Leufroyia*) *guadalmansae* Vera-Peláez, 2002 is considered a subjective junior synonym of *Leufroyia leufroyi* (Michaud, 1828).

The assemblage shows a relatively high level of endemism (37%). Both shallow and deeper-water taxa are represented. The shallow water assemblage is similar to that found in the tropical Mediterranean Pliocene of Italy (MPPMU1); we note in these shallower facies the first record for the European Neogene of the genus *Pseudodaphnella* Boettger, 1895. The deeper-water assemblage is similar in generic composition to that recorded for the northeastern Atlantic coast of Lusitania and West Africa at greater depths but contains most of the endemic species.

The strong predominance of planktotrophic-type protoconchs amongst the Estepona raphitomids is highlighted and we suggest that the emergence of non-planktotrophic forms in the Mediterranean is a relatively recent event, possibly driven by increasing areas of relative isolation within the Mediterranean since the Early Pliocene.

KEY WORDS: southern Spain, Upper Pliocene, Gastropoda, Raphitomidae, Conoidea, new species

Introduction

In this paper we continue to revise the turrids found in the astoundingly diverse Pliocene assemblage of Estepona in southwestern Spain (see Landau & Micali, 2021, p. 160 for other references to this series; Landau & Harzhauser, 2022a for Clavatulidae Gray, 1853; Landau & Harzhauser, 2022b for Borsoniidae Bellardi, 1875, Clathurellidae H. Adams & A. Adams, 1858, Horiaculidae Bouchet, Kantor, Sysoev & Puillandre, 2011, and Mitromorphidae Casey, 1904).

As with the Borsoniidae from Estepona, the raphitomids were initially discussed in a doctoral thesis submitted to the University of Málaga (date of thesis 1996 or 1997; both dates quoted in the taxonomic chresonymies of Vera-Peláez, 2002, but dated 1996 in the references section of

that paper; the year 1996 used herein, which is the date on the front page of the copy available to the present authors). Subsequently his findings were published in Vera-Peláez (2002), which covers all turrid families, except the Clavatulidae and the genus *Genota* Gray, 1841 in the Borsoniidae, which were published together with his wife (Vera-Peláez & Lozano-Francisco (2001a, 2001b).

The shortfalls of the paper published by Vera-Peláez (2002) were discussed by Landau & Harzhauser (2022b, p. 103), and will not be repeated in full, but in summary the chresonymy is randomly selected and mostly incomplete, the type setting 'unattractive', cramped and difficult to follow, especially for the plates, and the plates are dreadful: based on the illustrations in that work interpretation of some species included therein is almost impossible.

Age of the deposits

The Estepona assemblages are dated as earliest Piacenzian, Early Pliocene, an age corroborated by the assemblage of Euthecosomata (Janssen, 2004). They form part of the Mediterranean ecostratigraphic unit MPPMU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and lowest Piacenzian (see Landau *et al.*, 2011, text-fig. 9). For further discussion, see Landau & Micali (2021, p. 160).

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL) between 1997-2020 and by Henk Mulder between 2008-2021; to the latter we are extremely grateful for his tireless efforts and generosity in making his collection available to us. For a map of localities see Landau *et al.* (2003: 4, text-fig. 1). The material is housed in the Natural History Museum Vienna (NHMW).

A comprehensive chresonymy and distribution is given for each species, concentrating on fossil records, in which only illustrated records are included. For extant species a selection of references is given representing the species' geographical and/or ecological extension. In most turrids, both the protoconch and teleoconch are highly and complexly sculptured. We therefore find it useful to offer a species description for most species, especially as this is the first English language description for most of these taxa, in a field dominated by non-Anglo-Saxon literature. The descriptions for each species are based on the Estepona material. An exception is made when a recent and detailed description is available in English.

In most species the protoconch is typically multispiral, of 2.5-6 whorls, protoconch I often spirally striated, protoconch II with diagonally reticulated sculpture, indicating a planktotrophic development. This is indeed the case in the Estepona assemblages, where all raphitomids have this type of protoconch with the exception of some members of the genera *Andonia* Harris & Burrows, 1891, *Clathromangelia* Monterosato, 1884 and *Taranis* Jeffreys, 1870. All *Cyrellia* Kobelt, 1905, *Leufroyia* Monterosato, 1884, and *Raphitoma* Bellardi, 1847 species have multispiral protoconchs. To assess the number of protoconch whorls, we counted the nucleus as first half whorl. Therefore, all the species herein have a half whorl more than using the Verduin (1977) system adopted by Giannuzzi-Savelli *et al.* (2018, fig. 3).

The anal sinus is either subsutural, in 'reverse L-shape' on the subsutural ramp, asymmetrically 'U-shape', very shallow to rather deep, typically not constrained, but sometimes even almost tubular (Bouchet *et al.*, 2011). Rarely the sinus is broad 'V-shaped', with the apex at the shoulder (*e.g.*, *Taranis*).

For the *Raphitoma/Leufroyia/Cyrellia* group we have attempted to use some of the descriptive terminology suggested by Giannuzzi-Savelli *et al.* (2018) for shell profile (*ibid*, fig. 5), shell thickness (*ibid*, fig. 6), shape of sculp-

tural reticulation/cancellation (*ibid*, fig. 8), the types of tubercles (*ibid*, fig. 9), subsutural ramp (*ibid*, fig. 10), aspect of the outer lip (*ibid*, fig. 12), strength of the siphonal fasciole (*ibid*, fig. 13), length of the siphonal canal (*ibid*, fig. 14), and rib count (*ibid*, fig. 15).

We have also partly adopted the shell terminology used by Harzhauser *et al.* (2022, p. 8). For raphitomids the shells are categorised as small (<10 mm), medium (10-20 mm) or large (>20 mm), width is described as very broad (SL/MD <2.0), broad (SL/MD 2.0-2.5), moderately broad, (SL/MD = 2.5-2.7), moderately slender (SL/MD = >2.7-3.3), slender (SL/MD >3.3). Spire angle, apertural height/total height and apertural width/total width ratios have not been useful in distinguishing between species in present/day raphitomids and have not been used (RG-S unpublished information).

Abbreviations:

CO: Velerín conglomerates; **PA:** Rio del Padrón; **VC:** Velerín carretera; **VA:** Velerín Antena; **PQ:** Parque Antena; **EL:** El Lobillo; see Landau *et al.* (2003, p. 4, text-fig. 1).
NHMW Natural History Museum Vienna (Austria)
MMPE Museo Municipal de Paleontología de Estepona (Málaga).
AA Auctorum; name used in the sense of subsequent authors, and not in the sense as established by the original author.

Protoconch measurements:

dp = diameter protoconch, **hp** = height protoconch, **dp/hp** = diameter/height protoconch, **dv1** = diameter first protoconch whorl, **n** = diameter nucleus.

Correction to Clavatulidae

Harzhauser *et al.* (2022, p. 76) introduced the genus *Olegia* Harzhauser, Landau & R. Janssen, 2022 for a Clavatulidae genus from the European Miocene (Type species: *Olegia mandici* Harzhauser, Landau & R. Janssen, 2022). Unfortunately, those authors overlooked that *Olegia* was preoccupied by *Olegia* Shaposhnikov, 1979 [Insecta: Homoptera]. To solve this homonymy, we propose *Oleginina* Harzhauser, Landau & R. Janssen as replacement name (feminine).

We are grateful to Philippe Bouchet, who drew our attention to this *lapsus*.

Systematics

Systematics has been updated following Bouchet *et al.* (2017).

Family Raphitomidae Bellardi, 1875

Note – The Raphitomidae Bellardi, 1875 include a group of genera with highly diverse shells, many of which occur in deep-water. The molecular phylogeny of Puillandre

et al. (2011) considered Raphitomidae to be a highly supported clade and sister-family to the Mangeliidae Fischer, 1883b.

Genus *Andonia* Harris & Burrows, 1891

Type species – *Fusus bonellii* Bellardi & Michelotti, 1841, by typification of replacement name, Pliocene, Italy.

- 1873 *Genea* Bellardi, p. 205. Type species (by monotypy): *Fusus bonellii* Bellardi & Michelotti, 1841, Pliocene, Italy. Junior homonym of *Genea* Rondani, 1850 [Diptera].
- 1891 *Andonia* Harris & Burrows, p. 112. *Nom. nov. pro Genea* Bellardi, 1873, *non* Rondani, 1850 [Diptera].

Note – Vera-Peláez *et al.* (1999, p. 9) erected the subfamily Andoniinae for the genus *Andonia* Harris & Burrows, 1891 without description, rendering their taxon a *nomen nudum*. It was later validated with a description by Vera-Peláez (2002, p. 236). Andoniinae was synonymised with Raphitomidae Bellardi, 1875 by Bouchet *et al.* (2017, p. 34).

Andonia bonellii (Bellardi & Michelotti, 1841)

Plate 1, figs 1-4

- *1841 *Fusus Bonellii* Bellardi & Michelotti, p. 20, pl. 2, fig. 5.
- 1872 *Fusus Bonellii* Génée – D’Ancona, p. 252, pl. 14, fig. 4.
- 1873 *Genea Bonellii* (Bellardi & Michelotti) – Bellardi, p. 205, pl. 11, fig. 10.
- 1898 *Fusus Chiaie* Almera & Bofill, p. 22, pl. 2, fig. 3.
- 1920 *Mangelia (Mangeliella) Marcellinae* Hornung, p. 75, pl. 2, fig. 5.
- 1935 *Parvisipho (Andonia) Bonellii* Génée – Montanaro, p. 70, pl. 6, fig. 4.
- 1944 *Parvisipho (Andonia) bonellii* (Génée) – Wenz, p. 1157, fig. 3288.
- 1976 *Parvisipho (Andonia) bonellii* (Bellardi & Michelotti, 1840 [sic], Génée m.s.) – Pavia, p. 141, pl. 6, figs 11, 12, 14, 16.
- 1981 *Parvisipho (Andonia) bonellii* (Bellardi & Michelotti) – Moroni & Ruggieri, p. 99, fig. 1.
- 1986 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Reina, p. 227, figs. 1-4.
- 1992 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic], Génée m.s.) – Cavallo & Repetto, p. 138, fig. 369.
- 1992 *Andonia cf. transylvanica* Hoernes & Auinger, 1890 – Cavallo & Repetto, p. 138, fig. 370.
- 1996 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Vera-Peláez, p. 707, text-fig. 38a, d, 71, pl. 54, figs 1-4, 10.
- 2001 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic], Génée ms) – Silva, p. 551, pl. 24, figs 20-21.

- 2002 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Vera-Peláez, p. 237, pl. 8, figs N, Ñ, pl. 16, L, M.
- 2008 *Pseudoandonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Chirli & Richard, p. 70, pl. 14, fig. 3.
- 2010 *Andonia transylvanica* (Hoernes & Auinger, 1890) – Sosso & Dell’Angelo, p. 47, unnumbered fig. p. 63, top row right [*non Andonia transylvanica* (Hoernes & Auinger, 1890)].
- 2010 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic], Génée ms) – Sosso & Dell’Angelo, p. 47, unnumbered fig. p. 63, middle row left.
- 2011 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Landau *et al.*, p. 35, pl. 18, figs 8, 9.
- 2018 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Brunetti & Cresti, p. 96, fig. 393.
- 2018 *Andonia marcellinae* (Hornung, 1920) – Sosso *et al.*, p. 336, figs 80-86.
- 2019 *Andonia bonellii* [sic] (Bellardi & Michelotti, 1840 [sic]) – Cárdenas *et al.*, p. 214, fig. 8e.
- non* 1997 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Chirli, 39, pl. 10 figs 11-12 (= *Andonia wilhelminamariae* Landau & Mulder, 2020).

Material and dimensions – Maximum height 14.0 mm, width 3.5 mm. **CO**: NHMW 2020/0171/0005-0007 (3), NHMW 2020/0171/0008 (8). **VC**: NHMW 2020/0171/0009 (1), NHMW 2020/0171/0010 (3). **EL**: NHMW 2020/0171/0011 (10).

Description – Shell medium sized, slender fusiform (apical angle 18.7-23.7°). Protoconch tall conical multi-spiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on the last two whorls (Estepona specimen: dp = 550 µm, hp = 820 µm). Teleoconch of up to six tall, weakly convex whorls, separated by impressed, undulating suture. Axial sculpture of rounded orthocone to weakly opisthocline ribs (T2: 7-9, TP or TL: 7-10), about one-third width of their interspaces, overrun by narrow spiral cords, slightly narrower than their interspaces, 6-9 on first teleoconch whorl, 9-11 on penultimate whorl. Single secondary spiral developed in some interspaces. Close-set growth lines give finely cancellate appearance in spiral interspaces. Axials weakening on second half of penultimate whorl, obsolete on last whorl in fully adult specimens. Last whorl 56-62% total height, slender fusiform, subsutural ramp poorly delimited by slightly strengthened shoulder cord, broadly convex below, weakly constricted at base, sculptured by 20-24 subequal flattened cords, with single secondary in some interspaces mid-whorl. Base and siphonal fasciole not delimited. Aperture 34-41% total height, elongate; outer lip slightly thickened by varix, smooth within; anal sinus very broad, shallow U-shaped; siphonal canal medium length, slightly bent adaxially, wide, open, unnotched. Columella weakly excavated, smooth. Columellar and parietal callus poorly developed, weakly delimited, forming narrow callus rim.

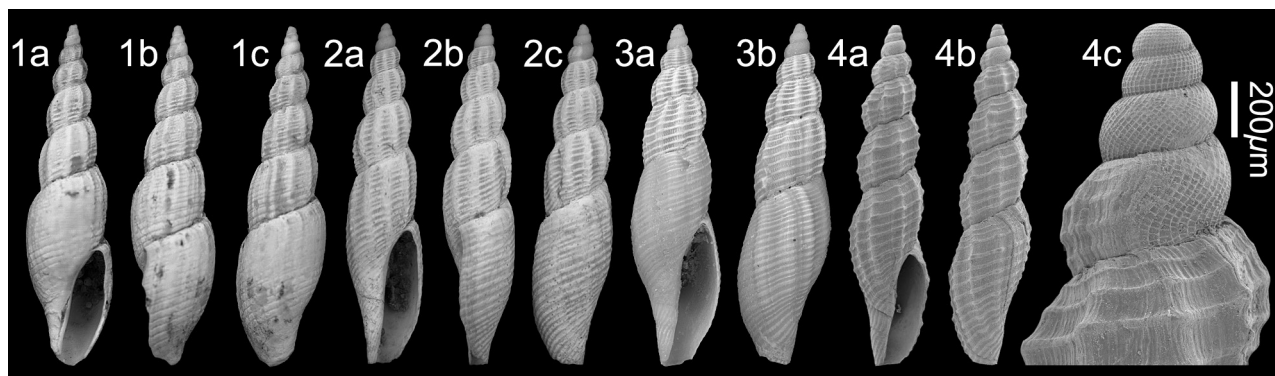


Plate 1. *Andonia bonellii* (Bellardi & Michelotti, 1841); 1. NHMW 2020/0171/0005, height 9.4 mm, width 2.3 mm; 2. NHMW 2020/0171/0006, height 8.5 mm, width 1.9 mm; 3. NHMW 2020/0171/0007, height 7.6 mm, width 1.8 mm (digital images). Velerín conglomerates. 4. NHMW 2020/0171/0009, height 6.5 mm, width 1.5 mm, 4c, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – As discussed by Moroni & Ruggieri (1981, p. 105) and Landau *et al.* (2013, p. 274) there are probably several species of *Andonia* Harris & Burrows, 1891 in the European Neogene that have not been described formally. The shell illustrated by Chirli (1997, pl. 10, figs 11, 12) as *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) with a non-planktotrophic type protoconch was recently described as *Andonia wilhelminariae* Landau & Mulder, 2020, based on material from Estepona (see below).

With ontogeny *Andonia bonellii* shows important changes in whorl shape and sculpture, and in large adult specimens the axial sculpture becomes obsolete on the last two whorls. There is also marked variability in sculpture within specimens at the same growth stage; the number of ribs and their strength is variable, as is the number of spiral cords and the presence of secondary spirals. The subsutural ramp is poorly delimited by a slightly strengthened cord in most, but not all specimens. Sosso *et al.* (2018, p. 337) argued that *Andonia marcellinae* (Hornung, 1920) described from the Lower Pliocene of Rio Torsero, Italy differed from *A. bonellii* in having more numerous axial ribs (10 vs 6–8 in *A. bonellii*) and spiral cords (11 vs 7–8 in *A. bonellii*). On which whorl the cord count was taken is not specified, but the holotype does indeed have 11 cords on the penultimate whorl. As can be seen in the rib/cord count given above, the number of sculptural elements found in the holotype of *A. marcellinae* fits within the range given for *A. bonellii* from Estepona, and it is herein considered a subjective synonym.

Similar *Andonia* specimens from the Atlantic Upper Miocene of northwestern France were illustrated by Landau *et al.* (2020, p. 42, pl. 37, figs 1–3). They differ from *A. bonellii* in being slightly less slender, in having fewer spiral cords on the subsutural ramp and there is no secondary spiral sculpture on any of the specimens. Unfortunately, the protoconch is not preserved in the French material, and the species was left in open nomenclature.

Distribution – Upper Miocene: Atlantic, southwestern

Spain (Cárdenas *et al.*, 2019); Proto-Mediterranean, Italy (Montanaro, 1935). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Cavallo & Repetto, 1992; Sosso & Dell’Angelo, 2010; Brunetti & Cresti, 2018; Sosso *et al.*, 2018). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002), France (Chirli & Richard, 2008).

Andonia wilhelminariae Landau & Mulder, 2020

Plate 2, figs 1–2

1997 *Andonia bonellii* (Bellardi & Michelotti, 1840 [sic]) – Chirli, 1997: 39, pl. 10 figs 11–12 [*non Andonia bonellii* (Bellardi & Michelotti, 1841)].

*2020 *Andonia wilhelminariae* Landau & Mulder, p. 47, figs 35, 36.

Material and dimensions – Maximum height 6.9 mm, width 2.2 mm. Holotype NHMW 2019/0167/0031, height 6.9 mm, width 2.2 mm; paratype 1 NHMW 2019/0167/0032, height 5.9 mm, width 2.0 mm; paratype 2 NHMW 2019/0167/0033, height 7.0 mm, width 2.0 mm; paratype 3 NHMW 2019/0167/0034, height 5.8 mm, width 1.8 mm.

Original description – “Shell small, slender fusiform. Protoconch paucispiral, dome-shaped, composed of two convex whorls, bearing fine, close-set spiral rows of micropustules. Junction with teleoconch delimited by beginning of adult sculpture. Teleoconch of 3.5 tall convex whorls, separated by impressed suture. Axial sculpture of rounded opisthocline ribs, broadening towards abapical suture, about half width of their interspaces, overrun by narrow spiral cords, slightly narrower than their interspaces, six on first teleoconch whorl, nine on penultimate whorl. Single secondary spiral developed in some interspaces. Close-set growth lines give finely cancellate appearance in spiral interspaces. Axials weaken on second half of penultimate whorl, obso-

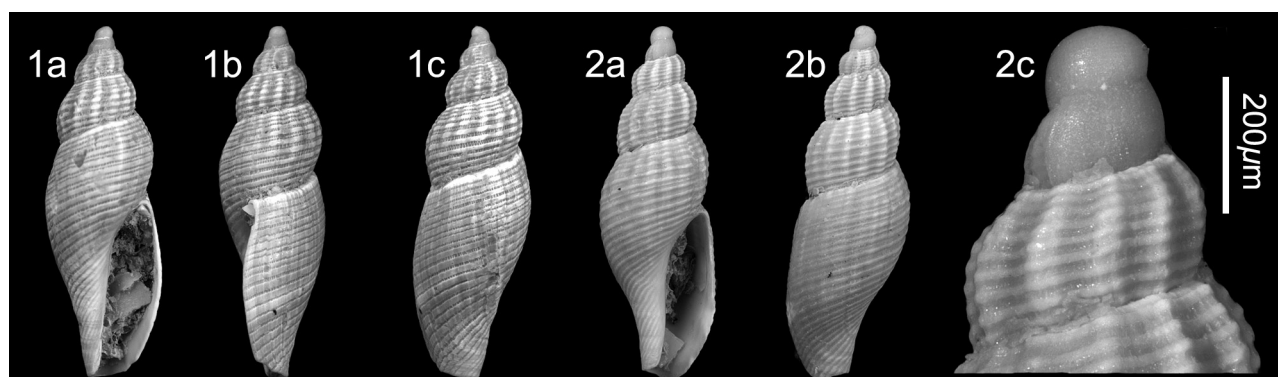


Plate 2. *Andonia wilhelminamariae* Landau & Mulder, 2020; 1. **Holotype** NHMW 2019/0167/0031, height 6.9 mm, width 2.2 mm; 2. **Paratype 1** NHMW 2019/0167/0032, height 5.9 mm, width 2.0 mm (digital images). El Lobillo, Estepona, Lower Pliocene, Upper Pliocene.

lete on last whorl. Last whorl slender fusiform, weakly constricted at base, sculptured by 22-26 subequal flattened cords, with single secondary in the interspaces mid-whorl in most specimens. Base and siphonal fasciole not delimited. Aperture elongate; outer lip slightly thickened by varix, smooth within; anal sinus very shallow U-shaped; siphonal canal medium length, straight, wide, open. Columella weakly excavated in upper third. Columellar callus poorly developed, forming narrow edge; parietal callus not thickened” (Landau & Mulder, 2020, p. 47).

Discussion – Both Moroni & Ruggieri (1981, p. 105) and Landau *et al.* (2013, p. 274) suggested that there were probably several species of *Andonia* Harris & Burrows, 1891 in the European Neogene that had not been formally described. *Andonia wilhelminamariae* Landau & Mulder, 2020 is a non-planktotrophic sister species to the Miocene-Pliocene Mediterranean and adjacent Atlantic *A. bonellii* (Bellardi & Michelotti, 1841). The teleoconch of the two species is extremely similar, slender, with axials that weaken on the last two whorls. However, they are immediately separated by their protoconchs; *A. bonellii* has a multispiral protoconch of a typically planktotrophic type (Vera-Peláez, 2002, pl. 16 figs l-m; Pl. 1, fig. 4c; *A. bonellii hoc opus*), whereas *A. wilhelminamariae* has a protoconch of about two whorls with a large nucleus. The specimen illustrated by Chirli (1997, pl. 10 figs 11-12) as *A. bonellii* is probably a juvenile of *A. wilhelminamariae*, as it is only 3.5 mm in height, and only the axially ribbed early teleoconch whorls are present. Landau *et al.* (2020, p. 42-43), described yet another *Andonia* species with non-planktotrophic development: *A. delgadoi* Landau, Van Dingenen & Ceulemans, 2020 from the Upper Miocene Tortonian Atlantic Ligerian Basin, northwest France, but that species has a much broader teleoconch.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1997). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Genus *Clathromangelia* Monterosato, 1884

Type species – *Pleurotoma granum* Philippi, 1844, by monotypy, present-day, Mediterranean.

1884 *Clathromangelia* Monterosato, p. 131.

1896 *Clathromangilia* Cossmann, p. 118. Incorrect subsequent spelling.

Note – Oliverio (1995) placed the genus in the Daphnellinae Casey, 1904 (= Raphitomidae Bellardi, 1875) rather than the traditional placement in the Mangeliidae/Mangeliinae Fischer, 1883b (*i.e.*, Glibert, 1954; Powell, 1966). Certainly, the protoconchs of the species here placed in *Clathromangelia* are similar to those placed in *Raphitoma*. Bouchet *et al.* (2011) suggested placement in the Clathurellidae H. & A. Adams, 1858, but no *Clathromangelia* species were included in their molecular work. Its placement in the Raphitomidae was confirmed based on molecular data by Fassio *et al.* (2019).

Oliverio (1995) discussed the identity of *Clathromangelia quadrillum* (Dujardin, 1837). This name has been used rather uncritically and extensively in the literature for fossil *Clathromangelia* specimens, including Vera-Peláez (2002), who was evidently unaware of Oliverio’s work. Oliverio noted that the type was likely lost, and reasonably assumed material from the Middle Miocene Faluns de Touraine to be topotypic. That material has a multispiral planktotrophic protoconch with typically raphitomid diagonally reticulated sculpture. This led him to conclude that “Lower Pliocene *Clathromangelia* of the quadrillum lineage from the Senese outcrops (present study) and from Spain (Gili & Martinell 1992), have a protoconch indicating a planktotrophic larval development, while all Recent species of the genus have a non-planktotrophic development. The non-planktotrophic Pleistocene to Recent species (which is also the type of the genus) is here called *C. granum* (Philippi), whilst the Lower Pliocene planktotrophic taxon is referred to as *C. quadrillum* (Dujardin)” (Oliverio, 1995, p. 197). However, we note that in the Estepona Pliocene all the *Clathromangelia* species have non-

planktotrophic type protoconchs, and the species in Estepona representing the *quadrillum* lineage is *granum* and not *quadrillum*. Also, during the Tortonian Early Miocene of NW France there was a whole radiation of *Clathromangelia* species with non-planktotrophic type protoconchs and quite varied teleoconch sculpture that evolved in the relatively isolated Ligerian Bay (Landau *et al.*, 2020).

***Clathromangelia acuticostata* nov. sp.**

Plate 3, figs 1-4.

Type material – Holotype NHMW 2020/0171/0497, height 5.5 mm, width 2.7 mm; paratype 1 NHMW 2020/0171/0498, height 4.2 mm, width 1.9 mm; paratype 2 NHMW 2020/0171/0499, height 5.1 mm, width 2.2 mm; paratype 3 NHMW 2020/0171/0500.

Other material – VC: NHMW 2020/0171/0501 (12). CO: NHMW 2020/0171/0675 (9).

Type locality – El Lobillo, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – name reflecting the sharp, elevated sculpture. *Clathromangelia* gender feminine.

Diagnosis – *Clathromangelia* species of minute size, paucispiral protoconch bearing spiral microsculpture,

teleoconch of two smooth, rapidly expanding whorls, low spire, large last whorl, siphonal canal wide.

Description – Shell small, broadly turritiform-fusiform, with relatively high conical spire (apical angle 44.2-45°). Protoconch paucispiral, of just over two whorls, second whorl shouldered, bearing microsculpture; protoconch I with spiral cordlets, protoconch II with irregular axial riblets interrupt spirals forming small cruxiform tubercles (Estepona specimen; dp = 470 μ m, hp = 500 μ m, dp/hp = 0.94, dV1 = 285 μ m, dn = 135 μ m). Junction with teleoconch marked by sinusigera. Teleoconch of up to four shouldered convex whorls, separated by narrowly impressed undulating suture. Axial sculpture of 12 sharp, elevated, orthocone ribs extending between sutures. Spiral sculpture of two sharp, elevated cords, roughly equal in strength to ribs, adapical delimiting subsutural ramp, abapical cord forming periphery, whorl profile between cords concave. Cords overrun, but not swollen, over ribs, forming small, pointed tubercles. No teleoconch microsculpture. Last whorl evenly convex, 63-66% of total height, moderately constricted at base, bearing four subequal primary spiral cords, axials extending over base, and further 5-7 tubercular cords over siphonal fasciole. Aperture subquadrate, 44-45% of total height; outer lip weakly thickened by labial varix, sharp edged, bearing four tubercles within, only D1 strongly developed in most specimens; anal sinus narrow, moderately deeply U-shaped, with apex placed mid-ramp; siphonal canal moderately short, bent slightly abaxially and recurved, shallowly notched at tip. Columella smooth, moderately excavated in upper third, straight below, twisted at fas-

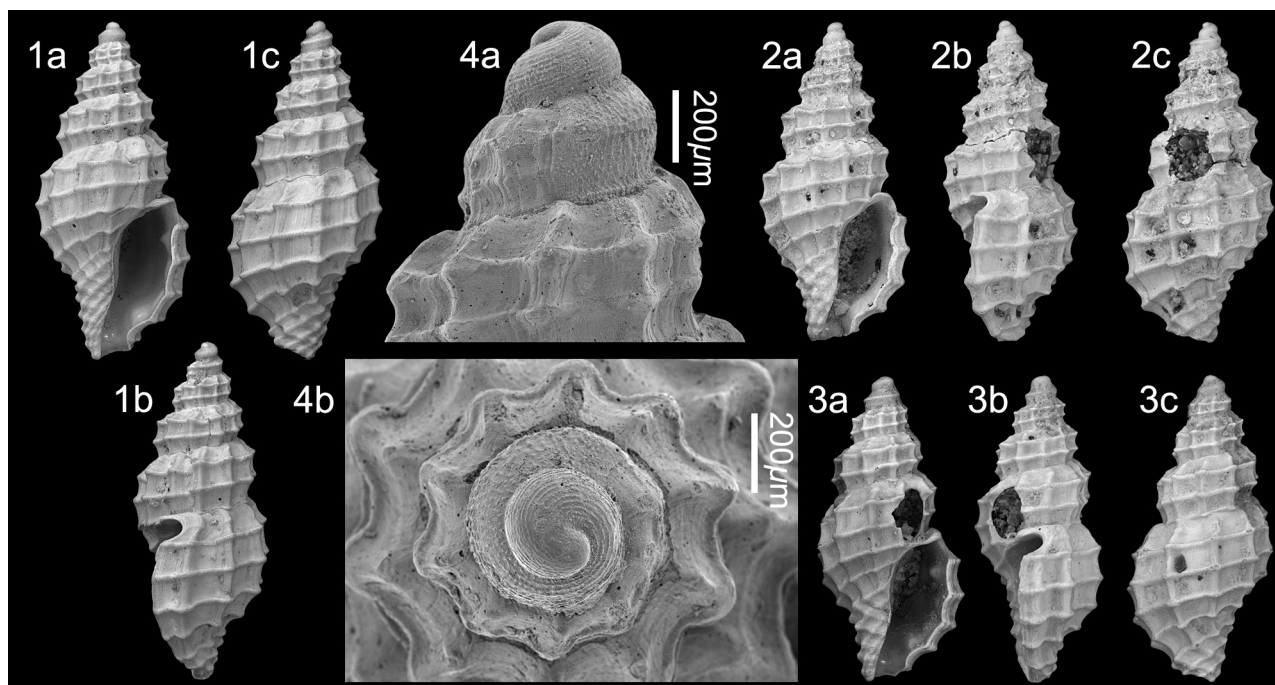


Plate 3. *Clathromangelia acuticostata* nov. sp.; 1. **Holotype** NHMW 2020/0171/0497, height 5.5 mm, width 2.7 mm; 2. **Paratype 1** NHMW 2020/0171/0498, height 4.2 mm, width 1.9 mm; 3. **Paratype 2** NHMW 2020/0171/0499, height 5.1 mm, width 2.2 mm (digital images); 4. **Paratype 3** NHMW 2020/0171/0500, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ciolo. Columellar and parietal callus slightly thickened, forming narrow callus rim; small parietal tubercle developed in some specimens.

Discussion – *Clathromangelia acuticostata* nov. sp. has only two spiral cords on the spire whorls which separates it from most of its congeners from the Pliocene of Italy revised by Oliverio (1995) [*i.e.* *C. loiselieri* Oberling, 1970, *C. elvirae* Oliverio, 1995, *C. tavianii* Oliverio, 1995 (three cords on spire whorls), *C. marinae* Oliverio, 1995 (four cords on last spire whorl), *C. strigillata* Pallary, 1904 (five cords on last spire whorl)]. *Clathromangelia granum* (Dujardin, 1837) has two primary cords on spire whorls (a third weaker one on the subsutural ramp on the last spire whorl; see Oliverio, 1995: figs 7-9), but differs in having a more elevated protoconch with stronger, wider spaced axial riblets. *Clathromangelia quadrillum* (Dujardin, 1837) has three cords on the penultimate whorl and differs from all the other species discussed above in having a planktotrophic type multispiral protoconch (see Oliverio, 1995: figs 18-21). *Clathromangelia fenestrata* (Millet, 1865) from the Upper Miocene and Lower Pliocene of northwestern France (Ceulemans *et al.*, 2018; Landau *et al.*, 2020) is the most similar species to *C. acuticostata* in teleoconch sculpture but differs in having a far more elevated and strongly carinate protoconch.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Clathromangelia granum (Philippi, 1844)

- 1836 *Pleurotoma rude* Philippi, p. 199, pl. 11, fig. 16 (*non* G.B. Sowerby I, 1834).
 1839 *Pleurotoma cancellata* Calcare, p. 5, fig. 1 (*non* Eichwald, 1830, *nec* Deshayes, 1834).
 *1844 *Pleurotoma granum* Philippi, p. 170 (*nom. nov. pro* *Pleurotoma rude* Philippi, 1836, *non* G.B. Sowerby I, 1834).
 2002 *Clathromangelia quadrillum* (Dujardin, 1837) – Vera Peláez, p. 207; pl. 4, figs E, F, pl. 13, figs E, F [*non* *Clathromangelia quadrillum* (Dujardin, 1837)].
 1995 *Clathromangelia granum* (Philippi, 1844) – Oliverio, p. 197, figs 7-9, 22-25.

Discussion – According to the description, the specimen illustrated by Vera Peláez (2002, pl. 4, figs E, F, pl. 13, figs E, F) from Parque Antena has a protoconch of about 2.5 whorls, with a carinate last whorl, and axial and spiral sculpture, forming reticulated pattern with tubercles. The teleoconch whorls bear 11-12 ribs crossed by 2-3 cords. Unfortunately, the very poor-quality reproduction of the plates in that work make interpretation difficult. Nevertheless, it is not *Clathromangelia quadrillum* (Dujardin, 1837) that has a planktotrophic type multispiral protoconch (see Oliverio, 1995, figs 18-21). The specimen probably represents *Clathromangelia granum* (Philippi, 1844), which matches the shell description given by Vera-

Peláez. We include this species in the discussion but cannot confirm its presence.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper). Lower and Middle Pleistocene: central and eastern Mediterranean (Oliverio, 1995). Present-day: central Mediterranean (Oliverio, 1995)

Clathromangelia marinae Oliverio, 1995

Plate 4, figs 1-3

- *1995 *Clathromangelia marinae* Oliverio, p. 200, figs 15, 30, 32.

Material and dimensions – Maximum height 5.0 mm, width 2.1 mm. CO: NHMW 2020/0171/0513-0515 (3), NHMW 2020/0171/0572 (7).

Description – Shell small, broadly turritiform-ovate, with medium-height conical spire (apical angle 52.5-53.4°). Protoconch paucispiral, of 2.1 convex whorls, protoconch I smooth, protoconch II weakly shouldered, bearing microsculpture; first whorl with coarse tubercles vaguely arranged axially, on second whorl tubercles coalescing into widely spaced axial ribs (Estepona specimen; dp = 425 µm, hp = 485 µm, dp/hp = 0.88, dV1 = 260 µm, dn = 120 µm). Junction with teleoconch marked by sinusigera. Teleoconch of up to four low convex whorls, separated by narrowly impressed weakly undulating suture. Axial sculpture of 12-13 narrow, elevated, rounded, orthocone ribs, extending between sutures. Spiral sculpture of two cords on first two teleoconch whorls, weaker third cord develops below suture on penultimate whorl: cords narrower than ribs, first cord weaker running over subsutural ramp, second cord delimiting subsutural ramp, abapical cord forming periphery, whorl profile between cords concave. Cords overrun, but not swollen, over ribs, forming small tubercles. No teleoconch microsculpture. Last whorl evenly convex, 67-68% of total height, weakly constricted at base, bearing one weaker cord over subsutural ramp, 4-5 subequal primary cords mid-whorl, axials extending over base, and further 4 or 5 tubercular cords over siphonal fasciole. Aperture subquadrate, 43-44% of total height; outer lip strongly thickened by labial varix, sharp edged, bearing bifid D1 and three further tubercles below; anal sinus narrow, moderately depth U-shaped, with apex placed mid-ramp; siphonal canal moderately short, bent slightly abaxially and recurved, shallowly notched at tip. Columella smooth, strongly excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus thickened, forming narrow callus rim; small parietal tubercle developed.

Discussion – The Estepona specimens are not identical to the holotype illustrated by Oliverio (1995, figs 15, 30, 32). They are matched in shell size (maximum height 4.5 mm Estepona vs 4 mm Italy), the protoconch has the same number of whorls [2.1 vs 2.1-2.2 (the 1.6-1.7

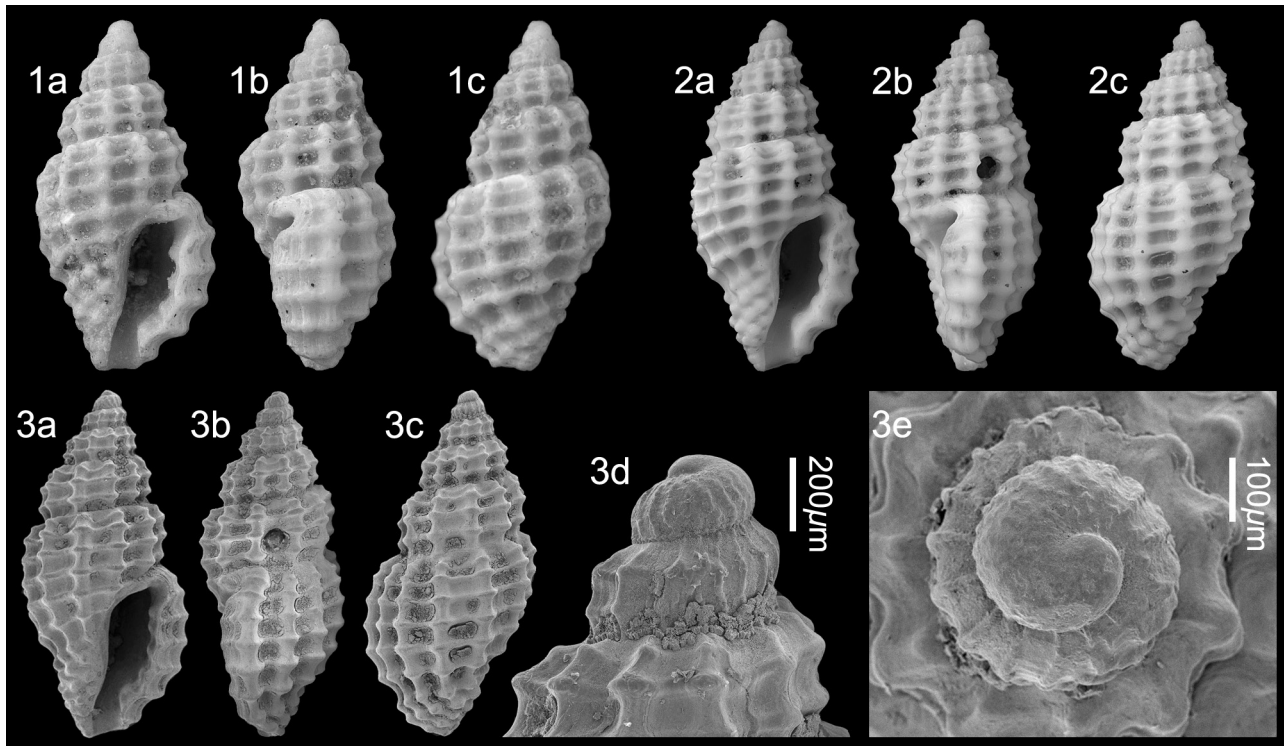


Plate 4. *Clathromangelia marinae* Oliverio, 1995; 1. NHMW 2020/0171/0513, height 4.5 mm, width 2.1 mm; 2. NHMW 2020/0171/0514, height 5.0 mm, width 2.1 mm (digital images); 2. NHMW 2020/0171/0515, height 4.4 mm, width 2.1 mm, 3d-e, detail of protoconch (SEM images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

whorls quoted in the species description does not count the nucleus] but is larger ($dp = 425 \mu\text{m}$ vs $360 \mu\text{m}$, *vide* Oliverio, 1995, p. 200). The protoconch microsculpture and shape are similar. The teleoconch sculpture is similar, but with about two fewer ribs and one extra cord on the penultimate whorl. The shape and orientation of the anal sinus are similar, the sinus is possibly broader in the Italian specimen. They share a strongly thickened and denticulate outer lip. We provisionally consider the Estepona specimens to be conspecific with *Clathromangelia marinae* but highlight the differences discussed above.

Clathromangelia marinae is most similar to *C. strigilata* Pallary, 1904 from the present-day eastern Mediterranean, but differs in its protoconch microsculpture and that species has an even greater number of spiral cords (5 on penultimate whorl).

Distribution – Lower Pliocene: central Mediterranean, Italy (Oliverio, 1995). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

***Clathromangelia mulderi* sp. nov.**

Plate 5, fig. 1

Type material – Holotype NHMW 2020/0171/0001, height 5.0 mm, width 2.1 mm.

Other material – Known from holotype only.

Type locality – Velerín conglomerates, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Name after Henk Mulder, enthusiastic collector of fossil molluscs and friend of the first author (BL). *Clathromangelia* gender feminine.

Diagnosis – *Clathromangelia* species of small size, paucispiral protoconch of two whorls, last carinate, teleoconch with narrow ramp, bearing 15 axial ribs and raised primary and secondary cords of almost equal strength, six labial denticles, D1 and D6 strongest, narrow anal sinus, short siphonal canal.

Description – Shell small, broadly fusiform, robust, weakly scalate spire (apical angle 40.4°). Protoconch paucispiral, composed of two convex whorls, last whorl strongly keeled just above mid-whorl (any surface microsculpture abraded). Junction with teleoconch sharply delimited. Teleoconch of four whorls with narrow sub-sutural ramp, weakly angular shoulder placed high, convex below, separated by superficial undulating suture. Axial sculpture of elevated, narrow, rounded, orthocline ribs, 15 on last whorl, equal in width to their interspaces. Spiral sculpture of narrower cords, two on first whorl, with single secondary intercalated on shoulder and between primaries on second whorl, rap-

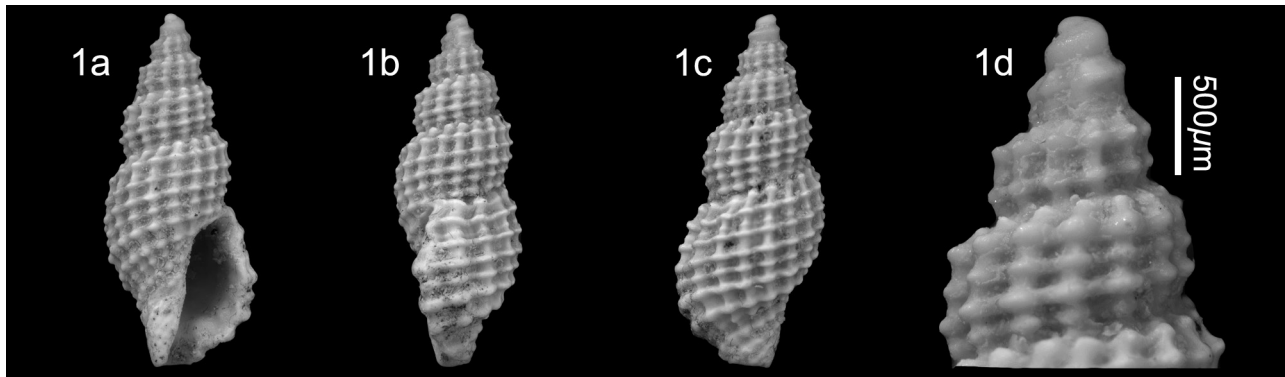


Plate 5. *Clathromangelia mulderi* nov. sp.; 1. **Holotype** NHMW 2020/0171/0001, height 5.0 mm, width 2.1 mm, 1d, detail of protoconch. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

idly becoming almost equal in strength to primaries. Third primary appears just above suture on penultimate whorl. Spirals overrun axials, forming small tubercles. Last whorl 64% total height, weakly inflated, subsutural ramp narrow, shoulder weakly angular, evenly convex below, moderately constricted at base; axials continue over base, nine spirals on last whorl plus further four over siphonal fasciole. Aperture ovate; outer lip thick, convex in profile, slightly flared just below mid-aperture, bearing six stout, poorly delimited denticles within, D1 and D6 strongest; anal sinus narrow, moderately deep, symmetrically U-shaped, with apex mid-subsutural ramp, delimited laterally by D1 within outer lip; siphonal canal short, open. Columella smooth, strongly excavated in upper third, straight below, slightly twisted at fasciole. Columellar callus poorly developed, forming narrow indented edge. Siphonal fasciole not sharply delimited.

Discussion – Although represented by a single specimen, *Clathromangelia mulderi* nov. sp. is distinctive and warrants description. It has no closely living relatives in European waters today but is most like some of its paucispiral congeners recently described from the Upper Miocene Tortonian of northwestern France. *Clathromangelia daisyae* Landau, Van Dingenen & Ceulemans, 2020 differs in not having the protoconch strongly keeled, lacking secondary spiral sculpture, and having longer siphonal fasciole. *Clathromangelia hakkennesi* Landau, Van Dingenen & Ceulemans, 2020 has the same type of strongly keeled protoconch, but differs in having more convex whorls, finer spiral sculpture, and having a longer siphonal fasciole. *Clathromangelia pereirae* Landau, Van Dingenen & Ceulemans, 2020 is similar in size and profile, but has fewer, broader ribs and only two spirals on all spire whorls. All these French Tortonian species have protoconch microsculpture. This is probably also true of the Estepona species, but it is worn and not preserved.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Clathromangelia oliverioi sp. nov.

Plate 6, figs 1-3

Type material – Holotype NHMW 2020/0171/0509, height 3.1 mm, width 1.6 mm; paratype 1, NHMW 2020/0171/0510, height 3.2 mm, width 1.5 mm; **Velerín carretera**, paratype 2, NHMW 2020/0171/0511, height 4.5 mm, width 1.9 mm; paratype 3, NHMW 2020/0171/0512, height 4.8 mm, width 2.1 mm; **Velerín conglomerates**.

Other material – Known from type series only.

Type locality – Velerín carretera, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Name after Marco Oliverio, Dipartimento di Biologia Animale e dell’Uomo, “La Sapienza” University of Roma, in recognition of his contribution to the knowledge of this genus. *Clathromangelia* gender feminine.

Diagnosis – *Clathromangelia* species of small size, paucispiral protoconch of two whorls with microsculpture of spiral rows of tubercles, cruciform on the last whorl, teleoconch of three shouldered whorls, bearing ten axial ribs and spiral sculpture of almost equal strength, two cords on spire whorls, forming coarsely cancellate sculpture tubercles at intersections, four labial denticles, D1 strongest.

Description – Shell small, broadly fusiform, with gradate spire (apical angle 46.8-53.3°). Protoconch paucispiral, of two whorls, second whorl shouldered, bearing microsculpture of spiral rows of tubercles, cruciform on the last whorl (dp = 460 μm, hp = 510 μm, dp/hp = 0.90, dV1 = 285 μm, dn = 145 μm). Junction with teleoconch marked by sinusigera. Teleoconch of up to three angular whorls, separated by superficial undulating suture. Axial sculpture of narrow, elevated, weakly prosocline ribs, ten on last whorl, extending between sutures, slightly weaker

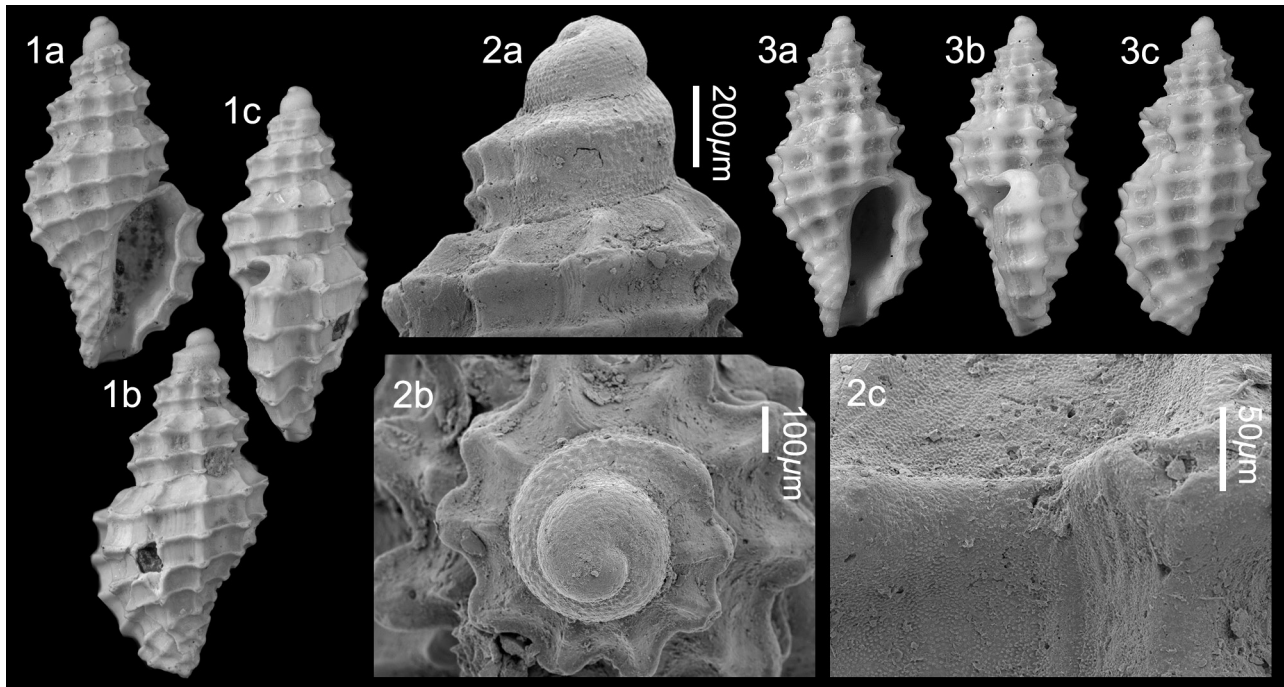


Plate 6. *Clathromangelia oliverioi* nov. sp.; 1. **Holotype** NHMW 2020/0171/0509, height 3.1 mm, width 1.6 mm (digital image); 2. **Paratype 1** NHMW 2020/0171/0510, height 3.2 mm, width 1.5 mm, 2a-b, detail of protoconch, 2c, detail of teleoconch microsculpture (SEM image). Velerín carretera. 3. **Paratype 2** NHMW 2020/0171/0511, height 3.6 mm, width 1.6 mm (digital image). Velerín conglomerates, Estepona, Lower Piacenzian, Upper Pliocene.

over subsutural ramp. Spiral sculpture of roughly equal strength, two cords on spire whorls, forming coarsely cancellate sculpture with small horizontally elongated tubercles at intersections. Teleoconch covered in very fine micropustules. Last whorl 67-70% of total height, with broad, concave subsutural ramp, sharply angled by shoulder cord, convex below, moderately constricted at base, bearing four subequal primary cords mid-whorl, axials extending weakened over base, and further five tubercular cords over siphonal fasciole. Aperture subquadrate, 47-49% of total height; outer lip strongly thickened by labial varix, sharp edged, bearing four tubercles within, D1 strongest, weakening abapically; anal sinus broad, distorting adapical part of outer lip, moderately deeply U-shaped, with apex placed on adapical half of ramp; siphonal canal moderately short, bent slightly abaxially and recurved, shallowly notched at tip. Columella smooth, moderately excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus weakly thickened, forming narrow callus rim; no parietal tubercle developed.

Discussion – *Clathromangelia oliverioi* nov. sp. is a very characteristic species, with its strongly angular whorls with sharp tubercles developed at the sculptural intersections, protoconch microsculpture predominantly composed of rows of tubercles, finely cruciform on the last whorl, and teleoconch covered in very fine micropustules. *Clathromangelia tavianii* Oliverio, 1995 (see below) also has two spirals on spire whorls, and the ribs and cords are of similar strength and width, but it differs in have an al-

most reticulated pattern on the protoconch, the teleoconch is slenderer fusiform, the whorls less angular, and the anal sinus is narrower. All the other species discussed by Oliverio (1995) differ immediately in their whorl profile.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Clathromangelia tavianii Oliverio, 1995

Plate 7, figs 1-4

*1995 *Clathromangelia tavianii* Oliverio, p. 198, figs 12, 13, 28, 31.

Material and dimensions – Maximum height 7.6 mm, width 3.0 mm. **CO**: NHMW 2020/0171/0506-0507 (2), NHMW 2020/0171/0508 (20). **VS**: NHMW 2020/0171/0505 (8). **EL**: NHMW 2020/0171/0502-0503 (2), NHMW 2020/0171/0504 (25).

Description – Shell small, broadly turritiform-fusiform, with relatively high conical spire (apical angle 49-50°). Protoconch paucispiral, of 2.25 whorls bearing microsculpture; protoconch I with spiral cordlets, protoconch II weakly shouldered, bearing minute axial riblets appear between spirals forming very irregular reticulated pattern (dp = 465 µm, hp = 470 µm, dp/hp = 0.99, dV1 = 285 µm, dn = 120 µm). Junction with teleoconch marked by sinusigera. Teleoconch of up to four convex whorls, separated by narrowly impressed undulating suture. Axial sculpture

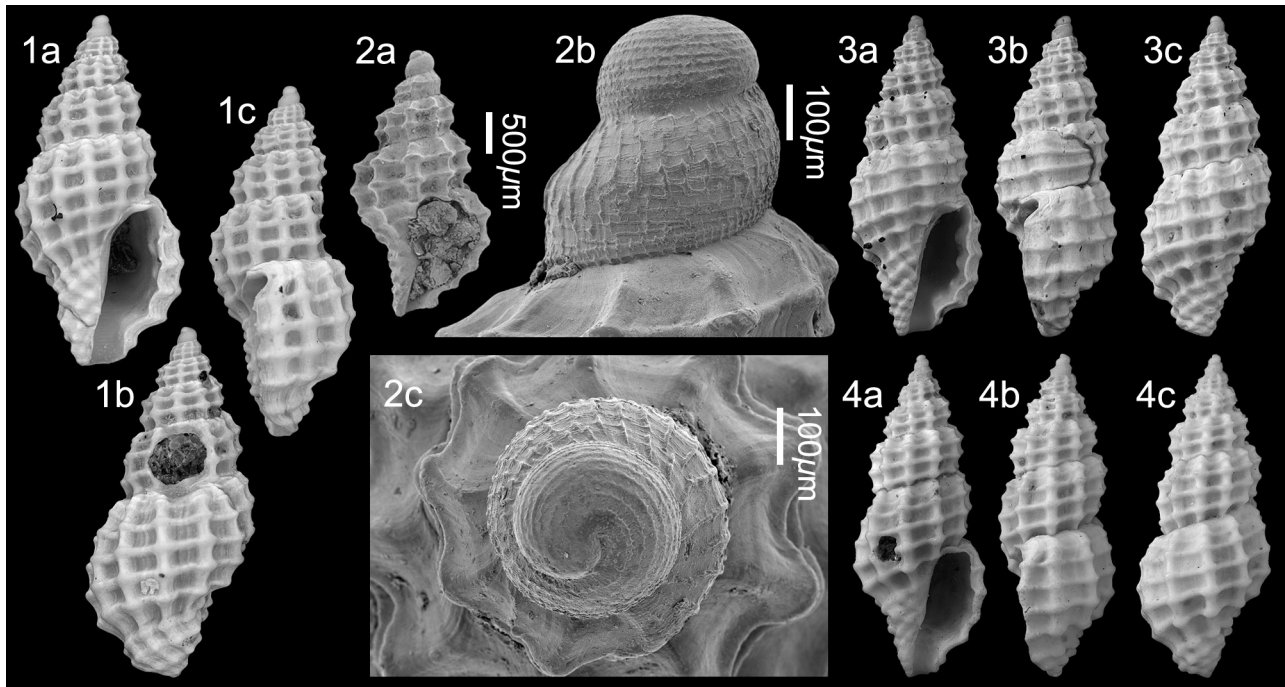


Plate 7. *Clathromangelia tavianii* Oliverio, 1995; 1. NHMW 2020/0171/0502, height 6.4 mm, width 2.9 mm (digital image); 2. NHMW 2020/0171/0503, detail of protoconch (SEM image). El Lobillo. 3. NHMW 2020/0171/0505, height 6.9 mm, width 2.7 mm; 4. NHMW 2020/0171/0506, height 7.6 mm, width 3.0 mm (digital images). Velerin conglomerates, Velerin, Estepona, Lower Pliocene, Upper Pliocene.

of 10-12 sharp, elevated, weakly opisthocline ribs, extending between sutures. Spiral sculpture of three sharp, elevated cords, slightly narrower than ribs, first cord weaker running over subsutural ramp, second cord delimiting subsutural ramp, abapical cord forming periphery, whorl profile between cords concave. Cords overrun, but not swollen, over ribs, forming small, pointed tubercles. No teleoconch microsculpture. Last whorl evenly convex, 61-65% of total height, moderately constricted at base, bearing two weaker cords over subsutural ramp, four subequal primary cords mid-whorl, axials extending over base, and further 5 or 6 tubercular cords over siphonal fasciole. Aperture ovate, 39-45% of total height; outer lip moderately thickened by labial varix, sharp edged, bearing four tubercles within, D1 strongest, weakening abapically; anal sinus narrow, moderately deeply U-shaped, with apex placed on adapical half of ramp; siphonal canal moderately short, bent slightly abaxially and recurved, shallowly notched at tip. Columella smooth, strongly excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus thickened, forming narrow callus rim; small parietal tubercle developed in some specimens.

Discussion – The Estepona specimens probably fit within the intraspecific variability of *Clathromangelia tavianii* Oliverio, 1995, described from the Lower Pliocene of Italy, although we have some reservations. The Estepona specimens are larger (maximum height 7.6 mm vs 4 mm, *vide* Oliverio, 1995, p. 198). The protoconch is larger with an extra half whorl [we note that in the original description the protoconch is described as 1.5 whorls, $dp = 340$

μm , although fig. 31 of Oliverio (1995) shows at least 1.75 whorls, if the nucleus is counted]. The teleoconch characters are the same: 10-12 axials, three cords on spire whorls, 10-11 spirals on the last whorl. However, the anal canal is directed more adapically than in the Italian specimens and the outer lip is not as strongly thickened. We provisionally consider the Estepona specimens to be conspecific with *Clathromangelia tavianii* but highlight the differences discussed above.

Other species with three cords on spire whorls: the present-day eastern Mediterranean *C. loiselierii* Oberling, 1970 has a quite different protoconch sculptured by widely spaced irregular axial riblets with almost no spiral elements. *Clathromangelia elvirae* Oliverio, 1995 from the Lower Pliocene of Italy, is very similar in protoconch and teleoconch characters to *C. tavianii*, but is even smaller (3.0 mm height, *vide* Oliverio, 1995), and has the anal canal directed more adapically, even more so than the Estepona specimens.

Distribution – Lower Pliocene: central Mediterranean, Italy (Oliverio, 1995). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

Genus *Clinura* Bellardi, 1875

Type species – *Murex calliope* Brocchi, 1814, by subsequent designation, Bellardi, 1877, Pliocene, Italy.

1875 *Clinura* Bellardi, p. 20.

***Clinura calliope* (Brocchi, 1814)**

Plate 8, figs 1-2

- *1814 *Murex Calliope* Brocchi, p. 436, pl. 9, fig. 15a, b.
 1847 *Pleurotoma calliope* Brocchi – Bellardi, p. 62, pl. 1, fig. 9.
 1877 *Clinura Calliope* (Brocch.) – Bellardi, p. 205, pl. 7, fig. 1.
 1890 *Clinura calliope* var. *minima* Sacco, p. 277.
 1896 *Clinura Calliope* (Brocchi) – Cossmann, p. 74, pl. 5, fig. 19.
 1904 *Clinura Calliope* var. *minima* Sacco, p. 49 (var. A of Bellardi, 1877).
 1937 *Clinura Calliope* var. *minima* Bell. – Montanaro, p. 189 [109], pl. 6 [9], fig. 32.
 1942 *Surculites (Clinura) calliope* (Brocchi) – Beets, p. 359, pl. 36, fig. 8, pl. 37, fig. 23.
 1944 *Surculites (Clinura) calliope* (Brocchi) – Wenz, p. 1390, fig. 3928.
 1955 *Pleurotomella (Clinuropsis) calliope* (Brocchi 1814) – Rossi Ronchetti, p. 305, fig. 163.
 1955 *Surcula (Clinura) calliope* (Brocchi) – Korobkov, p. 394, pl. 105, fig. 12.
 1963 *Clinura calliope* (Brocchi) – Charig, p. 291, fig. 3, pl. 47, figs 9-12.
 1966 *Clinura calliope* (Brocchi, 1814) – Powell, p. 140, pl. 23, fig. 1.
 1967 *Surculites (Clinura) calliope* (Brocchi) – Pelosio, p. 156 [56], pl. 45, figs 6, 7.
 1974 *Surculites (Clinura) calliope* (Brocchi) 1814 – Caprotti, p. 32, pl. 4, fig. 1.
 1978 *Murex calliope* Brocchi, 1814 – Pinna & Spezia, p. 146, pl. 31, fig. 2.
 1978 *Pleurotomella calliope* Brocchi [sic] – Cuscani Politi, p. 37, 42, pl. 4, fig. 4.
 1979 *Surculites (Clinura) calliope* (Brocchi, 1814) – Montefameglio *et al.*, p. 131, pl. 1, fig. 7.
 1992 *Clinura calliope* (Brocchi, 1814) – Cavallo & Repetto, p. 134, fig. 359.
 1997 *Surculites calliope* (Brocchi, 1814) – Chirli, p. 31, pl. 8, figs 11, 12.
 2002 *Clinura calliope* (Brocchi, 1814) – Vera-Peláez, p. 234, pl. 8, figs A, B, C.

Material and dimensions – Maximum height 23.0 mm, width 12.8 mm. VC: NHMW 2020/0171/0341-0342 (2), NHMW 2020/0171/0343 (2).

Description – Shell medium size, fragile, turritiform, very broadly biconic, with pagodiform gradate spire (apical angle 52.5-56.2°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture. Teleoconch of up to six angular whorls, with very broad, concave subsutural ramp, acutely angled at shoulder cord placed at about one-quarter whorl height, concave below, separated by shallow, linear suture. Sculpture on adapical three-quarters of subsutural ramp consisting of comma-shaped axial riblets of irregular length, most strongly developed below shoulder, weakening towards periphery; on abapical quarter of ramp 2 or 3 weak spiral threads, one further weak cord below shoulder. Axial sculpture reduced to rounded tubercles developed on shoulder cord, 18-20 on penultimate whorl. Last whorl tall, 69-72% of total height, with very broad, weakly concave subsutural ramp, angled at tuberculous shoulder cord, convex below, strongly constricted at base; narrow cords over base, with a single secondary intercalated in some interspaces; cords closer-set and weaker over siphonal fasciole. Aperture very broad, ovate; outer lip thin, sharply angled at shoulder, sharp edged, without varix, smooth within; anal sinus very broad, deep, asymmetrically U-shaped, occupying entire ramp, apex placed on adapical half of ramp; siphonal canal long, straight, unnotched. Columella smooth, straight, twisted at fasciole. Columellar and parietal callus not thickened, no callus rim.

Discussion – Bellardi's (1877) variety A from the Upper Miocene of Santa Agata, later named var. *minima* by Sacco (1904, p. 49), was said to differ in being smaller, with a more acute spire, weaker shoulder carina placed further from the suture, and the tubercles on the carina are sub-obsolete on the last whorl. The only specimen we have seen is the incomplete shell from Montegibbio illustrated by Montanaro (1937, pl. 6 [9], fig. 32), which does indeed seem to be slenderer, with a more elevated spire. Otherwise, the sculpture seems to fall within the range of that of the Pliocene specimens of *Clinura calliope* (Brocchi,

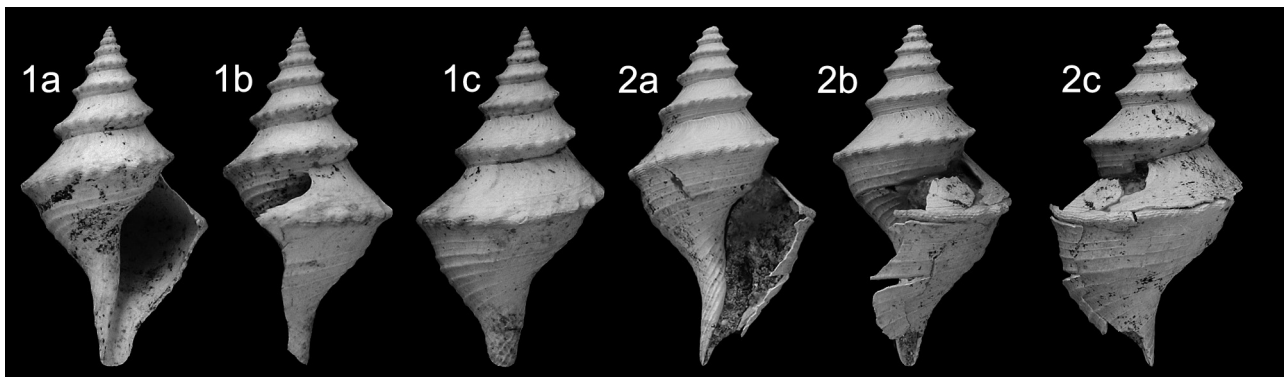


Plate 8. *Clinura calliope* (Brocchi, 1814); 1. NHMW 2020/0171/0341, height 17.0 mm, width 9.0 mm; 2. NHMW 2020/0171/0342, height 23.0 mm, width 12.8 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1814). We provisionally consider them conspecific and include the Upper Miocene specimens in the distribution, but further study with more plentiful material is required.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1847, 1877; Sacco, 1890, 1904; Montanaro, 1937). Lower Pliocene: central Mediterranean, Italy (Pelosio, 1967; Caprotti, 1974; Montefameglio *et al.*, 1979; Cavallo & Repetto, 1992; Chirli, 1992). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

Genus *Cyrillia* Kobelt, 1905

Type species – *Murex linearis* Montagu, 1803, by typification of replacement name, present-day, British Isles.

- 1884 *Cirillia* Monterosato, p. 133. Type species (by subsequent designation; Crosse, 1885): *Murex linearis* Montagu, 1803, present-day, British Isles. Junior homonym of *Cirillia* Rondani, 1856 [Diptera].
- 1905 *Cyrillia* Kobelt, p. 367. Type species (by typification of the replaced name): *Murex linearis* Montagu, 1803, present-day, British Isles. Emendation of *Cirillia* Monterosato, 1884, which is a junior homonym of *Cirillia* Rondani, 1856 [Diptera].
- 1967 *Cenodagreutes* E.H. Smith, p. 1. Type species (by original designation): *Cenodagreutes aethus* E.H. Smith, 1967, present-day, British Isles.
- 1977 *Lineotoma* Nordsieck, p. 59. Type species (by typification of replaced name): *Murex linearis* Montagu, 1803, present-day, British Isles. *Nom. nov. pro Cirillia* Monterosato, 1884, *non* Rondani, 1856 [Diptera].

Note – Based on molecular evidence, Fassio *et al.* (2019) recognised three major lineages within species traditionally placed in the genus *Raphitoma* Bellardi, 1847: *Raphitoma*, *Cyrillia* Kobelt, 1905 and *Leufroyia* Monterosato, 1884. This was again reinforced by Giannuzzi-Savelli *et al.* (2020) who repeated that *Cyrillia* was worthy of generic rank.

According Fassio *et al.* (2019) the genus *Cyrillia* includes biconic, small shelled species, with a slender spire composed of convex whorls, bearing reticulate sculpture, axially predominant, microsculpture of granules or pustules, a thickened outer lip, denticulate within, the two anteriormost denticles stronger. In their generic description they characterise the protoconch as multispiral, although the generic concept was widened by Landau *et al.* (2020) to include paucispiral species.

We draw attention to the revision of the extant Mediterranean Raphitomidae recently published (Giannuzzi-Savelli *et al.*, 2018), and adopt some of the nomenclature suggested in that paper for shell characteristics within these raphitomid genera (*Cyrillia*, *Leufroyia*, *Raphitoma*); shell outline and aspect (see Giannuzzi-Savelli *et al.*, 2018, figs 1, 2, 5-15). For protoconch whorl count we do count the

nucleus as first half whorl. Therefore, all the species herein have half whorl more than using the Verduin (1977) system adopted by Giannuzzi-Savelli *et al.* (2018).

Cyrillia clathrataeformis nov. sp.

Plate 9, fig. 1

Type material – Holotype NHMW 2020/0171/0560, height 5.8 mm, width 2.6 mm.

Other material – Known from holotype only.

Type locality – El Lobillo, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Name derived from Latin ‘*clathratus*, -a, -um’, adjective, meaning grated or latticed, reflecting sculpture. *Cyrillia* gender feminine.

Diagnosis – *Cyrillia* species of small size, multispiral protoconch with diagonally reticulated surface sculpture, teleoconch of 4.5 strongly convex whorls, 11 narrow axial ribs, three spirals on spire whorls forming pointed tubercles at intersections, last whorl with 5 primary cords plus four over fasciole, D1 developed only.

Description – Shell small, solid, broadly fusiform, tall spire (apical angle 44.5°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of 4.5 strongly convex whorls, with narrow, smooth, concave subsutural ramp bearing inconspicuous comma-shaped axial growth lines, shoulder hardly developed, convex below, separated by superficial, undulating suture. Axial sculpture predominant, composed of narrow, rounded weakly opisthocline ribs, 11 on last whorl, about half width of their interspaces. Spiral sculpture of three narrow cords on spire whorl,

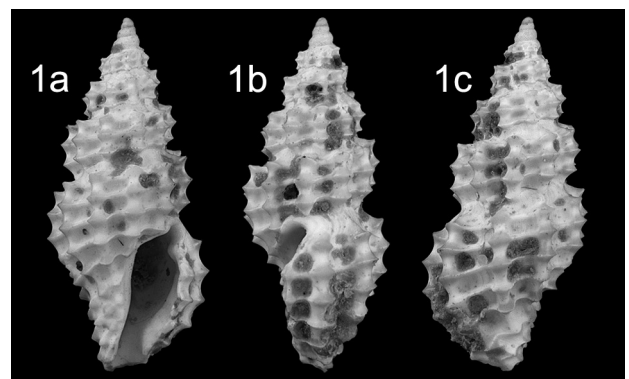


Plate 9. *Cyrillia clathrataeformis* nov. sp.; 1. **Holotype** NHMW 2020/0171/0560, height 5.8 mm, width 2.6 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

forming sharp tubercles over ribs; no secondary spiral sculpture. Last whorl 61% of total height, with narrow, concave subsutural ramp, evenly convex below, weakly to moderately constricted at base; axials weaken over base, five primary spirals, four somewhat tubercular cords over siphonal fasciole. Aperture ovate; outer lip moderately thickened by varix, sharp edged, smooth within, except distinct D1; anal sinus narrow, moderately deep, asymmetrically U-shaped, with apex mid-ramp; siphonal canal moderately length and width, strongly bent abaxially and recurved. Columella smooth, strongly excavated in upper third, straight below, moderately twisted at fasciole. Columellar and parietal callus sharply delimited, weakly thickened, forming narrow callus rim.

Discussion – *Cyrrillia clathrataeformis* nov. sp. is closely similar to *Cyrrillia linearis* (Montagu, 1803), which also occurs in the Estepona assemblages (see below) but differs in having fewer and narrower axial ribs and fewer cords that form sharp tubercles at the sculptural intersections. *Cyrrillia michalidesi* Landau, Van Dingenen & Ceulemans, 2020 from the Atlantic Upper Miocene, Tortonian, of northwestern France is immediately separated by its much finer spiral sculpture. *Cyrrillia georgesi* (Ceulemans, Van Dingenen & Landau, 2018) from the Atlantic Upper Pliocene of northwestern France also has more numerous spirals that are swollen, but not sharp over the ribs.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Cyrrillia linearis (Montagu, 1803)

Plate 10, figs 1-3

- *1803 *Murex linearis* Montagu, p. 261, pl. 9, fig. 4.
- 1804 *Murex elegans* Donovan, pl. 179, fig. 3 (*non* W. Wood, 1828).
- 1826 *Pleurotoma tricolor*, Risso, p. 215.
- 1829 *Pleurotoma muricoidea* de Blainville, p. 111, pl. 4, fig. 7.
- 1833 *Murex Cyrrilli* Scacchi, p. 24.
- 1843 *Fusus Buchananensis* MacGillivray, p. 170.
- 1848 *Clavatulula linearis* Mont. – S.V. Wood, p. 56, pl. 7, fig. 2.
- 1877 *Homotoma Raynevali* Bellardi, p. 274, pl. 8, fig. 24.
- 1882 *Clathurella linearis* Montagu – Bucquoy *et al.*, p. 96, pl. 14, figs 20, 21.
- 1910 *Peratotoma (Cirillia [sic]) linearis* Mtg. – Cerulli-Irelli, p. 59 (251), pl. 5 (36), figs 39-45.
- 1915 *Clathurella linearis* (Montagu) – Harmer, p. 237, pl. 28, figs 26-29.
- 1918 *Clathurella linearis* (Montagu) – Harmer, p. 379, pl. 38, figs 26-29, pl. 39, fig. 34.
- 1931 *Clathurella linearis* (Montagu) – Nobre, p. 80, pl. 29, figs 30-32.
- 1937 *Daphnella (Bellardiella) Raynevali* var. *crassior* Montanaro, p. 178 [148], pl. 8 [11], figs 27-29.
- 1943 *Raphitoma (Cirillia [sic]) linearis* (Montagu) –

Wenz, p. 1453, fig. 4111.

- 1963 *Comarmondia raynevali crassior* (Montanaro, 1937) – Venzo & Pelosio, p. 131, pl. 11, fig. 33.
- 1967 *Cenodagreutes coccyginus* E.H. Smith, p. 3, pl. 1, figs 3, 4, text-figs 4, 5.
- 1968 *Raphitoma (Cirillia [sic]) linearis* (Montagu) – Nordsieck, p. 178, pl. 30, fig. 94.60.
- 1977 *Raphitoma (Lineotoma) linearis* (Montagu) – Nordsieck, p. 59, pl. 20, fig. 153.
- 1979 *Lineotoma linearis* (Montagu, 1803) – Nordsieck & García-Talavera, p. 165, pl. 41, fig. 31.
- 1980 *Raphitoma linearis* (Montagu 1803) – Bogi *et al.*, p. 14, fig. 3.
- 1981 *Homotoma raynevali* Bellardi, 1877 – Ferrero Mortara *et al.*, p. 88, pl. 18, fig. 3.
- 1984 *Philbertia linearis* (Montagu, 1803) – Fretter & Graham, p. 535, fig. 368.
- 1988 *Raphitoma linearis* (Montagu, 1803) – Graham, p. 454, fig. 190.
- 1992 *Raphitoma linearis* (Montagu, 1803) – Cavallo & Repetto, p. 146, fig. 403.
- 1992 *Comarmondia raynevali* (Bellardi, 1877) – Cavallo & Repetto, p. 146, fig. 405.
- 1993 *Raphitoma (Cirillia [sic]) linearis* (Montagu, 1803) – González-Delgado, p. 46, pl. 4, figs 13, 14.
- 1997 *Raphitoma linearis* (Montagu, 1803) – Chirli, p. 83, pl. 23, figs 9-12.
- 1997 *Raphitoma raynevali* (Bellardi, 1877) – Chirli, p. 87, pl. 25, figs 1-4.
- 2001 *Raphitoma linearis* (Montagu, 1803) – Cachia *et al.*, p. 68, pl. 10, fig. 6.
- 2002 *Rimosodaphnella* cf. *raynevali* (Bellardi, 1877) – Vera-Peláez, p. 216 (not figured).
- 2002 *Raphitoma (Raphitoma) linearis* (Montagu, 1803) – Vera-Peláez, p. 232, pl. 7, figs Ñ, O.
- 2011 *Comarmondia raynevali* (Bellardi, 1877) – Landau *et al.*, p. 35, pl. 18, fig. 5.
- 2011 *Raphitoma linearis* (Montagu, 1803) – Chirli & Linse, p. 174, pl. 61, fig. 1.
- 2016 *Raphitoma linearis* (Montagu, 1803) – Høisæter, p. 21, figs 1A, 2A, 3A, 14-17.
- 2019 *Raphitoma linearis* (Montagu, 1803) – Cárdenas *et al.*, p. 214, fig. 8f.
- 2022 *Cyrrillia linearis* (Montagu, 1803) – J.D. Oliver *et al.*, p. 424, figs 36A-E, 43O.
- non* 2018 *Raphitoma linearis* (Montagu, 1803) – Brunetti & Cresti, p. 98, fig. 411 [= *Raphitoma* sp.].

Material and dimensions – Maximum height 7.3 mm, width 2.9 mm. **CO**: NHMW 2020/0171/0351 (2). **VC**: NHMW 2020/0171/0352-354 (3), NHMW 2020/0171/0355 (4), NHMW 2020/0171/0616 (1). **EL**: NHMW 2020/0171/0356 (4).

Description – Shell small, solid, moderately broadly fusiform, tall spire (apical angle 44.5-46°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture,

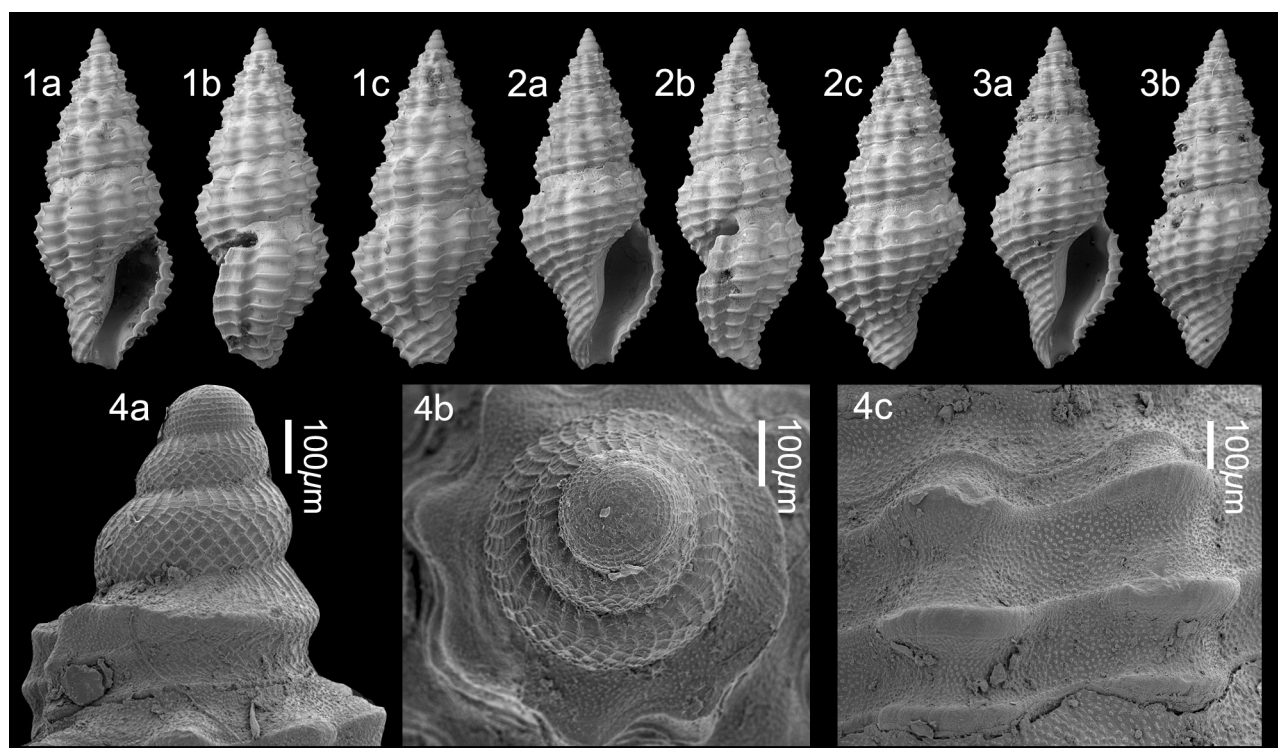


Plate 10. *Cyrillia linearis* (Montagu, 1803); 1. NHMW 2020/0171/0352, height 6.6 mm, width 2.7 mm; 2. NHMW 2020/0171/0353, height 7.0 mm, width 3.0 mm; 3. NHMW 2020/0171/0354, height 7.3 mm, width 2.9 mm (digital images); 4. NHMW 2020/0171/0616 (juvenile), 4a-b, detail of protoconch, 4c, detail of teleoconch microsculpture (SWEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of five convex whorls, with narrow, steeply inclined, smooth, concave subsutural ramp bearing inconspicuous comma-shaped axial growth lines, shoulder hardly developed, convex below, separated by weakly impressed, undulating suture. Axial sculpture predominant, composed of broad, rounded weakly orthocline to opisthocline ribs, 11-14 on last whorl, double the width of their interspaces. Spiral sculpture of two narrow elevated cords on first teleoconch whorl, third cord develops below suture on second whorl, four cords on penultimate whorl: no secondary spiral sculpture. Microsculpture of irregular micropustules developed. Last whorl 59-61% of total height, with narrow, concave subsutural ramp, evenly convex below, moderately constricted at base; axials weaken over base, nine primary spirals, six weakly tubercular cords over siphonal fasciole. Aperture ovate, 39-42% of total height; outer lip weakly thickened by varix, sharp edged, smooth within, except weak D1; anal sinus narrow, deep, asymmetrically U-shaped, with apex near shoulder; siphonal canal moderate length, moderately wide, strongly bent abaxially and recurved. Columella smooth, strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus sharply delimited, weakly thickened, forming narrow callus rim.

Discussion – *Cyrillia linearis* (Montagu, 1803) is most like *C. aequalis* (Jeffreys, 1867), which has a similar

present-day distribution, but differs in having a microsculpture of coalescent micropustules as opposed to isolated micropustules in *C. aequalis*, the sharper tubercles developed over the cords, and the somewhat tubercular cords over the siphonal fasciole, which are smooth in *C. aequalis* (Høisæter, 2016, p. 23). *Cyrillia georgesii* (Ceulemans, Van Dingenen & Landau, 2018) from the Atlantic Upper Pliocene of northwestern France is also closely similar, but that species is slenderer, and the larger tubercles are developed where the cords overrun the ribs.

Vera-Peláez (2002) recorded a single specimen from the Estepona assemblage as *Rimosodaphnella* cf. *raynevali* (Bellardi, 1877). As correctly pointed out by Bonfitto & Morassi (2013, p. 232) this species does not belong to the genus *Rimosodaphnella* Cossmann, 1916, and - following Bałuk (2003, p. 72) - placed Bellardi's species in the genus *Philbertia* Monterosato, 1884, which is now considered a synonym of *Raphitoma* Bellardi, 1847. Compared to typical *C. linearis*, the syntype of *Homotoma raynevali* figured by Ferrero Mortara *et al.* (1981, pl. 18, fig. 3) is slenderer, has a relatively short, inflated last whorl, more strongly constricted at the base, and a shorter siphonal canal. Sculpture seems to be similar in both species, although some authors have illustrated specimens with large tubercles developed on the cords as they overrun the ribs (*e.g.*, Chirli & Linse, 2011, p. 175, pl. 62, fig. 1). When compared with specimens illustrated by other authors (*e.g.*, Cavallo & Repetto, 1992, fig. 405;

Chirli, 1997, pl. 25, figs 1-4), the most constant difference seems to be a slightly shorter siphonal canal. In our opinion, *Homotoma raynevali* Bellardi, 1877 fits well within the range of the rather variable *C. linearis*. Therefore, Bellardi's species is herein considered a junior subjective synonym of *C. linearis*.

Distribution – Upper Miocene: Atlantic, southwestern Spain (Cárdenas *et al.*, 2019); central Proto-Mediterranean, Italy (Montanaro, 1937; Venzo & Pelosio, 1967). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848; Harmer, 1915); Atlantic, Guadalquivir Basin, S. Spain (González-Delgado, 1993); central Mediterranean, Italy (Chirli, 1997; Brunetti & Cresti, 2018). Upper Pliocene: North Sea Basin, Red Crag, England (S.V. Wood, 1848; Harmer, 1915); western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean (Bellardi, 1877; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914). Middle Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Pleistocene (indeterminate): Atlantic, England (Harmer, 1915, 1918). Present-day: Atlantic: Norway (Høisæter, 2016), Scotland (E.H. Smith, 1967), British Isles (Fretter & Graham, 1984; Graham, 1988), Galicia (Oliver *et al.*, 2022), south to Portugal (Nobre, 1931) and Canary Islands (Nordsieck & García-Talavera, 1979); western Mediterranean (Bucquoy *et al.*, 1882), central Mediterranean (Bogi *et al.*, 1980; Cachia *et al.*, 2001).

***Cyrillia saldubensis* nov. sp.**

Plate 11, figs 1-4

Type material – Holotype NHMW 2020/0171/0573, height 4.8 mm, width 2.2 mm; paratype 1 NHMW 2020/0171/0574, height 5.3 mm, width 2.7 mm; paratype 2 NHMW 2020/0171/0572, height 3.9 mm, width 1.9 mm; paratype 3, NHMW 2020/0171/0575, height 3.2 mm, width 1.7 mm.

Other material – Maximum height 5.3 mm, width 2.7 mm. **CO:** NHMW 2020/0171/0676 (6). **EL:** NHMW 2020/0171/0615 (11).

Type locality – El Lobillo, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Named after the Roman name for Estepona, Salduba. *Cyrillia* gender feminine.

Diagnosis – *Cyrillia* species of small size, relatively broad, multispiral protoconch with diagonally reticulated sculpture, teleoconch of 3.5 convex whorls, bearing 15 axial ribs and weaker, narrow spiral cords, ten tubercular cords over fasciole, micropustular surface sculpture, only D1 developed within outer lip.

Description – Shell small, solid, broadly fusiform, tall spire (apical angle 52.7°). Protoconch tall, conical mul-

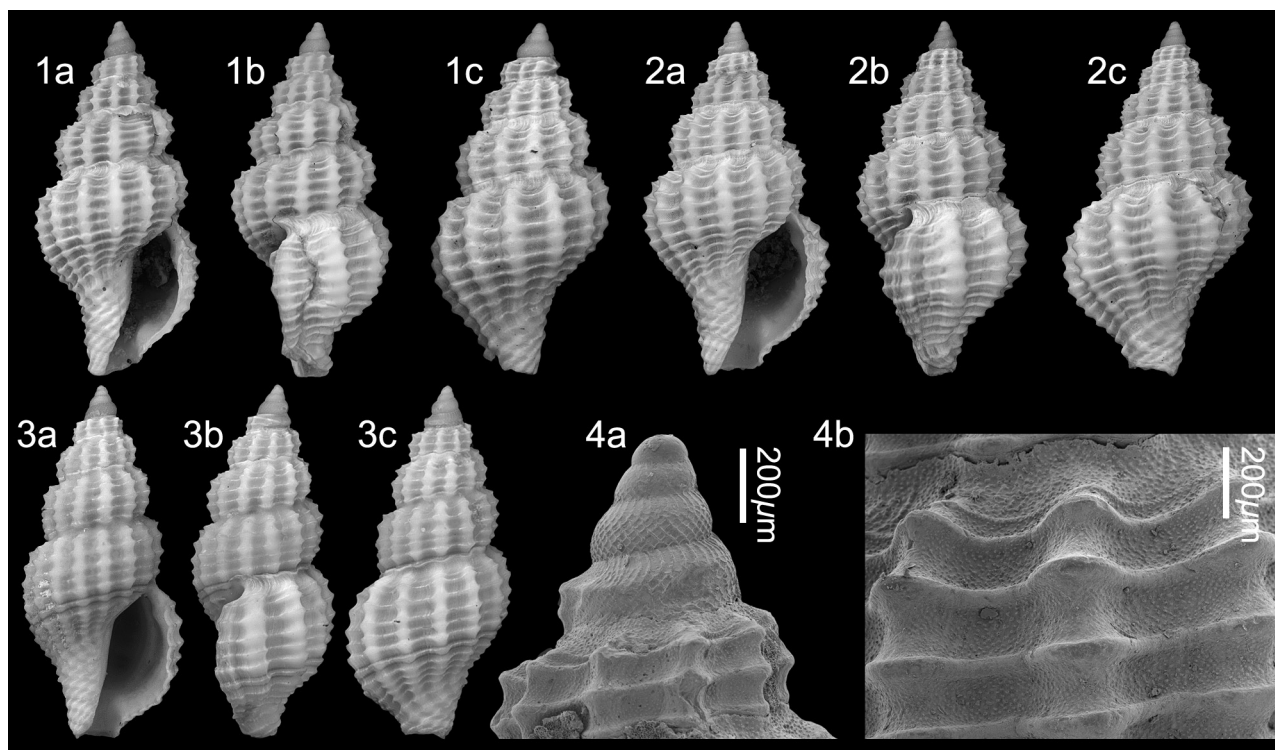


Plate 11. *Cyrillia saldubensis* nov. sp.; 1. **Holotype** NHMW 2020/0171/0573, height 4.8 mm, width 2.2 mm; 2. **Paratype 1** NHMW 2020/0171/0574, height 5.3 mm, width 2.7 mm; 3. **Paratype 2** NHMW 2020/0171/0572, height 3.9 mm, width 1.9 mm (digital image); 4. **Paratype 3** NHMW 2020/0171/0575, height 3.2 mm, width 1.7 mm, 4a, detail of protoconch, 4b, detail of teleoconch sculpture (SEM image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

tispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of 3.5 convex whorls, with narrow, smooth, concave subsutural ramp bearing inconspicuous comma-shaped axial growth lines, shoulder hardly developed, convex below, separated by weakly impressed, undulating suture. Axial sculpture predominant, composed of narrow, rounded orthocone ribs, 15 on last whorl, slightly narrower than their interspaces. Spiral sculpture of three narrow elevated cords on first teleoconch whorl, third cord develops below suture on penultimate whorl; no secondary spiral sculpture. Microsculpture of dense, irregular micropustules developed. Last whorl 66% of total height, with narrow, concave subsutural ramp, evenly convex below, moderately constricted at base; axials weaken over base, nine primary spirals, ten tubercular cords over siphonal fasciole. Aperture ovate, 45% of total height; outer lip weakly thickened by varix, sharp edged, smooth within, except weak D1; anal sinus narrow, relatively shallow, asymmetrically U-shaped, with apex on adapical half of ramp; siphonal canal moderate length, moderately wide, strongly bent abaxially and recurved, shallowly notched at tip. Columella smooth, weakly excavated in upper third, straight below, twisted at fasciole. Columellar and parietal callus moderately delimited, weakly thickened, forming narrow callus rim. Suggestion of colour pattern is preserved, consisting of two very narrow brown/orange horizontal stripes circling the base.

Discussion – *Cyrrillia saldubensis* nov. sp. differs from *Cyrrillia linearis* (Montagu, 1803) in being broader, with a wider apical angle, the ribs are more numerous and narrower, the last whorl is more inflated, and although there are the same number of primary cords on the last whorl, there are more cords over the siphonal fasciole that are more strongly tubercular than in *C. linearis*, which immediately separates it from *C. aequalis* (Jeffreys, 1867), which has smooth cords on the fasciole. It is also like the extant species *C. obesa* (Høisæter, 2016), endemic to the fjords on the western coast of Norway, but in that species the last whorl is more strongly and regularly inflated and more strongly constricted at the base. Moreover, that species is completely white and lacks the two coloured lines seen circling the base of the *Estepona* species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Genus *Daphnella* Hinds, 1844

Type species – *Pleurotoma lymneiformis* Kiener, 1840, by subsequent designation (Herrmannsen, 1847), present-day, Mauritius.

1844 *Daphnella* Hinds, p. 25.

Subgenus *Paradaphne* Laseron, 1954

Type species – *Daphnella botanica* Hedley, 1918, by original designation, present-day, New South Wales, Australia.

1954 *Paradaphne* Laseron, p. 44.

Note – Fassio *et al.* (2019) suggested that the West African ‘*Daphnella*-like’ species, *Raphitoma corimbensis* Rolán, Otero-Schmitt & Fernandes, 1998 and *Raphitoma bedoyai* Rolán, Otero-Schmitt & Fernandes, 1998 should be placed in the Antipodean subgenus *Paradaphne* Laseron, 1954. They suggested that *Daphnella*, as used currently, might be polyphyletic and likened the shell shape and sculpture to the type species *Daphnella botanica* Hedley, 1918. Although not previously recognised, this subgenus has a long geological history along the eastern Atlantic frontage, as *Daphnella gascognensis* Lozouet 2017, from the Upper Oligocene of France undoubtedly belongs within the same group.

Daphnella (Paradaphne) romani (Libassi, 1859)

Plate 12, figs 1-2

- *1859 *Pleurotoma (Clavatula) Romani* Libassi, p. 30, pl. 1, fig. 30.
- 1872 *Pleurotoma (Defrancia) admirabilis* Mayer, p. 234, pl. 14, fig. 7.
- 1910 *Daphnella Romanii* [sic] Libassi–Cerulli-Irelli, p. 60 [252], pl. 5 [36], figs 48, 49.
- 1914 *Daphnella Romanii* [sic] Libassi–Cipolla, p. 149 [45], pl. 13 [2], fig. 20.
- 1963 *Pleurotoma (Clavatula) Romani* Libassi – Moroni & Paonita, p. 29, pl. 2, fig. 30.
- 1877 *Daphnella Romanii* [sic] (Libassi.) – Bellardi, p. 283, pl. 8, fig. 31.
- 2002 *Daphnella (Daphnella) romanii* [sic] (Libassi, 1859) – Vera-Peláez, p. 215; pl. 5, figs G, H.
- 2010 *Daphnella romanii* [sic] (Libassi, 1859) – Sosso & Dell’Angelo, p. 48, unnumbered fig. p. 63, bottom row left.
- 2011 *Rimosodaphnella romanii* [sic] (Libassi, 1859) – Landau *et al.*, p. 35, pl. 18, fig. 3.
- 2018 *Daphnella romanii* [sic] (Libassi, 1859) – Brunetti & Cresti, p. 98, fig. 414.

Material and dimensions – Maximum height 13.6 mm, width 5.6 mm. **CO**: NHMW 2020/0171/0045 (4), NHMW 2020/0171/0046 (1). **VC**: NHMW 2020/0171/0047 (1). **EL**: NHMW 2020/0171/0048 (2).

Description – Shell medium-sized, fragile, broadly bi-conic-fusiform, with conical spire. Protoconch pointed conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (abraded on early protoconch whorls). Teleoconch of up to four very weakly shouldered, convex whorls, with poorly delimited subsutural ramp, separated

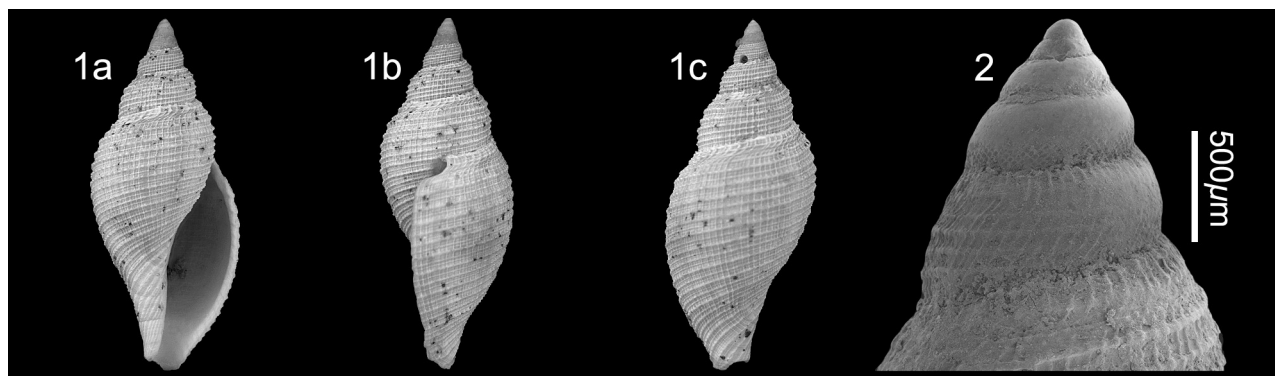


Plate 12. *Daphnella (Paradaphne) romani* (Libassi, 1859); 1. NHMW 2020/0171/0046, height 11.1 mm, width 4.7 mm (digital image). Velerín conglomerates. 2. NHMW 2020/0171/0047, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

by deeply impressed, linear suture. Sculpture of very close-set fine axials, overrun by slightly predominant spirals of primary and secondary strength, minute sharp tubercles developed where primary cords overrun ribs. Last whorl with poorly delimited, convex subsutural ramp, very weakly shouldered, broadly convex below, moderately constricted at base, spiral sculpture with cords of primary to tertiary strength regularly intercalated; siphonal fasciole with stronger, regular cords. Aperture elongate ovate; outer lip sharp, without varix, smooth within; anal sinus narrow, deep, inverted L-shaped, with apex just below suture; siphonal canal moderate length, slightly bent adaxially. Columella smooth, broadly and shallowly excavated, slightly twisted at fasciole. Columellar and parietal callus sharply delimited forming very narrow callus rim.

Discussion – We note that the original spelling of the name “*Romani*” is with one *-i*, and the subsequent Latinisation of the name by all later authors is not justified (ICZN 1999; Art. 31.1.3).

Daphnella (Paradaphne) romani (Libassi, 1859) was widely distributed in the Mediterranean and adjacent Atlantic Pliocene, but always uncommon. Its regularly convex whorls and finely reticulated sculpture with tiny sharp tubercles at the intersections make this species very characteristic and impossible to confuse with any other Pliocene raphitomid.

Daphnella gascognensis Lozouet 2017 from the Atlantic Upper Oligocene Adour Basin of France is remarkably similar in profile and sculpture but differs in having a shallower anal sinus. *Daphnella (Paradaphne) groeneweldi* Landau, Van Dingenen & Ceulemans, 2020, from the Upper Miocene of northwestern France is immediately separated by its unusually sculptured paucispiral protoconch and more convex teleoconch whorls. Today the genus is represented along the tropical West African coast by *D. (P.) corimbensis* (Rolán, Otero-Schmitt & Fernandes, 1998), which is closely similar to *D. (P.) romani*, but has an even more regularly fusiform profile, with a more superficial suture and a shorter siphonal canal, and *D. (P.) bedoyai* (Rolán, Otero-Schmitt & Fernandes,

1998), which is separated from both species by its axial sculpture, most evident on the early teleoconch whorls.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Bellardi, 1877; Moroni & Paonita, 1963; Sosso & Dell’Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Bellardi, 1877; Cipolla, 1914). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

Daphnella (s.l.) malacitana (Vera-Peláez, 2002)

Plate 13, figs 1-3

*2002 *Thatcherina malacitana* Vera-Peláez, p. 235, pl. 8, figs E, F, pl. 17, figs C’, E’.

Material and dimensions – Maximum height 20.4 mm, width 8.4 mm. **CO**: NHMW 2020/0171/0247 (1 complete), NHMW 2020/0171/0248 (1 spire fragment), NHMW 2020/0171/0249 (1 apertural fragment).

Description – Shell large, solid, broadly turritiform, with gradate spire (apical angle 49.6°). Protoconch tall, conical multispiral (apex missing), two convex whorls preserved with fine, diagonally reticulated sculpture. Teleoconch of six barrel-shaped whorls, separated by moderately narrow, deeply concave, canaliculate suture, delimited laterally by sharp-edged adapical primary spiral cord and medially by narrowly impressed suture. Axial sculpture of close-set comma-shaped riblets in subsutural gutter and narrow orthocline ribs restricted to first four teleoconch whorls, ten on second whorl, becoming wider-spaced and rapidly weakening and fading on fourth whorl. Spiral sculpture of narrow, strongly elevated, strap-like subequal cords, ten on penultimate whorl, separated by deep grooves; spirals incompletely interrupted by close-set axial growth lines, giving them finely gemmate appearance. Last whorl 62% of total height, with deep, narrow subsutural gutter, broadly convex below, moderately

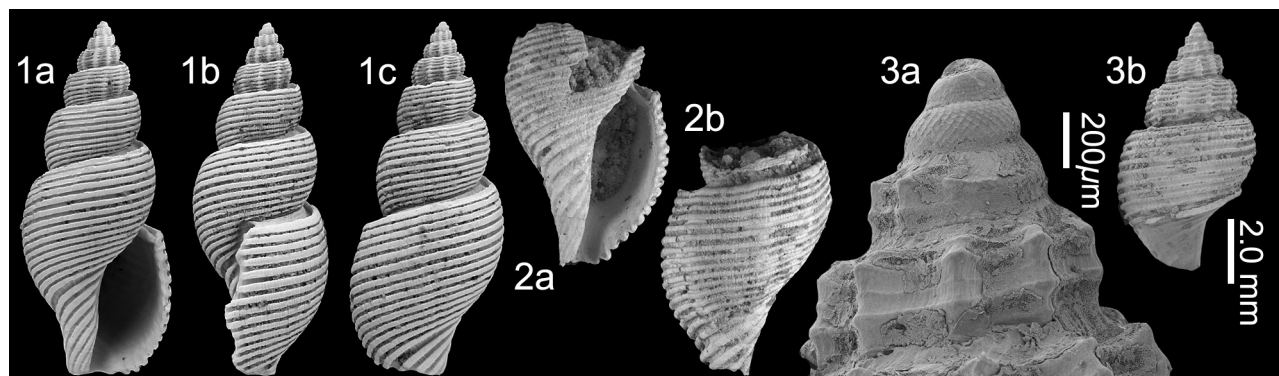


Plate 13. *Daphnella* (s.l.) *malacitana* (Vera-Peláez, 2002); 1. NHMW 2020/0171/0247, height 20.4 mm, width 8.4 mm; 2. NHMW 2020/0171/0248, height 7.6 mm, width 4.6 mm, apertural fragment (digital images); 3. NHMW 2020/0171/0249, height 7.3 mm, spire fragment (SEM image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

constricted at base; siphonal fasciole delimited by wider groove, bearing slightly broader cords. Aperture ovate, 41% of total height; outer lip not thickened (edged incomplete), without varix, smooth within; anal sinus narrow, moderate depth, asymmetrically U-shaped, occupying entire gutter, with apex in adapical half; siphonal canal short, wide (tip damaged). Columella smooth, moderately excavated in upper third, weakly concave below, slightly twisted at fasciole. Columellar and parietal callus not developed, forming narrow indented rim on which spirals are almost worn away.

Discussion – *Daphnella* (s.l.) *malacitana* (Vera-Peláez, 2002) is a most unusual species. The protoconch is typically raphitomid, making its placement in the family Raphitomidae Bellardi, 1875 undoubted. However, its teleoconch characters, with deep subsutural gutter, axials that do not persist on later adult whorls, and narrow cords separated by very deep grooves, is unusual for the family. Vera-Peláez (2002, p. 235) placed this species in his earlier described genus *Thatcherina* Vera-Peláez, 1998. However, the type species *T. carminis* Vera-Peláez, 2002, also from Estepona, is quite different. It has no axial ribs on its early whorls, a very broad subsutural platform and extremely deep reverse L-shaped anal sinus with the apex at the suture. Moreover, absolutely no inner lip callus is developed, so that the dorsal sculpture runs uninterrupted into the aperture, whereas in *R. malacitana* an indented inner lip rim is present on which the spiral sculpture is eroded. We provisionally leave this species in *Daphnella* sensu lato.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

Genus *Diaugasma* Melvill, 1917

Type species – *Daphnella epicharta* Melvill & Standen, 1903, by monotypy, present-day, Gulf of Oman.

1917 *Diaugasma* Melvill, p. 195.

Note – This genus includes small species, with an oliviform profile, protoconch multispiral and diagonally reticulate, smooth or microscopically striate teleoconch, spire whorls almost flat-sided, last whorl narrowly cylindrical tapering to a short, siphonal canal. The aperture is long, the outer lip thin, and the anal sinus hardly developed (Powell, 1966, p. 123).

The genus is not speciose, and today it has an Indo-West Pacific distribution. This is the first record of the genus in European faunas. The specimen illustrated by Landau *et al.* (2011, pl. 18, fig. 6) as *Diaugasma* sp. is best placed in the mangeliid genus *Kyllinia* Garilli & Galletti, 2007 (see below in discussion of *D. mediterranea* nov. sp.).

***Diaugasma mediterranea* nov. sp.**

Plate 14, fig. 1

Type material – Holotype NHMW 2020/0171/0570, height 9.5 mm, width 3.5 mm.

Other material – Known from holotype only.

Type locality – El Lobillo, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Name after the Mediterranean Sea, where it occurred during the Pliocene. *Diaugasma* gender feminine.

Diagnosis – *Diaugasma* species of small size, short, coeloconid spire, irregular growth rate resulting in bent spire, surface covered in fine spirals, no axials on early whorls, aperture large, anal sinus hardly developed.

Description – Shell small, moderately broadly oliviform, with low coeloconid spire (apical angle 53.9°). Protoconch not preserved. Teleoconch of four almost flat-sided whorls, the last whorl rapidly increasing in size, so that the spire is at an angle to the main shell axis and the narrowly impressed,

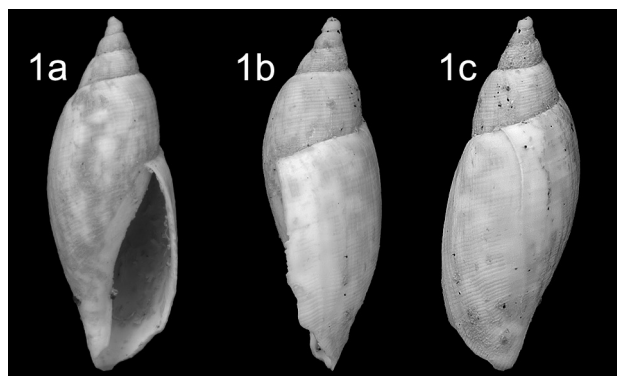


Plate 14. *Diaugasma mediterranea* nov. sp.; 1. **Holotype** NHMW 2020/0171/0570, height 9.5 mm, width 3.5 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

linear suture becomes increasingly oblique. Sculpture of very weak and narrow, crowded cords. Last whorl tall, 82% of total height, subcylindrical, moderately inflated, evenly and broadly rounded, subsutural ramp, collar, base and fasciole not delimited. Aperture elongate, 56% of total height, outer lip simple, smooth within; anal sinus hardly developed; siphonal canal incomplete, but probably moderately short. Columella smooth, broadly and weakly excavated. Columellar and parietal callus sharply delimited, weakly thickened, forming broad callus rim.

Discussion – The type species *Diaugasma epicharta* (Melvill & Standen, 1903) from the Gulf of Oman differs in its broader spire and more regular growth. *Diaugasma olyra* (Reeve, 1845) from the Indo-West Pacific is more closely similar in having a coeloconoid spire and fine spiral sculpture on the last whorl, but the spire is composed of a greater number of whorls, there is regular growth throughout, and fine but prominent axial growth lines are seen on the early whorls, absent in *Diaugasma mediterranea* nov. sp.

Landau *et al.* (2011, p. 35, pl. 18, fig. 6) illustrated a single specimen from the Atlantic Lower Pliocene Guadalquivir Basin of southwestern Spain as *Diaugasma* sp. In their discussion they compared it to *D. marchadi* (Knudsen, 1956), which is now placed in the genus *Kyllinia* Garilli & Galletti, 2007. The Guadalquivir Basin species has a thickened outer lip and a shallow, but well-developed anal sinus, and is better placed in the mangeliid genus *Kyllinia* than *Diaugasma*.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Genus *Favriella* Hornung, 1920

Type species – *Daphnella* (*Favriella*) *weberi* Hornung, 1920, by monotypy, Pliocene, Italy.

1920 *Favriella* Hornung, p. 76.

Note – This genus includes small, broadly fusiform species, with a strongly gradate spire, sharply shouldered whorls above mid-whorl height, the last whorl sharply angular at the shoulder and strongly constricted at the base, with a relatively long, twisted siphonal canal. The protoconch, multispiral with diagonally reticulated sculpture and carinate last portion is typical for the family. Teleoconch sculpture consists of narrow orthocline ribs, obsolete over the subsutural ramp, spinous at the shoulder, and weak spiral cords (Powell, 1966, p. 125).

Powell (1966, p. 125) referring to the original generic description quoted “*Sinus described as sutural, but with no indication of its depth; nor do the illustrations help in this respect*”. Janssen (1972) re-examined type material and concluded that the anal sinus was very broad and shallow, and placed on the subsutural ramp. This description was confirmed by Sosso *et al.* (2018, p. 340-341).

Favriella cipriani (Hornung, 1920)

Plate 15, figs 1-4

- *1920 *Daphnella* (*Rimosodaphnella*) *Cipriani* Hornung, p. 75, pl. 2, fig. 6.
- 1976 *Favriella weberi* Hornung, 1920 – Pavia, p. 144, pl. 6, figs 15, 17-19 [*non Favriella weberi* (Hornung, 1920)].
- 1996 *Favriella weberi* (Hornung, 1920) – Vera-Peláez, p. 712, text-fig. 72, pl. 54, figs 5-9 [*non Favriella weberi* (Hornung, 1920)].
- 2002 *Favriella weberi* (Hornung, 1920) – Vera-Peláez, p. 237, pl. 8, figs G, H, I, J, pl. 16, figs N, Ñ [*non Favriella weberi* (Hornung, 1920)].
- 2018 *Favriella cipriani* (Hornung, 1920) – Sosso *et al.*, p. 341, figs 43-49.
- 2018 *Favriella* sp. A – Brunetti & Cresti, p. 100, fig. 418.

Material and dimensions – Maximum height 6.6 mm, width 2.7 mm. VC: NHMW 2020/0171/0144-0147 (4), NHMW 2020/0171/0148 (5).

Description – Shell small, fragile, moderately broad, with pagodiform gradate spire (apical angle 42.5-45.1°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, squarely reticulated sculpture, diagonal on protoconch II, last half whorl shouldered (Estepona specimens: dp = 680 µm, 885 µm, dp/hp = 0.77). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of up to four acutely shouldered whorls, with broad, straight-sided subsutural ramp, sharply angled at shoulder cord, convex below, separated by narrowly impressed, weakly undulating suture. Axial sculpture predominant; consisting of narrow, raised ribs, only developing on abapical half of subsutural ramp, strongest and slightly spinous at shoulder, orthocline to weakly prosocline below shoulder, eight on last whorl. Spiral sculpture of fine scabrous cords; fine secondary cords on adapical portion of ramp; below, four primary cords, second forming shoulder cord, with sin-

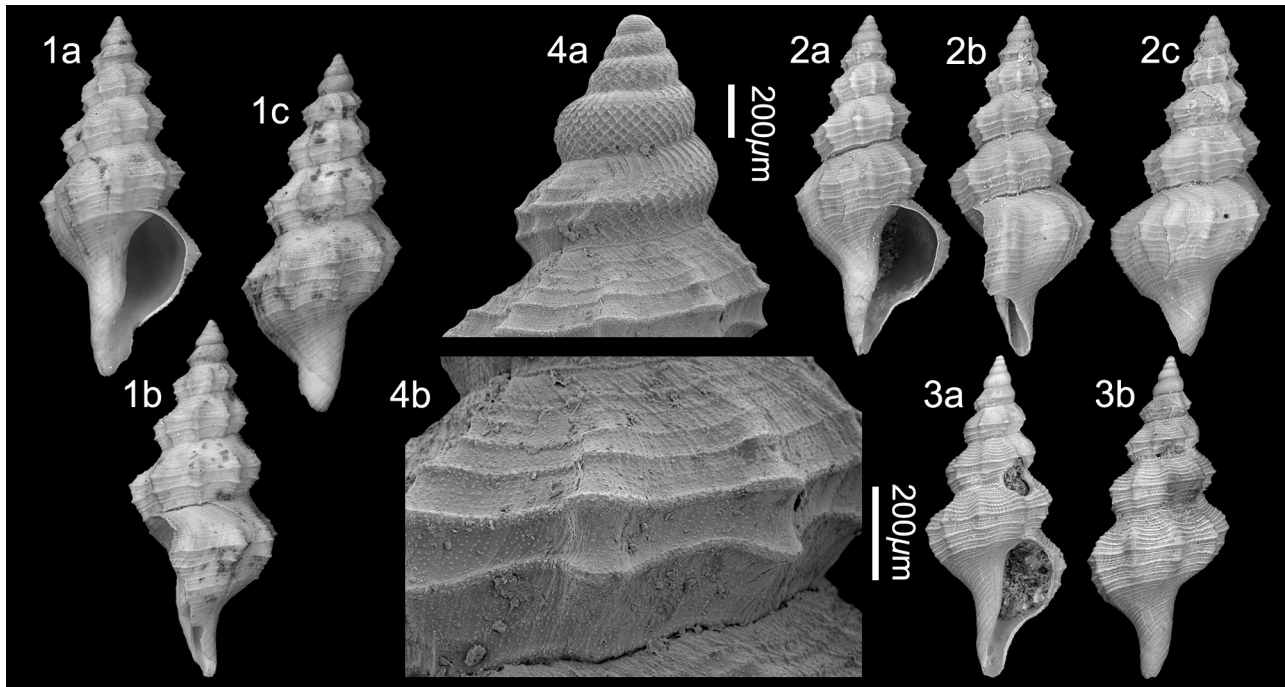


Plate 15. *Favriella ciprianii* (Hornung, 1920); 1. NHMW 2020/0171/0144, height 6.6 mm, width 2.7 mm; 2. NHMW 2020/0171/0145, height 6.4 mm, width 2.6 mm; 3. NHMW 2020/0171/0146, height 5.8 mm, width 2.3 mm (digital images); 4. NHMW 2020/0171/0147, 4a, detail of protoconch, 4b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Pliocene, Upper Pliocene.

gle secondary thread intercalated on penultimate whorl. Microsculpture of widely spaced micropustules roughly aligned in horizontal rows covers entire surface. Last whorl 60-64% of total height, with broad, weakly convex to weakly concave subsutural ramp, sharply angled at shoulder cord, convex below, weakly angled at basal cord, strongly constricted at base; ribs not extending beyond basal cord, fine scabrous cords continue over base, slightly stronger over siphonal fasciole. Aperture ovate, 43-46% of total height; outer lip weakly thickened by labial varix, sharp edged, smooth within; anal sinus very broad, moderately shallow U-shaped, asymmetrical, with apex below mid-ramp; siphonal canal moderately long, recurved, bent abaxially. Columella weakly and broadly excavated, strongly twisted at fasciole, unnotched. Columellar and parietal callus slightly thickened, sharply delimited, forming narrow callus rim.

Discussion – The specimens from Estepona are slightly different from the lectotype of *Daphnella* (*Rimosodaphnella*) *ciprianii* Hornung, 1920 from the Lower Pliocene of Rio Torsero, Italy (illustrated by Sosso *et al.*, 2018, figs 43-49) in having the primary cords slightly more developed and more spinous at the sculptural intersections. However, we consider this difference to fall within the species variability. The specimen illustrated by Brunetti & Cresti (2018, p. 100, fig. 418) from the Lower Pliocene of Italy as *Favriella* sp. A is very similar to the Estepona ones. For comparison with *Favriella weberi* (Hornung, 1920), see under that species. *Favriella sinulosa* (Sorgenfrei, 1958) from the Middle Miocene North Sea Basin of Ger-

many is closely similar in profile and sculpture, but that species is smaller, has a broader protoconch with a very strong carina on the last whorl, and has stronger primary spiral sculpture on the teleoconch.

Distribution – Lower Pliocene: central Mediterranean, Italy (Hornung, 1920; Pavia, 1976; Brunetti & Cresti, 2018; Sosso *et al.*, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Favriella tumidula (Bellardi, 1877)

Plate 16, figs 1-3

- 1877 *Raphitoma tumidula* (Brugn.) – Bellardi, p. 314, pl. 9, fig. 30.
- 1937 *Daphnella* (*Raphitoma*) *tumidula*? Bell. – Montanaro, p. 155[185], pl. 8 [11], figs 57, 58.
- 1976 *Pleurotomella* (*P.*) *tumidula* (Bellardi, 1877, Brugnone m.s.) – Pavia, p. 150, pl. 8, figs 29-31.
- 1992 *Pleurotomoides tumidula* (Brugnone, 1875 [sic]) – Cavallo & Repetto, p. 138, fig. 367.
- 2002 *Rimosodaphnella tumidula* (Brugnone, 1864 [sic]) – Vera-Peláez, p. 216; pl. 5, fig. K.
- 2010 *Favriella tumidula* (Bellardi, 1877, Brugnone ms) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 63, bottom row right.
- 2018 *Favriella tumidula* (Brugnone, 1875 [sic]) – Brunetti & Cresti, p. 100, fig. 416.

Material and dimensions – Maximum height 7.7 mm,

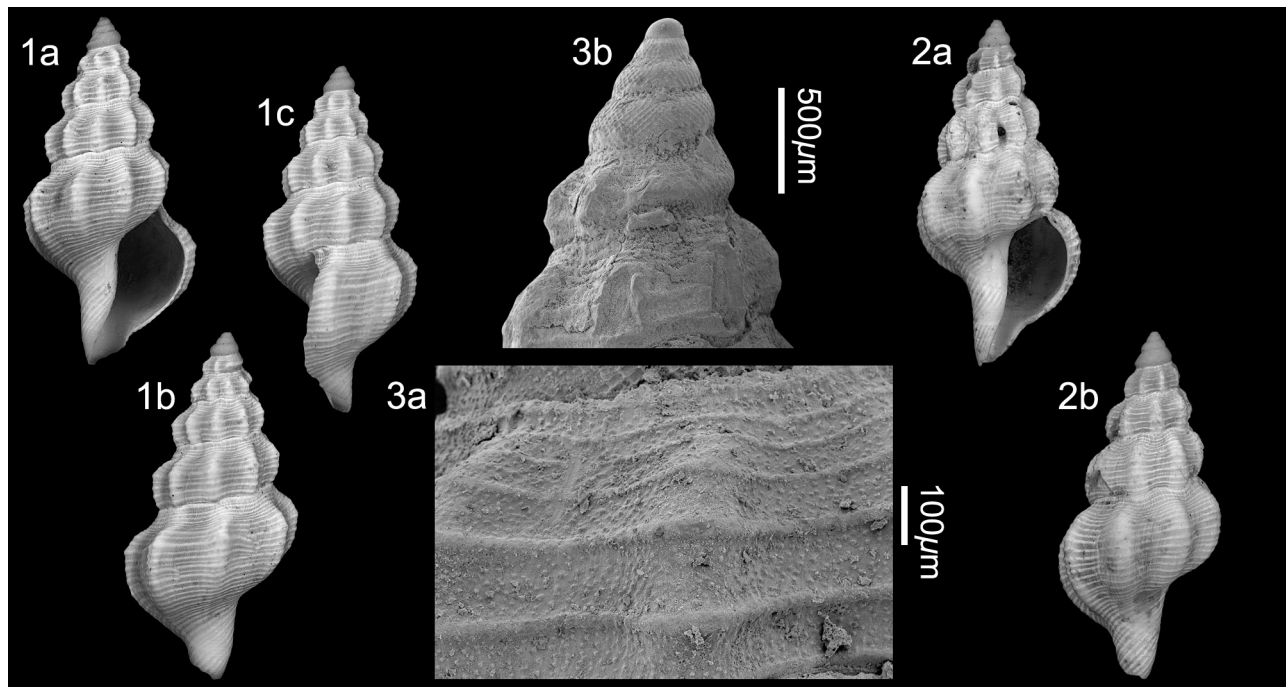


Plate 16. *Favriella tumidula* (Bellardi, 1877); 1. NHMW 2020/0171/0482, height 7.4 mm, width 3.5 mm; 2. NHMW 2020/0171/0483, height 7.7 mm, width 3.2 mm (digital images); 3. NHMW 2020/0171/0484, detail of protoconch (SEM image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

width 3.2 mm. **CO:** NHMW 2020/0171/0482-0484 (3), NHMW 2020/0171/0485 (7). **VC:** NHMW 2020/0171/0636 (1). **EL:** NHMW 2020/0171/0677 (2).

Description – Shell small, medium thickness, broad, with gradate spire (apical angle 46.9–47.6°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II (Estepona specimen; $dp = 820 \mu\text{m}$, $hp = 1015 \mu\text{m}$, $dp/hp = 0.81$). Teleoconch of up to four strongly shouldered whorls, with broad, weakly concave subsutural ramp, roundly angled at shoulder cord, convex below, separated by narrowly impressed, undulating suture. Axial sculpture strongly predominant; consisting of narrow, raised ribs, about one-third width of their interspaces, weak over subsutural ramp, stronger and orthocline below shoulder, 5–8 on last whorl. Spiral sculpture of fine cords; on first whorl two weak cords on subsutural ramp, three primary cords below, adapical delimiting shoulder, single secondary spiral intercalated from penultimate whorl. Entire surface covered in fine axial growth lines, slightly more prominent and arcuate over ramp, and scattered micropustules. Last whorl 63% of total height, with broad subsutural ramp, adapical half concave, abapical convex, obtusely angled at shoulder, convex below, strongly constricted at base; base and fasciole poorly delimited; axials weakening over base, fine spirals of alternating strength over base and siphonal fasciole. Aperture wide, ovate, 43% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus shallow, moderately narrow, asymmetrically U-shaped, occupying adapical half of ramp,

with apex at just below suture; siphonal canal moderate length, strongly recurved. Columella strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus hardly thickened, poorly delimited, forming narrow callus rim.

Discussion – *Favriella tumidula* (Bellardi, 1877) differs from its two Estepona congeners *F. cipriani* (Hornung, 1920) and *F. weberi* (Hornung, 1920) in being squatter and more roundly shouldered. *Drillia dora* Boettger, 1902 from the Middle Miocene Paratethys of Romania is closely similar in profile and sculpture (see Zilch, 1934, pl. 17, fig. 25). It was placed in *Favriella* at subgenus rank by Bałuk (2003, p. 68). It differs from *Favriella tumidula* (Bellardi, 1877) in being taller spired, with more numerous and more regularly convex whorls, and the axial ribs are fewer, broader, and strongly opisthocline.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Montanaro, 1937). Lower Pliocene: central Mediterranean, Italy (Pavia, 1976; Cavallo & Repetto, 1992; Sosso & Dell’Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Bellardi, 1877).

Favriella weberi (Hornung, 1920)

Plate 17, fig. 1

*1920 *Daphnella* (*Favriella*) *Weberi* Hornung, p. 76, pl. 2, fig. 7.

- 1944 *Daphnella (Favriella) weberi* Hornung – Wenz, p. 1455, fig. 4120.
- 1966 *Favriella weberi* (Hornung, 1920) – Powell, p. 125, pl. 20, fig. 4.
- 1972 *Favriella weberi* (Hornung, 1920) – Janssen, p. 52, pl. 10, fig. 4.
- 1976 *Favriella weberi* (Hornung, 1920) – Pavia, p. 144, pl. 6, fig. 15.
- 1992 *Favriella weberi* (Hornung, 1920) – Cavallo & Repetto (*partim*), p. 138, fig. 371 (right fig. only).
- 1998 *Favriella weberi* Hornung, 1920 [*sic*] – Bogi & Cauli, p. 130, fig. 4.
- 2008 *Favriella weberi* (Hornung, 1920) [*sic*] – Chirli & Richard, p. 68, pl. 13, fig. 9.
- 2010 *Favriella weberi* Hornung, 1920 [*sic*] – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 64, top row left.
- 2018 *Favriella weberi* (Hornung, 1920) – Brunetti & Cresti, p. 100, fig. 417.
- 2018 *Favriella weberi* (Hornung, 1920) – Sosso *et al.*, p. 339, figs 35-42.
- non* 1976 *Favriella weberi* Hornung, 1920 – Pavia, p. 144, pl. 6, figs 15, 17-19 [= *Favriella cipriani* (Hornung, 1920)].
- non* 1996 *Favriella weberi* (Hornung, 1920) – Vera-Peláez, p. 712, pl. 54, figs 5-9 [= *Favriella cipriani* (Hornung, 1920)].
- non* 2002 *Favriella weberi* (Hornung, 1920) – Vera-Peláez, p. 237, pl. 8, figs G, H, I, J, pl. 16, figs N, Ñ [= *Favriella cipriani* (Hornung, 1920)].

Material and dimensions – Maximum height 10.6 mm, width 5.2 mm. **VC:** NHMW 2020/0171/0156 (1), NHMW 2020/0171/0157 (1).

Description – Shell medium sized, fragile, with broad pagodiform spire (apical angle 50.5°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture. Junction with teleoconch sharply delimited by sinusigera. Teleoconch of up to five sharply angled whorls, with broad, weakly concave subsutural ramp, sharply angled at shoulder cord, convex below, separated by narrowly impressed, undulating suture. Axial sculpture predominant; consisting of raised, narrow ribs, only developing on abapical half of subsutural ramp, strongest at shoulder forming horizontally elongated spines, orthocline below shoulder, 12 on last whorl. Spiral sculpture on first whorl of two weak cords on subsutural ramp, two primary cords below, adapical delimiting shoulder, secondary and tertiary cords intercalated from second whorl, later whorls with fine scabrous cords of primary to tertiary strength. Last whorl 65% of total height, with broad, weakly concave subsutural ramp, sharply angled at narrow shoulder cord, convex below, strongly constricted at base, base and fasciole poorly delimited; ribs not extending over base, fine scabrous cords of alternating strength continue over base and siphonal fasciole. Aperture wide, ovate, 49% of total height; outer lip very thin, angled at shoulder, sharp

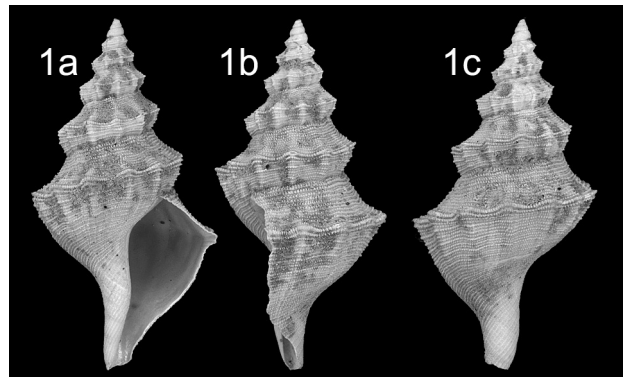


Plate 17. *Favriella weberi* (Hornung, 1920); 1. NHMW 2020/0171/0156, height 10.6 mm, width 5.2 mm (digital image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

edged, without varix, smooth within; anal sinus not developed; siphonal canal moderately long, recurved. Columella strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus hardly thickened, sharply delimited, forming narrow callus rim.

Discussion – The specimen from Estepona closely matches the lectotype recently figured by Sosso *et al.* (2018, figs 35-42) from the Lower Pliocene of Rio Torsero, Ceriale, Italy. *Favriella cipriani* (Hornung, 1920) described from the same Pliocene Rio Torsero assemblage differs in being slenderer, in having a narrower apical angle, with less angular more regularly convex whorls, in having a relatively larger and more inflated last whorl, and in having a slightly deeper U-shaped anal sinus. The specimens illustrated by Vera-Peláez (2002, pl. 8, figs G, H, I, J, pl. 16, figs N, Ñ) as *Favriella weberi* (Hornung, 1920) are, in our opinion, more characteristic of *Favriella cipriani*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Hornung, 1920; Pavia, 1976; Cavallo & Repetto, 1992; Bogi & Cauli, 1998; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018; Sosso *et al.*, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002), France (Chirli & Richard, 2008).

Genus *Gymnobela* Verrill, 1884

Type species – *Gymnobela engonia* Verrill, 1884, by subsequent designation, Cossmann, 1896, present-day, NW Atlantic.

- 1884 *Gymnobela* Verrill, p. 157.
- 1968 *Majox* Nordsieck, p. 182. Type species (by original designation): *Pleurotomella bairdi* Verrill & S. Smith *in* Verrill, 1884, present-day, NW Atlantic.
- 1968 *Watsonaria* Nordsieck, p. 182. Type species (by monotypy): *Clathurella watsoni* Dautzenberg, 1889, present-day, Azores.

Note – The genus *Gymnobela* Verrill, 1884 has been used to place small to moderate sized, thin-shelled, ovate-biconic shells, with a relatively short spire, angular shoulder, and inflated last whorl with a short ‘spout-like’ siphonal canal, a multispiral protoconch covered in diagonally cancellate sculpture, teleoconch sculpture of flexuous ribs overrun by close-set spiral cords more or less tuberculate at the shoulder, and a shallow, reverse L-shape anal sinus, occupying entire shoulder slope (Powell, 1966, p. 133). Bouchet & Warén (1980, p. 48) expanded to genus concept to include other small to medium-sized deep-water NW Atlantic species with more solid shells, more fusiform shell shape, tall to low spires, almost smooth to coarsely reticulated sculpture, and short to medium length siphonal canal. More recently, Criscione *et al.* (2021) considered *Gymnobela* to be an artificial assemblage of several unrelated, mostly undescribed, genus-level lineages. We use the genus in the sense of Bouchet & Warén (1980) until a molecular phylogeny of the extant northeastern Atlantic species within this group is available.

Gymnobela brevis (Bellardi, 1847)

Plate 18, figs 1-3

- 1842 *Pleurotoma abbreviata* Sismonda, p. 33 (*nomen nudum*).
- *1847 *Pleurotoma brevis* Bellardi, p. 19, pl. 1, fig. 15.
- 1847 *Pseudotoma brevis* Bell. – Michelotti, p. 289, pl. 9, fig. 10.
- 1877 *Pseudotoma brevis* Bell. – Bellardi, p. 222, pl. 7, fig. 15.
- 1957 *Genotia brevis pliorecens* Ruggieri, p. 82, pl. 1, fig. 2.
- 1968 *Genota (Pseudotoma) brevis* (Bellardi, 1847) – Robba, p. 610, pl. 46, fig. 7.
- 1974 *Genota (Pseudotoma) brevis pliorecens* Ruggieri, 1957 – Caprotti, p. 34, pl. 4, fig. 3.
- 1976 *Genota brevis f. pliorecens* Ruggieri – Marasti & Raffi, p. 197, pl. 2, fig. 5.
- 1979 *Genota (Pseudotoma) brevis* (Bellardi, 1847) – Montefameglio *et al.*, p. 191, pl. 1, fig. 20.
- 1981 *Pseudotoma brevis* (Bellardi, 1847) – Ferrero Mortara *et al.*, p. 82, pl. 17, fig. 5.
- 1992 *Pseudotoma brevis* (Bellardi, 1847) – Cavallo & Repetto, p. 136, fig. 362.
- 1996 *Gymnobela pliorecens* (Ruggieri, 1957) – Vera-Peláez, p. 661, 34g, h, 66, pl. 49, figs 1-8.
- 1997 *Genota brevis* (bellardi, 1847) – Chirli, p. 102, pl. 29, figs 3, 4.
- 2002 *Gymnobela brevis* (Bellardi, 1847) – Vera-Peláez, p. 227, pl. 7, figs A, B, C, pl. 15, figs C, D.
- 2008 *Pseudotoma brevis* (Bellardi, 1847) – Chirli & Richard, p. 64, pl. 12, fig. 9.
- 2018 *Pseudotoma brevis brevis* (Bellardi, 1847) – Brunetti & Cresti, p. 92, fig. 372.
- non 1854 *Pseudotoma brevis* Bell. – Hörnes, p. 333, pl. 36, fig. 4 (undescribed species).

non 1885 *Gymnobela brevis* Verrill, p. 417 [= *Gymnobela aquilarum* (Watson, 1882)].

non 1973 *Gymnobela brevis* Verrill, 1885 – Morris, p. 251, pl. 69, fig. 15 [= *Gymnobela aquilarum* (Watson, 1882)].

Material and dimensions – Maximum height 9.3 mm, width 5.1 mm. VC: NHMW 2020/0171/0018-0020 (3), NHMW 2020/0171/0021 (3).

Description – Shell small, fragile, very broad ovate-biconic, with relatively low gradate spire (apical angle 59.4-61.3°). Protoconch tall, conical multispiral, of three convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl riblets over subsutural third, diagonally reticulated below (Estepona specimen; dp = 565 μ m, hp = 620 μ m, dp/hp = 0.91). Teleoconch of up to 4.5 shouldered whorls, with moderate width, concave subsutural ramp, sharply angled at shoulder cord, convex below, separated by deeply impressed, linear suture. Axial sculpture strongly predominant; consisting of narrow, ribs, arcuate over subsutural ramp, opisthocline below, about 20 on penultimate whorl. Spiral sculpture weak, with two strengthened cords, one just below suture on ramp, second delimiting shoulder, forming small tubercles at sculptural intersections; flattened cords separated by narrow, shallow grooves below shoulder; cord immediately below shoulder weakly tubercular in some specimens. Last whorl inflated, 70-71% of total height, with relatively narrow, concave subsutural ramp, angled at tubercular shoulder cord, convex below, strongly constricted at base; ribs weakening over base, cords strengthening. Aperture wide, ovate, 49-53% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus very shallow and broad, hardly developed, with apex at shoulder; siphonal canal moderately short, slightly bent adaxially and recurved. Columella broadly excavated mid-height, twisted at fasciole, unnotched. Columellar and parietal callus not thickened, sharply delimited, forming broad indented rim.

Discussion – Ruggieri (1957) erected the chronosubspecies *Genotia brevis pliorecens* for a form from the Lower Calabrian, Lower Pleistocene of Italy that was said to differ from the type in being slenderer, with a stronger carina, the subsutural ramp concave, the presence of a narrow granular subsutural cord, and having fewer and more elevated ribs. The specimens from Estepona have a concave subsutural ramp and exhibit the subsutural cord typical of the subspecies *pliorecens*, but further examination of Italian specimens from Lugnano (Piacenza) and Ciuciano (Siena) show this to be a rather variable character. The concavity of the subsutural ramp is also variable within a population from a single locality. The number and strength of the ribs is also variable as seen in the series illustrated (Pl. 18, figs 1, 2). These observations do not support the erection of the chronosubspecies *pliorecens*, which is placed in synonymy of the nominotypical taxon.

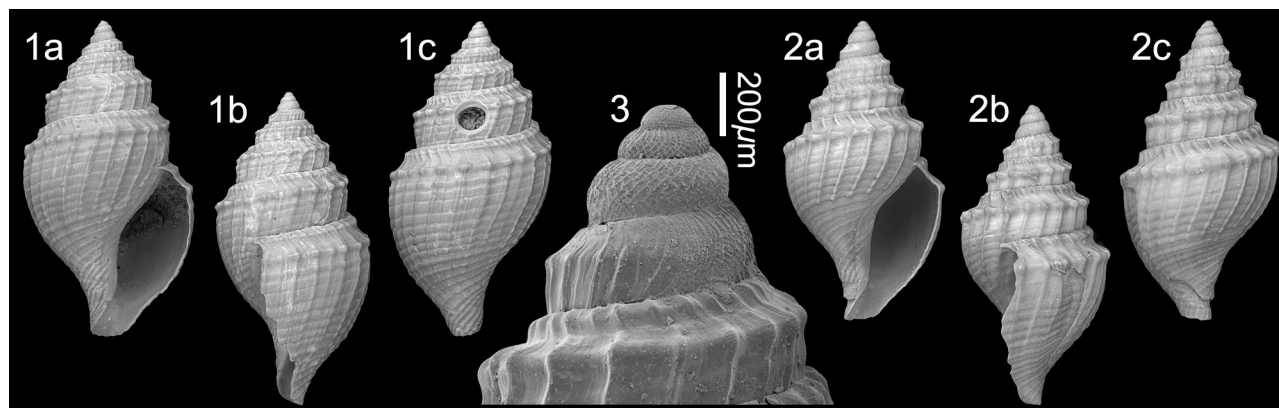


Plate 18. *Gymnobela brevis* (Bellardi, 1847); 1. NHMW 2020/0171/0018, height 9.3 mm, width 5.1 mm; 2. NHMW 2020/0171/0019, height 5.7 mm, width 2.9 mm; 3. NHMW 2020/0171/0019, detail of protoconch (1, 2 digital images, 3 SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Gymnobela brevis (Bellardi, 1847) is closely similar to the type species *Gymnobela engonia* Verrill, 1884, an extant deep-water species from the northwestern Atlantic, but that species differs in having a taller, more gradate spire, more rounded shoulder, broader ribs, and narrow rounded cords separated by wider interspaces as opposed to broad flattened cords separated by narrow, shallow grooves.

Already Bellardi (1877, p. 222) doubted that the Viennese specimens, described by Hörnes (1854), were conspecific with his *Gymnobela brevis* and Hoernes & Auinger (1891) separated it as “var.” from the type. The Paratethyan species differs from the Italian species in its more contracted base and the marked angulation of the last whorl. Moreover, the spiral row of nodes on the shoulder of the spire whorls is closer to the abapical suture in the Paratethyan species but above mid-whorl in *Gymnobela brevis*.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1847, 1877; Robba, 1968; Ferrero Mortara *et al.*, 1981). Lower Pliocene: central Mediterranean, Italy (Caprotti, 1974; Montefameglio *et al.*, 1979; Cavallo & Repetto, 1992; Chirli, 1997; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002), France (Chirli & Richard, 2008), central Mediterranean, Italy (Marasti & Raffi, 1976).

***Gymnobela galerita* (Philippi, 1844)**

Plate 19a, figs 1-3; plate 19b, figs 1-2

- *1844 *Pleurotoma galeritum* Philippi, p. 172, pl. 26, fig. 15.
- 1847 *Pleurotoma Rochettae* Bellardi, p. 69, pl. 4, fig. 1.
- 1862 *Pleurotoma subasperum* Brugnone, p. 5, pl. 1, fig. 1.
- 1876 *Pleurotoma galerita* Philippi – Foresti, p. 25, pl. 1, figs 3-5.
- 1877 *Drillia galerita* (Phil.) – Bellardi, p. 123, pl. 4, fig. 13.
- 2002 *Gymnobela pelagia* Vera-Peláez, p. 228, pl. 7, figs D, E, F, pl. 15, figs G, H.

2010 *Gymnobela galerita* (Philippi, 1844) – Sosso & Dell’Angelo, p. 48, unnumbered fig. p. 64, top row right.

2018 *Gymnobela pelagia* Vera-Peláez, 2002 – Tabanelli, p. 6, fig. 5.

non 1918 *Drillia galerita* (Philippi) – Harmer, p. 378, pl. 39, fig. 36 (worn shell: unidentifiable).

Material and dimensions – Maximum height 15.6 mm, width 6.3 mm. **CO:** NHMW 2020/0171/0027 (12). **VC:** NHMW 2020/0171/0028-0030 (3), NHMW 2020/0171/0031 (20). **EL:** NHMW 2020/0171/0678 (5).

Description – Shell of medium size and thickness, broadly ovate-biconic, with gradate spire (apical angle 43.8–48.2°). Protoconch tall, conical multispiral, of 3.5 convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl riblets over subsutural third, diagonally reticulated below (Estepona specimen; dp = 680 µm, hp = 795 µm, dp/hp = 0.86). Teleoconch of up to five shouldered whorls, with broad, concave subsutural ramp, roundly angled at elevated, thickened narrow shoulder cord, weakly convex below, separated by shallow, linear suture. Axial sculpture of close-set, deeply comma-shaped axial riblets over subsutural ramp, most strongly developed just below suture and weak opisthocline ribs commencing at shoulder where they form weak tubercles, rapidly weakening further below, subobsolete on last whorl. Spiral sculpture of fine threads on subsutural ramp, crossing riblets, giving ramp finely reticulated appearance, thickened shoulder cord, one further primary cord below on spire whorls. Teleoconch surface covered in tiny, irregularly placed, crowded micropustules. Last whorl with moderately broad to broad, 63–64% of total height, with broad concave subsutural ramp, sharply angled at thickened shoulder cord, convex below, strongly constricted at base; base and fasciole not delimited; axials subobsolete on last whorl, except for vague tubercles at shoulder; spirals very fine, of primary to tertiary strength, continued

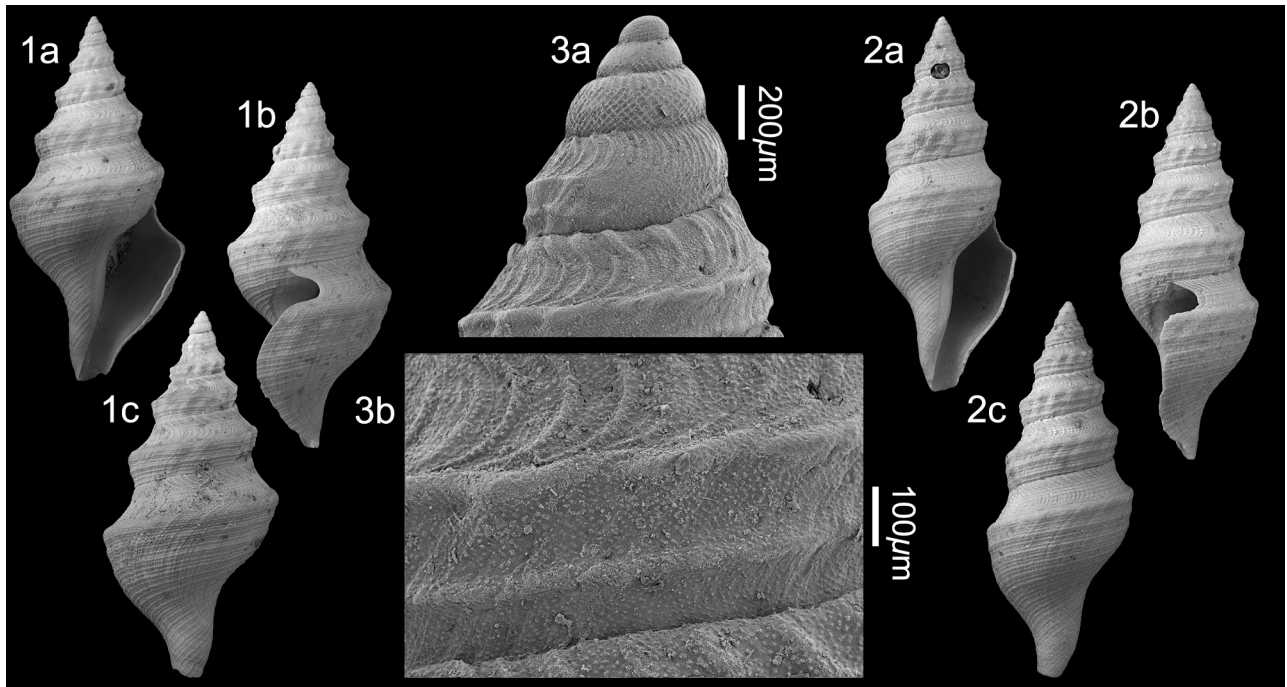


Plate 19a. *Gymnobela galerita* (Philippi, 1844); 1. NHMW 2020/0171/0028, height 10.0 mm, width 4.7 mm; 2. NHMW 2020/0171/0029, height 9.6 mm, width 3.8 mm; 3. NHMW 2020/0171/0030, 3a, detail of protoconch, 3b, detail of teleoconch microsculpture (1, 2 digital images, 3 SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

over base and fasciole. Aperture broad, ovate, 46-49% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus broad, deep, asymmetrically U-shaped, occupying entire ramp, with apex just below mid-ramp; siphonal canal moderate length, slightly bent adaxially and recurved, unnotched. Columella smooth, strongly excavated in upper third, straight below, moderately twisted at fasciole. Columellar and parietal callus not thickened, sharply delimited forming narrow callus rim.

Discussion – The identity of this species is problematic. According to Tabanelli (2018, p. 6), *Drillia galerita* (Phil.) *sensu* Bellardi (1877, p. 123, pl. 4, fig. 13) *non* Philippi (1844, p. 172, pl. 26, fig. 15) is *Gymnobela pelagia* Vera-Peláez, 2002. That author illustrated a specimen from the Upper Pliocene Piacenzian of Pietramora (Ravenna, Italy) (Tabanelli, 2018, fig. 5) that certainly looks conspecific with the Estepona material. However, Tabanelli did not mention that Bellardi (1877, p. 123) placed in his chresonymy of *D. galerita* a species he previously described as *Pleurotoma rochettae* Bellardi, 1847 (spelt *P. Rocchettae* [sic] in Bellardi, 1877). Therefore, the earliest name for this species is *Gymnobela rochettae* (Bellardi, 1847). Whether this is a senior synonym of *Pleurotoma galeritum* Philippi, 1844 (Pl. 19b, figs 1-2) described as fossil from Calabria (stratum not specified) is unclear. The original figure shows a relatively slender shell, similar to that figured here (Pl. 19a, fig. 2). It is most likely that this is the earliest name available for the species and it is used herein. Already Foresti (1876, p. 25) included *Pleurotoma Rochettae* Bellardi, 1847

and *Pleurotoma subasperum* Brugnone, 1862 (see Plate 19b) in his chresonymy of *Pleurotoma galerita*. To this we add *Gymnobela pelagia* Vera-Peláez, 2002; all are considered junior subjective synonyms. It is likely that Vera-Peláez (2002, p. 229) was unaware of any of these species names, as none are discussed in his new species comparison. Only the extant *G. abyssorum* [sic] (correct spelling *abyssorum*) (Locard, 1897) was compared that differs in having a more rounded shoulder and a shorter siphonal canal.



Plate 19b. *Pleurotoma subasperum* Brugnone, 1862; MCZR M14-16760. 1. Lectotype; height 23.0 mm, width 9.2 mm, specimen figured by Brugnone (1862, pl. 1, fig. 1); 2. Paralectotype; height 9.0 mm, width 4.6 mm. Altavilla, Palermo, Pliocene (digital image courtesy of MCRZ, taken by Carlo Smriglio).

Tabanelli (2018, p. 6) erected the taxon *Gymnobela santorsolae* from the Upper Pliocene of Italy and compared it to *G. pelagia*. The differences between the two are quite clear, as stated by Tabanelli: *G. pelagia* is thicker-shelled, taller, the surface covered in finer spiral cords and the much stronger ribs forming well defined tubercles at the shoulder. *Gymnobela santorsolae* seems to have a glossy, polished surface, which is not a feature of the genus *Gymnobela*, which has a dull surface (see Bouchet & Warén, 1980, p. 48). It might be better placed in the genus *Theta* Clarke, 1959, which includes shells like those of *Gymnobela*, but with more polished surface instead of dull and the upper postlarval protoconch whorls are somewhat shouldered. Either way, *G. galerita* is also not congeneric with other species placed in the genus *Gymnobela* as it clearly has a U-shaped sinus and not a reverse L-shaped one. Until a revision of the extant members of this group is available, we keep this species in *Gymnobela* (s.l.).

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Tabanelli, 2018).

Gymnobela lozanoi (Vera-Peláez, 2002)

Plate 20, figs 1-2

*2002 *Rimosodaphnella lozanoi* Vera-Peláez, p. 216, pl. 5, fig. L, pl. 16, figs D, E, F.

Material and dimensions – Maximum height 13.8 mm, width 5.9 mm. VC: NHMW 2020/0171/0053-54 (2), NHMW 2020/0171/0595 (1), NHMW 2020/0171/0055 (8).

Description – Shell medium sized, fragile, broad, with strongly gradate spire (apical angle 52.6°). Protoconch pointed, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl riblets over subsutural third, diagonally reticu-

lated below (dp = 845 μ m, hp = 980 μ m, dp/hp = 0.86). Teleoconch of up to five strongly shouldered coronate whorls, with broad, concave subsutural ramp, angled at elevated, thickened shoulder cord, straight-sided below, tapering inwards to superficial, linear suture. Axial sculpture predominant, composed of comma-shaped riblets over subsutural ramp; very fine, sharp, low, opisthocline, arched ribs below shoulder, 16-20 on penultimate whorl; ribs thickened and extending slightly adapically at shoulder giving coronate appearance. Spirals reduced to flattened cords, except at shoulder where 3 or 4 cords strengthened to form elevated, rounded shoulder carina. Last whorl 66% of total height, with broad, strongly concave subsutural ramp delimited by coronate shoulder carina, convex below, moderately constricted at base, axials weakening over base, spirals strengthening over base and siphonal fasciole; base and fasciole not delimited. Aperture subquadrate, 50% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus broad, shallow, reverse L-shaped, occupying entire ramp; siphonal canal moderate length, broad, slightly bent adaxially and recurved, unnotched. Columella smooth, weakly excavated in upper half, moderately twisted at fasciole. Columellar and parietal callus sharply delimited forming narrow callus rim.

Discussion – Vera-Peláez (2002) originally described this species in the genus *Rimosodaphnella* Cossmann, 1916. However, that genus has been applied rather uncritically in the literature (see generic note for *Rimosodaphnella*), and the shell characters fit better the deep-water genus *Gymnobela* Verrill, 1884, in the wider sense used by Bouchet & Warén (1980).

Gymnobela lozanoi (Vera-Peláez, 2002) is immediately separated from all its congeners by its even more strongly shouldered whorls than usual for the genus, forming an almost tabulate spire, and the coronate aspect of the shoulder carina, which is formed by 3-4 closely spaced and elevated cords. Of the extant deep-water NE Atlantic species reviewed by Bouchet & Warén (1980), the most similar is *G. chyta* (Watson, 1881), but that species is slenderer, the subsutural ramp is more inclined, the

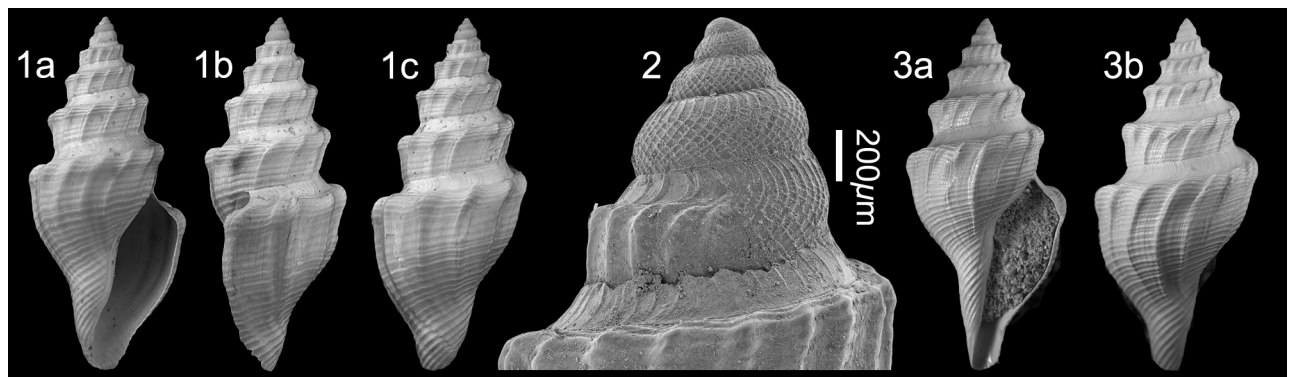


Plate 20. *Gymnobela lozanoe* (Vera-Peláez, 2002); 1. NHMW 2020/0171/0053, height 11.5 mm, width 5.2 mm (digital image); 2. NHMW 2020/0171/0054, detail of protoconch (SEM image); 3. NHMW 2020/0171/0595, height 8.3 mm, width 3.9 mm (digital image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

shoulder is weaker, the shoulder carina less elevated, and the siphonal canal is shorter.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

***Gymnobela ovum* Vera-Peláez, 2002**

Plate 21, figs 1-3

*2002 *Gymnobela ovum* Vera-Peláez, p. 229, pl. 7, figs G, H, pl. 15, figs E, F.

Material and dimensions – Maximum height 19.9 mm, width 9.1 mm. **CO:** NHMW 2020/0171/0026 (2). **VC:** NHMW 2020/0171/0022-0024 (3), NHMW 2020/0171/0025 (8). **EL:** NHMW 2020/0171/0679 (1).

Description – Shell medium sized, relatively fragile, broadly biconic, with gradate spire (apical angle 51.4–55°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl riblets over subsutural third, diagonally reticulated below (dp = 895 µm, hp = 960 µm, dp/hp = 0.93). Teleoconch of up to seven angular whorls, with broad, weakly concave subsutural ramp, angled at shoulder, straight sided to weakly concave below, separated by shallow, linear suture. Sculpture on adapical two-thirds of subsutural ramp consisting of comma-shaped axial riblets crossed by close-set spiral threads, giving finely reticulated appearance, with minute tubercles developed at intersections; on abapical third of

ramp and below shoulder, irregular, interrupted, finely beaded spiral threads. Axial sculpture only developed at shoulder, represented by small, axially elongated, opisthocline shoulder tubercles, subobsolete by penultimate whorl. Teleoconch surface covered in close-set rows of tiny micropustules. Last whorl with broad, 65–66% of total height, with weakly concave subsutural ramp, angled at shoulder, convex below, strongly constricted at base, base and fasciole not delimited; fine spiral threads of roughly alternate strength continued over base and fasciole irregularly beaded. Aperture broad, ovate, 49–51% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus broad, deep, reverse L-shaped, with apex on adapical half of ramp; siphonal canal moderate length, straight, unnotched. Columella smooth, moderately excavated in upper third, straight below, very weakly twisted at fasciole. Columellar and parietal callus not thickened, sharply delimited forming narrow callus rim.

Discussion – *Gymnobela ovum* Vera-Peláez, 2002 is the largest of its congeners in the Estepona assemblages. It is most like *Gymnobela pelagia* Vera-Peláez, 2002, with which it co-occurs, but differs in being more broadly fusiform, the shoulder is angled, but is not delimited by a thickened cord as it is in *G. pelagia*, the axial sculpture is weaker, the anal canal shallower and the siphonal canal shorter. The teleoconch microsculpture consists of rows of tiny micropustules, whereas in *G. pelagia* they are irregularly placed.

Several of the northwestern Atlantic extant species discussed by Bouchet & Warén, (1980) are similar. *Gymnobela homoeotata* (Watson, 1886) is the most similar in

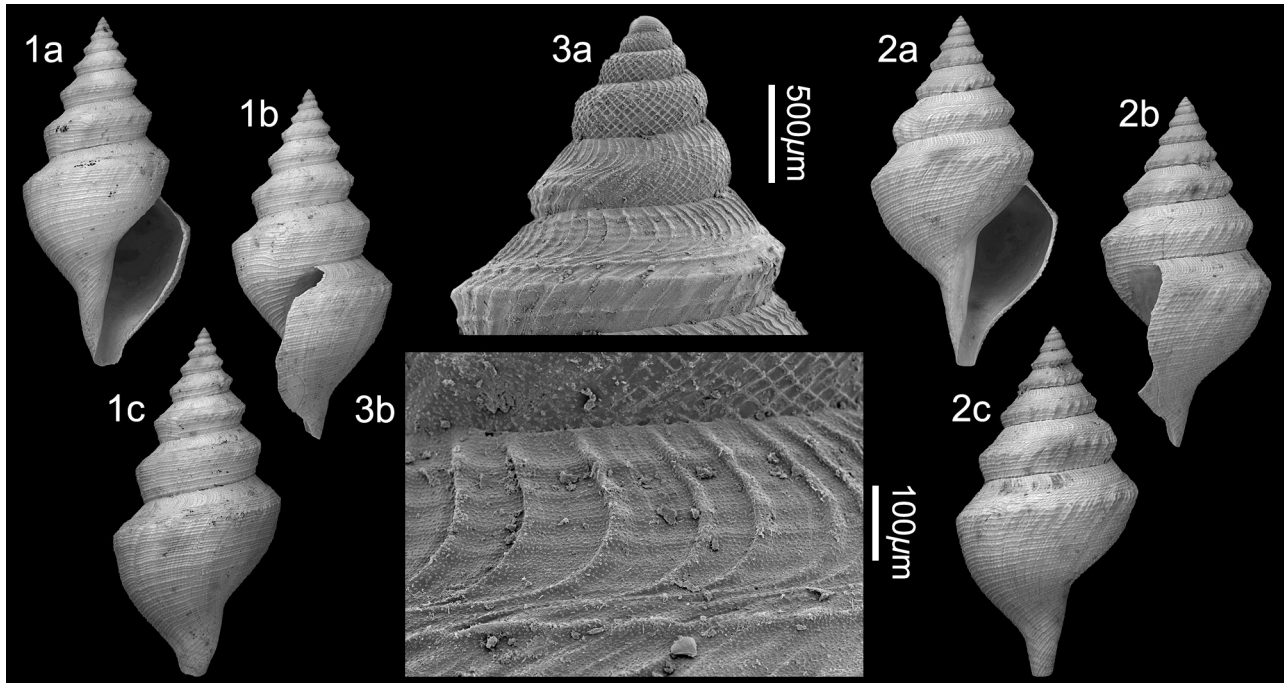


Plate 21. *Gymnobela ovum* Vera-Peláez, 2002; 1. NHMW 2020/0171/0022, height 19.9 mm, width 9.1 mm; 2. NHMW 2020/0171/0023, height 14.9 mm, width 7.6 mm; 3. NHMW 2020/0171/0024, 3a, detail of protoconch, 3b, detail of teleoconch microsculpture (1-2, digital images, 3, SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

profile and sculpture but differs in having stronger ribs that persist onto the last whorl, and broader spiral cords that are not finely beaded. *Gymnobela frielei* (Verrill, 1885) also has stronger ribs, like those of *G. homoeotata*, but differs in having a shorter siphonal canal.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

Gymnobela salinasi (Calcara, 1841)

Plate 22, figs 1-2

- *1841 *Pleurotoma Salinasi* Calcara, p. 53, pl. 2, fig. 5.
- 1842 *Pleurotoma lanciae* Testa, p. 2.
- 1872 *Pleurotoma (Defrancia) caveola* Mayer, p. 234, pl. 14, fig. 8.
- 1877 *Daphnella Salinasi* (Calc.) – Bellardi, p. 284, pl. 8, fig. 32.
- 1904 *Daphnella Salinasi* var. *pliocostulatissima* Sacco, p. 53, pl. 14, fig. 1.
- 1914 *Daphnella Salinasi* Calcara – Cipolla, p. 150 [46], pl. 13 [2], fig. 21.
- 1992 *Rimosodaphnella salinasi* (Calcara, 1841) – Cavallo & Repetto, p. 138, fig. 372.
- 1996 *Rimosodaphnella salinasii* [sic] (Calcara, 1841) – Vera-Peláez, p. 621, text-figs 32c, d, 35b, 58, pl. 46, figs 1, 2, 5, 7, 9, 11.
- 2002 *Rimosodaphnella salinasii* [sic] (Calcara, 1841) – Vera-Peláez, p. 215; pl. 5, figs I, J, pl. 16, figs A, B, C.
- 2010 *Daphnella salinasi* (Calcara, 1841) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 63, bottom row centre.
- 2018 *Daphnella salinasi* (Calcara, 1841) – Brunetti & Cresti, p. 100, fig. 415.

?non 1958 *Daphnella* aff. *salinasi pliocostulatissima* Sacco – Hölzl, p. 277, pl. 22, fig. 7.

Material and dimensions – Maximum height 13.6 mm, width 5.6 mm. **CO:** NHMW 2020/0171/0049 (1). **VC:** NHMW 2020/0171/0050-51 (2), NHMW 2020/0171/0052 (8).

Description – Shell medium sized, fragile, broadly turritiform, with gradate spire (apical angle 56.5°). Protoconch tall, conical multispiral, of 3.75 convex whorls, with small nucleus; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl riblets over subsutural third, diagonally reticulated below (Estepona specimen; dp = 300 μm, hp = 345 μm, dp/hp = 0.87, dV1 = 200 μm, dn = 140 μm). Teleoconch of up to four sharply shouldered whorls, with broad, weakly concave subsutural ramp, sharply angled at shoulder cord, convex below, separated by narrowly impressed, linear suture. Spiral sculpture predominant, composed of one weak thread towards periphery of subsutural ramp, and two narrow, elevated primary cords; adapical delimiting shoulder, abapical cord placed mid-height between shoulder and suture, delimiting periphery; very fine threads of secondary and tertiary strength intercalated. Axial sculpture of comma-shaped riblets over subsutural ramp, extremely fine opisthocline axial ribs below shoulder, 18-20 on penultimate whorl, giving surface wide reticulated pattern, with tiny tubercles developed at intersections. Last whorl tall and broad, about 76% of total height; broad, weakly concave subsutural ramp, sharply shouldered, convex below, moderately strongly constricted at base, bearing three elevated carinate primary cords mid-whorl, 6 further cords over base, becoming closer spaced abapically, 9-10 slightly stronger cords over fasciole; base and fasciole poorly delimited. Aperture wide, ovate, 56 % of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus broad, deep, reverse L-shaped, with apex on adapical half of ramp; siphonal canal moderate length, hardly twisted, unnotched. Columella smooth, moderately excavated in upper third, straight below, hardly twisted at fasciole. Columellar and parietal callus hardly developed forming very narrow rim of callus wash.

Discussion – *Gymnobela salinasi* (Calcara, 1841) is a highly characteristic species, immediately separated from *G. romani* (Libassi, 1859) by having a strongly gradate spire and three carinate primary cords on the last whorl. Like *G. romani*, it was widely distributed in the Mediterranean and adjacent Atlantic Pliocene, but al-

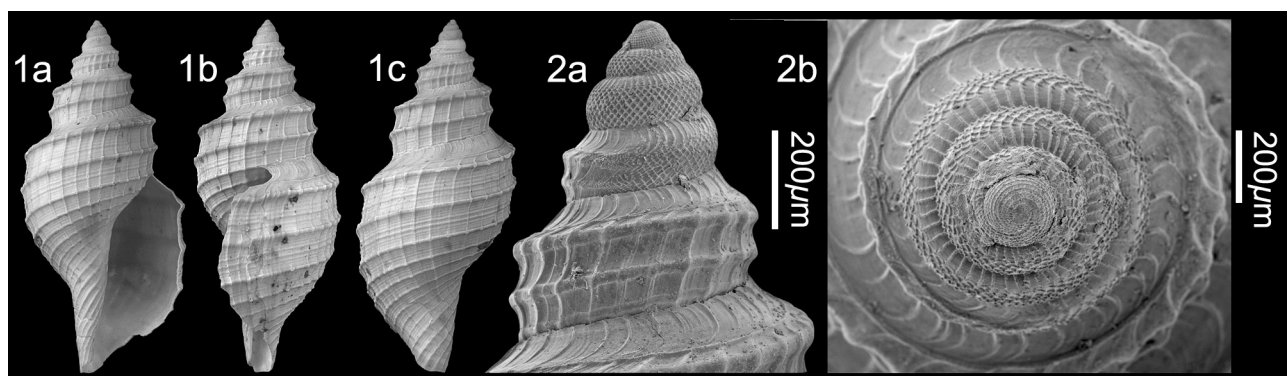


Plate 22. *Gymnobela salinasi* (Calcara, 1841); 1. NHMW 2020/0171/0050, height 10.1 mm, width 4.7 mm (digital image); 2. NHMW 2020/0171/0051, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ways uncommon. It is most like the coarsely sculptured form of *G. subaraneosa* (Dautzenberg & Fischer, 1896), a deep-water species from the NE Atlantic and Mediterranean (see Bouchet & Warén, 1980, fig. 114), but the cancellation is finer in that species.

The record of *Daphnella* aff. *salinasi pliocostulatissima* Sacco of Hölzl (1958, p. 277, pl. 22, fig. 7) from the Lower Miocene Burdigalian Kaltenbach-Graben of Austria is based on a single small specimen. The illustration is too poor to make identification reliable, and it is excluded from the synonymy.

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Gili & Martinell, 1994); central Mediterranean, Italy (Bellardi, 1877; Cavallo & Repetto, 1992; Sosso & Dell’Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002); central Mediterranean, Italy (Mayer, 1872; Cipolla, 1914).

Gymnobela sphaera (Vera-Peláez, 2002)

Plate 23, fig. 1

*2002 *Pleurotomella* (*Pleurotomella*) *sphaera* Vera-Peláez, p. 226, pl. 6, figs P, O (*lapsus*; P, Q stated in text, in figure is P, O), pl. 17, figs Z, A’.

Material and dimensions – Holotype VL/G672.001.001 (MMPE coll.), height 11.0 mm, width 6.0 mm, Velerín carretera. Known only from holotype.

Description – Shell medium sized, fragile, broadly ovate, with conical gradate spire (apical angle 56.3°). Protoconch conical, multispiral, of three convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture. Teleoconch of up to 5.5 convex whorls, with narrow subsutural ramp, rounded at poorly delimited shoulder, convex below, separated by strongly oblique, narrowly impressed, linear suture delimiting periphery. Axial sculpture predominant; comma-shaped growth lines over subsutural ramp, low, narrow orthocone ribs below shoulder, 18 on first whorl, increasing in number abapically to 30 on last whorl, about one-third width of their interspaces. Spiral sculpture of narrow cords overrunning ribs, forming small, rounded tubercles at the intersections, with single secondary intercalated from the penultimate whorl. Last whorl strongly inflated, about 71% of total height; relatively narrow, weakly concave subsutural ramp, hardly shouldered, regularly convex below, moderately constricted at base; axials continue over base ending at fasciole, fasciole bearing about six stronger cords; base not delimited, fasciole moderately delimited. Aperture very wide, ovate, 55% of total height; outer lip very thin (edge incomplete), smooth within; anal sinus broad, deep, inverted L-shaped; siphonal canal incomplete. Columella smooth, moderately excavated in upper half, straight below, weakly twisted at fasciole. Columellar and parietal callus forming narrow rim of callus rim (adapted from

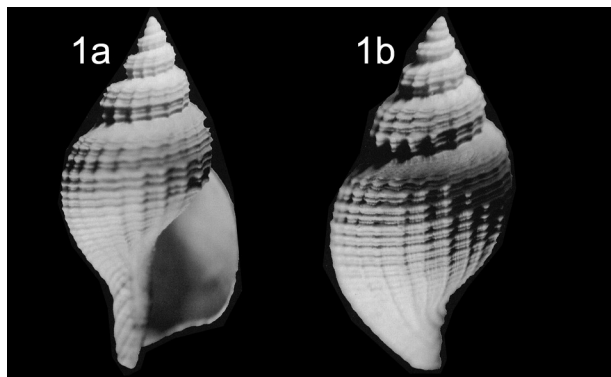


Plate 23. *Gymnobela sphaera* (Vera-Peláez, 2002); 1. **Holotype** VL/G672.001.001 (MMPE coll.), height 11.0 mm, width 6.0 mm (specimen figured by Vera-Peláez, 2002, pl. 6, figs P, O). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

original description and illustration; Vera-Peláez, 2002, p. 226, pl. 6, figs P, O, pl. 17, figs Z, A’).

Discussion – *Gymnobela sphaera* (Vera-Peláez, 2002) was based on a single specimen from the deeper water assemblage at Velerín carretera. It does indeed seem different enough from all other turrids to warrant description. Unfortunately, it also seems exceedingly uncommon, as no further specimens have been found in the material at hand. It was originally placed in the genus *Pleurotomella* Verrill, 1872, but the rather broad shell, inflated last whorl, reverse L-shaped anal sinus, and probably relatively short siphonal canal (if the outer lip where complete) make placement in the genus *Gymnobela* Verrill, 1884 (*sensu* Bouchet & Warén, 1980, p. 48) more likely. Several of the extant NE Atlantic deep-water species reviewed by Bouchet & Warén (1980) have strongly inflated shells, of which the most similar are *G. lamyi* (Dautzenberg, 1925), but that species has more numerous axial ribs resulting in a more finely reticulated sculpture, and *G. leptoglypta* (Dautzenberg & Fischer, 1896), which is very similar in sculpture to *G. lamyi*, with a finer reticulated sculpture than *G. sphaera*, but differs from both in having a clearly delimited subsutural ramp and angled shoulder.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

Genus *Leufroyia* Monterosato, 1884

Type species – *Pleurotoma leufroyi* Michaud, 1828, by subsequent designation, Crosse, 1885, present-day, Mediterranean.

1884 *Leufroyia* Monterosato, p. 134.

Note – Fassio *et al.* (2019) characterised species within the genus *Leufroyia* Monterosato, 1884 as being suboval

to fusiform, medium to large for the family, with a slender spire composed of regularly convex whorls, undulating axial ribs and numerous finer, low spiral cords, microsculpture of growth lines, but no pustules, a smooth outer lip devoid of denticles and short to long siphonal canal. In their generic description they characterise the protoconch as multispiral, although in this work we include paucispiral species.

Leufroyia concinna (Scacchi, 1836)

Plate 24, fig. 1

- *1836 *Pleurotoma concinna* Scacchi, p. 12, fig. 18.
- 1839 *Fusus Boothii* J. Smith, p. 50, pl. 1, fig. 1.
- 1867 *Defrancia leufroyi* var. *carosula* Jeffreys, p. 367.
- 1877 *Homotoma Michaudi* Bellardi, p. 276.
- 1877 *Pleurotoma (Defrancia) concinna* Scacchi – Monterosato 1877, p. 43, pl. 5, fig. 1
- 1878 *Pleurotoma linearis* var. *major-violacea* Monterosato, p. 106.
- 1883 *Clathurella concinna* Scacchi – Bucquoy *et al.*, p. 98, pl. 14, fig. 5.
- 1904 *Peratotoma? (Leufroyia) Michaudi* (Bell.) Sacco, p. 53, pl. 13, figs 55, 56.
- 1905 *Clathurella (Cyrillia) linearis concinna* Scacchi – Kobelt, p. 368, pl. 96, figs 6, 7.
- 1910 *Peratotoma (Leufroyia) concinna* Scacchi – Cerulli-Irelli, 60 [252], pl. 5[36], fig. 47.
- 1914 *Peratotoma (Leufroyia) concinna* Scacchi – Cipolla, 175 [71], pl. 14 [3], figs. 25, 26.
- 1915 *Clathurella concinna* (Scacchi) – Harmer, p. 236, pl. 28, figs 22, 23.
- 1968 *Raphitoma (Cirillia [sic]) concinna* (Scacchi, 1836) – Nordsieck, p. 178, pl. 30, fig. 94.62.
- 1977 *Raphitoma (Leufroyia) concinna* (Scacchi, 1836) – Nordsieck, p. 60, pl. 20, fig. 159.
- 1979 *Raphitoma (Leufroyia) scacchii* De Casa & Hallgass, p. 6, pl. 1 [*non R. scacchii* Bellardi, 1847].
- 1974 *Philbertia leufroyi* (Scacchi, 1836) – Hubendick & Warén, p. 28, fig. 222 [*non Leufroyia leufroyi* (Michaud, 1828)].
- 1979 *Lineotoma concinna* form *maderensis* Nordsieck

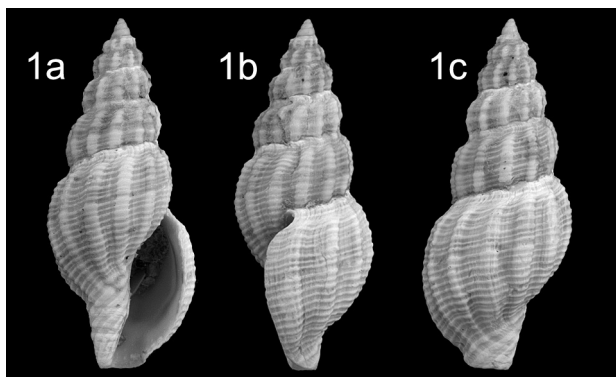


Plate 24. *Leufroyia concinna* (Scacchi, 1836); 1. NHMW 2020/0171/0562, height 8.8 mm, width 3.3 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

& García-Talavera, p. 166, pl. 41, fig. 34.

- 1980 *Raphitoma concinna* (Scacchi, 1836) – Bogi *et al.*, p. 14, fig. 1.
- 1984 *Raphitoma leufroyi* (Michaud, 1828) – Fretter & Graham, p. 538, fig. 371 [*non Leufroyia leufroyi* (Michaud, 1828)].
- 1988 *Raphitoma leufroyi* (Michaud, 1828) – Graham, p. 460, fig. 193 [*non Leufroyia leufroyi* (Michaud, 1828)].
- 1997 *Raphitoma michaudi* (Bellardi, 1877) – Chirli, p. 84, pl. 24, figs 1-4.
- 2001 *Raphitoma concinna* (Scacchi, 1836) – Cachia *et al.*, p. 64, pl. 9, fig. 10.
- 2005 *Raphitoma concinna* (Scacchi, 1836) – Repetto *et al.*, p. 39, 216, fig. 888.
- 2011 *Raphitoma michaudi* (Bellardi, 1877) – Chirli & Linse, p. 174, pl. 61, fig. 2.
- 2016 *Raphitoma (Leufroyia) concinna* (Scacchi, 1836) – Høisaeter, p. 25, figs 2F, 3D, 21-23.
- 2018 *Raphitoma leufroyi* (Michaud, 1828) – Wigham & Graham, p. 137, fig. 161 [*non Leufroyia leufroyi* (Michaud, 1828)].
- 2020 *Leufroyia concinna* (Scacchi, 1836) – Giannuzzi-Savelli *et al.*, p. 446, figs 9-13.

Material and dimensions – Height 8.8 mm, width 3.3 mm. **EL:** NHMW 2020/0171/0562 (1).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2020, p. 453).

Discussion – *Leufroyia concinna* (Scacchi, 1836) has often been misidentified as *L. leufroyi* (Michaud, 1828), but can be separated from this and all other extant European *Leufroyia* species by the constant presence of pinkish or purple areas on parts of the shell and the numerous brown spiral cords on all whorls. This is preserved in the illustrated specimen from Estepona (Pl. 24, fig. 1). In the absence of any colour preservation the two are difficult, if not impossible, to distinguish based solely on shell characters.

Leufroyia pseudoconcinna (Ceulemans, Van Dingenen & Landau, 2018) from the lower Pliocene of northwestern France has an almost identical teleoconch but is immediately separated by its paucispiral protoconch.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Tropeano *et al.*, 1984; Tabanelli & Segurini 1995; Chirli, 1997). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1915); western Mediterranean, Estepona Basin, southern Spain (this paper); central Mediterranean, Italy (Cipolla, 1914). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic Norway (Hubendick & Warén, 1974; Høisaeter, 2016), British Isles (Fretter & Graham, 1984; Wigham & Graham, 2018), Madeira (Nordsieck & García-Talavera, 1979), Canary Islands (Giannuzzi-Savelli *et al.*, 2020), entire Mediterranean (Bucquoy *et al.*, 1883; Giannuzzi-Savelli *et al.*, 2020; Cachia *et al.*, 2001).

***Leufroyia desmoulinsi* (Bellardi, 1847)**

Plate 25, figs 1-3

- *1847 *Raphitoma Desmoulinsi* Bellardi, p. 91, pl. 4, fig. 16.
 1877 *Homotoma Desmoulinsi* Bell. – Bellardi, p. 278, pl. 8, fig. 26.
 1914 *Daphnella (Bellardiella) Desmoulinsi* Bell. – Cipolla, 156 [52], pl. 14 [3], fig. 3.
 1981 *Homotoma desmoulinsi* (Bellardi, 1847) – Ferrero Mortara *et al.*, p. 89, pl. 18, fig. 2.
 non 1997 *Raphitoma desmoulinsi* Bellardi, 1847 – Chirli, p. 74, pl. 21, figs 8-10 (= *Belidaphne* sp.).
 non 2002 *Belidaphne desmoulinsi* [sic] (Bellardi, 1847) – Vera-Peláez, p. 222, pl. 6, fig C, D (= ?*Pleurotomoides* sp.).

Material and dimensions – Maximum height 14.5 mm, width 5.5 mm. CO: NHMW 2020/0171/0377-0379 (3), NHMW 2020/0171/0380 (1).

Description – Shell medium sized, moderately broadly fusiform, solid, with cyrtocooid spire (apical angle 42.4-51°). Protoconch (incomplete), small, conical multispiral, 2.5 convex whorls preserved with fine, diagonally reticulated sculpture, last whorl keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of 5.5 whorls, separated by narrowly impressed, linear suture. First three teleoconch whorls with moderately broad, steep, weakly concave, sub-sutural ramp, poorly delimited by low rounded shoulder; opisthocline axial ribs developed below shoulder, 9-10 on second whorl, broadening towards suture, overrun by narrow spirals, three on first whorl, secondaries developed in interspaces from second whorl rapidly strengthening and equal to primaries on third whorl. On second half of third whorl axials broaden and weaken, so that last two whorls are evenly convex and devoid of axial sculpture. Close-set axial growth lines strengthening abapically, weakly beading spirals. Last whorl 65-68% total height, weakly inflated, with narrow, subsutural ramp not delimited, marked by slight

concavity to profile below suture, whorl evenly convex below, weakly constricted at base; narrow, subequal spirals over entire whorl; siphonal fasciole indistinct, weakly rounded, bearing coarser spirals. Aperture 44-46% total height, ovate; outer lip thin, slightly thickened by labial varix, sharp edged, smooth within; anal sinus moderate width, asymmetrically U-shaped, with apex placed on adapical third of ramp; siphonal canal short, broad, unnotched. Columella smooth, broadly and weakly excavated. Columellar and parietal callus slightly thickened, sharply delimited, forming narrow indented callus edge.

Discussion – Chirli (1997) misinterpreted Bellardi's species and illustrated a mangeliid species as *R. desmoulinsi*. Vera-Peláez (2002) recognised Chirli's shell to belong in his new genus *Belidaphne* and illustrated a shell from Estepona similar to Chirli's under the trivial name *B. desmoulinsi* [sic]. A syntype of Bellardi's species from Villavernia was illustrated by Ferrero Mortara *et al.* (1981, pl. 18, fig. 2) and clearly represents a raphitomid and, although incomplete, the protoconch bears the typical finely diagonally reticulated post-nuclear microsculpture seen in the family. Unlike *Leufroyia desmoulinsi* that is a raphitomid, *Raphitoma semicostata* Bellardi, 1847 (for syntype see Ferrero Mortara *et al.*, 1981, pl. 18, fig. 7) is a mangeliid and therefore the genus *Belidaphne* is available and will be reviewed later in this series.

The specimens from Estepona are closely similar to the syntype and the specimen illustrated by Cipolla (1914, pl. 14 [3], fig. 3) from the Upper Pliocene of Italy, although there are slightly fewer axial ribs on the early teleoconch whorls (9-10, vs 12-13, *vide* Cipolla, 1914), and the axial sculpture becomes obsolete slightly earlier, so that the last two whorls lack ribs as opposed to the last 1.5 whorls. These small differences are considered to fit within intraspecific variability.

Leufroyia stria (Calcare, 1839), with which it co-occurs in the Estepona deposits, is most similar to *L. desmoulinsi* in that they both lack axial sculpture on the late whorls, but *L. stria* differs in having a taller, gradate spire with more convex whorls, the subsutural ramp more clearly

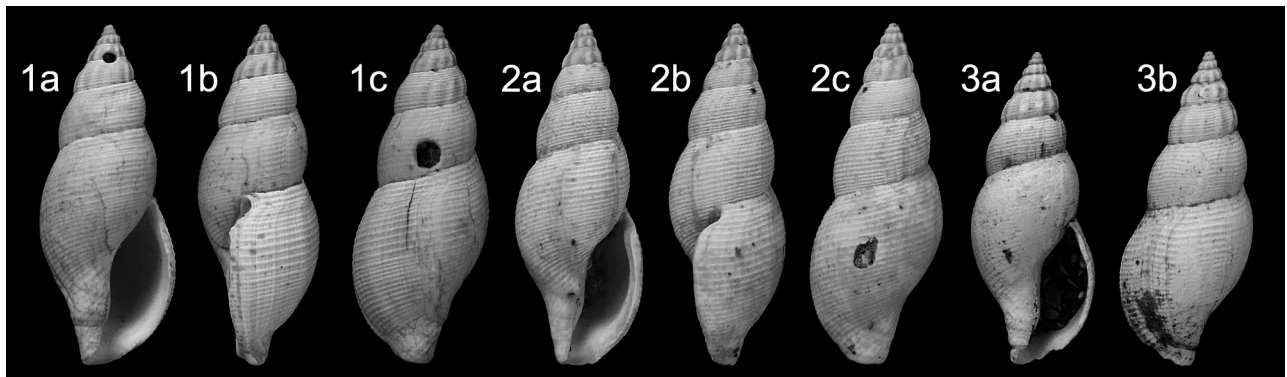


Plate 25. *Leufroyia desmoulinsi* (Bellardi, 1847); 1. NHMW 2020/0171/0377, height 12.6 mm, width 5.0 mm; 2. NHMW 2020/0171/0378, height 14.5 mm, width 5.5 mm; 3. NHMW 2020/0171/0379, height 12.0 mm, width 4.6 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

delimited, irregular spiral sculpture, the last whorl far more inflated, the base more constricted, and a longer siphonal canal.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Bellardi, 1847, 1877). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper); central Mediterranean, Italy (Bellardi, 1877; Cipolla, 1914).

***Leufroyia erronea* Monterosato, 1884**

Plate 26, fig. 1

- 1872 *Defrancia leufroyi* var. *coralligena* Monterosato, p. 51 (*nomen nudum*).
- *1884 *Leufroyia erronea* Monterosato, p. 134.
- 1997 *Comarmondia inflata* (De Cristofori & Jan, 1832) – Chirli, p. 91, pl. 26, figs 5, 6 [*non Leufroyia inflata* (De Cristofori & Jan, 1832)].
- 2008 *Raphitoma erronea* (Monterosato, 1884) – Pusateri & Giannuzzi-Savelli, p. 124, fig. 15.
- 2018 *Raphitoma erronea* (Monterosato, 1884) – Appolloni *et al.*, p. 60, figs 22M, N.
- 2018 *Raphitoma erronea* (Monterosato, 1884) – Manousis *et al.*, p. 21, figs 11A-E.
- 2020 *Leufroyia erronea* Monterosato, 1884 – Giannuzzi-Savelli *et al.*, p. 454, figs 14-16.
- 2022 *Leufroyia erronea* Monterosato, 1884 – J.D. Oliver *et al.*, p. 426, figs 38A-F, 43H.
- non 2001 *Raphitoma* cf. *erronea* (Monterosato, 1884) – Cachia *et al.*, p. 66, pl. 10, fig. 3 [= *Leufroyia villaria* (Pusateri & Giannuzzi-Savelli, 2008)].
- non 2003 *Raphitoma* (*Leufroyia*) *erronea* (Monterosato, 1884) – Mifsud, p. 44, fig. 15 [= *Leufroyia villaria* (Pusateri & Giannuzzi-Savelli, 2008)].

Material and dimensions – Height 8.2 mm, width 3.4 mm. CO: NHMW 2020/0171/0360 (1).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2020, p. 457).

Discussion – *Leufroyia erronea* Monterosato, 1884 differs from all other *Leufroyia* species in its subovate profile, wide aperture, very short siphonal canal and the stronger and more closely spaced spiral cords. It differs from *L. concinna* (Scacchi, 1836) in lacking the brown coloured bands and pinkish/purple areas, and in its larger protoconch. From *L. leufroyi* (Michaud, 1828) it differs in lacking the dark brown or blackish blotches and in its larger protoconch, which is never darkly coloured. *Leufroyia villaria* (Pusateri & Giannuzzi-Savelli, 2008) has a slenderer shell, more gradate whorls and thinner spiral cords (Giannuzzi-Savelli *et al.*, 2020, p. 458).

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1997). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

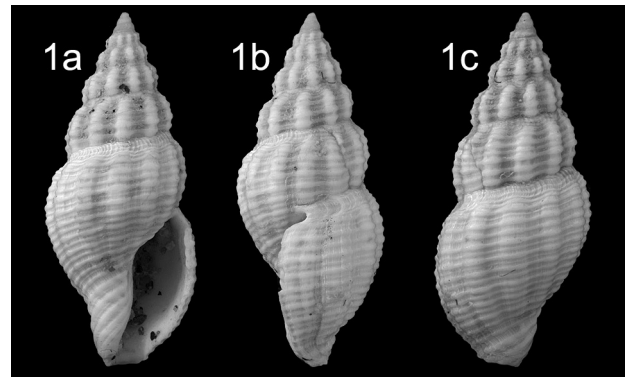


Plate 26. *Leufroyia erronea* Monterosato, 1884; 1. NHMW 2020/0171/0360, height 8.2 mm, width 3.4 mm (digital image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Present-day: Northeast Atlantic from Great Britain to Portugal (Giannuzzi-Savelli *et al.*, 2020; J.D. Oliver *et al.*, 2022), central Mediterranean (Appolloni *et al.*, 2018; Giannuzzi-Savelli *et al.*, 2020), eastern Mediterranean (Manousis *et al.*, 2018).

***Leufroyia gradata* nov. sp.**

Plate 27, fig. 1

Type material – Holotype NHMW 2020/0171/0596, height 11.2 mm, width 4.3 mm.

Other material – Known from holotype only.

Type locality – Velerín sands, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian, Upper Pliocene.

Etymology – Latin ‘gradatus, -a, -um’, adjective meaning furnished with steps, referring to the strongly stepped spire. *Leufroyia* gender feminine.

Diagnosis – *Leufroyia* species of medium size, thin shelled, with strongly gradate spire, multispiral protoconch with diagonally reticulated microsculpture, spire whorls tabulate, sculpture of nine narrow axial ribs over-run by narrow spirals of primary to tertiary strength; three primary cords on penultimate whorl.

Description – Shell medium sized, thin, moderately broadly turreted, with tall gradate spire (apical angle 43.5°). Protoconch tall, conical multispiral, of about 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture (poorly preserved), last whorl weakly keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of five tall tabulate whorls, with weakly inclined, moderate-width, smooth, concave subsutural ramp, sharply angled at shoulder, weakly convex below, separated by superficial

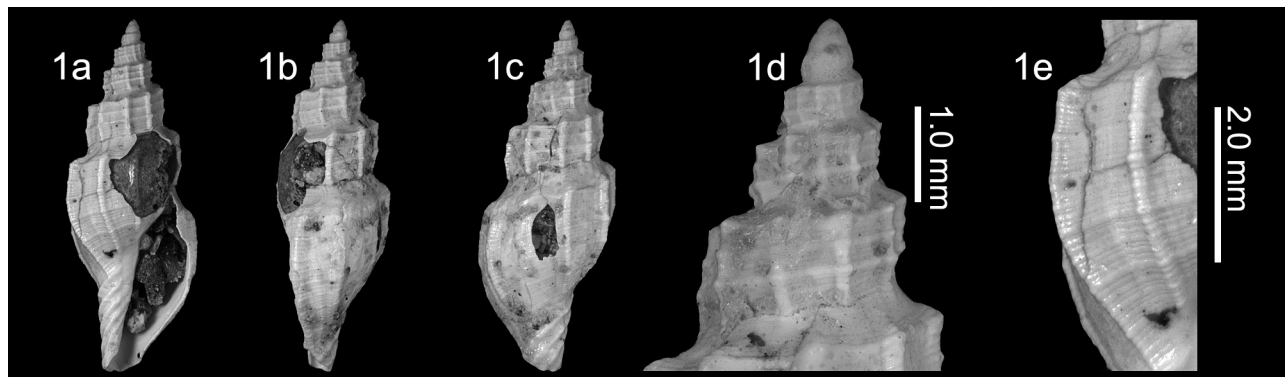


Plate 27. *Leufroyia gradata* nov. sp.; 1. **Holotype** NHMW 2020/0171/0596, height 11.2 mm, width 4.3 mm (digital image). Velerín sands, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

undulating suture. Axial sculpture of narrow, elevated, weakly prosocline ribs, nine on last whorl, much narrower their interspaces. Spiral sculpture overruns ribs without forming spines or tubercles, three primary cords on first teleoconch whorl, secondaries intercalated in interspaces on second whorl, tertiaries on penultimate whorl. Last whorl 67% of total height, subsutural ramp strongly concave, sharply angled at shoulder, weakly convex below, moderately constricted at base; axials persist over base, ending at siphonal fasciole, fasciole sharply delimited, bearing six smooth cords. Aperture elongate-ovate, 50% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus moderate width and depth, asymmetrically U-shaped, with apex just above mid-ramp; siphonal canal long, narrow, straight, unnotched. Columella smooth, moderately excavated in upper third, straight below, hardly twisted at fasciole. Columellar and parietal callus poorly delimited, hardly thickened, forming narrow irregular callus rim.

Discussion – *Leufroyia gradata* nov. sp. is a very characteristic species, with its slender gradate profile, tabulate whorls, very thin and widely spaced axial ribs and broadly cancellate sculpture, with crowded spirals of primary to tertiary strength without spines or tubercles developed at the intersections. It has no closely similar congeners living in the NE Atlantic or Mediterranean today. The only Pliocene Mediterranean species that can be compared is *Leufroyia volutella* (Kiener, 1839) (see Giannuzzi-Savelli *et al.*, 2020, figs 21D, E), which is also elongated and has narrow axial ribs, but that species is immediately separated by its rounded, non-tabulate whorls. Moreover, the ribs are more strongly opisthocline, and the spirals are of equal strength and not strongly separated into primary to tertiary strength as in *L. gradata*. We find no other European Neogene species with which we can usefully compare this new taxon.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Leufroyia inflata (De Cristofori & Jan, 1832)

Plate 28, figs 1-2

- *1832 *Pleurotoma inflata* De Cristofori & Jan, p. 9.
- 1877 *Homotoma inflata* (Jan) – Bellardi, p. 276.
- 1910 *Daphnella* (*Bellardiella*) *inflata* Jan – Cerulli-Irelli, p. 63 [254], pl. 6 [37], figs 1-4.
- 1971 *Cythara* (*Atoma*) *inflata* (De Cr. e Jan, 1832) – Pinna, p. 430, pl. 77, fig. 16.
- 1974 *Philbertia inflata* (Jan, 1832) – Malatesta, p. 435, pl. 31, fig. 10.
- 1978 *Pleurotoma inflata* de Cristofori & Jan, 1832 – Pinna & Spezia, p. 158, pl. 40, fig. 1.
- 2010 *Leufroya* [*sic*] *inflata* (De Cristofori & Jan, 1832) – Sosso & Dell’Angelo, p. 47, p. 63 unnumbered fig. middle row centre.
- 2011 *Comarmondia inflata* (Cristofori & Jan, 1832) – Landau *et al.*, p. 35, pl. 18, fig. 4.
- 2011 *Clathurella inflata* (De Cristofori & Jan, 1832) – Chirli & Linse, p. 168, pl. 58, fig. 1.
- 2020 *Pleurotoma inflata* De Cristofori & Jan, 1832 – Giannuzzi-Savelli *et al.*, p. 464, figs 21A-C.
- non 1836 *Pleurotoma inflata* De Cr. et Jan – Philippi, p. 197, pl. 11, fig. 24 [= *Leufroyia leufroyi* (Michaud, 1828)].
- non 1873 *Raphitoma inflata* De Cr. et Jan – Cocconi p. 63, pl. 1, figs 15, 16 [= *Leufroyia volutella* (Kiener, 1839)].
- non 1904 *Peratotoma* (*Leufroyia*) *inflata* Jan – Sacco, p. 53, pl. 13, fig. 54 [= *Leufroyia volutella* (Kiener, 1839)].
- non 1914 *Peratotoma* (*Leufroyia*) *inflata* Jan – Cipolla, p. 176 [72], pl. 14 [3], fig. 27 [= *Leufroyia villaria* (Pusateri & Giannuzzi-Savelli, 2008)].
- non 1997 *Comarmondia inflata* (De Cristofori & Jan, 1832) – Chirli, p. 91, pl. 26, figs 5, 6 [= *Leufroyia erronea* Monterosato, 1884].

Material and dimensions – Maximum height 14.1 mm, width 6.3 mm **VC**: NHMW 2020/0171/0424 (1). **EL**: NHMW 2020/0171/0425 (1).

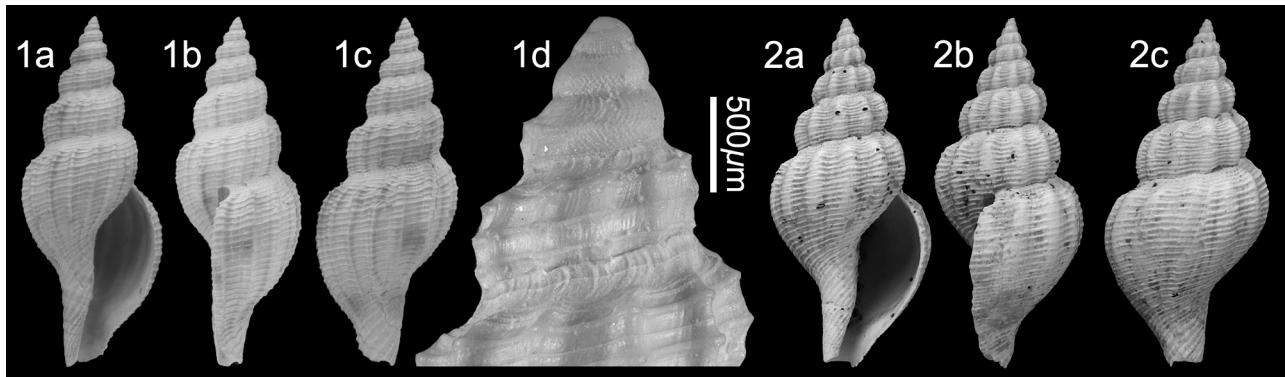


Plate 28. *Leufroyia inflata* (De Cristofori & Jan, 1832); 1. NHMW 2020/0171/0424, height 17.1 mm, width 6.9 mm, 1d, detail of protoconch. Velerín carretera, Velerín. 2. NHMW 2020/0171/0425, height 14.1 mm, width 6.3 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell medium sized, solid, broadly ovato-pupoid, with tall conical spire (apical angle 43.5°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine squarely reticulated sculpture, diagonal on protoconch II, last whorl moderately keeled, with riblets over subsutural ramp, diagonally reticulated below keel. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to six convex, weakly shouldered whorls, with relatively wide, weakly inclined and weakly concave subsutural ramp, shoulder rounded, poorly delimited, convex below, separated by superficial undulating suture. Axial sculpture of narrow, elevated, weakly opisthocline ribs, 15 on last whorl, less than half width of their interspaces, weaker over subsutural ramp. Close-set, comma-shaped axial riblets over subsutural ramp. Spiral sculpture of fine cords, about seven primaries on penultimate whorl forming rectangular reticulated sculpture, with 3-4 weaker cords over subsutural ramp; primaries overrun axials forming small tubercles; secondary spiral threads of variable strength intercalated and in variable number of interspaces from penultimate whorl. Last whorl inflated, 67% of total height, with narrow, weakly concave subsutural ramp, broadly convex below, strongly constricted at base; axials weaken over base, spirals of alternate strength, 12-14 slightly stronger cords over siphonal fasciole; base indistinct, fasciole relatively well delimited. Aperture ovate, 50% of total height; outer lip thin, hardly thickened by varix, smooth within; anal sinus narrow, shallow, asymmetrically U-shaped, with apex on adapical half of ramp; siphonal canal long, bent slightly adaxially, shallowly notched. Columella smooth, moderately excavated just above mid-height, weakly twisted at fasciole. Columellar and parietal callus not developed.

Discussion – This species is rather variable in the inflation of the last whorl and the strength of the axial sculpture. The lectotype figured by Pinna & Spezia (1978, pl. 40, fig. 1) is similar in width to the specimens from Estepona (Pl. 28, fig. 1), but has stronger axial sculpture. Cerulli-Irelli (1910, p. 63 [255]) considered *Pleurotoma inflata* De Cristofori & Jan, 1832 and *P. volutella* distinct

species, whereas Cipolla (1914, p. 73) considered them to represent a single variable species. Giannuzzi-Savelli *et al.* (2020, p. 466) again considered them different species. *Pleurotoma inflata* has lower, wider axial ribs that are orthocline or slightly prosocline as opposed to distinctly opisthocline in *P. volutella*, and it has more prominent and more numerous spiral cords.

Leufroyia erronea Monterosato, 1884 differs in having a suboval profile, wider aperture, and much shorter siphonal canal. The extant West African and Mediterranean *L. villaria* (Pusateri & Giannuzzi-Savelli, 2008) differs from *L. inflata* in having a less arched spire, narrower, weaker, opisthocline as opposed to orthocline or slightly prosocline ribs, narrower and less dense spiral cords separated by wider interspaces, more ovate aperture, and shorter siphonal canal.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Pinna, 1971; Sosso & Dell'Angelo, 2010; Giannuzzi-Savelli *et al.*, 2020). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper); central Mediterranean, Italy (Cipolla, 1914; Malatesta, 1974). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Giannuzzi-Savelli *et al.*, 2020); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

***Leufroyia leufroyi* (Michaud, 1828)**

Plate 29, figs 1-3

- *1828 *Pleurotoma Leufroyi* Michaud, p. 121, pl. 1, figs 5, 6.
- 1831 *Murex zonalis* Delle Chiaje, pl. 84, fig. 1, 7.
- 1836 *Pleurotoma inflata* De Cr. et Jan – Philippi, p. 197, pl. 11, fig. 24 [*non Leufroyia inflata* (De Cristofori & Jan, 1832)].
- 1844 *Pleurotoma Cyrilli* O.G. Costa, p. 54.
- 1847 *Murex caudicula* ex Chiereghini ms. Nardo, p. 59, figs 723, 724.

- 1883 *Clathurella leufroyi* var. *albida* Bucquoy, Dautzenberg & Dollfus, p. 96.
- 1883 *Clathurella leufroyi* Michaud – Bucquoy *et al.*, p. 95, pl. 14, figs 3, 4.
- 1891 *Clathurella leufroyi* Michaud – Locard, p. 68, fig. 54.
- 1891 *Clathurella mirabilis* Locard, p. 69.
- 1904 *Peratotoma (Leufroya [sic]) leufroyi* (Michd.) – Sacco, p. 53, pl. 13, figs 52, 53.
- 1910 *Peratotoma (Leufroyia) leufroyi* Michaud – Cerrulli-Irelli, p. 59 [251], pl. 5 [36], fig. 46.
- 1914 *Peratotoma (Leufroyia) leufroyi* Michaud – Cippolla, p. 174 [70], pl. 14 [3], fig. 24.
- 1931 *Clathurella leufroyi* (Michaud) – Nobre, p. 52, pl. 32, fig. 4.
- 1943 *Raphitoma (Leufroyia) leufroyi* – Wenz, p. 1453, fig. 4114.
- 1968 *Raphitoma (Leufroyia) leufroyi* (Michaud) – Nordsieck, p. 179, pl. 30, fig. 94.70.
- 1977 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – Nordsieck, p. 60, pl. 20, fig. 157.
- 1979 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – De Casa & Hallgass 1979, p. 6 pl. 1.
- 1979 *Leufroyia leufroyi* (Michaud, 1828) – Nordsieck & García-Talavera, p. 165, pl. 41, fig. 33.
- 1980 *Raphitoma leufroyi* (Michaud 1828) – Bogi *et al.*, p. 14, fig. 2.
- 1984 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – Van Aartsen *et al.*, p. 45, fig. 219.
- 1992 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – Cavallo & Repetto, p. 146, fig. 404.
- 1996 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – Vera-Peláez (*partim*), p. 744, pl. 56, figs 8, 9 (only).
- 1998 *Raphitoma leufroyi* (Michaud, 1828) – Rolán *et al.*, p. 108, figs 26-28.
- 2001 *Raphitoma leufroyi* (Michaud, 1828) – Cachia *et al.*, p. 67, pl. 10, fig. 5.
- 2002 *Raphitoma (Leufroyia) guadalmanseae* Vera-Peláez, p. 233, pl. 7, figs T, U, pl. 15, fig. Ñ.
- 2005 *Raphitoma leufroyi* (Michaud, 1828) – Rolán, p. 172, fig. 789.
- 2005 *Raphitoma leufroyi* (Michaud, 1828) – Repetto *et al.*, p. 39, 218, fig. 900.
- 2008 *Raphitoma leufroyi* (Michaud, 1828) – Pusateri & Giannuzzi-Savelli, p. 124, figs 5, 7, 9, 14.
- 2011 *Raphitoma leufroyi* (Michaud, 1828) – Hernández *et al.*, p. 230, figs 76L-M.
- 2013 *Raphitoma leufroyi* (Michaud, 1828) – Landau *et al.*, p. 271, pl. 45, fig. 8.
- 2020 *Leufroyia leufroyi* (Michaud, 1828) – Giannuzzi-Savelli *et al.*, p. 438, figs 4-8 (*cum syn.*).
- non 1854 *Pleurotoma leufroyi* Mich. – Hörnes, p. 373, pl. 40, fig. 16 [= *Leufroyia conspicua* (Eichwald, 1830)].
- non 1912 *Mangilia [sic] leufroyi* Michd. – Friedberg, p. 226, pl. 14, fig. 8 [= *Leufroyia conspicua* (Eichwald, 1830)].
- non 1915 *Clathurella leufroyi* (Michaud) – Harmer, p. 235, pl. 28, figs 13-15 193 [= *Leufroyia concinna* (Scacchi, 1836)].
- non 1878 *Pleurotoma leufroyi* (Mich.) – Nyst, pl. 3, fig. 14 [= *Leufroyia pseudoleufroyi* (Marquet, 1998)].
- non 1882 *Pleurotoma leufroyi* (Mich.) – Nyst, p. 50 [= *Leufroyia pseudoleufroyi* (Marquet, 1998)].
- non 1915 *Clathurella leufroyi* (Michaud) – Harmer, p. 235, pl. 28, figs 13-15 193 [= *Leufroyia pseudoleufroyi* (Marquet, 1998)].
- non 1938 *Mangelia (Leufroyia) leufroyi* var. *praecedens* Dollfus & Dautzenberg in Peyrot, p. 285, pl. 5, figs 40, 56 [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1954 *Philbertia (Leufroyia) leufroyi* f. *praecedens* Dollfus et Dautzenberg in Peyrot, 1938 – Glibert, p. 60, pl. 7, figs 8a, b, c [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1960 *Raphitoma (Leufroyia) leufroyi* Michaud, 1828 – Glibert, p. 17, pl. 4, fig. 19, pl. 5, fig. 7 [= *Leufroyia pseudoleufroyi* (Marquet, 1998)].
- non 1964 *Raphitoma (Leufroyia) leufroyi* Michaud, 1827 [*sic*] – Brébion, p. 611, pl. 15, fig. 5 [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1964 *Raphitoma (Leufroyia) leufroyi* var. *praecedens* Dollfus et Dautzenberg in Peyrot, 1938 – Brébion, p. 613 [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1964 *Raphitoma (Leufroyia) leufroyi* var. *selecta* Millet, 1854 – Brébion, p. 614, pl. 15, fig. 6 [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1964 *Raphitoma (Leufroyia) leufroyi* var. *milleti* Brébion, p. 615, pl. 15, fig. 7 (*nomen nudum*) [= *Leufroyia aldrovandi* (Millet, 1865)].
- non 1968 *Mangelia leufroyi* (Michaud, 1828) – Zelinskaya *et al.*, p. 224, pl. 50, figs 40-41 [= *Leufroyia conspicua* (Eichwald, 1830)].
- non 1974 *Philbertia leufroyi* (Scacchi, 1836) – Hubendick & Warén, p. 28, fig. 222 [= *Leufroyia concinna* (Scacchi, 1836)].
- non 1984 *Raphitoma leufroyi* (Michaud, 1828) – Fretter & Graham, p. 538, fig. 371 [= *Leufroyia concinna* (Scacchi, 1836)].
- non 1988 *Raphitoma leufroyi* (Michaud, 1828) – Graham, p. 460, fig. 193 [= *Leufroyia concinna* (Scacchi, 1836)].
- non 1992 *Raphitoma (Leufroyia) leufroyi* (Michaud, 1828) – Cavallo & Repetto, p. 146, fig. 404 (= *Cyrellia* sp.).
- non 2003 *Peratotoma leufroyi* (Michaud, 1828) – Batuk, p. 73, pl. 29, fig. 12 [= *Leufroyia conspicua* (Eichwald, 1830)].
- non 2018 *Raphitoma leufroyi* (Michaud, 1828) – Wigham & Graham, p. 137, fig. 161 [= *Leufroyia concinna* (Scacchi, 1836)].

Material and dimensions – Maximum height 13.6 mm, width 5.5 mm. CO: NHMW 2020/0171/0357-0358 (2), NHMW 2020/0171/0350 (5), NHMW 2020/0171/0561 (1).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2020, p. 444).

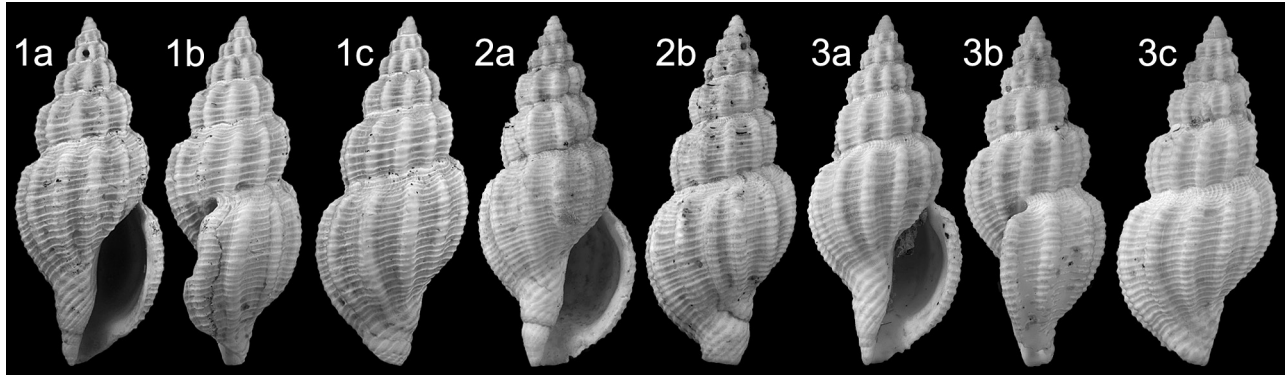


Plate 29. *Leufroyia leufroyi* (Michaud, 1828); 1. NHMW 2020/0171/0561, height 10.0 mm, width 4.1 mm; 2. NHMW 2020/0171/0357, height 13.0 mm, width 5.5 mm; 3. NHMW 2020/0171/0358, height 9.2 mm, width 3.8 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – Høisæter (2016, p. 28) discussed the relationship and taxonomic history of Atlantic and Mediterranean records for this species and concluded that in the North Atlantic outside the Mediterranean, specimens of this group belonged to *Leufroyia concinna* (Scacchi, 1836) [= *L. boothi* (J. Smith, 1839)], and those within the Mediterranean were *L. leufroyi* (Michaud, 1828). *Leufroyia concinna* differs in having weaker axial sculpture and lacking the characteristic colour pattern seen in *L. leufroyi* (for further discussion see under *L. concinna*). *Leufroyia guadalmanasae* (Vera-Peláez, 2002) was based in a single specimen from the Parque Antena locality. The original discussion is confusing; “*R. guadalmanasae está emparentada con las especies actuales R. leufroyi (Michaud, 1828) y R. concinna (Scacchi, 1836) de las que difiere por presentar las cóstulas de sutura a sutura, sin rampa sutural, el perfil de las vueltas es más convexo y los cordones son más anchos que en R. guadalmanasae* [*R. guadalmanasae* is closely related to the present-day species *R. leufroyi* (Michaud, 1828) and *R. concinna* (Scacchi, 1836), from with it differs in having the ribs extending between the sutures, without subsutural ramp, the whorl profile is more convex and the ribs are wider than in *R. guadalmanasae*].” (Vera-Peláez, 2002, p. 234). The holotype shows a shell with weakly convex, clearly shouldered whorls with a narrow, well-developed subsutural ramp and relatively narrow ribs. It is possible that the comparison in Vera-Peláez is a *lapsus* and was meant to read that *R. guadalmanasae* differs from *R. leufroyi* and *R. concinna* in having less convex whorls, a well-developed subsutural ramp, and narrower ribs. In any case, the poorly illustrated holotype represents a specimen of *L. leufroyi* and Vera-Peláez’s species is herein considered a junior subjective synonym. *Leufroyia ferrierii* Brunetti & Della Bella, 2006 described from the Lower Pliocene of Italy is closely similar to *L. leufroyi* but said to differ in having finer sculpture and the ribs terminating at the anal sinus and not continuing to the suture. The holotype illustrated also seems slightly more elongate than usual for *L. leufroyi*.

Distribution – Middle Miocene: eastern Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.*, 2013).

Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper); central Mediterranean, Italy (Sacco, 1904; Cipolla, 1914; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Present-day: Atlantic coast of France south to Portugal, Azores, Madeira and Canary Islands (Hernández *et al.*, 2011; Giannuzzi-Savelli *et al.*, 2020), Cape Verde Islands (Rolán, 2005), western Mediterranean (Bucquoy *et al.*, 1883; Van Aartsen *et al.*, 1984), entire Mediterranean (Cachia *et al.*, 2001; Repetto *et al.*, 2005; Pusateri & Giannuzzi-Savelli, 2008; Giannuzzi-Savelli *et al.*, 2020).

Leufroyia montagui (Bellardi, 1877)

Plate 30, figs 1-3

- *1877 *Homotoma Montagui* Bellardi, p. 272.
- 1881 *Homotoma Montagui* Bell. – Cocconi, p. 20
- 1904 *Peratotoma Montagui* (Bell.) – Sacco, p. 52, pl. 13, figs 45, 46.
- 1904 *Peratotoma Montagui* var. *ligusticostatissima* Sacco, p. 52.
- 1981 *Homotoma montagui* Bellardi, 1877 – Ferrero-Mortara *et al.*, p. 88, pl. 19, fig. 4. [syntype figured]
- 1994 *Raphitoma montagui* (Bellardi, 1847 [sic!]) – Gili & Martinell, p. 352
- 2018 *Raphitoma* aff. *linearis* (Montagu, 1803) – Brunetti & Cresti, p. 98, fig. 412 [non *Cyrrillia linearis* (Montagu, 1803)].

Material and dimensions – Maximum height 6.9 mm, width 3.1 mm. **CO:** NHMW 2020/0171/0138-0139 (2), NHMW 2020/0171/0140 (1). **VC:** NHMW 2020/0171/0141 (1), NHMW 2020/0171/0142 (8). **EL:** NHMW 2020/0171/0143 (3).

Description – Shell small, robust, relatively squat, broadly subpupoid, with strongly gradate spire (apical angle 57-58.8°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine squarely

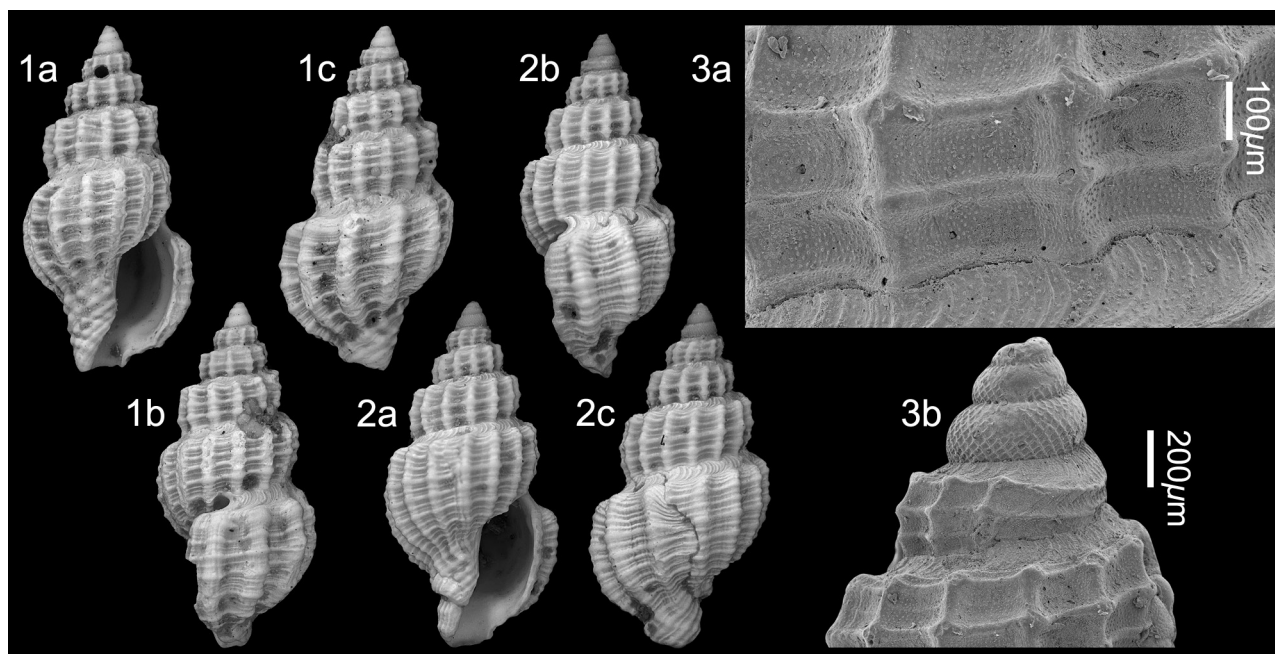


Plate 30. *Leufroyia montagui* (Bellardi, 1877); 1. NHMW 2020/0171/0138, height 6.9 mm, width 3.1 mm; 2. NHMW 2020/0171/0139, height 6.5 mm, width 2.9 mm (digital images). Velerín conglomerates. 3. NHMW 2020/0171/0414 juvenile, 3a, detail of teleoconch microsculpture, 3b, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

reticulated sculpture, diagonal on protoconch II, last whorl moderately keeled (Estepona specimen; $dp = 620 \mu\text{m}$, $hp = 695 \mu\text{m}$, $dp/hp = 0.89$). Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to 4.5 strongly shouldered whorls, with broad, weakly concave, subhorizontal subsutural ramp, sculptured by close-set comma-shaped riblets, sharply angled at shoulder, weakly convex below, separated by narrowly impressed, undulating suture. Axial sculpture predominant, composed of narrow, rounded orthocone ribs, 13-14 on last whorl, one-third width of their interspaces, subobsolete over subsutural ramp. Spiral sculpture of three narrow primary cords forming rectangular reticulated sculpture, with elongated tubercles developed at sculptural intersections; secondary thread intercalated on penultimate whorl. Entire surface covered in fine micropustules roughly aligned in horizontal rows. Last whorl 61-64% of total height, profile and sculpture as described above, evenly convex below shoulder, strongly constricted at base; axials and narrow cords of alternating strength persisting over base, six weakly tubercular cords over siphonal fasciole; base indistinct, fasciole well delimited. Aperture ovate, 43% of total height; outer lip moderately thickened by varix, smooth within, except 1-2 weak adapical tubercles at lateral edge of anal canal and 1-2 tubercles abapically at lateral edge of siphonal canal; anal sinus moderately narrow, deep, inverted L-shaped; siphonal canal short, bent adaxially, strongly recurved, unnotched. Columella smooth, strongly excavated in upper third, straight, strongly twisted at fasciole. Columellar and parietal callus hardly developed, poorly delimited, forming narrow indented callus rim.

Discussion – *Leufroyia montagui* (Bellardi, 1877) is a very characteristic species, with its small size, solid shell, squat shell shape, strongly gradate spire and sculpture composed of rounded orthocone ribs and spiral cords of alternating strength. Despite this, it has seldom been reported in the literature. Of the living Mediterranean and NE Atlantic *Leufroyia* species revised by Giannuzzi-Savelli *et al.* (2020) only the squatter forms of *L. erronea* Monterosato, 1884 are vaguely similar, but that species is never as squat and the whorls are less tabulate, the shoulder rounded rather than angular. In the Atlantic Upper Miocene of northwestern France *L. annegienae* Landau, Van Dingenen & Ceulemans, 2020 has a similar gradate spire, but is immediately separated by its paucispiral protoconch.

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Gili & Martinell, 1994); central Mediterranean, Italy (Bellardi, 1877). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Leufroyia stria (Calcare, 1839)

Plate 31, figs 1-3

- 1838 *Pleurotoma semiplicata* Bonelli in Michelotti, p. 396 (*nomen nudum*).
- *1839 *Pleurotoma stria* Calcare, p. 11, pl. 1, fig. 5.
- 1841 *Pleurotoma semiplicata* Bon. Bellardi & Michelotti, p. 11, pl. 1, figs 2, 3.
- 1844 *Pleurotoma semiplicatum* Bon. – Philippi, p. 174, pl. 26, fig. 18.

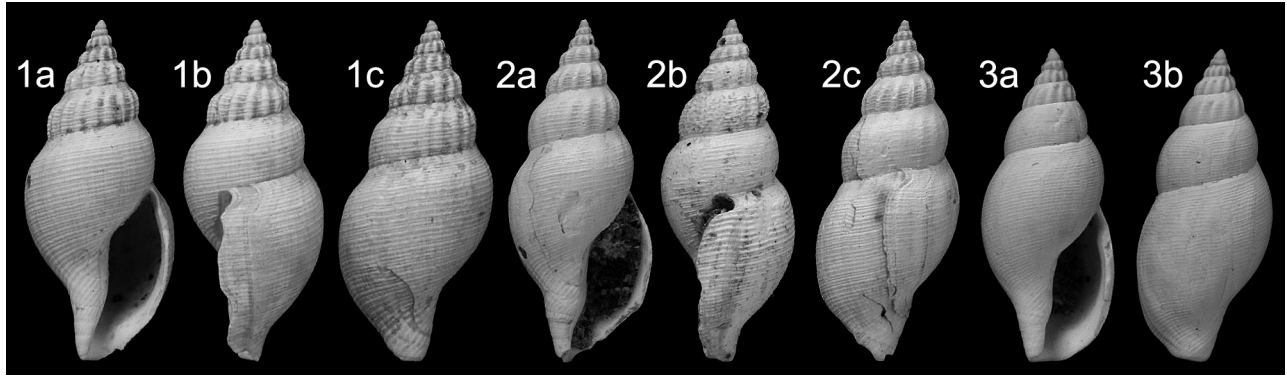


Plate 31. *Leufroyia stria* (Calcara, 1839); 1. NHMW 2020/0171/0373, height 14.0 mm, width 6.0 mm; 2. NHMW 2020/0171/0374, height 16.0 mm, width 6.3 mm; 2. NHMW 2020/0171/0375, height 10.7 mm, width 4.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

- 1862 *Pleurotoma semiplicatum minus* Brugnone, p. 29, fig 30 [*sic* for 22]
 1877 *Homotoma stria* (Calc.) – Bellardi, p. 277, pl. 8, fig. 25.
 1910 *Daphnella* (*Bellardiella*) *stria* Calc. – Cerulli-Irelli, p. 61 [253], pl. 5 [36], figs 54-57.
 1914 *Daphnella* (*Bellardiella*) *stria* Calcara – Cipolla, p. 155 [51], pl. 14 [3], figs 1, 2.
 1915 *Bellardiella stria* (Calcara) – Harmer (*partim*), p. 243, pl. 29, fig. 1 (only).
 1982 *Raphitoma* (*Leufroiya* [*sic*]) *stria* (Calcara, 1840 [*sic*]) – Martinell, p. 110, pl. 1, figs 19-20.
 1992 *Comarmondia stria* (Calcara, 1839) – Cavallo & Repetto, p. 146, fig. 407.
 1997 *Comarmondia stria* (Calcara, 1839) – Chirli, p. 93, pl. 26, figs 10-12.
 1998 *Comarmondia stria* (Calcara, 1839) – Bogi & Cauli, p. 130, fig. 6.

Material and dimensions – Maximum height 16.0 mm, width 6.3 mm. **CO:** NHMW 2020/0171/0373-0375 (3), NHMW 2020/0171/0376 (3). **VC:** NHMW 2020/0171/0680 (1).

Description – Shell medium sized, robust, broadly fusiform, with conical spire (apical angle 48.5-55.9°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to six convex, weakly shouldered whorls, with moderately broad, concave subsutural ramp, shoulder roundly angled, convex below, with periphery at abapical suture, suture superficial, weakly undulating. Axial sculpture of rounded, weakly elevated and weakly opisthocline ribs, subobsolete over subsutural ramp, 13-16 on early spire whorls, slightly narrower than their interspaces that fade on second half of penultimate whorl, absent on last whorl. Spiral sculpture of low, fine cords, about six primaries on penultimate whorl, with one secondary of almost equal strength intercalated in interspaces, further fine cords of roughly alternate strength over ramp. Last whorl strongly

inflated, 67-70% of total height, with weakly concave to straight-sided subsutural ramp, rounded at shoulder, convex below, moderately constricted at base; narrow spirals of alternate strength over entire surface, 12-14 slightly stronger cords over siphonal fasciole; base and fasciole not delimited. Aperture ovate, 48-49% of total height; outer lip thin, very slightly thickened by varix, smooth within; anal sinus relatively broad, shallow, asymmetrically U-shaped, occupying entire ramp, with apex on adapical half; siphonal canal moderately short, slightly bent adaxially and recurved, unnotched. Columella smooth, strongly excavated just above mid-height, straight below, moderately twisted at fasciole. Columellar and parietal callus not thickened, forming narrow indented callus margin.

Discussion – The multispiral protoconch with diagonally reticulated pattern is typically raphitomid, and we agree with Della Bella & Scarponi (2007, p. 25) in placing this species in that family.

Leufroyia stria (Calcara, 1839) is most similar to *L. desmoulinsi* (Bellardi, 1847) in that they both lack axial sculpture on the late whorls, but *L. stria* differs in having a taller, gradate spire with more convex whorls, the subsutural ramp more clearly delimited, irregular spiral sculpture, the last whorl far more inflated, the base more constricted, and a longer siphonal canal.

Harmer (1915, p. 243, pl. 29, fig. 2) recorded this species from the North Sea Basin Upper Pliocene Red Crag of England based on an incomplete worn specimen that is, in our opinion, unidentifiable with any degree of confidence. We therefore exclude the English record from the chresonymy and distribution herein.

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Martinell, 1982; Gili & Martinell, 1994); central Mediterranean, Italy (Bogi & Cauli, 1998), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Bellardi, 1877; Cipolla, 1914; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

***Leufroyia* aff. *stria* (Calcara, 1839)**

Plate 32, fig. 1

Material and dimensions – Height 9.1 mm, width 4.3 mm. **EL:** NHMW 2020/0171/0563 (1).

Description – Shell small, of medium thickness, broadly fusiform, with conical spire (apical angle 49.7°). Protoconch tall, conical multispiral (incomplete); post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of five convex, weakly shouldered whorls, with narrow, concave subsutural ramp, shoulder placed high, roundly angled, convex below, with periphery at abapical suture, suture superficial, weakly undulating. Axial sculpture of broad, rounded, weakly elevated and weakly opisthocline ribs, subobsolete over subsutural ramp, 12 on penultimate whorl, broader than their interspaces that fade on second half of the last whorl. Spiral sculpture of fine, low cords of alternating strength. Last whorl moderately inflated, 69% of total height, with narrow, concave subsutural ramp, rounded at high shoulder, broadly convex below, moderately constricted at base; narrow spirals of alternate strength over entire surface, slightly stronger cords over siphonal fasciole; base and fasciole not delimited. Aperture ovate, 50% of total height; outer lip thin, very slightly thickened by varix, smooth within; anal sinus of moderate width, relatively shallow, asymmetrically U-shaped, occupying entire ramp, with apex mid-ramp; siphonal canal moderately short, slightly bent adaxially, not recurved, unnotched. Columella smooth, strongly excavated just above mid-height, straight below, moderately twisted at fasciole. Columellar and parietal callus not thickened, forming narrow indented callus margin.

Discussion – This species is similar to *Leufroyia stria* (Calcara, 1839), but differs in having a more evenly fusiform profile, the last whorl less inflated, the axial ribs are less numerous, broader, and persist onto the first half of the last whorl, and the subsutural ramp is more strongly

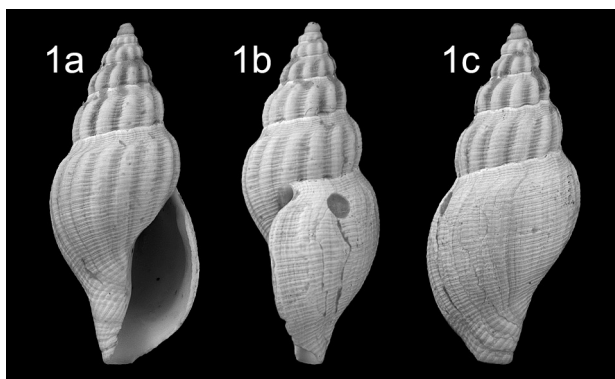


Plate 32. *Leufroyia* aff. *stria* (Calcara, 1839); 1. NHMW 2020/0171/0563, height 9.1 mm, width 4.3 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

delimited and concave. We do not think it is conspecific with *Leufroyia stria*, but with the scant material at hand we refrain from formally describing it. *Leufroyia desmoulinsi* (Bellardi, 1847) is slenderer fusiform in profile, the subsutural ramp is hardly delimited, and the axial ribs fade earlier in ontogeny.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Genus *Lusitanops* Nordsieck, 1968

Type species – *Pleurotomella lusitanica* Sykes, 1906, by original designation, present-day, Portugal.

1968 *Lusitanops* Nordsieck, p. 181.

***Lusitanops bermejensis* (Vera-Peláez, 2002)**

Plate 33, figs 1-3

*2002 *Xantodaphne* [*sic*] *bermejensis* Vera-Peláez, p. 230, pl. 6, figs R, S, pl. 17, fig. B'.

Material and dimensions – Maximum height 9.3 mm, width 5.0 mm. **VC:** NHMW 2020/0171/0074-0076 (3), NHMW 2020/0171/0077 (8).

Description – Shell small, fragile, very broadly globose fusiform, with low, conical spire (apical angle 60.5–66.3°). Protoconch broadly conical, multispiral, of 4–4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture ($dp = 770 \mu\text{m}$, $hp = 900 \mu\text{m}$, $dp/hp = 0.86$). Junction with teleoconch marked by sinusigera. Teleoconch of up to three evenly convex whorls, subsutural ramp not developed, separated by narrowly impressed, linear suture. Sculpture of very fine, close-set, strongly sinuous axial riblets and fine irregular flattened cords separated by grooves only visible in axial interspaces. No microsculpture developed. Last whorl tall, greatly inflated, 78–79% of total height, slightly concave in subsutural area, broadly convex below, moderately constricted at base; riblets weakening over base, base covered by numerous fine cords less flattened over siphonal fasciole. Aperture very broad, ovate, 53–61% of total height; outer lip very thin, sharp edged, without varix, smooth within, somewhat flared abapically; anal sinus very broad and shallow, asymmetrically U-shaped; siphonal very canal short and wide, broadly and shallowly notched. Columella smooth, broadly and shallowly excavated. Columellar and parietal callus not developed, with surface sculpture running into aperture.

Discussion – The shell profile of *Xantodaphne bermejensis* Vera-Peláez, 2002 is most like that of deep-water Atlantic species placed by Bouchet & Warén (1980, p. 82) in the genus *Lusitanops* Nordsieck, 1968. However, species in that genus have no distinct sinus zone, whereas the Estepona species has a shallow, but distinct U-shaped

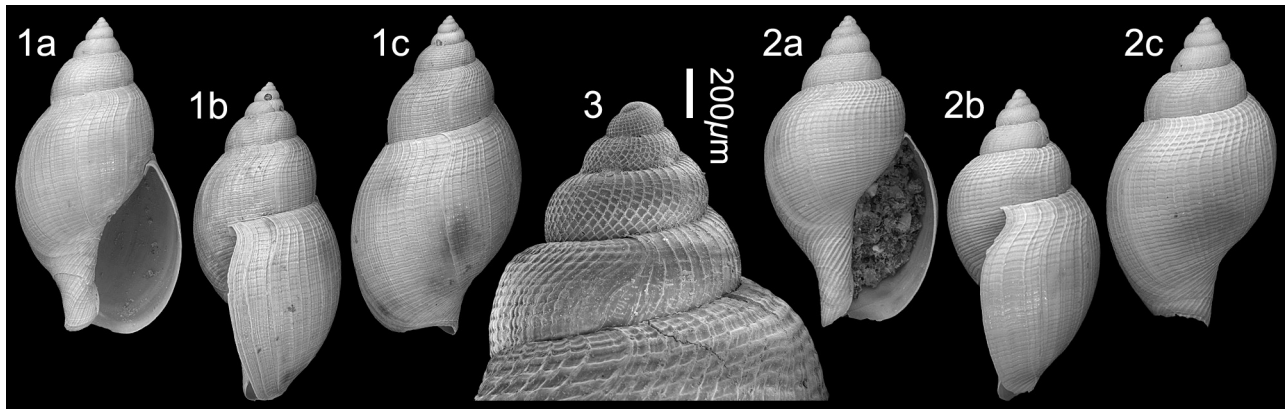


Plate 33. *Lusitanops bermejensis* (Vera-Peláez, 2002); 1. NHMW 2020/0171/0074, height 9.3 mm, width 5.0 mm; 2. NHMW 2020/0171/0075, height 5.6 mm, width 3.0 mm (digital images); 2. NHMW 2020/0171/0076, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

anal sinus. It is also not typical of *Xanthodaphne* Powell, 1942, as species in that genus have a reverse L-shaped sinus. On balance, we prefer to place this species in the genus *Lusitanops*.

The Estepona species is most like the type species *L. lusitanica* (Sykes, 1906), but is even broader, more inflated, with a wider aperture, and the outer lip is more flared abapically. In having a strongly inflated last whorl *L. bermejensis* is most like two other deep-sea northeastern Atlantic species: *L. cingulata* Bouchet & Warén, 1980 and *L. macrapex* Bouchet & Warén, 1980 but in both of these the inflation of the last whorl is most marked mid-whorl and the siphonal canal is longer than it is in the Estepona species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

Genus *Metuonella* Sorgenfrei, 1958

Type species – *Daphnella grippi* Kautsky, 1925, by original designation, Miocene, Germany.

1958 *Metuonella* Sorgenfrei, p. 76.

Note – This genus is very similar to *Favriella* Hornung, 1920, in including species with sharply angulate whorls, squamose or scabrose cords, and a shallow anal sinus. Indeed Powell (1966, p. 125) suggested that they may be synonymous. Bouchet & Warén (1980, p. 45) synonymised *Metuonella* with *Benthomangelia* Thiele, 1925, family Mangeliidae Fischer, 1883. However, the protoconch in *Metuonella* species has the diagonally reticulated pattern associated with raphitomid taxa but is not keeled. The type species *M. grippi* (Kautsky, 1925) from the Miocene of Germany is much taller spired than *Favriella* species and rather fusinid in profile, very similar to the Estepona species. We therefore keep them as separate genera.

Metuonella eufusinus Vera-Peláez, 2002

Plate 34, figs 1-4

1997 *Metuonella grippi* (Kautsky, 1925) – Vera-Peláez, p. 717, text-fig 38h, i, 73 [*non Metuonella grippi* (Kautsky, 1925)].

*2002 *Metuonella eufusinus* Vera-Peláez, p. 237, pl. 8, figs K, L, M, pl. 17, figs E', F'.

Material and dimensions – Maximum height 19.8 mm, width 5.8 mm. **CO:** NHMW 2020/0171/0170-0171(2), NHMW 2020/0171/0172 (6), NHMW 2020/0171/0597 (1). **VC:** NHMW 2020/0171/0173 (1), NHMW 2020/0171/0174 (2). **VS:** NHMW 2020/0171/0175 (2). **EL:** NHMW 2020/0171/0681 (5).

Description – Shell medium sized, slender fusiform, with tall spire (apical angle 37.1°). Protoconch tall, turbiniform, multispiral, of 3.25 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (dp = 660 µm, hp = 780 µm, dp/hp = 0.85, dV1 = 105 µm, dn = 60 µm). Teleoconch of up to six tall, angularly shouldered whorls, with broad, straight sided to weakly convex, steeply sloping subsutural ramp delimited by shoulder cord, convex below, separated by narrowly impressed, linear suture. Axial sculpture of 7-10 narrow, weakly prosocline ribs, about half width of their interspaces, overrun by narrow granular spiral cords of alternating strength, giving surface finely squamose appearance. Entire surface covered in very fine micro-pustules. Last whorl 60-61% of total height, with broad weakly convex subsutural ramp, weakly angled at shoulder, convex below, strongly constricted at base; primary to tertiary spirals all very narrow, continuing over base, axials weakening at peribasal cord, subobsolete over base, about ten slightly stronger cords over siphonal fasciole; base delimited by slightly strengthened peribasal cord, fasciole not delimited. Aperture ovate; outer lip not thickened by varix, smooth within; anal sinus not developed; siphonal canal long, bent slightly abaxially, unnotched. Columella smooth, moderately excavated in

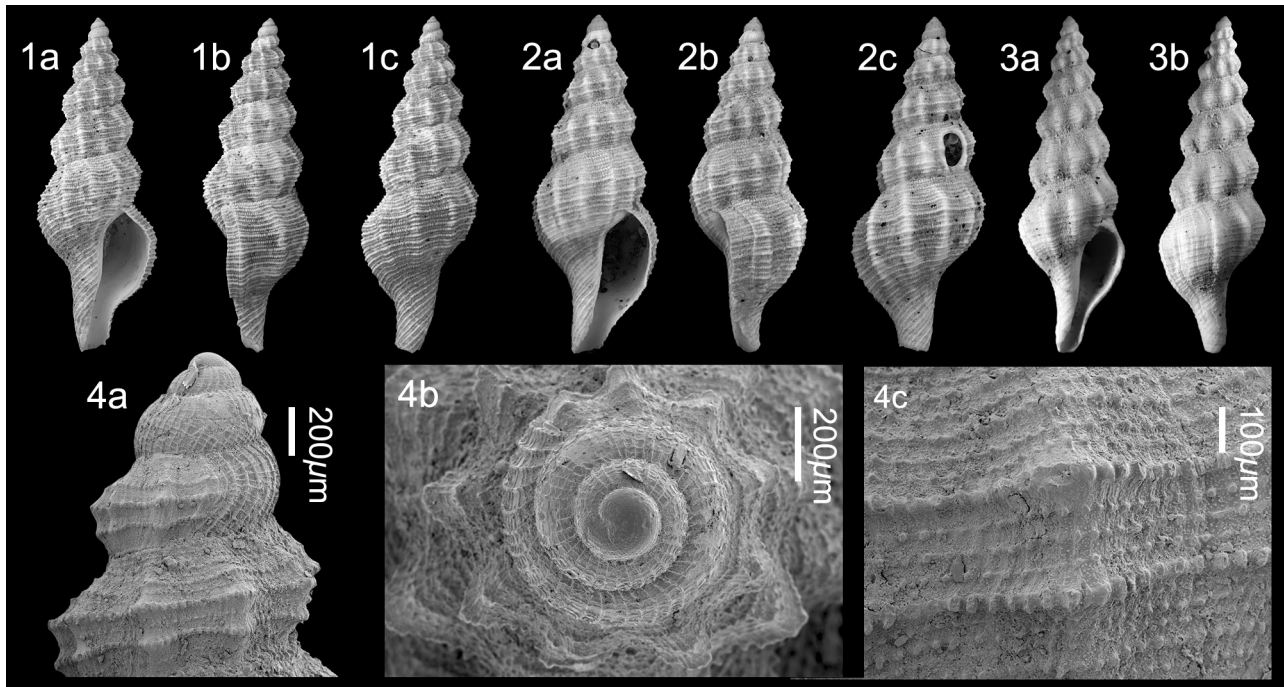


Plate 34. *Metuonella eufusinus* Vera-Peláez, 2002; 1. NHMW 2020/0171/0170, height 13.2 mm, width 4.8 mm; 2. NHMW 2020/0171/0171, height 10.6 mm, width 3.9 mm; 3. NHMW 2020/0171/0597, height 8.4 mm, width 2.7 mm (digital images). Velerín conglomerates. 4. NHMW 2020/0171/0173, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

upper third, straight below, weakly twisted at fasciole. Columellar and parietal callus sharply delimited, hardly thickened, forming very narrow callus rim.

Discussion – *Metuonella eufusinus* Vera-Peláez, 2002 is extremely similar to the type species, *M. grippi* (Kautsky, 1925), widespread in the North Sea Basin Miocene. It differs in being larger, in having protoconch with fewer whorls (3.25 whorls vs 4 *vide* Sorgenfrei, 1958, pl. 62, fig. 212; R. Janssen & Wienrich *in* Wienrich, 2007, pl. 114, fig. 1), and having fewer spiral cords at the protoconch teleoconch boundary (3 vs 6-7, *vide* Sorgenfrei, 1958, pl. 62, fig. 212; R. Janssen & Wienrich *in* Wienrich, 2007, pl. 114, fig. 1). The width of the axials does not separate the two species, as suggested by Vera-Peláez (2002, p. 238).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

Genus *Microandonia* nov. gen.

Type species – *Microandonia minutissima* nov. sp., Pliocene, Spain.

Other species included – Monotypic.

Diagnosis – Small, low spired, moderately broadly fusiform shell, with paucispiral dome-shaped protoconch bearing rows of irregular microtubercles, teleoconch of two rapidly expanding whorls, separated by linear suture

becoming increasingly oblique abapically, surface bearing subobsolete spiral cords, last whorl evenly convex, without subsutural ramp, base or fasciole delimited, aperture elongate and broad; outer lip simple, smooth within; anal sinus very broad and shallow U-shaped; siphonal canal short, wide, possibly broadly notched, columella weakly excavated, smooth, with poorly developed inner callus rim.

Etymology – Compound name reflecting suspected systematic position close to the genus *Andonia* Harris & Burrows, 1891, but even smaller in size. Gender feminine.

Discussion – This genus is erected for the single species *Microandonia minutissima* nov. sp. From Estepona, which cannot be placed in any known genus group. We suspect that it is most closely affiliated to the raphitomid genus *Andonia* Harris & Burrows, 1891, but deviates significantly from the type species *Andonia bonellii* (Bellardi & Michelotti, 1840) (see under that genus) in having a short spire, being relatively broad as opposed to slender in most *Andonia* species and having much reduced sculpture with no axial element.

Microandonia minutissima nov. sp.

Plate 35, figs 1-2

Type material – Holotype NHMW 2020/0171/0365, height 5.0 mm, width 2.0 mm; paratype 1: height 5.9 mm, width 2.2 mm.

Other material – Known from type series only.

Type locality – El Lobillo, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Latin ‘*minutus*’, adjective meaning small, superlative form.

Diagnosis – *Microandonia* species of small size, paucispiral protoconch bearing spiral microsculpture, teleoconch of two smooth, rapidly expanding whorls, low spire, large last whorl, siphonal canal wide.

Description – Shell small, moderately broad fusiform, with low spire (apical angle 45.3-49.3°). Protoconch paucispiral, dome-shaped, consisting of 1.5 whorls bearing spiral cordlets that on the last whorl become interrupted forming spiral rows of irregular tubercles ($dp = 350 \mu\text{m}$, $hp = 240 \mu\text{m}$, $dp/hp = 1.45$, $dV1 = 255 \mu\text{m}$, $dn = 135 \mu\text{m}$). Teleoconch of two rapidly expanding whorls, separated by narrowly impressed, linear suture becoming increasingly oblique abapically. First teleoconch whorl weakly convex bearing subobsolete spiral cords. No axial sculpture. Last whorl 84-86% total height, relatively broad, evenly convex, without ramp or shoulder developed, base and fasciole not delimited. Aperture 56-60% total height, broad, elongate; outer lip simple, smooth within; anal sinus very broad and shallow U-shaped; siphonal canal short, wide, possibly broadly notched (tip slightly damaged). Columella weakly excavated, smooth. Columellar and parietal callus poorly developed, weakly delimited,

forming narrow, poorly delimited callus rim.

Discussion – *Microandonia minutissima* nov. sp. can only be compared to the *Andonia* species with a paucispiral protoconch described from the European Neogene assemblages. It is immediately separated from *Andonia wilhelminamariae* Landau & Mulder, 2020, with which it co-occurs in the El Lobillo assemblage, by its much smaller size, lower dome-shaped protoconch, and almost complete lack of sculpture on teleoconch whorls. *Andonia delgadoi* Landau, Van Dingenen & Ceulemans, 2020 from the Upper Miocene Tortonian Atlantic Ligerian Basin, northwest France is quite different in profile, again larger, with a teleoconch composed of a greater number of convex, sculptured whorls.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Genus *Pleurotomella* Verrill, 1872

Type species – *Pleurotomella packardii* Verrill, 1872, by monotypy, present-day, northeastern United States.

1872 *Pleurotomella* Verrill, p. 15.

1954 *Tasmadaphne* Laseron, p. 46. Type species (by original designation): *Tasmadaphne spicula* Laseron, 1954, present-day, New South Wales, Australia.

1954 *Fusidaphne* Laseron, p. 47. Type species (by original designation): *Fusidaphne bullata* Laseron, 1954, present-day, New South Wales, Australia.

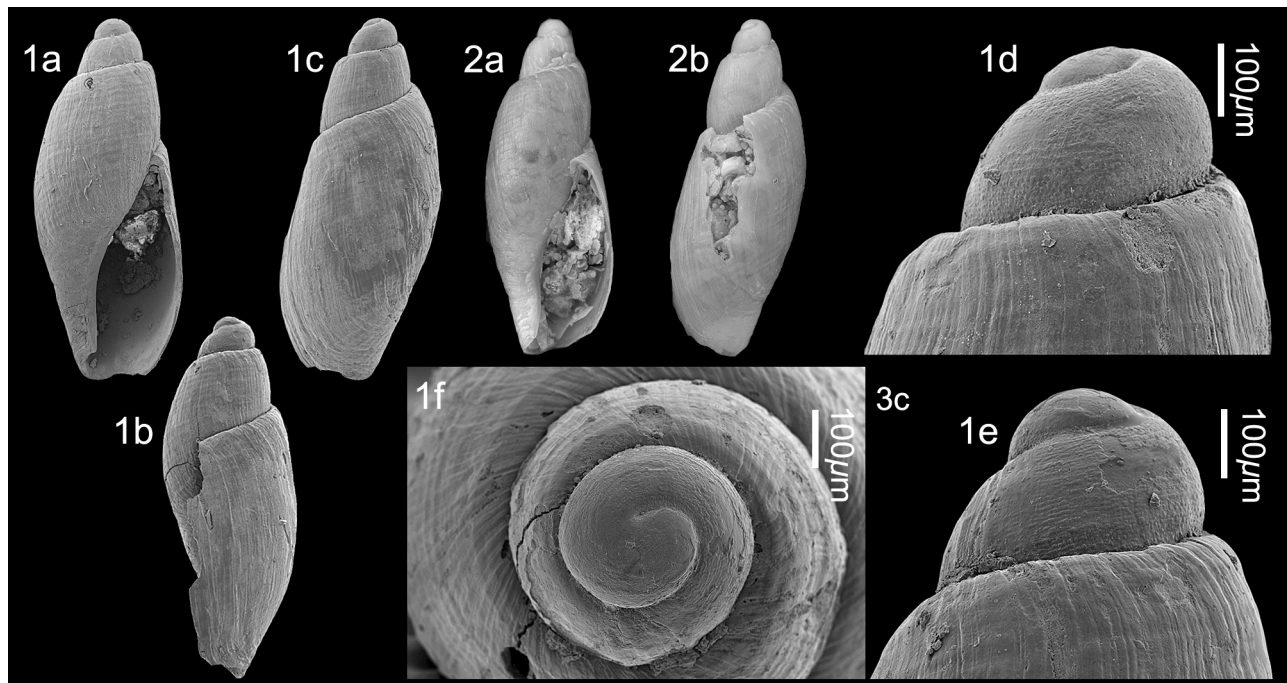


Plate 35. *Microandonia minutissima* nov. sp.; 1. **Holotype** NHMW 2020/0171/0365, height 5.0 mm, width 2.0 mm, 1d-f, detail of protoconch (SEM image); 2. Paratype 1 NHMW 2020/0171/0366, height 5.9 mm, width 2.2 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

- 1966 *Anomalotomella* Powell, p. 132. Type species (by original designation): *Pleurotomella anomalapex* Powell, 1951, present-day, Falkland Islands.
- 1968 *Azorita* Nordsieck, p. 184. Type species (by original designation): *Pleurotoma bureaui* Dautzenberg & H. Fischer, 1897, present-day, Azores.

Note – We use this genus in the more restricted sense of Bouchet & Warén (1980, p. 34) to include rather this shelled species, with a multispiral protoconch covered in diagonally reticulate surface sculpture, strongly inflated whorls teleoconch whorls with predominantly axial sculpture, and a deep anal sinus. This is primarily a deep-water genus and all the *Pleurotomella* Verrill, 1872 specimens from Estepona come from the deeper-water deposits of Velerín carretera. Further molecular data is needed to confirm whether this group is monophyletic (Criscione *et al.*, 2021).

***Pleurotomella antemnaensis* Vera-Peláez, 2002**

Plate 36, fig. 1

- *2002 *Pleurotomella (Pleurotomella) antemnaensis* Vera-Peláez, p. 225, pl. 6, figs M, N, pl. 15, figs A, B.

Material and dimensions – Holotype VL/ G480.001.001 (MMPE coll.), height 12.7 mm, width 5.0 mm, Parque Antena. Known only from holotype.

Description – Shell medium sized, thin, broad, turriculate-gradate spire (apical angle 45.6°). Protoconch tall, pointed, conical multispiral, of 4.5 convex whorls: post-nuclear whorls with fine, diagonally reticulated sculpture, last half whorl moderately keeled (dp = 850 µm, hp = 800 µm, dp/hp = 1.06). Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of four relatively broad, strongly shouldered whorls, with broad, concave subsutural ramp; shoulder angular at peripheral cord, convex below, separated by narrowly impressed, undulating suture. Axial sculpture predominant, composed of 8-11 [*sic*] elevated, opisthocline [*sic*] ribs developed only below shoulder, about one-third width of their interspaces. Spiral sculpture on spire whorl of two narrow elevated cords, abapical forming periphery; plus, sinuous threads over ramp. Last whorl 62% of total height, with very broad, concave subsutural ramp, mid-whorl portion compressed, strongly constricted at base; axials narrow and weaken over base, stronger cords over siphonal fasciole. Aperture ovate, 44% of total height; outer lip incomplete, smooth within; anal sinus deep, broad, inverted L-shaped, occupying entire ramp; siphonal canal moderately long, bent abaxially. Columella smooth, strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus forming narrow rim (adapted from original description and illustration; Vera-Peláez, 2002, pl. 6, figs M, N, pl. 15, figs A, B).

Discussion – The description given above is adapted from the original description and illustration. Sculpture

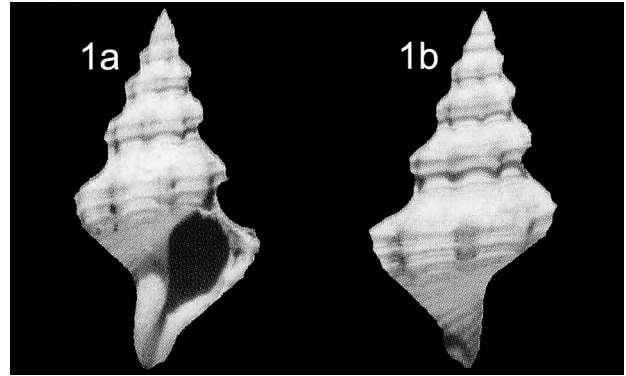


Plate 36. *Pleurotomella antemnaensis* Vera-Peláez, 2002; 1. **Holotype** VL/G480.001.001 (MMPE coll.), height 12.7 mm, width 5.0 mm (specimen figured by Vera-Peláez, pl. 6, figs M, N). Parque Antena, Estepona, Lower Piacenzian, Upper Pliocene.

over the subsutural ramp and base is unclear, and is interpreted as precisely as possible, although there may be some error. The ribs were described as opisthocline, although to the present authors they look orthocline.

Pleurotomella antemnaensis Vera-Peláez, 2002 was erected based on a single specimen from the deeper-water Parque Antena locality. Unfortunately, no further specimens are present in the material available. It seems to be very similar to the species described herein as *Pleurotomella turrita* nov. sp. However, they are unlikely conspecific, as the holotype of *P. antemnaensis* at a height of 12.7 mm is composed of four teleoconch whorls, whereas the largest specimen of *P. turrita* is smaller, 11.8 mm, and composed of seven teleoconch whorls. The protoconch also seems different, more pointed. For further discussion see under *P. turrita*.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

***Pleurotomella cf. gibbera* Bouchet & Warén, 1980**

Plate 37, fig. 1

- cf. *1980 *Pleurotomella gibbera* Bouchet & Warén, p. 41, figs 93, 220.
- 2002 *Pleurotomella (Pleurotomella) eurybrocha* (Dautzenberg & Fischer, 1896) – Vera-Peláez, p. 225, pl. 6, figs Ñ, O [*non Pleurotomella eurybrocha* (Dautzenberg & Fischer, 1896)].
- cf. 2009 *Pleurotomella gibbera* Bouchet & Warén, 1980 – Martins *et al.*, p. 65, figs 242-244.
- cf. 2016 *Pleurotomella gibbera* Bouchet & Warén, 1980 – Negri & Corselli, p. 70, figs 16a-c.
- cf. 2022 *Pleurotomella gibbera* Bouchet & Warén, 1980 – J.D. Oliver *et al.*, p. 414, figs 31, 43M.

Material and dimensions – Maximum height 7.2 mm, width 3.0 mm. VC: NHMW 2020/0171/0489 (1), NHMW 2020/0171/0491 (3).

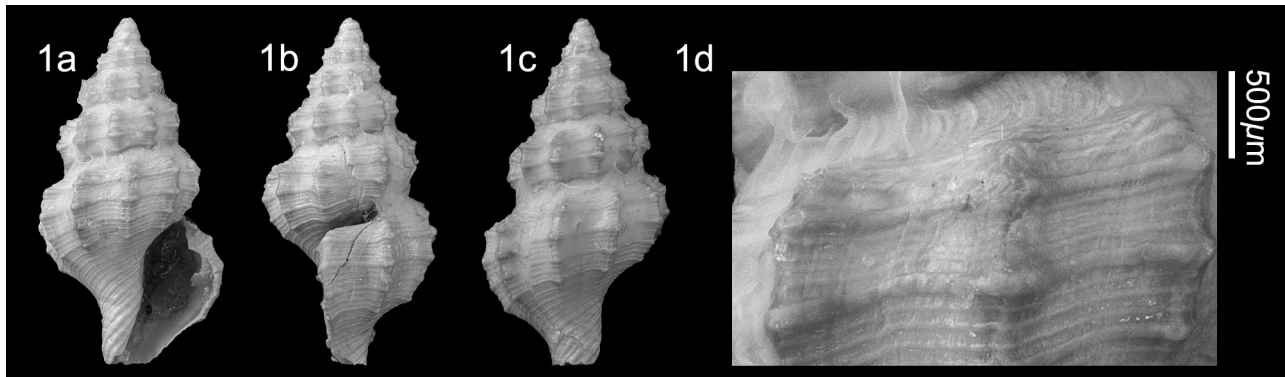


Plate 37. *Pleurotomella* cf. *gibbera* Bouchet & Warén, 1980; 1. NHMW 2020/0171/0489, height 6.7 mm, width 3.1 mm, 1d, detail of teleoconch sculpture (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell small, thin, relatively squat, broad, with low gradate spire (apical angle 45.3-53.6°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to five strongly shouldered whorls, with broad, concave subsutural ramp; adapical half bearing close-set comma-shaped axial growth lines, abapical half with two spiral cords above shoulder cord. Shoulder rounded, strongly convex below, separated by narrowly impressed, undulating suture. Axial sculpture predominant, composed of elevated, rounded orthocline ribs, 10-11 on last whorl, one-third the width of their interspaces. Spiral sculpture of three equal primary spirals on spire whorls, slightly swollen over intersections, with secondary and tertiary sculpture intercalated from penultimate whorl. Prominent, close set growth lines give surface finely reticulated appearance. No teleoconch microsculpture. Last whorl broad, 60-63% of total height, obtusely angled at shoulder and base, spirals of primary to tertiary strength between shoulder and basal cords, alternate strength over base, 8-9 slightly stronger cords of subequal strength over siphonal fasciole. Aperture ovate, 40-42% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus extremely deep, narrow, inverted L-shaped, occupying smooth portion of ramp; siphonal canal moderately short, straight, unnotched. Columella smooth, moderately excavated in upper third, straight below, moderately twisted at fasciole. Columellar and parietal callus sharply delimited, hardly thickened, forming narrow callus rim.

Discussion – Vera-Peláez (2002, p. 225, pl. 6, figs Ñ, O) considered these Estepona specimens to be conspecific with the present-day deep-water NE Atlantic *Pleurotomella eurybrocha* (Dautzenberg & Fischer, 1896). However, that species differs in having an extra protoconch whorl, in having a smoother subsutural ramp, slightly greater number of ribs, and lacking the crowded secondary and tertiary spiral sculpture seen in the Estepona specimens, so that the reticulated sculpture consists of relatively large, smooth squares, or at most with a sin-

gle secondary intercalated in some of the interspaces on the last whorl (see Bouchet & Warén, 1980, figs 92, 224, 225). The Estepona specimens are more like *Pleurotomella gibbera* Bouchet & Warén, 1980. The holotype of that species has a more solid shell, thicker ribs and fewer secondary spiral threads intercalated between the primary spiral cords. *Pleurotomella demosia* (Dautzenberg & Fischer, 1896), another deep-water NE Atlantic species differs in having a protoconch with only two whorls, the subsutural ramp is less concave, and the ribs are more numerous and broader.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

***Pleurotomella obesula* nov. sp.**

Plate 38, figs 1-3

Type material – Holotype NHMW 2020/0171/0580, height 6.1 mm, width 3.1 mm; paratype 1 NHMW 2020/0171/0581, height 5.2 mm, width 2.5 mm; paratype 2 NHMW 2020/0171/0582 (juvenile).

Other material – VC: NHMW 2020/0171/0583 (2).

Type locality – Velerín carretera, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Latin ‘*obesus*, -a, -um’, adjective meaning fat, referring to the globose shape of the last whorl. *Pleurotomella* gender feminine.

Diagnosis – *Pleurotomella* species of small size, multi-spiral protoconch with diagonally reticulated microsculpture and strongly keeled last whorl, teleoconch of three whorls bearing 8-9 axial ribs overrun by two primary cords with single secondary intercalated on penultimate whorl, last whorl strongly inflated mid-whorl, strongly constricted at base, long siphonal canal.

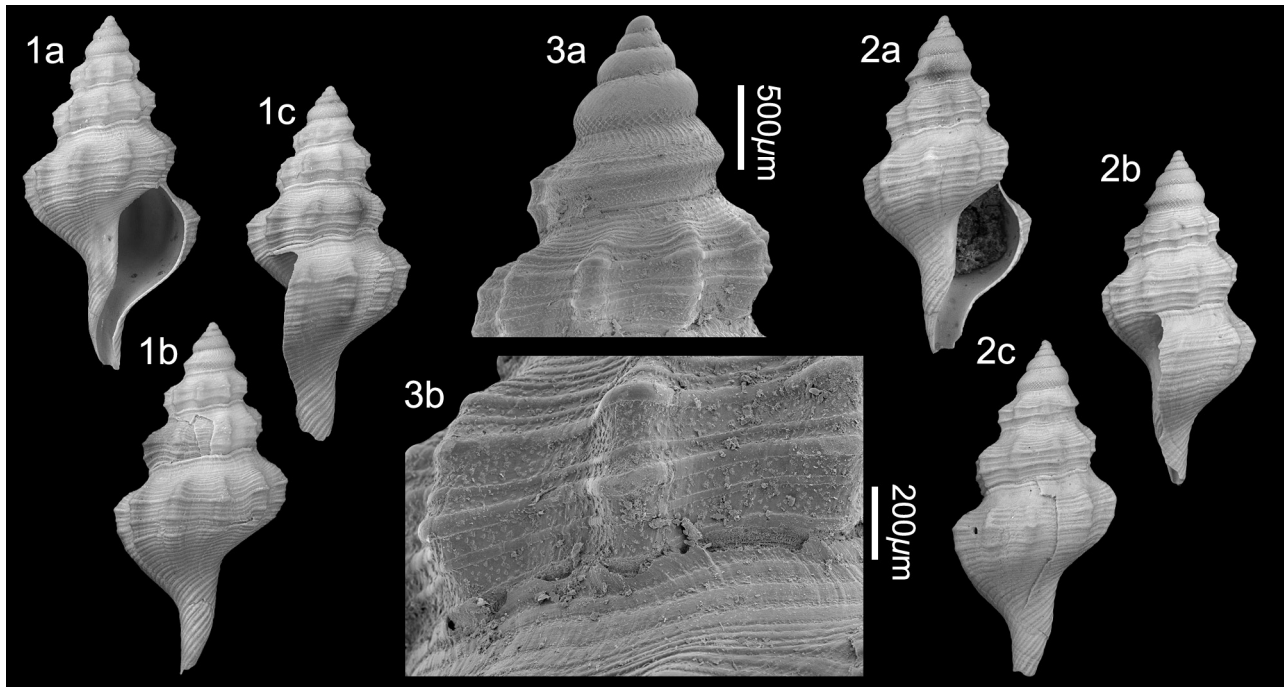


Plate 38. *Pleurotomella obesula* nov. sp.; 1. **Holotype** NHMW 2020/0171/0580, height 6.1 mm, width 3.1 mm; 2. **Paratype 1** NHMW 2020/0171/0581, height 5.2 mm, width 2.5 mm (digital images); 3. **Paratype 2** NHMW 2020/0171/0582, 3a, detail of protoconch, 3b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell small, fragile, squat, broadly turri-form, with short gradate spire (apical angle 55.1–57.1°). Protoconch tall, broad conical multispiral, of four convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl strongly keeled, with one spiral thread developed above keel and one below, further thicker cord develops in apposition to abapical suture. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to three low, strongly shouldered whorls, with broad, concave subsutural ramp, angled at shoulder cord, convex below, separated by narrowly impressed, weakly undulating suture. Axial sculpture predominant, composed of narrow, elevated orthocline to weakly opisthocline rounded ribs starting on abapical half of subsutural ramp, 8–9 on last whorl, about one-third width of their interspaces. Inconspicuous comma-shaped axial riblets on adapical half of subsutural ramp. Spiral sculpture of fine secondary cords on adapical half of ramp; below, two primary cords, adapical forming shoulder, with single secondary thread intercalated on penultimate whorl. Last whorl low, 68–70% of total height, with profile and sculpture as described above, strongly convex below shoulder and strongly constricted at base; axials weakening below shoulder, not extending over base, narrow spirals of alternate strength over base and siphonal fasciole. Aperture ovate, 51–53% of total height; outer lip thin (incomplete), smooth within; anal sinus deep, inverted L-shaped, occupying entire ramp, with apex on adapical portion of ramp; siphonal canal moderately long, strongly twisted, weakly recurved, unnotched.

Columella smooth, strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus weakly delimited, hardly thickened, forming callus wash with spiral sculpture visible through callus.

Discussion – With its squat profile, low whorls, strongly constricted base and strongly twisted columella this species is reminiscent of the present-day North Atlantic *Pleurotomella packardi* Verrill, 1872. The sculpture is also similar, except the ribs being less opisthocline than they are in *P. packardi*. However, the two clearly differ in their protoconch; *P. packardi* has a low dome-shaped protoconch (Bouchet & Warén, 1980, fig. 216), whereas *Pleurotomella obesula* nov. sp. has a larger, more elevated conical protoconch composed of more whorls, and the last whorl is strongly keeled.

The shell illustrated by Vera-Peláez (2002, pl. 6, figs K, L, pl. 14, figs M, N) as *P. packardi* has a conical pointed protoconch, quite unlike the low dome-shaped protoconch illustrated by Bouchet & Warén, and we do not believe it to be that species. It does not seem to be *P. obesula* either, as the protoconch, although conical, is composed of fewer whorls and the last whorl is not carinate (2002, pl. 14, figs M, N). The teleoconch (2002, pl. 6, figs K, L) is also less squat, with a different whorl profile, especially the last whorl is far less constricted at the base, and the siphonal canal is less twisted.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

***Pleurotomella tumens* (Bellardi, 1877)**

Plate 39, figs 1-3

- 1877 *Homotoma tumens* Bellardi, p. 266, pl. 8, fig. 22.
 1937 *Daphnella* (*Bellardiella*) *tumens* Bell. – Montanaro, p. 147 [177], pl. 8 [11], figs 25, 26.
 1981 *Homotoma tumens* Bellardi, 1877 – Ferrero Mortara *et al.*, p. 87, pl. 16, fig. 14.
 1996 *Pleurotomella* (*Pleurotomella*) *tumens* (Bellardi, 1877) – Vera-Peláez, p. 641, text-fig 34b, 35g, 62, pl. 47, figs 1, 2, 5, 7, 9.
 2002 *Pleurotomella* (*Pleurotomella*) *packardi* Verrill, 1872 – Vera-Peláez, p. 224, pl. 6, figs K, L, pl. 14, figs M, N [*non Pleurotomella packardi* Verrill, 1872].

Material and dimensions – Maximum height 8.5 mm, width 3.9 mm. VC: NHMW 2020/0171/0492-0494 (3), NHMW 2020/0171/0495 (1).

Description – Shell small, fragile, squat, broadly turritiform, with medium-height gradate spire (apical angle 46-7-47.2°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl hardly keeled (*Estepona* specimens; dp = 640 µm, hp = 750 µm, dp/hp = 0.85). Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to 4.5 low, strongly shouldered whorls, with broad, concave subsutural ramp, roundly angled at shoulder cord, convex below, separated by narrowly impressed, weakly undulating suture. Axial sculpture predominant, composed of narrow, elevated weakly opisthocline rounded ribs starting on abapical

half of subsutural ramp, ten on last whorl, about one-third to one-quarter width of their interspaces. Prominent comma-shaped axial riblets on adapical half of subsutural ramp. Spiral sculpture of two narrow cords on abapical half of subsutural ramp, two primary cords below, adapical forming shoulder, with secondary threads intercalated below shoulder on penultimate whorl. Last whorl 67-69% of total height, with profile and sculpture as described above, strongly convex at shoulder and strongly constricted at base; axials weakening below shoulder, not extending over base, narrow spirals of alternate strength over base and siphonal fasciole. Aperture ovate, 52-56% of total height; outer lip thin, smooth within; anal sinus deep, inverted L-shaped, occupying entire ramp, with apex on adapical portion of ramp; siphonal canal long, strongly twisted, weakly recurved, unnotched. Columella smooth, strongly excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal not developed.

Discussion – Vera-Peláez (2002, p. 224) considered *Homotoma tumens* Bellardi, 1877 a junior subjective synonym of *Pleurotomella packardi* Verrill, 1872, without further discussion. A syntype of *H. tumens* from the Lower Pliocene of Italy was figured by Ferrero Mortara *et al.* (1981, pl. 16, fig. 14). The specimen is incomplete, and the aperture broken back, but it differs from *P. packardi* in having less inflated whorls, narrower apical angle, the shoulder placed higher and more angular, the axial ribs, especially on the spire whorls, less strongly opisthocline, and the siphonal canal longer, although this is exaggerated by the aperture being incomplete.

The shell illustrated by Vera-Peláez (2002, pl. 6, figs K,

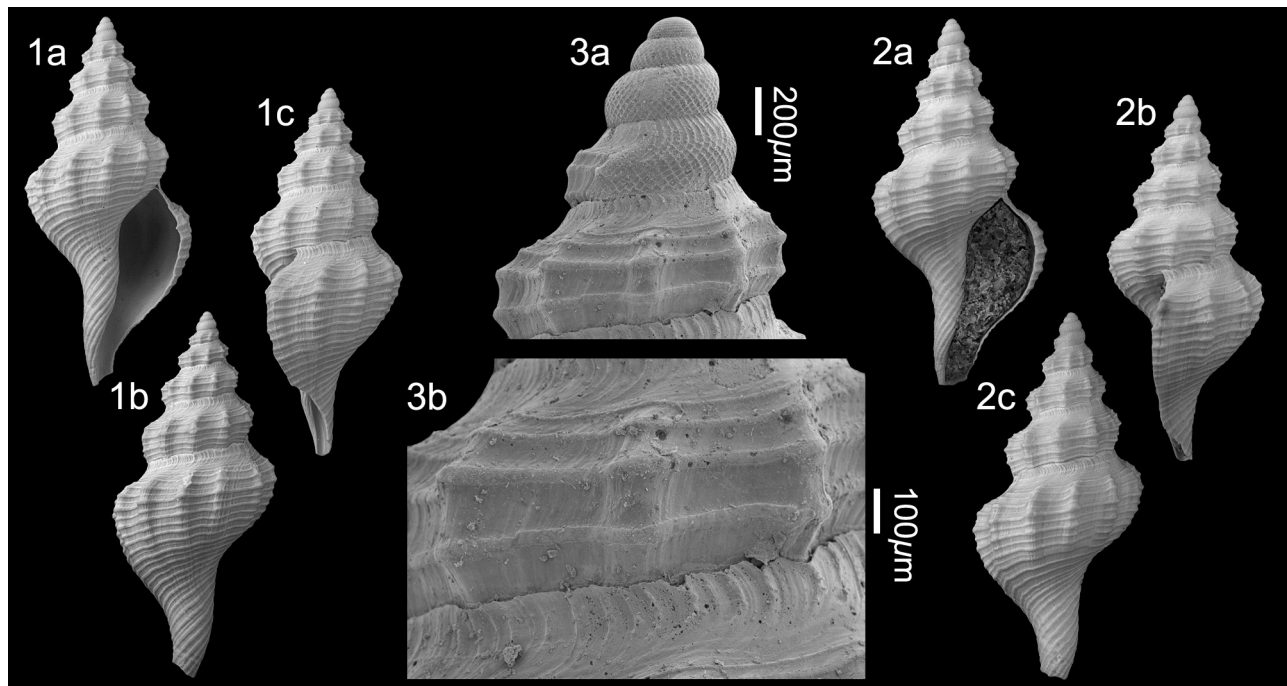


Plate 39. *Pleurotomella tumens* (Bellardi, 1877); 1. NHMW 2020/0171/0492, height 8.5 mm, width 3.9 mm; 2. NHMW 2020/0171/0493, height 7.0 mm, width 3.3 mm (digital images); 3. NHMW 2020/0171/0494, 3a, detail of protoconch, 3b, detail of teleoconch sculpture (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

L, pl. 14, figs M, N) as *P. packardi* has a pointed conical protoconch, quite unlike the low dome-shaped protoconch illustrated by Bouchet & Warén (1980, fig. 216) for *P. packardi*. Indeed, those authors noted that “*P. packardi* shows some variation in the sculpture of the adult shell but is always easy to identify because of its blunt protoconch” (1980, p. 38). The teleoconch of the Estepona specimen does not fit with the illustrations in Bouchet & Warén (1980, figs 96, 97) either; it is less squat, the subsutural ramp on the last whorl is less concave, the ribs are less sinuous, and the columella is far less twisted than in *P. packardi*. We consider the Estepona specimens to be conspecific with *P. tumens*, which is removed from the synonymy of *P. packardi*. The main difference between the Estepona specimens and that illustrated by Ferrero Mortara *et al.* is the even longer siphonal canal in the Italian specimen. However, as stated above, the aperture is broken back, exaggerating the length of the canal.

In shell profile and teleoconch sculpture *P. tumens* is similar to *Pleurotomella obesula* nov. sp., with which it co-occurs, but that species is immediately separated by its more pointed protoconch composed of four whorls, with a strongly carinate last protoconch whorl. The protoconch in *P. tumens* is hardly carinate. Moreover, the teleoconch whorls are slightly squatter in *P. obesula*, and the primary spiral cords more strongly distinguished from secondary cords than in *P. tumens*.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Montanaro, 1937). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

***Pleurotomella turrita* nov. sp.**

Plate 40, figs 1-2

Type material – Holotype NHMW 2020/0171/0584, height 11.8 mm, width 4.9 mm; paratype 1 NHMW 2020/0171/0585 (juvenile), height 6.2 mm, width 2.5 mm; paratype 2 NHMW 2020/0171/0586 (juvenile), height 7.2 mm, width 3.1 mm.

Other material – Known from type series only.

Type locality – Velerín carretera, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Latin ‘*turritus*, -a, -um’, adjective meaning tower-shaped, referring to the very high spire for the genus. *Pleurotomella* gender feminine.

Diagnosis – *Pleurotomella* species of medium size, thin shelled, with tall gradate spire, multispiral protoconch with diagonally reticulated microsculpture, up to seven teleoconch whorls with prominent comma-shaped axial

riblets just below suture, 11-12 narrow axial ribs below shoulder overrun by three primary spirals.

Description – Shell medium sized, thin, relatively short last whorl, tall gradate spire (apical angle 32.4-39.1°). Protoconch tall, conical multispiral, of four convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to seven relatively low, strongly shouldered whorls, with moderately broad, concave subsutural ramp; adapical half or ramp bearing very strong, relatively widely spaced, comma-shaped axial riblets, abapical half with one or two weak spiral cords above shoulder cord. Shoulder strongly rounded, angular at peripheral cord, convex below, separated by narrowly impressed, linear suture. Axial sculpture predominant, composed of narrow, elevated orthocline to weakly opisthocline ribs developed only below shoulder, 11-12 on last whorl, half to one-third width of their interspaces. Spiral sculpture on first teleoconch whorl of two narrow elevated cords, abapical forming periphery; third primary cords develops above suture on third whorl plus 1 or 2 weaker cords just above shoulder or abapical portion of subsutural ramp; fourth primary appears just above suture on fourth whorl, fifth on penultimate whorl. Last whorl low, about 50% of total height, with deeply concave subsutural ramp, strongly convex at shoulder and strongly constricted at base; axials narrow and weaken over base, single secondary spiral intercalated in interspaces, fine regular cords over siphonal fasciole. Aperture ovate, 36-38% of total height; outer lip thin (incomplete), smooth within; anal sinus extremely deep and broad, inverted L-shaped, occupying smooth portion of ramp; siphonal canal moderate length, twisted and recurved, unnotched. Columella smooth, moderately excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus sharply delimited, hardly thickened, forming callus wash with spiral sculpture visible through callus in parietal area.

Discussion – *Pleurotomella turrita* nov. sp. differs from all its congeners in having a relatively tall spire in relation to the last whorl. Of the extant North-East Atlantic congeners (see Bouchet & Warén, 1980, figs 86-99) *P. benedicti* Verrill & Smith in Verrill, 1884 is the most similar, but differs in the shell proportions discussed above and the concave portion of the subsutural ramp is not as broad, with the axial riblets denser than in *P. turrita*.

Vera-Peláez (2002, p. 225, pl. 6, figs M, N) described *Pleurotomella antemnaensis* based on a single specimen from the deeper-water deposits of Parque Antena, part of the Estepona assemblage. The photographs of the holotype are over-exposed and give little information, except for the shell profile and that there seem to be two cords on the spire whorls and three (possibly more) on the last whorl. It is not unlike *P. turrita* in spire whorl profile and in having two cords on the early teleoconch whorls. However, we do not believe them to be conspecific. The holotype of *P. antemnaensis* has four teleoconch whorls and a height of 12.7 mm (including protoconch). This is slightly

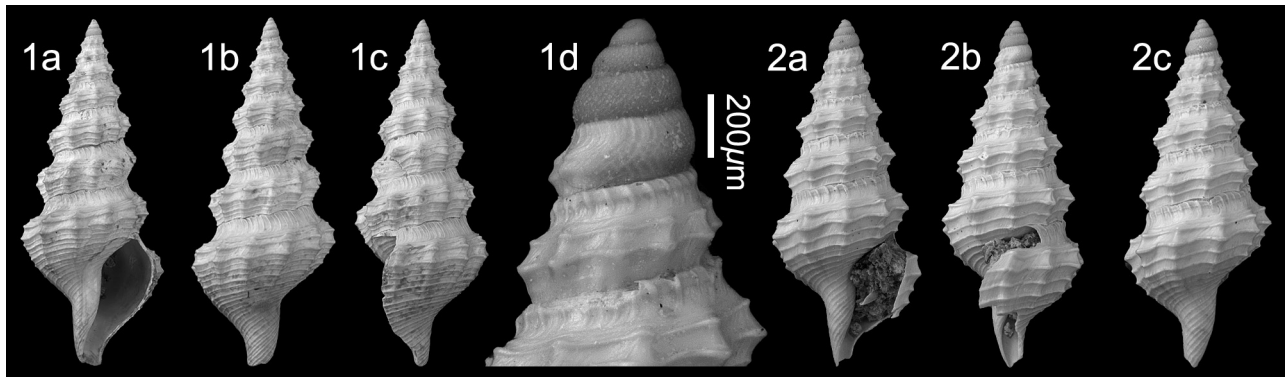


Plate 40. *Pleurotomella turrita* nov. sp.; 1. **Holotype** NHMW 2020/0171/0584, height 11.8 mm, width 4.9 mm; 2. **Paratype 1** NHMW 2020/0171/0585, height 6.2 mm, width 2.5 mm (juvenile) (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

larger than the holotype of *P. turrita* that has seven teleoconch whorls. Moreover, the apical angle is broader in *P. antemnaensis* and the ratio between last whorl/total height more normal for the genus (about 2/3) than the relatively tall spire and short last whorl seen in *P. turrita*. Lastly, the original description in Vera-Peláez (2002, p. 226) mentions “*La escultura de la rampa sutural consiste en cordoncillos aplanados y sinuosos. [Sculpture on the sutural ramp consists of flattened sinuous cordlets.]*” and does not mention the very prominent comma-shaped riblets on the concave portion of the ramp.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Genus *Pseudodaphnella* Boettger, 1895

Type species – *Pleurotoma philippinensis* Reeve, 1843, by original designation, present-day, Philippines.

1895 *Pseudodaphnella* Boettger, p. 58.

Note – The genus is characterised by small to moderate-sized species, with a small, dome-shaped protoconch of 2-3 whorls bearing microsculpture, axial sculpture of rounded ribs extending between sutures overridden by closely spaced cords and beaded or weakly spinose intersections, ovate last whorl, smooth columella, very short unnotched or weakly notched siphonal canal, and the sinus is sutural. A variously maculated colour pattern of red-brown spots arranged in rows overlying the crests of the ribs is characteristic (Powell, 1966, p. 128).

Molecular phylogeny by Fedosov & Puillandre (2012) found the genera *Kermia* W.R.B. Oliver, 1915 and *Pseudodaphnella* Boettger, 1895 to be monophyletic and closely related. Today the genus is restricted to the Indo-West Pacific. This is the first time the genus has been recognised in European faunas. However, a more critical generic revision of the European raphitomids may well place other species in this genus, for example *Clathurella* (*Clathromangalia*) *annamariaeae* Boettger, 1902 from the

Middle Miocene Paratethys of Romania.

This is not the only Indo-West Pacific raphitomid genus present in the European Neogene that has not been recognised previously. *Microdaphne* McLean, 1971 is represented in the Atlantic Lower Miocene Aquitanian of France by *Mangelia merignacensis* Peyrot, 1931 and in the Paratethyan Middle Miocene Badenian of Romania by *Peratotoma* (*Cordieria*) *microhystrix* Boettger, 1902. The presence of *Thetidos* Hedley, 1899 in the Atlantic Upper Oligocene Chattian of France was recently reported by Lozouet (2017, p. 69).

Pseudodaphnella iberica nov. sp.

Plate 41, figs 1-2

Type material – Holotype NHMW 2020/0171/0241 height 6.8, width 3.0 mm; paratype 1 NHMW 2020/0171/0242 height 6.2, width 3.0 mm.

Other material – Maximum height 6.8, width 3.0 mm. CO: NHMW 2020/0171/0243 (6).

Type locality – Velerín conglomerates, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Named after the Iberian Peninsula. *Pseudodaphnella* gender feminine.

Diagnosis – *Pseudodaphnella* species of small size, ovate-biconic profile, teleoconch of five convex whorls, 7-8 broad, rounded ribs, wider than their intervals, 3-4 spirals on spire whorls, slightly swollen at intersections, aperture subquadrate with well-developed D1 and parietal pad, short siphonal canal, colour pattern of rows of large spots over ribs, two rows on last whorl.

Description – Shell small, solid, broad ovate-biconic, with conical spire (apical angle 52.4-59.8°). Protoconch

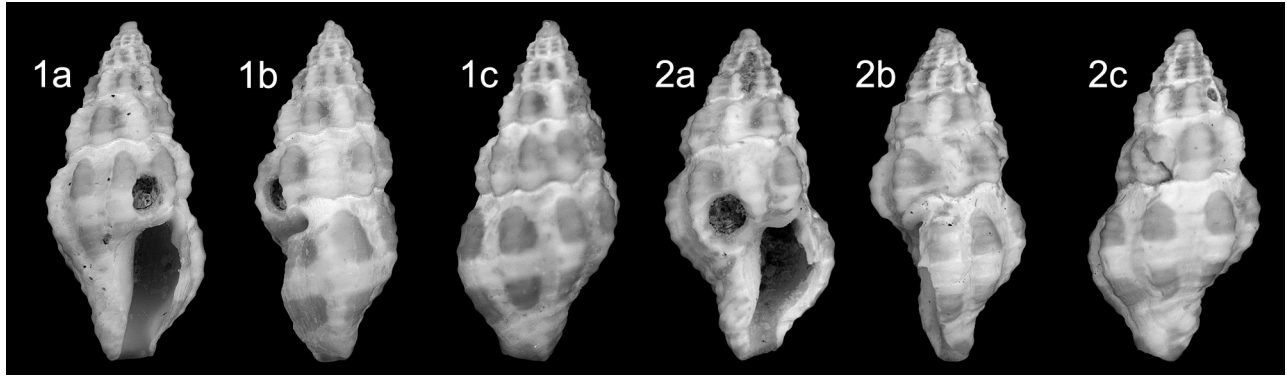


Plate 41. *Pseudodaphnella iberica* nov. sp.; 1. **Holotype** NHMW 2020/0171/0241, height 6.8 mm, width 3.0 mm; 2. **Paratype 1** NHMW 2020/0171/0242, height 6.2 mm, width 3.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

incomplete, but probably multispiral. Teleoconch of up to five convex whorls, with narrow, smooth, slightly concave subsutural ramp bearing shallow comma-shaped axial growth lines, shoulder not developed, convex below with periphery at about one-third whorl height, separated by superficial, undulating suture. Axial sculpture predominant, composed of broad, rounded weakly opisthocline ribs, 7-8 on last whorl, slightly wider than their interspaces. Spiral sculpture of three narrow cords on first teleoconch whorl, with fourth appearing at shoulder on penultimate whorl, slightly swollen over the ribs; no secondary spiral sculpture. No microsculpture. Last whorl 65-66% of total height, with narrow, concave subsutural ramp, evenly convex below, weakly to moderately constricted at base; axials weaken over base, eight primary spirals, plus one weaker over ramp, four low, broad cords over siphonal fasciole. Aperture subquadrate, 41% of total height; outer lip moderately thickened by varix placed a short distance behind sharp lip edge, smooth within, except moderately strong adapical tubercle (D1) at lateral edge of anal canal; anal sinus sutural, narrow, shallow, inverse L-shaped, occupying smooth portion of ramp; siphonal canal short, slightly recurved, unnotched. Columella smooth, very strongly excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus sharply delimited, slightly thickened, forming broad callus rim; strong parietal tubercle developed. Colour pattern preserved of large orange blotch over roughly alternate axial cords on spire whorls, on last whorl blotches developed over ribs in three horizontal bands placed over shoulder, base and siphonal fasciole.

Discussion – *Pseudodaphnella iberica* nov. sp. is quite unlike any other raphitomid in the European Neogene assemblages. Colour pattern of darker blotches over the ribs is preserved in most specimens and is seen in extant members of the genus (e.g., *P. lineata* Fedosov & Puillandre, 2012 and *P. phaeogranulata* Fedosov & Puillandre, 2012)

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

***Pseudodaphnella velerinensis* nov. sp.**

Plate 42, figs 1-2

Type material – Holotype NHMW 2020/0171/0244 height 6.6, width 3.2 mm; paratype 1 NHMW 2020/0171/0245 height 6.1, width 3.2 mm.

Other material – Maximum height 6.8, width 3.0 mm. **CO:** NHMW 2020/0171/0246 (1).

Type locality – Velerín conglomerates, Velerín, Estepona, Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

Etymology – Named after the type locality of Velerín. *Pseudodaphnella* gender feminine.

Diagnosis – *Pseudodaphnella* species of small size, squat ovate-biconic profile, teleoconch of four convex whorls, 9-10 broad, low, rounded ribs, wider than their intervals, 3-4 spirals on spire whorls, slightly swollen at intersections, aperture subquadrate with strong D1 and weaker parietal pad, short siphonal canal, colour pattern of horizontal bands, two on last whorl.

Description – Shell small, solid, broad ovate-biconic, with conical spire (apical angle 59.2-64.7°). Protoconch missing. Teleoconch of up to four low convex whorls, with narrow, smooth, slightly concave subsutural ramp, separated by superficial, undulating suture. Axial sculpture predominant, composed of broad, low, rounded orthocline to weakly opisthocline ribs, 9-10 on last whorl, slightly wider than their interspaces. Spiral sculpture of three narrow cords on first teleoconch whorl, with fourth appearing at shoulder on penultimate whorl, slightly swollen over the ribs; no secondary spiral sculpture. No microsculpture. Last whorl 66-70% of total height, with narrow, weakly concave subsutural ramp, evenly convex below, weakly to moderately constricted at base; axials weaken over base, eight primary spirals, plus one weaker

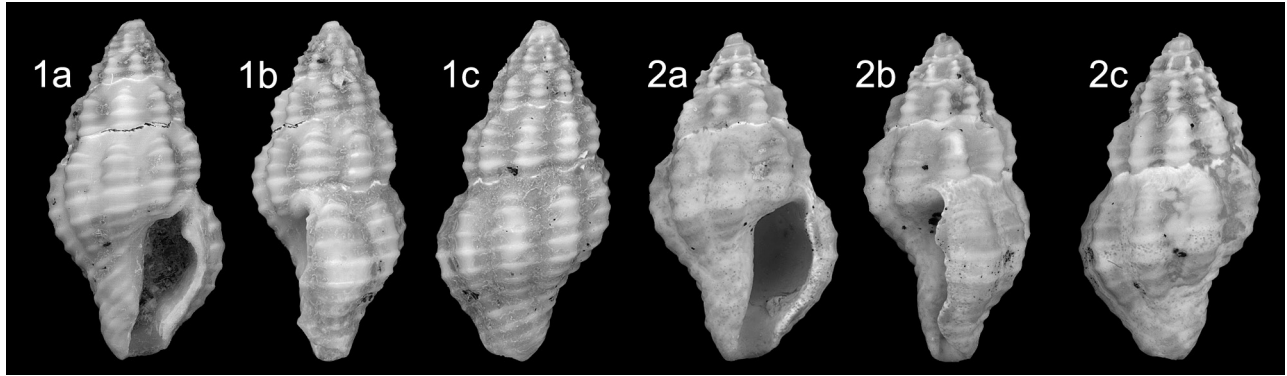


Plate 42. *Pseudodaphnella velerinensis* nov. sp.; 1. **Holotype** NHMW 2020/0171/0244, height 6.6 mm, width 3.2 mm; 2. **Paratype 1** NHMW 2020/0171/0245, height 6.1 mm, width 3.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

over ramp, four low, broad cords over siphonal fasciole. Aperture subquadrate, 43-47% of total height; outer lip moderately thickened by varix placed a short distance behind sharp lip edge, smooth within, except strong adapical tubercle (D1) at lateral edge of anal canal; anal sinus sutural, narrow, shallow, inverse L-shaped, occupying smooth portion of ramp; siphonal canal short, slightly recurved, unnotched. Columella smooth, very strongly excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus sharply delimited, slightly thickened, forming broad callus rim; weak to moderate parietal tubercle developed. Colour pattern preserved suggesting two broad horizontal bands of colour, one below the subsutural ramp, the other over the base.

Discussion – *Pseudodaphnella velerinensis* nov. sp. is closely similar to *Pseudodaphnella iberica* nov. sp., and both co-occur in the shallower water facies of the Velerín conglomerates. *Pseudodaphnella velerinensis* differs in being broader, squatter, the teleoconch with one whorl less, the ribs are lower and broader, and they differ in their colour pattern, placed in the same position on the last whorl, but horizontal bands vs rows of spots in *P. iberica*. Horizontal bands are also seen in some extant congeners (see Blatterer, 2019, pl. 180, fig. 17; pl. 181, fig. 18; *Pseudodaphnella* sp. 1 and 2)

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Genus *Raphitoma* Bellardi, 1847

Type species – *Raphitoma histrix* Bellardi, 1847, by subsequent designation, Monterosato, 1872, Pliocene, Italy.

- 1847 *Raphitoma* Bellardi, p. 16.
 1875 *Homotoma* Bellardi, p. 22. Type species (by subsequent designation; Powell, 1966): *Murex reticulatus* Renier, 1804, present-day, Italy. Junior homonym of *Homotoma* Guérin-Méneville, 1844 [Hemiptera].

- 1884 *Cordieria* Monterosato, p. 131. Type species (by subsequent designation; Crosse, 1885): *Murex reticulatus* Brocchi, 1814, Pliocene, Italy. Junior homonym of *Cordieria* Rouault, 1848.
 1884 *Philbertia* Monterosato, p. 132. Type species (by subsequent designation; Crosse, 1885): *Pleurotoma bicolor* Risso, 1826, present-day, Mediterranean.
 1891 *Peratotoma* Harris & Burrows, p. 133. Type species (by subsequent designation; Powell, 1966): *Murex reticulatus* Renier, 1804, present-day, Italy. *Nom. nov. pro Homotoma* A. Bellardi, 1875, non Guérin-Méneville, 1844 [Hemiptera].
 1968 *Cyrtoides* Nordsieck, p. 176. Type species (by original designation): *Pleurotoma rudis* Scacchi, 1836, present-day, Mediterranean.

Note – Fassio *et al.* (2019) characterised species within the genus *Raphitoma* Bellardi, 1847 as being turreted to biconic-pupoid, small to medium sized for the family, with a slender spire composed of regularly convex whorls, bearing reticulate sculpture, with the axials predominant, granular microsculpture present in some species, a thickened denticulate outer lip, and a very short to moderately long siphonal canal. The protoconch was described as multispiral or paucispiral with reticulate sculpture. As noted under the generic note for *Cyrilla* Kobelt, 1905, we adopt the descriptive terms for shell features suggested by Giannuzzi-Savelli *et al.* (2018).

***Raphitoma contigua* (Monterosato, 1884)**

Plate 43, figs 1-3

- 1882 *Clathurella purpurea philberti* Mich. – Bucquoy *et al.*, p. 91, pl. 14, figs 13- 15 [(non *Raphitoma philberti* (Michaud, 1829)].
 *1884 *Philbertia contigua* Monterosato, p. 133 (*nom. nov. pro Clathurella purpurea philberti* of Bucquoy *et al.*, 1882; non *Pleurotoma philberti* Michaud, 1829).
 1965 *Clathurella contigua* Monterosato – Ruggieri & Greco, p. 53, pl. 7, figs 7-8.

- 2002 *Raphitoma (Raphitoma) purpurea* (Montagu, 1803) – Vera-Peláez, p. 232, pl. 7, fig. P, pl. 15, figs M, N.
 2011 *Raphitoma philberti* (Michaud, 1829) – Chirli & Linse, p. 175, pl. 61, fig. 3 [*non Raphitoma philberti* (Michaud, 1829)].
 2012 *Raphitoma contigua* (Monterosato, 1884) – Pusa-teri *et al.*, p. 41, figs 1-3.
 2018 *Raphitoma contigua* (Monterosato, 1884) – Manousis *et al.*, p. 10, figs 6d-f.
 2018 *Raphitoma contigua* (Monterosato, 1884) – Giannuzzi-Savelli *et al.*, p. 52, figs 54, 56A (*cum syn.*).

Material and dimensions – Maximum height 11.3 mm, width 4.4 mm. **CO:** NHMW 2020/0171/0237-0239(2), NHMW 2020/0171/0240 (11). **EL:** NHMW 2020/0171/0633 (1).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2018, p. 55).

Discussion – Similar extant congeners with a multispiral protoconch: *R. lineolata* (Bucquoy, Duatzenberg & Dollfus, 1883), with a similar present-day distribution to *R. contigua* (Monterosato, 1884), differs in being slenderer, thinner shelled, with a narrower aperture, and lacks the narrow subsutural ramp; the Mediterranean *R. atropurpurea* (Locard & Caziot, 1900) is also slenderer; *R. densa* is more densely sculptured; the exclusively Atlantic *R. oblonga* (Jeffreys, 1867) has a narrower aperture. All these species differ in their colour patterns (Giannuzzi-Savelli *et al.*, 2018), which cannot be relied upon in fossil material. The Mediterranean *R. alternans* (Monterosato, 1884) is slenderer than *R. contigua* (Monterosato, 1884) and has a paucispiral protoconch. For further comparison and discussion see Giannuzzi-Savelli *et al.* (2018, p. 52-56).

The only other fossil record for the species is from the Lower Pleistocene (Milazziano) of Italy and the record in Chirli & Linse [as *Raphitoma philberti* (Michaud, 1829)] for the Gelasian and Calabrian Pleistocene of Rhodes Island, Greece. Its presence in the Estepona Pliocene constitutes the oldest confirmed stratigraphic occurrence.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper). Lower Pleistocene: central Mediterranean, Italy (Ruggieri & Greco, 1965), eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present day: Confirmed records only throughout the Mediterranean (Giannuzzi-Savelli *et al.*, 2018), unconfirmed Atlantic records from Galicia and Guernsey Island (Giannuzzi-Savelli *et al.*, 2018).

***Raphitoma echinata* (Brocchi, 1814) sensu AA**
 Plate 44, figs 1-2

- 1804 *Murex reticulatus* Lister – Renier, p. ix (name rejected by ICZN Opinion 316)
 *1814 *Murex echinatus* Brocchi, p. 423, pl. 8, fig. 3.
 1904 *Peratotoma reticulata* (Ren.) – Sacco, p. 52, pl. 13, fig. 38.
 1904 *Peratotoma reticulata* var. *pliocurta* Sacco, p. 52, pl. 13, fig. 39.
 1904 *Peratotoma reticulata* var. *pliosubacostata* Sacco, p. 52, pl. 13, fig. 40.
 1910 *Peratotoma reticulata* Ren. – Cerulli-Irelli, p. 57 [249], pl. 5 [36], figs 25-32.
 1914 *Mangilia [sic] (Clathurella) reticulata* Renier – Cipolla, p. 143 [39], pl. 13 [2], figs 13, 14.
 1937 *Daphnella (Bellardiella) reticulata* (Ren.) – Montanaro, p. 178 [148], pl. 8 [11], figs 30, 31.
 1963 *Raphitoma (Raphitoma) reticulata* (Renier, 1804) – Venzo & Pelosio, p. 132, pl. 11, fig. 34.
 1971 *Raphitoma (Raphitoma) hystrix [sic]* (De Cr. e Jan, 1832) [*sic*] – Pinna, p. 430, pl. 76, fig. 1 [*non Raphitoma hystrix* Bellardi, 1847].
 1974 *Philbertia cordieri* (Payraudeau, 1826) – Malatesta, p. 434, pl. 31, fig. 9 [*non Raphitoma cordieri* (Payraudeau, 1826)].
 1976 *Raphitoma (R.) reticulata* (Renierj [*sic*]) – Pavia, p. 114, pl. 8, fig. 22.
 1976 *Raphitoma echinata* (Brocchi, 1814) – Caprotti, p. 12, pl. 17, fig. 20.
 1983 *Raphitoma (Raphitoma) reticulata* (Renier, 1804) – Aimone & Ferrero Mortara, p. 297, pl. 1, fig. 3.
 1983 *Raphitoma reticulata* (Renier, 1804) – Menesini &

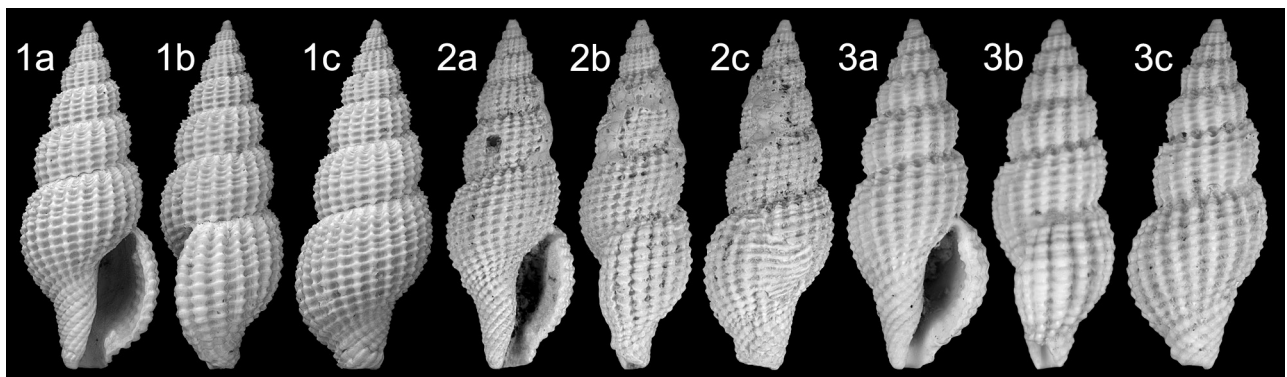


Plate 43. *Raphitoma contigua* (Monterosato, 1884); 1. NHMW 2020/0171/0237, height 11.3 mm, width 4.4 mm; 2. NHMW 2020/0171/0238, height 9.0 mm, width 3.3 mm; 3. NHMW 2020/0171/0239, height 8.2 mm, width 3.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

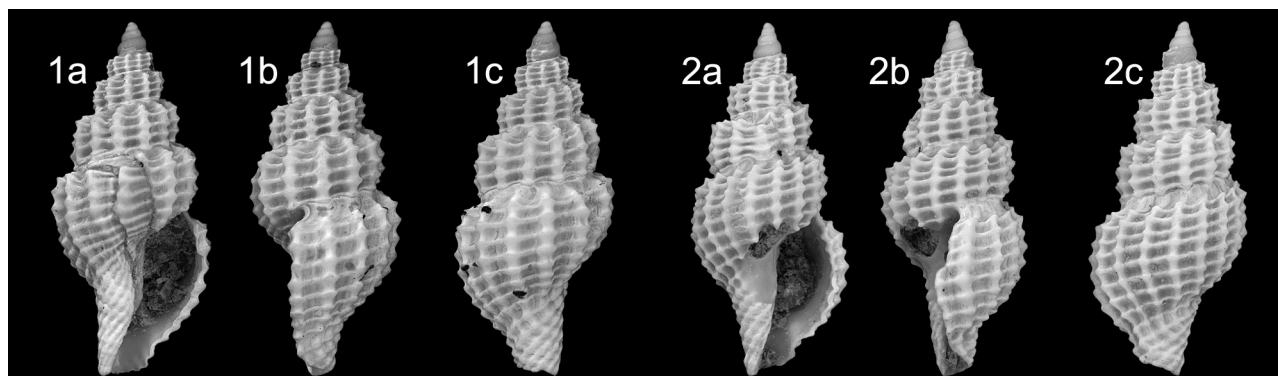


Plate 44. *Raphitoma echinata* (Brocchi, 1814) *sensu* AA; 1. NHMW 2020/0171/0548, height 5.3 mm, width 2.3 mm; 2. NHMW 2020/0171/0569, height 5.2 mm, width 2.1 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

- Ughi, p. 237, pl. 2, fig. 12.
- 1992 *Raphitoma echinata* (Brocchi, 1814) – Cavallo & Repetto, p. 146, fig. 402.
- 1997 *Raphitoma echinata* (Brocchi, 1814) – Chirli, p. 76, pl. 22, figs 1-3.
- 2010 *Raphitoma echinata* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 64, middle row right.
- 2011 *Raphitoma echinata* (Brocchi, 1814) – Landau *et al.*, p. 33, pl. 18, fig. 1.
- 2018 *Raphitoma echinata* (Brocchi, 1814) – Brunetti & Cresti, p. 98, fig. 408.
- 2018 *Raphitoma echinata* (Brocchi, 1814) *sensu* AA – Giannuzzi-Savelli *et al.*, p. 9, figs 16A, B, 63F.
- 2019 *Raphitoma echinata* (Brocchi, 1814) *sensu* AA – Giannuzzi-Savelli *et al.*, p. 58, figs 8-10, 28.
- non* 1978 *Murex echinatus* Brocchi, 1814 – Pinna & Spezia, p. 148, pl. 36, fig. 3 [*Raphitoma cordieri* (Payraudeau, 1826)].
- non* 2002 *Raphitoma* (*Raphitoma*) *echinata* (Brocchi, 1814) – Vera-Peláez, p. 231, pl. 7, figs K, L [= *Raphitoma hispidella* Pusateri & Giannuzzi-Savelli, 2019].
- non* 2011 *Raphitoma echinata* (Brocchi, 1814) – Chirli & Linse, p. 173, pl. 60, fig. 2.
- non* 2018 *Raphitoma echinata* (Brocchi, 1814) – Manousis *et al.*, p. 27, fig. 21c [= *Raphitoma hispidella* Pusateri & Giannuzzi-Savelli, in Giannuzzi-Savelli *et al.*, 2019].
- non* 2020 *Murex echinatus* Brocchi, 1814 – Pelorce & Horst, p. 28, fig. 3 [*Raphitoma cordieri* (Payraudeau, 1826)].

Material and dimensions – Maximum height 5.3 mm, width 2.3 mm. **CO:** NHMW 2020/0171/0632 (6). **EL:** NHMW 2020/0171/0548 (1), NHMW 2020/0171/0569 (1).

Description – Shell small, solid, subpupoid, gradate spire (apical angle 46–49°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited

by flexuous sinusigera. Teleoconch of up to 4.5 sharply shouldered whorls, with moderately narrow, smooth, slightly concave subsutural ramp bearing inconspicuous comma-shaped axial growth lines, angled at shoulder, weakly convex below, separated by narrowly impressed, undulating suture. Axial sculpture of sharp, narrow, elevated orthocline ribs, 12–14 on last whorl, one-third width of their interspaces. Spiral sculpture of subordinate, consisting of three sharp, elevated, evenly spaced primary cords on first teleoconch whorl. On second whorl further cord develops on abapical portion of subsutural ramp, resulting cancellation rectangular, with small tubercles developed at intersections. No teleoconch microsculpture. Last whorl 63–65% of total height, shape and sculpture as described above, shoulder angular, placed high, convex below, moderately constricted at base; axials persist over base; eight sharp cords; fasciole with 7 weakly tubercular cords. Aperture ovate, 45% of total height; outer lip moderately thickened, bearing denticles within; anal sinus narrow, shallow U-shaped, occupying smooth portion of ramp; siphonal canal moderate length and width, bent adaxially and recurved, unnotched. Columella smooth, excavated in upper half, twisted at fasciole. Columellar and parietal callus sharply delimited, hardly thickened, forming narrow callus rim.

Discussion – This species is highly problematic as the type material consists of three different species. The lectotype fixed by Pinna & Spezia (1978) is a *Raphitoma cordieri* (Payraudeau, 1826) *sensu* AA. The second specimen refers to a *Cyrrillia* sp. The third specimen is similar to what modern authors have interpreted as one of the morphotypes of *R. echinata*. Therefore, we use the annotation *R. echinata sensu* AA. This matter is pending an application to the ICZN to establish the name (RG-S personal information).

Distribution – Lower Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Upper Miocene: central Proto-Mediterranean, Italy (Montanaro, 1937; Venzo & Pelosio, 1963). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Bellardi, 1877; Pavia, 1976; Chirli, 1997; Sosso

& Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Cipolla, 1914; Caprotti, 1976; Aimone & Ferrero Mortara, 1983; Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Menesini & Ughi, 1983), eastern Mediterranean, Rhodes Island, Greece (Chirli & Linse, 2011). Present-day: ?Atlantic, Channel coast of France (Locard, 1891).

***Raphitoma erinacea* (Bellardi, 1877)**

Plate 45, fig. 1

- *1877 *Homotoma erinaceus* Bellardi, p. 267, pl. 8, fig. 23.
- 1981 *Homotoma erinaceus* Bellardi, 1877 – Ferrero-Mortara *et al.*, p. 87, pl. 16, fig 13.
- 1997 *Raphitoma erinacea* (Bellardi, 1877) – Chirli, p. 77, pl. 22, figs 5, 6.
- 2002 *Raphitoma (Raphitoma) erinacea* (Bellardi, 1877) – Vera-Peláez, p. 231, pl. 7, figs M, N, pl. 15, figs K, L.

Material and dimensions – Height 8.3 mm, width 3.7 mm. **EL:** NHMW 2020/0171/0549 (1), NHMW 2020/0171/0598 (1), NHMW 2020/0171/0550 (8).

Description – Shell small, of medium thickness, broad ovato-pupoid, tall gradate spire (apical angle 47.5°). Protoconch tall, conical multispiral, of 3.5 convex whorls; post-nuclear whorls with fine, diagonally reticulated sculpture, last whorl moderately keeled. Junction with teleoconch sharply delimited by flexuous sinusigera. Teleoconch of up to 4.5 convex shouldered whorls, with narrow, slightly concave subsutural ramp bearing inconspicuous comma-shaped axial growth lines, rounded at weak, high-placed shoulder, convex below, separated by weakly impressed, undulating suture. Axial sculpture predominant of narrow, elevated orthocone ribs, 16 on last whorl, one-third width of their interspaces. Spiral sculpture consisting of three equally spaced, elevated primary cords on first teleoconch whorl. On second whorl further cord develops just above suture, on penultimate whorl single secondary intercalated in interspaces.

Resulting cancellation elongated rectangular, with small spinous tubercles developed at intersections. No teleoconch microsculpture. Last whorl 63% of total height, subsutural ramp narrow, concave, shoulder hardly developed, evenly rounded below, moderately constricted at base; axials persist over base; 13 spiral cords of almost equal strength below ramp, with occasional tertiary thread intercalated; fasciole with ten weakly tubercular cords. Aperture ovate, 45% of total height; outer lip thickened by weak labial varix, sharp edged, smooth within; anal sinus sutural, moderate width and depth, inverted L-shaped, occupying smooth portion of ramp, with apex near suture; siphonal canal moderate length and width, slightly bent adaxially and recurved, unnotched. Columella smooth,

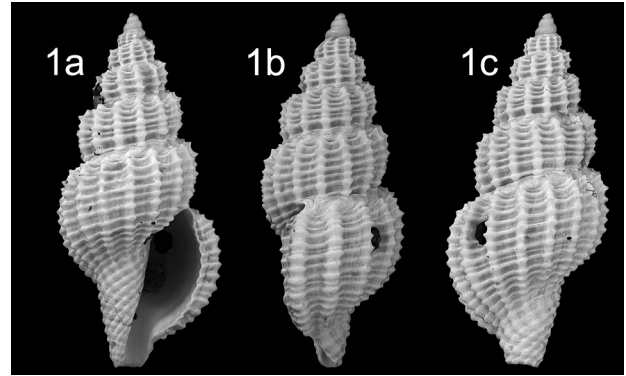


Plate 45. *Raphitoma erinacea* (Bellardi, 1877); 1. NHMW 2020/0171/0549, height 8.3 mm, width 3.7 mm (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

moderately excavated in upper third, straight below, hardly twisted at fasciole. Columellar and parietal callus poorly delimited, hardly thickened, forming narrow callus rim.

Discussion – *Raphitoma erinacea* (Bellardi, 1877) is very similar to *R. pumila* (Monterosato, 1890) but differs in being slenderer, with fewer axial ribs, it has seven spiral cordlets above the aperture vs 5-6 in *R. pumila*, the cancellate sculpture is coarser, the inside of the outer lip is smooth vs denticulate in *P. pumila*, and it is devoid of microsculpture, whereas *P. pumila* has densely disseminated microgranules.

Raphitoma echinata (Brocchi, 1814) and *R. erinacea* (Bellardi, 1877) both belong within the same species group. *Raphitoma erinacea* differs mainly in having secondary cords developed in the interspaces between the primaries on the last 1-2 whorls resulting in a more narrowly rectangular cancellate sculpture. The axial ribs are also slightly wider than they are in *R. echinata*, making the sculpture more strongly axially dominant.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1997). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Bellardi, 1877).

***Raphitoma hispidella* Pusateri & Giannuzzi-Savelli, 2019**

Plate 46, figs 1-3

- 1890 *Cordieria cordieri* var. *hispidella* Monterosato, p. 187 (*non Raphitoma hispidella* Bellardi, 1877).
- 2002 *Raphitoma (Raphitoma) echinata* (Brocchi, 1814) – Vera-Peláez, p. 231, pl. 7, figs K, L [*non Raphitoma echinata* (Brocchi, 1814) *sensu* AA].
- 2018 *Cordieria hispidella* Monterosato, 1890 – Appolloni *et al.*, p. 65, figs 220-P.
- 2018 *Raphitoma echinata* (Brocchi, 1814) – Manousis *et al.*, p. 27, fig. 21c [*non Raphitoma echinata* (Brocchi, 1814)].

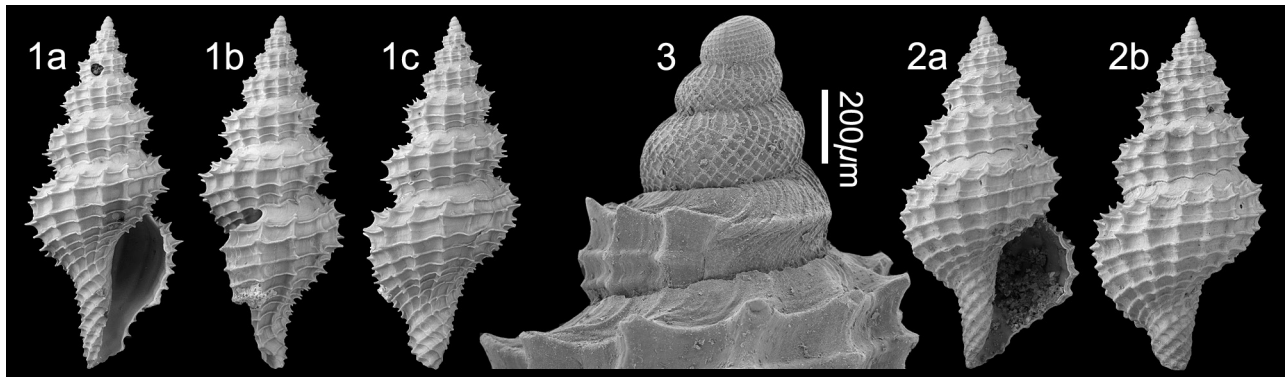


Plate 46. *Raphitoma hispidella* Pusateri & Giannuzzi-Savelli, 2019, height 11.2 mm, width 4.9 mm; 2. NHMW 2020/0171/0536, height 10.6 mm, width 5.0 mm (digital images); 3. NHMW 2020/0171/0537, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

*2019 *Raphitoma hispidella* Pusateri & Giannuzzi-Savelli in Giannuzzi-Savelli *et al.*, p. 58, figs 1-7 (*nom. nov. pro Cordieria cordieri* var. *hispidella* Monterosato, 1890) (*cum syn.*).

Material and dimensions – Maximum height 12.5 mm, width 5.2 mm. VC: NHMW 2020/0171/0535-0537 (3), NHMW 2020/0171/0538 (4).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2019, p. 65).

Discussion – Originally described as a subspecies of *R. cordieri* (Payraudeau, 1826), it differs consistently from that species in being smaller sized, having a wide concave subsutural ramp instead of sloping, a larger protoconch composed of a greater number of whorls (3 whorls, 600 x 509 µm vs 2.3 whorls, 475 x 350 µm; *vide* Giannuzzi-Savelli *et al.*, 2019, p. 65), more gradate profile, developing sharper spinous tubercles at the sculptural intersections, the cancellate sculpture is rectangular as opposed to subquadrate in *R. cordieri*, and the siphonal fasciole bears more numerous cords (8-9 vs 6-7) with weaker tubercles. *Raphitoma echinata* (Brocchi, 1814) *sensu* AA is more robust, has stronger denticles within the aperture, and a shorter siphonal canal. For further discussion see Giannuzzi-Savelli *et al.* (2019, p. 65).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper). Present-day: Atlantic, France to Spain, entire Mediterranean (Giannuzzi-Savelli *et al.*, 2019).

***Raphitoma histrix* Bellardi, 1847**

Plate 47, figs 1-3

1832 *Pleurotoma histrix* de Cristofori & Jan, p. 10 (*nomen nudum*).

*1847 *Raphitoma histrix* Bellardi, p. 85, pl. 4, fig. 14.

1862 *Pleurotoma histrix* Jan – Brugnone, p. 28, pl. 1, fig. 21.

1904 *Peratotoma histrix* (Jan) [*sic*] – Sacco, pl. 13, fig. 37.

1910 *Peratotoma histrix* Jan [*sic*] – Cerulli-Irelli, p. 56 [248], pl. 5 [36], figs 22-24.

1915 *Clathurella hystrix* [*sic*] (Jan) – Harmer (*partim*), p. 240, pl. 28, fig. 24 (not fig. 25 = *Raphitoma antonjansei* Marquet, 1998).

1944 *Raphitoma (Raphitoma) histrix* (Jan) [*sic*] – Wenz, p. 1452, fig. 4180.

1966 *Raphitoma hystrix* [*sic*] (Cristofori & Jan, 1832) – Powell, p. 125, pl. 20, figs 6, 7.

1978 *Pleurotoma hystrix* [*sic*] de Cristofori & Jan, 1832 [*sic*] – Pinna & Spezia, p. 157, pl. 14, fig. 1.

1997 *Raphitoma histrix* (Jan in Bellardi, 1847) [*sic*] – Chirli, p. 81, pl. 23, figs 5-7.

1996 *Raphitoma (Raphitoma) hystrix* [*sic*] (De Cristofori & Jan, 1832) [*sic*] – Vera-Peláez, p. 731, text-figs 39a, 74, pl. 55, figs 1, 2, 5-10.

2002 *Raphitoma (Raphitoma) hystrix* [*sic*] (De Cristofori & Jan, 1832) [*sic*] – Vera-Peláez, p. 231, pl. 7, figs I, J, pl. 15, figs I, J, pl. 17, figs G', H'.

2011 *Raphitoma histrix* (Jan in Bellardi, 1847) [*sic*] – Chirli & Linse, p. 173, pl. 60, fig. 3.

2018 *Raphitoma hystrix* [*sic*] Bellardi, 1847 [*sic*] – Brunetti & Cresti, p. 98, fig. 410.

2018 *Raphitoma histrix* Bellardi, 1847 – Giannuzzi-Savelli *et al.*, p. 6, figs 17-18A, 21A (*cum syn.*).

non 1872 *Pleurotoma hystrix* [*sic*] Jan [*sic*] – S.V. Wood, p. 41, pl. 6, fig. 3 (= *Raphitoma antonjansei* Marquet, 1998).

non 1878 *Pleurotoma histrix* Jan [*sic*] – Nyst, pl. 3, fig. 13 (= *Raphitoma antonjansei* Marquet, 1998).

non 1882 *Pleurotoma histrix* Jan [*sic*] – Nyst, p. 46 (= *Raphitoma antonjansei* Marquet, 1998).

non 1960 *Raphitoma histrix* Jan, 1832 [*sic*] – Glibert, p. 17, pl. 4, fig. 18 (= *Raphitoma antonjansei* Marquet, 1998).

non 1964 *Raphitoma hystrix* [*sic*] Jan, 1832 [*sic*] – Brébion, p. 603, pl. 14, figs 32-34 [= *Raphitoma dellabelorum* Landau *et al.*, 2020].

non 1965 *Raphitoma hystrix* [*sic*] Jan, 1832 [*sic*] – Van Reg-

teren Altena, p. 42, pl. 18, fig. 171 (= *Raphitoma antonjansei* Marquet, 1998).

non 1971 *Raphitoma (Raphitoma) hystrix* [sic] (De Cr. e Jan, 1832) [sic] – Pinna, p. 430, pl. 76, fig. 1 [= *Raphitoma echinata* (Brocchi, 1814) *sensu* AA].

Material and dimensions – Maximum height 14.0 mm, width 4.9 mm. **CO:** NHMW 2020/0171/0012 (9). **VC:** NHMW 2020/0171/0013-0014 (2), NHMW 2020/0171/0015 (2). **EL:** NHMW 2020/0171/0016 (1), NHMW 2020/0171/0017 (3).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2018, p. 6).

Discussion – As noted by Giannuzzi-Savelli *et al.* (2018, p. 9), *Pleurotoma hystrix* De Cristofori & Jan (1832, p. 10) is *nomen nudum* and thus unavailable (ICZN, 1999: Art. 12.1 & 12.3). The authorship goes to Bellardi (1847, p. 85) spelled *hystrix*, although referring to De Cristofori & Jan's taxon. Confusion regarding the type specimen was also discussed by those authors, and a neotype designated. *Raphitoma antonjansei* Marquet, 1998, *nom. emend.*, from the Pliocene North Sea Basin, but in that species the protoconch is multispiral, composed of 2.75 whorls, the last half whorl strongly carinate and the teleoconch sculpture is more coarsely reticulated composed of fewer axial and spiral elements. Although described from the North Sea Basin Pliocene, Giannuzzi-Savelli *et al.* also recorded it from the Pliocene of Italy. The *R. hystrix* species group also includes two species with a paucispiral protoconch, *R. pseudohystrix* (Sykes, 1906) and *R. dellabellaorum* Landau, Van Dingenen & Ceulemans, 2020 from the Upper Miocene and Lower Pliocene of NW France. We note that Vera-Peláez (2002, p. 233) recorded *Raphitoma (Philbertia) pseudohystrix* from the Estepona assemblage of Velerín antenna, based on an apical fragment with the protoconch preserved. The description given by the author certainly agrees with that of *R. pseudohystrix*, but unfortunately the fragment was not illustrated, and we cannot confirm its occurrence (see under that species). For further comparison of this species group see Ceulemans *et al.* (2018, p. 110, 111, table 1), Giannuzzi-Savelli

et al. (2018) and Landau *et al.* (2020, p. 71).

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Pinna, 1971; Chirli, 1997; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002); central Mediterranean, Italy (Bellardi, 1877). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Raphitoma pseudohystrix (Sykes, 1906)

- *1906 *Clathurella pseudohystrix* Sykes, p. 187.
- 1964 *Raphitoma hystrix* Jan, 1832 – Brébion, p. 603, pl. 14, figs 32-34 [*non Raphitoma hystrix* Bellardi, 1847].
- 1984 *Raphitoma pseudohystrix* Sykes, 1906 [sic] – Carrozza, p. 152, figs 1, 2.
- 1984 *Raphitoma divae* Carrozza, p. 152, figs 3, 4.
- 1986 *Raphitoma pseudohystrix* Sykes, 1906 [sic] – Bogi *et al.*, p. 27, figs 9-16.
- 1987 *Raphitoma pseudohystrix* (Sykes, 1906) – Smriglio *et al.*, p. 384, 215, pl. 1, figs 12-14.
- 2002 *Raphitoma (Philbertia) pseudohystrix* (Sykes, 1906) – Vera-Peláez, p. 233, not figured.
- 2009 *Raphitoma pseudohystrix* (Sykes, 1906) – Segers *et al.*, p. 40, 215, pl. 46, fig. 6.
- 2018 *Raphitoma pseudohystrix* (Sykes, 1906) – Poggiani & Micali, p. 203, fig. 1.
- 2018 *Raphitoma pseudohystrix* (Sykes, 1906) – Giannuzzi-Savelli *et al.*, p. 11, figs 19-20, 21B (*cum syn.*).
- non 2018 *Raphitoma pseudohystrix* (Sykes, 1906) – Ceulemans *et al.*, p. 110, pl. 5, figs 1-3 [= *Raphitoma dellabellaorum* Landau, Van Dingenen & Ceulemans, 2020]

Material and dimensions – Apical fragment. No collection number or size is given by Vera-Peláez (2002, p. 233). Locality is from Velerín antenna (2002, p. 241).

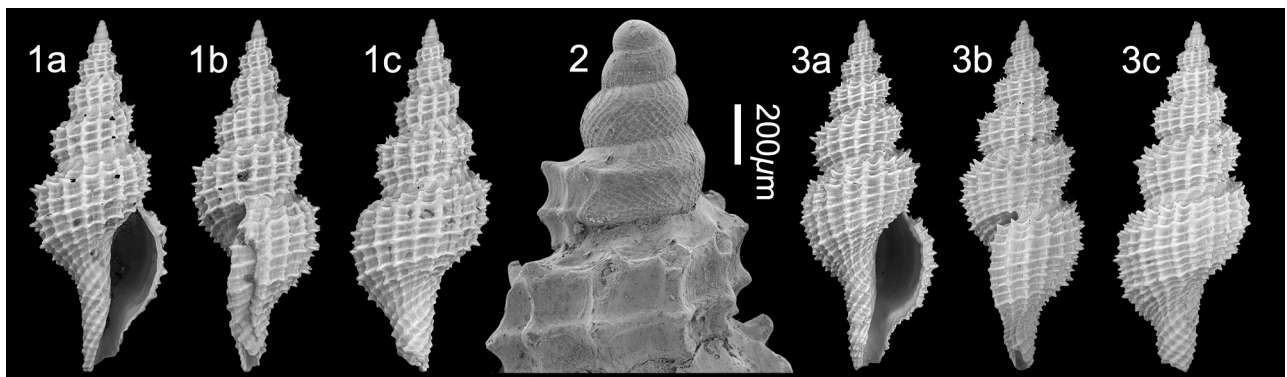


Plate 47. *Raphitoma hystrix* Bellardi, 1847; 1. NHMW 2020/0171/0013, height 10.5 mm, width 4.0 mm; 2. NHMW 2020/0171/0014, detail of protoconch. Velerín carretera, Velerín. 3. NHMW 2020/0171/0015, height 13.7 mm, width 5.2 mm (1, 3, digital images; 2, SEM image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Description – For detailed description of the species see Giannuzzi-Savelli *et al.* (2018, p. 14). Description of Estepona specimen: “*fragmento apical de la concha con la protoconcha y 3 vueltas de teleoconcha, concha turriculada-escalariforme, delgada, elevada, de vueltas estrechas, de perfil algo convexo. Desarrollo larvario no planctotrófico. Protoconcha paucispiral, de 2 vueltas turriculadas-escalariformes, pequeña. El radio nuclear ocupa la mitad del diámetro de la la vuelta, está aplanado apicalmente y desplazado abaxialmente. Las vueltas embrionarias son convexas, cuya escultura consiste en micropapilas puntiformes desarrollados en sentido espiral. Esta escultura está presente en las 2 vueltas. La última vuelta de protoconcha presenta una carena bien desarrollada adapicalmente, entre la sutura sutura adapical y la carena aparecen microcóstulas axiales filiformes prosoclinas, abapicalmente a la carena se observan microcordones espirales puntiformes. La teleoconcha es turriculada-escalariforme. Las 3 primeras vueltas presentan una escultura axial de 10 cóstulas axiales opisthoclina aplanadas lateralmente y la espiral de 2 cordones rectos sobresalientes aplanados lateralmente, la conjunción de ambas esculturas da lugar a un retículo con rectángulos, formando nodos espinosos en los puntos de intersección. Líneas de crecimiento opistolinas. Sutura superficial, sinuosa. Vueltas restantes rotas [apical fragment with protoconch and three teleoconch whorls, shell turriculate-gradate, slender, tall, with somewhat convex narrow whorls. Larval development non-planktotrophic. Protoconch paucispiral, small, composed of two turriculate-gradate whorls. Nucleus half width of the whorl, flattened, displaced abaxially. Embryonic whorls convex, entire surface bearing spirally arranged micropustules. Last protoconch whorl with well-developed carina adapically, between the suture and the carina fine punctiform spiral cordlets. Teleoconch turriculate-gradate. First three whorls with 10 opisthoclinal axial ribs flattened laterally, and 2 raised, straight spiral cords, flattened laterally, forming reticulated pattern, with spinous tubercles developed at intersections. Growth lines opisthoclinal. Suture superficial, sinuous. Remaining whorls broken].” (Vera-Peláez, 2002, p. 233).*

Discussion – Vera-Peláez (2002, p. 233) recorded *Raphitoma* (*Philbertia*) *pseudohystrix* from the Estepona assemblage of Velerín antenna, based on an apical fragment with the protoconch preserved. The description given agrees with that of *R. pseudohystrix*, but unfortunately the fragment was not illustrated, and we cannot confirm its occurrence. *Raphitoma dellabellaorum* Landau, Van Dingenen & Ceulemans, 2020 from the Upper Miocene and Lower Pliocene of NW France also has a paucispiral protoconch but differs from *R. pseudohystrix* most importantly in its spiral sculpture. There are three spirals at the protoconch/teleoconch boundary, with a fourth developing at the abapical suture immediately after the boundary, whereas there are only two spirals at the protoconch/teleoconch boundary and first two teleoconch whorls in *R. pseudohystrix*. On later whorls the spirals are more numerous and subequal in strength in *R. dellabellaorum*, whereas in *R. pseudohystrix* they are less numerous and

of alternating strength. Other differences are that on average *R. dellabellaorum* has more numerous axial ribs on last whorl 20-30 (12-29[14] for extant *R. pseudohystrix*), although their ranges overlap, and there are no denticles developed within the outer lip. Both species have 6-10 cordlets above the aperture on the last whorl (up to 9 for extant *R. pseudohystrix*), and 7-9 cords on the siphonal canal.

Today *R. pseudohystrix* is a rather deep-water species (120-700 m depth and bathyal) (Giannuzzi-Savelli *et al.*, 2018, p. 15), and associated with white coral (Smriglio *et al.*, 1987).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002). Lower Pleistocene: central Mediterranean, Italy (Giannuzzi-Savelli *et al.*, 2018). Present-day: Atlantic: Madeira (Segers *et al.*, 2009), western and central Mediterranean (Carrozza, 1984; Bogi *et al.*, 1986; Giannuzzi-Savelli *et al.*, 2018).

Raphitoma pumila (Monterosato, 1890)

Plate 48, fig. 1

- 1878 *Pleurotoma* (*Homotoma*) *reticulata* var. *pumila* Monterosato, 1878: 106 (*nomen nudum*).
- *1890 *Cordieria reticulata* var. *pumila* Monterosato, 1890, p. 187.
- 2019 *Raphitoma pumila* (Monterosato, 1890) – Giannuzzi-Savelli *et al.*, p. 58, figs 1-7.

Material and dimensions – Maximum height 11.3 mm, width 5.1 mm. CO: NHMW 2020/0171/0545-0546 (2), NHMW 2020/0171/0547 (10).

Description – For detailed description see Giannuzzi-Savelli *et al.* (2019, p. 58).

Discussion – *Raphitoma pumila* (Monterosato, 1890) is quite similar to *R. echinata* (Brocchi, 1814), but differs being squatter, with a wider apical angle, having stronger

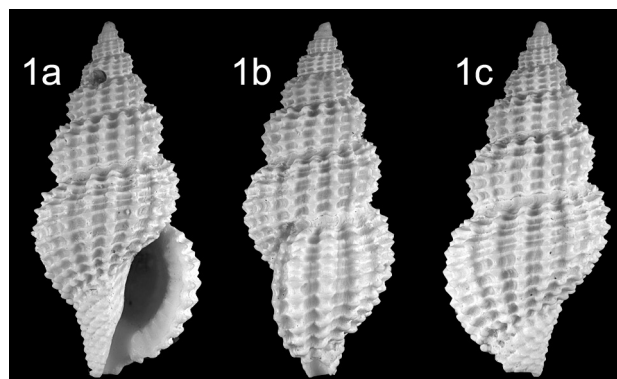


Plate 48. *Raphitoma pumila* (Monterosato, 1890); 1. NHMW 2020/0171/0546, height 9.5 mm, width 4.4 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

axial ribs, lower last whorl, less inclined suture, a thicker labial varix, and a shorter siphonal canal (*fide* Giannuzzi-Savelli *et al.* 2019, p. 59). This is the first fossil record for the species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper). Present-day: western and central Mediterranean (Giannuzzi-Savelli *et al.*, 2019).

Genus *Rimosodaphnella* Cossmann, 1916

Type species – *Murex textilis* Brocchi, 1814, by original designation, Pliocene, Italy.

1916 *Rimosodaphnella* Cossmann, p. 229.

Note – The genus *Rimosodaphnella* includes species of moderate size (up to 16 mm), tall spire, convex whorls, short last whorl and a tail-like anterior canal, cancellate sculpture of strong axial ribs crossed by narrower to equal spiral cords, and a deep reverse L-shaped anal sinus.

In the literature on European fossils, the genus has been used rather uncritically to include species with quite different protoconch and teleoconch morphology (Powell, 1966; Vera-Peláez, 2002; Landau *et al.*, 2011, *inter alia*) and the only European species that can be included in the genus with certainty is the type species. *Rimosodaphnella lappanni* Schnetler *in* Schnetler & Beyer, 1990 from the Upper Oligocene, Chattian, of Denmark is closely similar to *R. textile* (Brocchi, 1814), and might be a synonym of this rather variable species (see Bonfitto & Morassi, 2013, p. 232).

Its presence in extant faunas was reviewed by Bonfitto & Morassi (2013), who included only one eastern Atlantic species in the genus: *Pleurotoma morra* Dall, 1881, and three species in the Indo-West Pacific region. Those authors highlighted the Tethyan origin of the genus that extended its range to the Indo-West Pacific through connections to the eastern Proto-Mediterranean prior to the late Serravallian (Harzhauser *et al.*, 2002), disappeared from the Mediterranean due to climatic cooling after the Piacenzian Upper Pliocene, and today survives in the warmer waters of tropical eastern Atlantic (Bonfitto & Morassi, 2013).

Rimosodaphnella textile (Brocchi, 1814)

Plate 49, figs 1-5

- *1814 *Murex textile* Brocchi, p. 423, pl. 8, fig. 14.
- 1859 *Pleurotoma (Mangelia) Savi* Libassi, p. 31, pl. 1, fig. 24.
- 1896 *Bellardiella textilis* Br. – Cossmann, p. 128, pl. 5, figs 33-34.
- 1904 *Bellardiella? textilis* (Br.) – Sacco, p. 54, pl. 14, figs 7, 8.
- 1904 *Bellardiella? textilis* var. *recurvata* Sacco, p. 54,

pl. 14, figs 9, 10.

- 1904 *Bellardiella? textilis* var. *apertspirata* Sacco, p. 54, pl. 14, figs 11, 12.
- 1914 *Daphnella (Bellardiella) gracilis* Brocchi – Cipolla, p. 151 [47], pl. 13 [2], fig. 22.
- 1914 *Daphnella (Bellardiella) gracilis* var. *Savii* [*sic*] Libassi – Cipolla, p. 152 [48], pl. 13 [2], fig. 23.
- 1937 *Daphnella (Bellardiella) textilis* var. *raricosta* Montanaro, p. 177 [147], pl. 8 [11], figs 23, 24.
- 1944 *Daphnella (Rimosodaphnella) textilis* (Brocchi) – Wenz, p. 1455, fig. 4119.
- 1955 *Daphnella (Daphnella) (Daphnella) textile* (Brocchi 1814) – Rossi Ponchetti, p. 303, fig. 162.
- 1963 *Pleurotoma (Mangelia) Savi* Libassi – Moroni & Paonita, p. 29, pl. 2, fig. 24.
- 1966 *Rimosodaphnella textile* (Brocchi, 1814) – Powell, p. 124, pl. 20 figs 2, 3.
- 1978 *Murex textile* Brocchi, 1814 – Pinna & Spezia, p. 153, pl. 48, fig. 3.
- 1992 *Rimosodaphnella textile* (Brocchi, 1814) – Cavallo & Repetto, p. 138, fig. 373.
- 1996 *Rimosodaphnella textile* (Brocchi, 1814) – Vera-Peláez, p. 613, text-figs 32a, b, 35a, 57, pl. 45, figs 1-3, 6, 8, 10.
- 1997 *Raphitoma textilis* (Brocchi, 1814) – Chirli, p. 89, pl. 25, figs 9-12.
- 2002 *Rimosodaphnella textile* (Brocchi, 1814) – Vera-Peláez, p. 215; pl. 5, figs U, V, W, pl. 14, figs G, H.
- 2010 *Rimosodaphnella textilis* [*sic*] (Brocchi, 1814) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 64, top row centre.
- 2013 *Rimosodaphnella textilis* [*sic*] (Brocchi, 1814) – Bonfitto & Morassi, p. 231, fig. 1A.

Material and dimensions – Maximum height 9.5 mm, width 3.5 mm. **CO:** NHMW 2020/0171/0060 (14). **VC:** NHMW 2020/0171/0056-59 (4), NHMW 2020/0171/0570 (1 juvenile), NHMW 2020/0171/0571 (20). **EL:** NHMW 2020/0171/0061 (12).

Description – Shell small, fragile, slender turritiform, with tall gradate spire (apical angle 41.2-42.7°). Protoconch conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture; last half whorl weakly shouldered with arcuate axial riblets above shoulder, diagonally reticulated below (Estepona specimen; dp = 565 µm, hp = 640 µm, dp/hp = 0.88). Junction marked by sinusigera. Teleoconch of up to six weakly shouldered whorls, with moderate width, concave subsutural ramp, rounded at shoulder, convex below, separated by moderately impressed, weakly undulating suture. Axial sculpture predominant, composed of comma-shaped riblets over subsutural ramp, rounded opisthocline ribs developed at shoulder and continuing to abapical suture, slightly narrower to equal in width to their interspaces, 18-20 on penultimate whorl, overrun by narrow spirals, two on first teleoconch whorl, three on second, with single secondary cord intercalated from penultimate whorl in some specimens; spirals slightly horizontally swollen

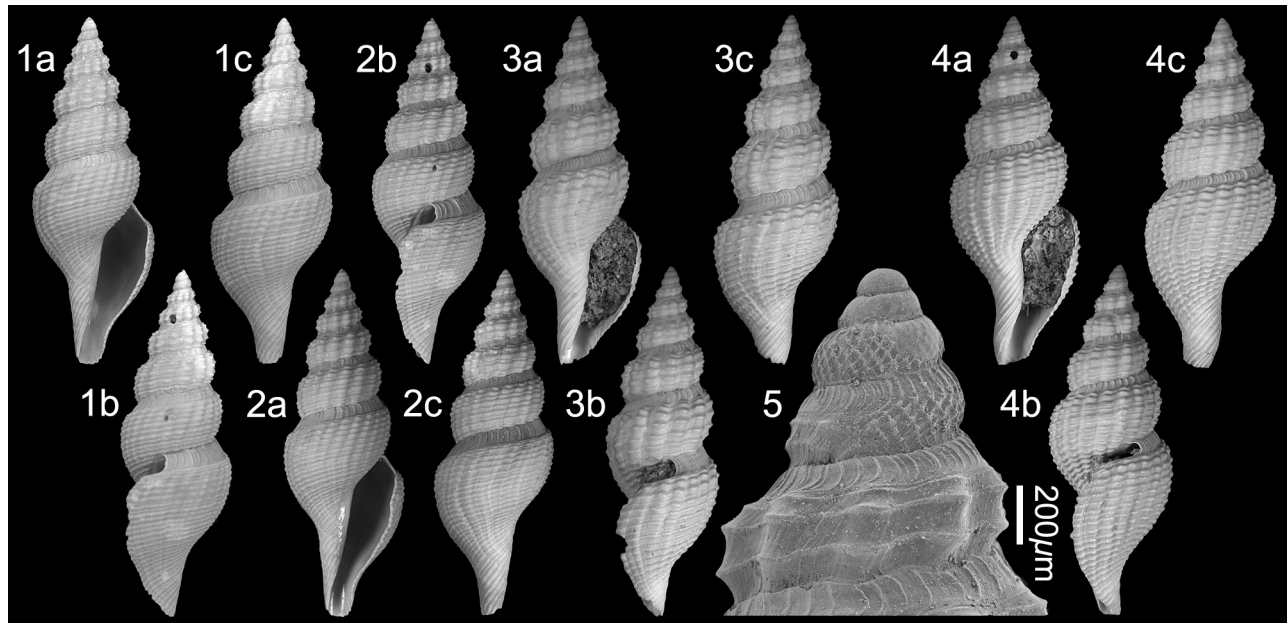


Plate 49. *Rimosodaphnella textile* (Brocchi, 1814); 1. NHMW 2020/0171/0056, height 9.8 mm, width 3.4 mm; 2. NHMW 2020/0171/0057, height 9.6 mm, width 3.3 mm; 3. NHMW 2020/0171/0058, height 9.6 mm, width 3.3 mm; 4. NHMW 2020/0171/0059, height 9.6 mm, width 3.3 mm (digital images); 5. NHMW 2020/0171/0570, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

over ribs. Last whorl 60–64% of total height, with moderate width, slightly concave subsutural ramp, convex below, shoulder weakly developed, moderately strongly constricted at base, bearing close-set narrow cords of alternating strength, axials weakening over base; siphonal fasciole with slightly stronger cords; base and fasciole not delimited. Aperture elongate-subquadrate, 44–46% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus broad, deep, reverse L-shaped, occupying entire ramp; siphonal canal long, slightly bent adaxially and recurved, unnotched. Columella smooth, weakly excavated in upper third, straight below, weakly twisted at fasciole. Columellar and parietal callus sharply delimited, forming narrow callus rim.

Discussion – *Rimosodaphnella textile* (Brocchi, 1814) is a very characteristic species, although rather variable in the strength of its sculpture. As discussed under the generic note, all other European Pliocene species placed by authors in this genus, belong elsewhere. *Daphnella* (*Bellardiella*) *textilis* var. *borealis* Kautsky, 1925 from the Middle Miocene North Sea Basin of Germany has a very similar profile and teleoconch sculpture, but the protoconch places it in the family Clathurellidae H. Adams & A. Adams, 1858, in the genus *Pleurotomoides* Bronn, 1831 (see R. Janssen & Wienrich in Wienrich, 2007, p. 688, pl. 113, fig. 3, pl. 148, fig. 6).

Distribution – Upper Miocene (Tortonian): Proto-Mediterranean, Italy (Montanaro, 1937). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Cavallo & Repetto, 1992; Chirli, 1997; Sosso

& Dell’Angelo, 2010), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002), France (Cossmann, 1896); central Mediterranean, Italy (Cipolla, 1904; Bonfitto & Morassi, 2013).

Genus *Taranis* Jeffreys, 1870

Type species – *Trophon moerchii* Malm, 1861, by original designation, present-day, Sweden.

- 1870 *Taranis* Jeffreys, p. 447.
- 1926 *Fenestrosyrinx* Finlay, p. 56, 254. Type species (by original designation): *Turris bicarinatus* Suter, 1915, Pleistocene, New Zealand.
- 1934 *Allo* Jousseume, p. 69. Type species (by monotypy): *Allo allo* Jousseume, 1934, present-day, Red Sea.
- 1934 *Feliciella* Lamy in Jousseume, p. 69. Type species (by monotypy): *Feliciella jousseumei* Lamy, 1934, present-day, Red Sea. Unnecessary substitute name for *Allo* Jousseume, 1934, by Lamy, considered to be improperly formed; *F. jousseumei* itself is a substitute name for *Allo allo*.

Note – The systematic position of the genus *Taranis* Jeffreys, 1870 within Raphitomidae Bellardi, 1875 was resolved by Bouchet *et al.* (2011, p. 286). Today this is a deeper water genus with a wide distribution in the northern Atlantic, Red Sea, Philippines, Australia, and New Zealand (Powell, 1966, p. 55).

***Taranis circumflexa* (Hornung, 1920)**

Plate 50, figs 1-4

- *1920 *Pleurotoma circumflexa* Hornung, p. 72, pl. 2, fig. 2.
 1979 *Taranis circumflexa* (Hornung) – Montefameglio *et al.*, p. 191, pl. 1, fig. 16.
 1984 *Taranis circumflexa* (Hornung, 1920) – Bernasconi & Robba, p. 295, pl. 5, fig. 5.
 1992 *Taranis circumflexa* (Hornung, 1920) – Cavallo & Repetto, p. 144, fig. 396.
 1996 *Taranis circumflexa* (Hornung, 1920) – Vera-Peláez, p. 521, text-fig. 43, pl. 41, figs 1-9.
 1997 *Taranis circumflexa* (Hornung, 1920) – Tabanelli, p. 14, pl. 1, fig. 1, pl. 2, fig. 1.
 2002 *Taranis circumflexa* (Hornung, 1920) – Vera-Peláez, p. 213; pl. 4, figs N', Ñ', O', P', pl. 12, figs M, N.
 2007 *Taranis circumflexa* (Hornung, 1920) – Della Bella & Scarponi, p. 73, figs 143-146.
 2010 *Taranis circumflexa* (Hornung, 1920) – Sosso & Dell'Angelo, p. 46, unnumbered fig. p. 62 middle row right, bottom row left.
 2018 *Taranis circumflexa* (Hornung, 1920) – Brunetti & Cresti, p. 92, fig. 374.
 2018 *Taranis circumflexa* (Hornung, 1920) – Sosso *et al.*, p. 338, figs 56-63.

Material and dimensions – Maximum height 9.5 mm, width 3.5 mm. **CO:** NHMW 2020/0171/0062 (8). **VC:** NHMW 2020/0171/0063-66 (3), NHMW 2020/0171/0067 (35).

Description – Shell small, usually squat, broad, with low spire, occasionally elevated (apical angle 42.2-55.7°). Protoconch paucispiral, of 1.5 convex whorls covered in close-set, irregular, punctiform spiral threads, with large nucleus (Estepona specimen; dp = 535 µm, dp = 505 µm, dp/hp = 1.06, dV1 = 440 µm, dn = 270 µm). Junction with teleoconch marked by series of sinuous axial riblets, initially closely spaced, wider spaced abapically. Teleoconch of up to 4.5 strongly angular whorls, with sharp, elevated peripheral keel placed mid-whorl, whorl profile concave above and below. Axials sharp, about 20 on penultimate whorl, prosocline above keel, opisthocline below, weakly spinous over keel. Surface covered in fine irregular micro-pustules. Last whorl 58-66% of total height, with broad, concave subsutural ramp, sharply angled at keel, concave immediately below, rounded at base, strongly constricted at siphonal fasciole, bearing 4 or 6 cords over base, very weak cords over fasciole. Aperture ovate-pyriform, 37-47% of total height; anal sinus broad V-shaped, with apex placed at peripheral keel; siphonal canal short, bent adapically, unnotched. Columella smooth, broadly excavated in upper half, straight below, twisted at fasciole. Columellar and parietal callus forming narrow callus rim.

Discussion – This is a very characteristic species that cannot be confused with any other Estepona raphitomid. Most specimens are rather squat, although the occasional specimen is taller spired (Pl. 50, fig. 1). The axial sculpture is relatively constant; the most variable character being the spiral sculpture over the base.

The genus *Taranis* Hornung, 1920 is not speciose in Europe. In the fossil record *Taranis dellabellai* Tabanelli,

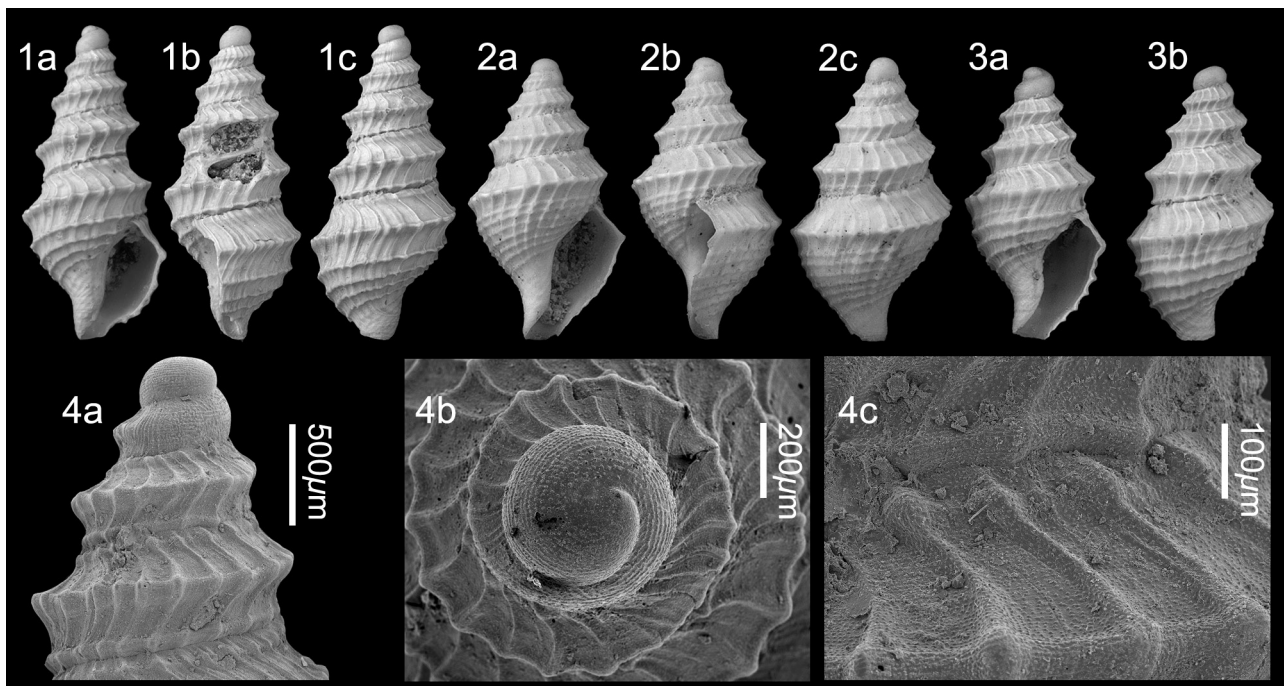


Plate 50. *Taranis circumflexa* (Hornung, 1920); 1. NHMW 2020/0171/0063, height 4.7 mm, width 1.9 mm; 2. NHMW 2020/0171/0064, height 4.3 mm, width 2.0 mm; 3. NHMW 2020/0171/0065, height 3.7 mm, width 1.7 mm (digital images); 4. NHMW 2020/0171/0066, 4a-b, detail of protoconch, 4c detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1997 from the Pleistocene of Italy has a paucispiral protoconch with similar microsculpture but has a more depressed first whorl. According to Tabanelli (1997, p. 11) the protoconch micropustular sculpture is finer in *T. dellabellae* and the micropustules on the first teleoconch whorl are loosely arranged in spiral rows, as opposed to randomly in *T. circumflexa*. This last difference is not obvious in the protoconch illustrations given by Della Bella & Scarponi (2007, figs 143 vs 147). The peripheral keel is not as prominent and placed lower, closer to the abapical suture, at about one-third whorl height as opposed to mid-whorl in *T. circumflexa*, resulting in *T. dellabellae* having a more regularly conical spire profile.

In the extant faunas the European species all have paucispiral protoconchs. *Taranis borealis* Bouchet & Warén, 1980 is immediately separated by its fine reticulated microsculpture. *Taranis laevisculpta* Monterosato, 1880 and *T. moerchii* (Malm, 1861) (*T. alexandrina* Sturany 1896 is considered a junior subjective synonym) both have similar protoconch microsculpture, but *T. moerchii* has much finer teleoconch sculpture. *Taranis laevisculpta* is more similar, but is even squatter, the peripheral keel is also placed mid-whorl, but it less elevated, and there are fewer cords over the base. The Caribbean *T. malmi* (Dall, 1889) has a multispiral protoconch, with coarse obliquely reticulated microsculpture (see Bouchet & Warén, 1980). *Taranis circumflexa* inhabited the lower circumlittoral to upper bathyal zone (Della Bella & Scarponi, 2007, p. 74). In Estepona it is found in both the shallow and deeper water deposits, although far more abundant in the deeper-water ones.

Distribution – Lower Pliocene: central Mediterranean, Italy (Hornung, 1920; Montefameglio *et al.*, 1979; Bernasconi & Robba, 1984; Cavallo & Repetto, 1992; Della Bella & Scarponi, 2007; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018; Sosso *et al.*, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002). Lower Pleistocene: central Mediterranean, Italy (Tabanelli, 1997).

Genus *Teretia* Norman, 1888

Type species – *Pleurotoma teres* Reeve, 1844, by typification of replaced name, present-day, Mediterranean.

1883 *Teres* Bucquoy, Dautzenberg & Dollfus, p. 187. Type species (by original designation): '*Pleurotoma anceps* Eichwald, 1830', present-day, Mediterranean. Junior homonym of *Teres* Boettger, 1878 [Clausiliidae].

1888 *Teretia* Norman, p. 8. Type species (by typification of replacement name): *Pleurotoma teres* (Reeve, 1844), present-day, Mediterranean. Proposed as an emendation of *Teres* Bucquoy, Dautzenberg & Dollfus, 1883, and later used as a substitute name for it as *Teres* is preoccupied. Bucquoy, Dautzenberg & Dollfus fixed *Pleurotoma anceps* Eichwald, 1830, as the type species of *Teres*, but

they used the name *P. anceps* for a present-day Mediterranean species and listed '*Pleurotoma teres* Forbes (non Reeve)' in its synonymy. However, *Pleurotoma anceps* Eichwald, 1830, is a Miocene species (*hoc opus*; see under *T. teres*). The name *Pleurotoma teres* Reeve, 1844, was established for the present-day species.

Note – In the Estepona assemblages the genus *Teretia* Norman, 1888 is represented by eight species, one of which is described as new. To our knowledge, this is the highest diversity of the genus in any single European assemblage. Today the genus is associated with lower shelf and upper bathyal habitats of the NE Atlantic and the Mediterranean (Bouchet & Warén, 1980, p. 82). Almost all the specimens come from the deeper-water assemblage of Velerín carretera. The protoconch is multispiral with fine diagonal reticulated microsculpture in all species. They differ in their teleoconch sculpture, profile and presence/absence and type of micropustules that cover the teleoconch in some species.

The Estepona species of *Teretia* can be separated into two groups: those with prominently carinate whorls, *T. elegantissima* (Foresti, 1868), *T. inflatissima* nov. sp., *T. monterosatoi* (Cipolla, 1914), *T. pentacariniifera* Vera-Peláez, 2002 and *T. turritelloides* (Bellardi, 1847) and those without a prominent carina *T. cf. multicingula* (Seguenza, 1880), *T. policarinarum* Vera-Peláez, 2002, and *T. teres* (Reeve, 1844).

***Teretia elegantissima* (Foresti, 1868)**

Plate 51, figs 1-3

- *1868 *Pleurotoma elegantissima* Foresti, p. 60, pl. 2, figs 10-13.
- 1877 *Clinura elegantissima* (Foresti) – Bellardi, p. 208, pl. 7, fig. 2.
- 1997 *Teretia monterosatoi* (Cipolla, 1914) – Chirli (*partim*), p. 95, pl. 27, fig. 10 only [not fig. 8-9 = *T. monterosatoi* (Cipolla, 1914)].
- 2003 *Teretia elegantissima* (Foresti, 1868) – Brunetti & Vecchi, p. 50, pl. 1, figs 1-6, pl. 3, fig. 5.
- 2010 *Teretia elegantissima* (Foresti, 1868) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 64, middle row left.

Material and dimensions – Maximum height 13.3 mm, width 6.0 mm. **CO:** NHMW 2020/0171/0078 (1). **VC:** NHMW 2020/0171/0079-81 (3), NHMW 2020/0171/0082 (2).

Description – Shell medium sized, fragile, broadly turritiform, with tall, gradate pagodiform spire (apical angle 44.8-54°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture, last quarter whorl carinate (Estepona specimen; dp = 720 µm, hp = 1130 µm, dp/hp = 0.64). Teleoconch of up to five extremely strongly carinate whorls, with very broad, concave subsutural ramp,

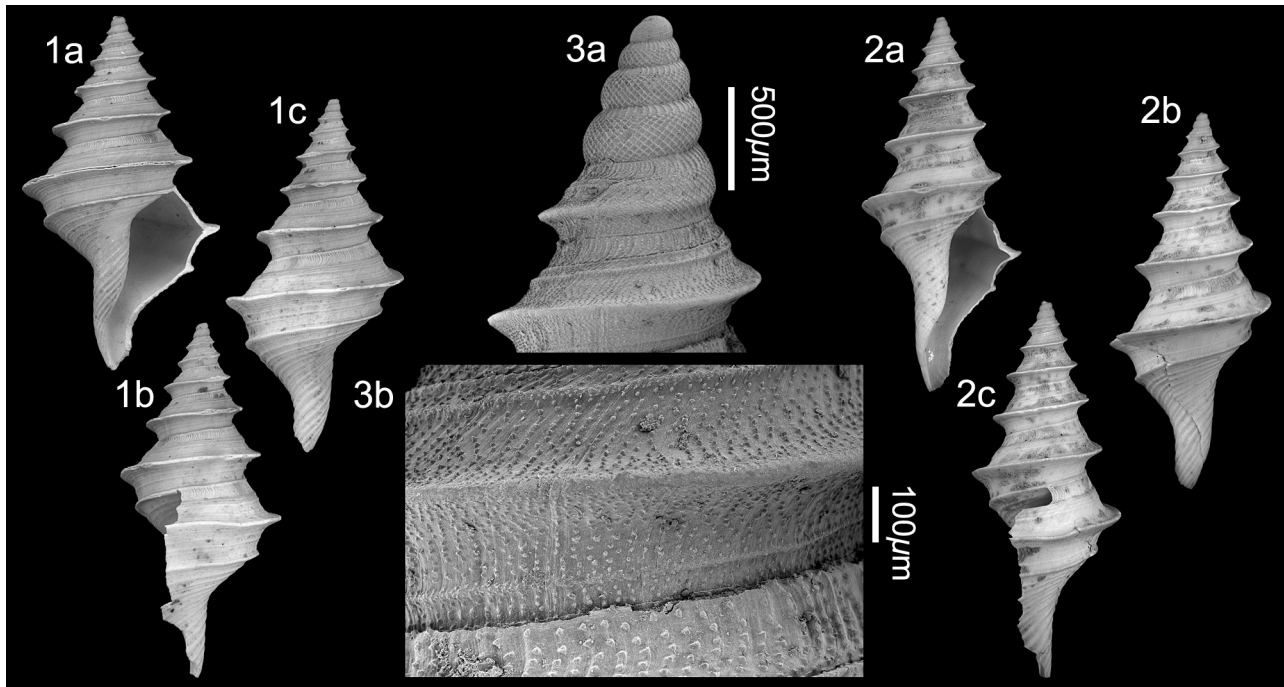


Plate 51. *Teretia elegantissima* (Foresti, 1868); 1. NHMW 2020/0171/0079, height 11.4 mm, width 5.7 mm; 2. NHMW height 10.9 mm, width 4.9 mm (digital images); 3. NHMW 2020/0171/0066, 3a, detail of protoconch, 3b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

sharply carinate at shoulder, strongly concave below, separated by narrowly impressed, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped axial riblets, cut by extremely fine spiral threads finely beading riblets. Spiral sculpture on first teleoconch whorl of three cords; two finer cords adjacent to each suture, mid-cord elevated and carinate; abapically further weak cords developed on outer two thirds of subsutural ramp and below shoulder; penultimate whorl with up to five weak cords over subsutural ramp, shoulder carina forming extremely elevated keel, two weak cords below shoulder. Surface covered in very fine micropustules arranged in spiral rows. Last whorl 64–66% of total height, with shape and sculpture as described above, extremely strongly carinate at shoulder, convex below, with second weaker carina developed at level of insertion outer lip delimiting strongly constricted base; base and siphonal fasciole with slightly stronger cords. Aperture ovate, 49–50% of total height; outer lip very thin (edge incomplete), angular at shoulder carina, without varix, smooth within; anal sinus very deep, reverse L-shaped; siphonal canal long, recurved, bent abaxially, unnotched. Columella smooth, moderately excavated in upper third, straight below, strongly twisted at fasciole. Columellar and parietal callus reduced to broad, thin callus wash, extending onto venter, but not obscuring spiral sculpture on venter.

Discussion – *Teretia elegantissima* (Foresti, 1868) has the most strongly keeled whorls of all the Estepona *Teretia* species. It is most like *T. monterosatoi* (Cipolla, 1914), which also has strongly keeled whorls, but apart from the keel being even stronger, in *T. elegantissima* only

the cord at the carina is well developed, whereas later adult whorls in *T. monterosatoi* have five prominent spiral cords. *Teretia candela* Horro & Rolán, 2017 from the present-day Canaries and West Sahara was compared to *T. elegantissima* in its original description, but the central carina is far more prominent in the extinct species.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1997; Brunetti & Vecchi, 2003; Sosso & Dell’Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Brunetti & Vecchi, 2003).

***Teretia inflatissima* nov. sp.**

Plate 52, figs 1–2

Type material – Holotype NHMW 2020/0171/0083, height 4.8 mm, width 3.2 mm; paratype 1 NHMW 2020/0171/0084, height 3.6 mm, width 2.4 mm; paratype 2 NHMW 2020/0171/0085, height 7.1 mm, width 5.0 mm.

Other material – Maximum height 7.1 mm, width 5.0 mm. VC: NHMW 2020/0171/0086 (1).

Type locality – Velerín carretera, Estepona, Andalusia, S. Spain.

Type stratum – unnamed beds, Lower Piacenzian age, Upper Pliocene.

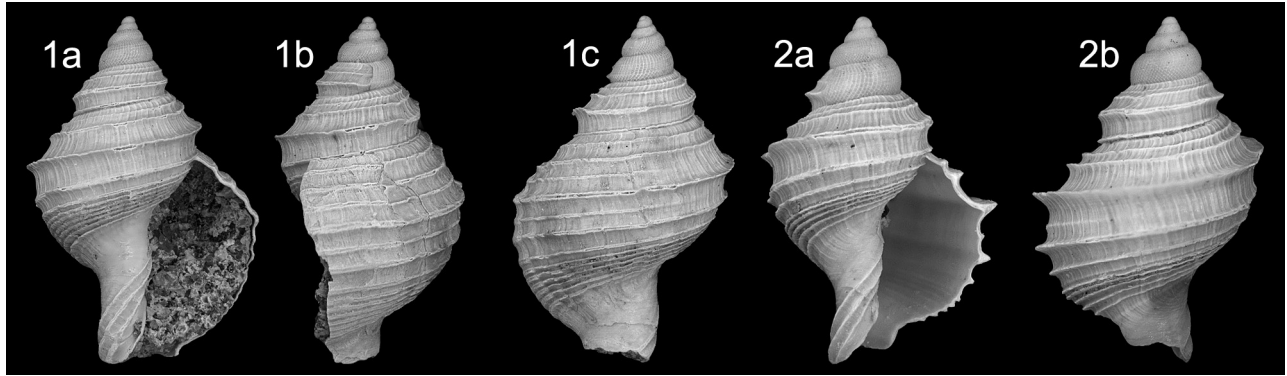


Plate 52. *Teretia inflatissima* nov. sp.; 1. **Holotype** NHMW 2020/0171/0083, height 4.8 mm, width 3.2 mm; 2. **Paratype 1** NHMW 2020/0171/0084, height 3.6 mm, width 2.4 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Pliocene, Upper Pliocene.

Etymology – Latin ‘*inflatus, -a*’ adjective, meaning swollen, using superlative, reflecting strongly globose profile. *Teretia* gender feminine.

Diagnosis – *Teretia* species of small size, strongly inflated last whorl, with four spiral cords on penultimate whorl: two on subsutural ramp, third forming shoulder, fourth above lower suture, base with series of seven close-set spirals, smooth neck between basal spirals and four cords on siphonal fasciole. No teleoconch microsculpture.

Description – Shell small, fragile, very broadly globose turritiform, with low spire (apical angle 65.4–66.6°). Protoconch relatively broad for genus, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture, last quarter whorl weakly carinate. Teleoconch of up to two carinate whorls, with broad, weakly convex subsutural ramp, sharply carinate at shoulder placed just below mid-whorl, concave below, separated by narrowly impressed, linear suture. Spiral sculpture on first teleoconch whorl of four spiral cords; adapical two cords closer-spaced, placed on subsutural ramp, upper cord weakest, third cord sharp, carinate, forming shoulder, fourth cord just above suture. Close-set, orthocone, shallow comma-shaped axial riblets in all spiral interspaces. No microsculpture developed. Last whorl greatly inflated, about 75% of total height, sculpture as described above with two closer-set cords on subsutural ramp, strongly carinate at sharp shoulder cord, broadly convex below, fourth cord placed at level of insertion of outer lip delimiting strongly constricted base; series of seven close set cords cover adapical two-thirds of base, lower third forming distinct smooth neck between base and siphonal fasciole bearing four further cords. Aperture very broad, ovate, about 59% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus very deep, reverse L-shaped; siphonal canal short, slightly recurved, broadly notched at tip. Columella moderately excavated in upper third, straight below, strongly twisted at fasciole; spiral sculpture on venter running into aperture. Columellar and parietal callus not developed.

Discussion – *Teretia inflatissima* nov. sp. is far more globose than any of its relatively slender fusiform congeners in the Estepona assemblages and differs in its basal and fasciolar sculpture. Most *Teretia* species bear more or less sharp cords on the base and siphonal fasciole, usually weakening and closer set abapically. In *T. inflatissima* the adapical two-thirds of the base bear a series of close-set cords that are less sharp than is typical for the genus, and there is a smooth neck between the basal cords and four stouter cords over the siphonal fasciole. This form of sculpture is not seen in any other European extinct or extant *Teretia* species. Moreover, the surface does not bear any micropustules.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Teretia monerosatoi (Cipolla, 1914)

Plate 53, figs 1-2

- 1859 *Pleurotoma Turritelloides* Bell. – Libassi, p. 33 [non *Pleurotoma turritelloides* Bellardi, 1847].
- *1914 *Daphnella (Teretia) Monerosatoi* Cipolla, p. 160 [56], pl. 14 [3], fig. 6 [nom. nov. pro *Pleurotoma turritelloides* Libassi, 1859, non *Pleurotoma turritelloides* Bellardi, 1847].
- 1997 *Teretia monerosatoi* (Cipolla, 1914) – Chirli (*partim*), p. 95, pl. 27, figs 8-9 [not fig. 10 = *T. elegantissima* (Foresti, 1868)].
- 2003 *Teretia monerosatoi* (Cipolla, 1914) – Brunetti & Vecchi, p. 54, pl. 1, figs 7-9, pl. 3, fig. 4.
- 2004 *Teretia monerosatoi* (Cipolla, 1914) – Repetto & Lacroce, p. 194, 200, pl. 1, fig. 5.
- 2008 *Teretia monerosatoi* (Cipolla, 1914) – Chirli & Richard, p. 70, pl. 14, fig. 2.

Material and dimensions – Maximum height 8.7 mm, width 3.4 mm. **CO:** NHMW 2020/0171/0095 (12). **VC:** NHMW 2020/0171/0096-97 (2), NHMW 2020/0171/0098 (4).

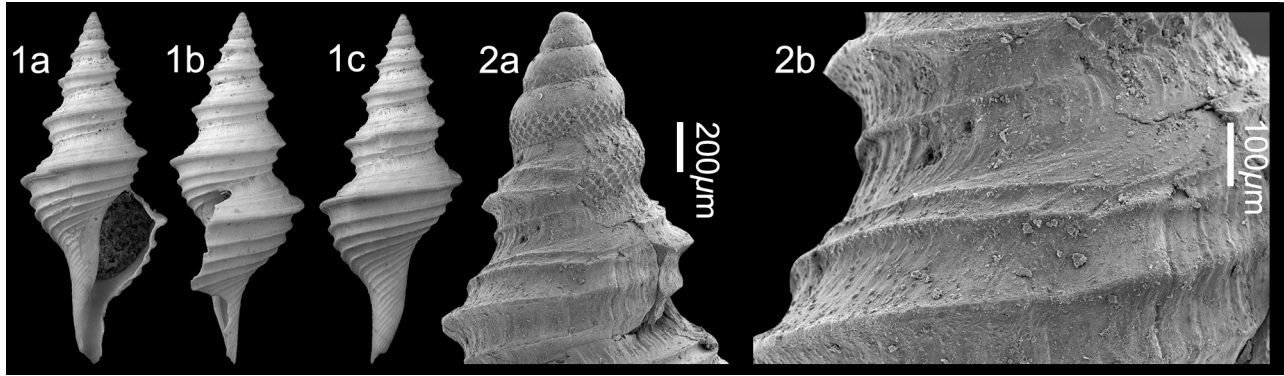


Plate 53. *Teretia monterosatoi* (Cipolla, 1914); 1. NHMW 2020/0171/0096, height 8.5 mm, width 3.2 mm (digital image); 2. NHMW 2020/0171/0097, 2a, detail of protoconch, 2b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell small, fragile, moderately broadly turritiform, with tall, gradate spire (apical angle about 43.3°). Protoconch tall, conical multispiral, of four convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture, last quarter whorl carinate (Estepona specimen; $dp = 530 \mu\text{m}$, $hp = 785 \mu\text{m}$, $dp/hp = 0.66$). Teleoconch of up to five strongly carinate whorls, with broad, concave subsutural ramp, sharply carinate at shoulder, concave below, separated by superficial, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped axial riblets. Remaining sculpture of sharp elevated carinate cords; on first teleoconch whorl three cords, placed just below and above suture, and far more elevated cord mid-whorl. Abapically two further weaker cords develop, one at lateral edge of axially sculptured medial portion of subsutural ramp, second at abapical suture, so that last two spire whorls bear five sharp cords, central cord, placed mid-whorl, becomes broader and even more elevated, delimiting periphery. Surface covered in very fine, scattered micropustules. Last whorl with shape and sculpture as described above, strongly carinate at shoulder, convex below, moderately constricted at base, with two more cords developed over base, further cords closer-set and less sharp over siphonal fasciole. Aperture broad, ovate, about 50% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus deep, reverse L-shaped; siphonal canal long, weakly recurved, unnotched. Columella smooth, broadly and weakly excavated, moderately twisted at fasciole. Columellar and parietal callus weakly thickened, sharply delimited, forming broad callus rim extending somewhat onto venter in columellar region.

Discussion – *Teretia monterosatoi* (Cipolla, 1914) is separated from its Estepona congeners in having the medial carina extremely sharp and elevated and somewhat thickened, much more so than in *T. pentacarinifera* Vera-Peláez, 2002 or *T. teres* (Forbes, 1844), which also have carinate whorls. Like *T. pentacarinifera*, it has scattered micropustular sculpture, absent in *T. teres*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Repetto & Lacroce, 2004). Upper Pliocene: west-

ern Mediterranean, Estepona Basin, Spain (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Cipolla, 1914).

Teretia cf. multicingula (Seguenza, 1880)

Plate 54, fig. 1

cf. *1880 *Homotoma multicingula* Seguenza, p. 258, pl. 16, fig. 21.

cf. 2003 *Teretia multicingula* (Seguenza, 1879 [sic]) – Brunetti & Vecchi, p. 52, pl. 2, fig. 11.

2018 *Teretia multicingula* (Seguenza, 1880) – Brunetti & Cresti, p. 100, fig. 424.

Material and dimensions – Maximum height 6.6 mm, width 2.8 mm. **CO:** NHMW 2020/0171/0099 (1), NHMW 2020/0171/0100 (5).

Description – Shell small, fragile, broadly turritiform, with tall, gradate spire (apical angle about 42.2°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture, last quarter whorl carinate. Teleoconch of up to five convex whorls; subsutural ramp narrow, slightly concave, shoulder rounded, poorly delimited, convex below, separated by narrowly impressed, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped growth lines. Remaining sculpture of low cords; three at teleoconch junction, central cord slightly stronger. On second to penultimate whorl two weaker cords on abapical half of subsutural ramp, stronger shoulder cord, two slightly weaker cords below; very fine, crowded opisthocline riblets composed of rows of micropustules present in all spiral interspaces. Last whorl about 60% of total height; subsutural ramp narrow, strongly rounded below, moderately constricted at base; further close-set, subequal cords over base and siphonal fasciole; base and fasciole not delimited. Aperture ovate, about 42% of total height; outer lip thin, sharp edged, without varix, smooth within; anal sinus deep, reverse L-shaped; siphonal canal moderately long, weakly recurved, unnotched. Columella smooth, strongly exca-

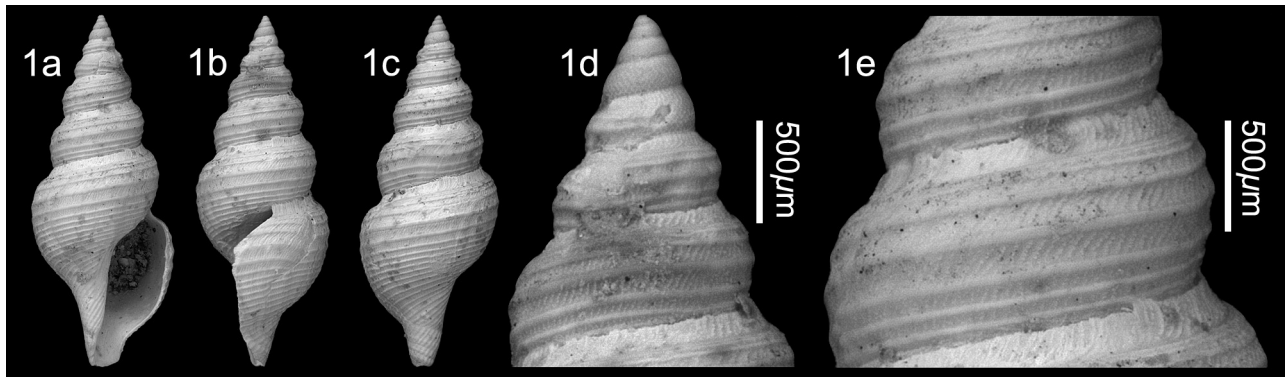


Plate 54. *Teretia cf. multicingula* (Seguenza, 1880); 1. NHMW 2020/0171/0099, height 6.6 mm, width 2.8 mm, 1d, detail of protoconch, 1e, detail of teleoconch sculpture (digital image). Velerín carretera, Velerín, Estepona, Lower Pliocenic, Upper Pliocene.

vated in upper third, straight below, weakly twisted at fasciole. Columellar and parietal callus weakly thickened, sharply delimited, narrow callus rim.

Discussion – As far as we are aware, after the original description, this species has only been recorded by Brunetti & Cresti (2018, fig. 424). The Estepona specimen is undoubtedly conspecific with that illustrated by Brunetti & Cresti. Seguenza's (1880, pl. 16, fig. 21) original drawing was refigured by Brunetti & Vecchi (2003, pl. 2, fig. 11). In most shell characters the specimens are comparable, but Seguenza's specimen has closer-set spiral cords. In the absence of further comparative material revealing the intraspecific sculptural variability, we are unsure if they represent the same species.

Teretia multicingula (Seguenza, 1880) is immediately separated from all its congeners in having very fine and strongly opisthocline axial riblets composed of rows of micropustules in all the spiral interspaces, except immediately below the suture on the adapical half of the subsutural ramp. The cords are also lower, especially the shoulder cord that is hardly stronger than the rest and not carinate.

In profile and sculpture *T. multicingula* is very similar to *T. strongyla* (Dall, 1927) (see Horro & Rolán, 2017, fig. 3) from the western Atlantic, but that species lacks the prominent, crowded opisthocline riblets seen between the spiral cords in the Estepona specimen. The cords also seem to be more regular in strength and spacing in *T. strongyla*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

***Teretia pentacarinifera* Vera-Peláez, 2002**

Plate 55, figs 1-2

*2002 *Teretia pentacarinifera* Vera-Peláez, p. 223, pl. 6, figs I, J, pl. 17, figs X, Y.

Material and dimensions – Maximum height 8.3 mm, width

3.3 mm. **VC:** NHMW 2020/0171/0087-88 (2), NHMW 2020/0171/0089 (22). **EL:** NHMW 2020/0171/0090 (4).

Description – Shell small, fragile, moderately broadly turritiform, with tall, gradate spire (apical angle about 41°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (dp = 580 µm, hp = 870 µm, dp/hp = 0.67). Teleoconch of up to five convex carinate whorls, with broad, subsutural ramp, carinate at shoulder, weakly convex below, separated by superficial, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped axial growth lines. Remaining sculpture of sharp elevated carinate cords; on first teleoconch whorl three cords, placed just below and above suture, and more elevated cord mid-whorl. Abapically two further cords develop, one at lateral edge of axially sculptured medial portion of subsutural ramp, second at abapical suture, so that last two spire whorls bear five sharp cords, middle cord, placed mid-whorl, sharper and more elevated, delimiting periphery. Surface covered in very fine, scattered micropustules. Last whorl about 62% of total height, with shape and sculpture as described above, rounded below shoulder carina, strongly constricted at base, with four more cords developed over base, further cords closer-set and less sharp over siphonal fasciole; base and fasciole not delimited. Aperture ovate, 45% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus deep, reverse L-shaped; siphonal canal moderate length, straight, unnotched. Columella smooth, moderately excavated in upper third, straight below, hardly twisted at fasciole. Columellar and parietal callus not thickened, sharply delimited forming narrow callus rim.

Discussion – *Teretia pentacarinifera* Vera-Peláez, 2002 differs from *Teretia teres* (Forbes, 1844), with which it coexists in the Estepona assemblages, in having five primary cords on the penultimate and last whorl above the level of the insertion of the outer lip, in lacking secondary spirals, and in having micropustular sculpture, absent in *T. teres*. Vera-Peláez (2002, p. 223) placed the specimen from the Pliocene of Italy illustrated by Cavallo & Repet-

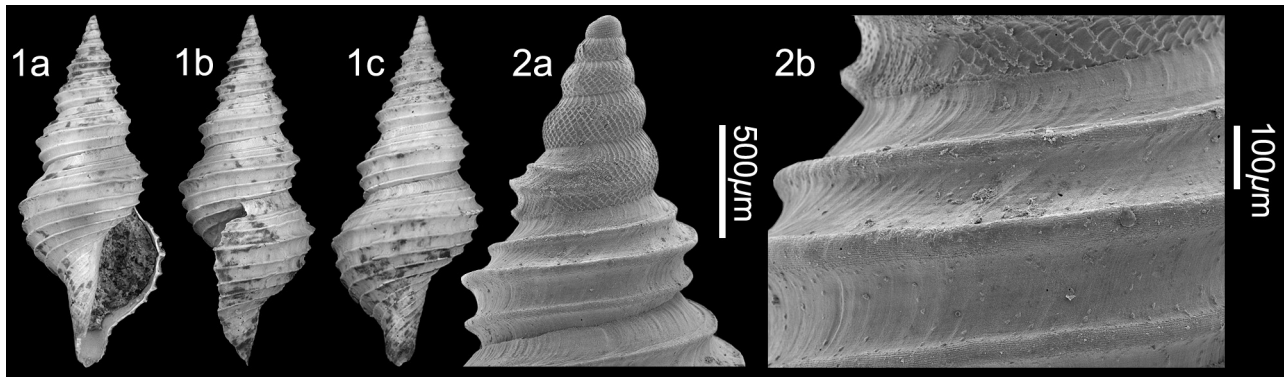


Plate 55. *Teretia pentacarinifera* Vera-Peláez, 2002; 1. NHMW 2020/0171/0087, height 7.7 mm, width 3.0 mm (digital image); 2. NHMW 2020/0171/0088, 2a, detail of protoconch, 2b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

to (1992, p. 134, fig. 356) as *Stenodrillia sulcinensis* (Bellardi, 1877) in their chresonymy of *T. pentacarinifera*. A syntype of *S. sulcinensis* from the Miocene of Italy was illustrated by Ferrero Mortara *et al.* (1981, pl. 13, fig. 9) and seems to be a *Microdrillia* Casey, 1903 species. The specimen figured by Cavallo & Repetto does seem to be a *Teretia* species, but not *T. pentacarinifera*, which has sharper cords and especially a more carinate periphery, and, as the trivial name would suggest, five primary cords, whereas the specimen illustrated by Cavallo & Repetto has more numerous cords (about 8 on the last whorl) that are lower and more rounded.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

***Teretia policarinarum* Vera-Peláez, 2002**

Plate 56, figs 1-3

*2002 *Teretia policarinarum* Vera-Peláez, p. 223, pl. 6, figs G, H, pl. 17, figs V, W.

Material and dimensions – Maximum height 9.1 mm, width 3.3 mm. CO: NHMW 2020/0171/0091-0093 (3), NHMW

2020/0171/0094 (7). VC: NHMW 2020/0171/0631 (1).

Description – Shell small, fragile, slender turritiform, with tall, gradate spire (apical angle 37-37.5°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (dp = 540 µm, hp = 840 µm, dp/hp = 0.64). Teleoconch of up to six convex whorls, with relatively narrow, subsutural ramp, rounded at poorly delimited shoulder, regularly convex below, separated by narrowly impressed, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped growth lines. Remaining sculpture of narrow cords; on first teleoconch whorl three cords, adapical two close-set, mid-cord stronger, abapical just above suture. Abapically further cords develop, penultimate whorl with five primary cords, shoulder cord slightly stronger, and secondary cords of irregular strength intercalated: secondary above shoulder cord strongest. Microsculpture of scattered micropustules present. Last whorl 53-59% of total height, with shape and sculpture as described above, rounded at shoulder, strongly constricted at base, with one or two secondaries of irregular strength in interspaces mid-whorl, secondaries above and below shoulder cord relatively strong, five more closer-set primary cords over base, further weaker cords

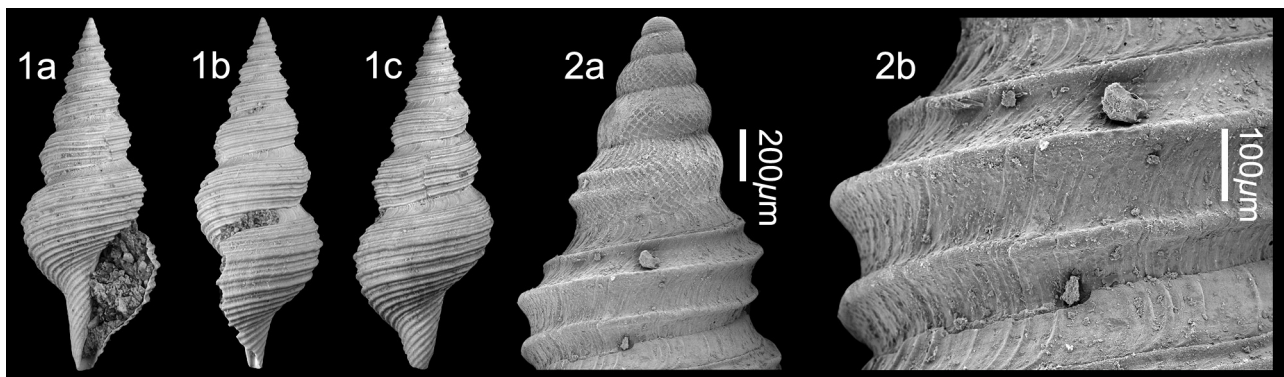


Plate 56. *Teretia policarinarum* Vera-Peláez, 2002; 1. NHMW 2020/0171/0091, height 7.0 mm, width 2.7 mm (digital images); 3. NHMW 2020/0171/0093, 3a, detail of protoconch, 3b, detail of teleoconch microsculpture (SEM image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

over siphonal fasciole; base and fasciole not delimited. Aperture ovate, 36-42% of total height; outer lip very thin (incomplete), without varix, smooth within; anal sinus deep, reverse L-shaped; siphonal canal moderate length, weakly recurved, unnotched. Columella smooth, moderately excavated in upper third, straight below, slightly twisted at fasciole. Columellar and parietal callus not thickened, well delimited, forming broad indented rim extending over medial border of venter in columellar region.

Discussion – *Teretia polycarinatum* Vera-Peláez, 2002 is like *T. teres* (Forbes, 1844), in having weakly carinate whorls, but differs in having five primary spirals on the penultimate whorl with a few relatively strongly developed secondaries, whereas *T. teres* has three strong cords (fourth in apposition with the suture) and much weaker secondary sculpture, and in having micropustular sculpture over the teleoconch. In having five primary cords it is similar to *T. pentacarinifera* Vera-Peláez, 2002, but in that species the whorls are more strongly carinate at the shoulder, the primary spirals are sharper, and secondary spirals are absent.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

Teretia teres (Reeve, 1844)

Plate 57, figs 1-3

- *1844 *Pleurotoma teres* Forbes in Reeve, pl. 19, sp. 161.
- 1844 *Pleurotoma teres* Forbes in Reeve, p. 412, pl. 10 fig. 3
- 1845 *Fusus La Viae* Calcara, p. 281.
- 1851 *Mangelia teres* Forbes – Forbes & Hanley, p. 462, pl. 113, figs 1, 2.
- 1859 *Mangelia teres* Forbes – G.B. Sowerby II, pl. 19 fig. 7
- 1859 *Mangelia teres* var. *alba* Jeffreys, p. 199.
- 1846 *Pleurotoma boreale* [sic!] Lovén, p. 14.
- 1862 *Pleurotoma minutum* var. *polyzonatum* Brugnone, p. 17, fig. 10.
- 1878 *Raphitoma anceps* Eichw. – Sars, p. 219, pl. 17 fig. 9 [non *Teretia anceps* (Eichwald, 1830)].
- 1882 *Pleurotoma anceps* Eichwald – Bucquoy *et al.*, p. 87, fig. 1 [non *Teretia anceps* (Eichwald, 1830)].
- 1891 *Pleurotoma anceps* Eichwald – Locard, p. 52 fig. 37 [non *Teretia anceps* (Eichwald, 1830)].
- 1912 *Clathurella anceps* var. *soluta* Marshall, p. 297.
- 1973 *Philbertia teres* (Forbes, 1844) – Hubendick & Warén, p. 43, figs 189, 190.
- 1976 *Teretia anceps* (Eichwald) – Pavia, p. 114, pl. 8, figs 25, 26 [non *Teretia anceps* (Eichwald, 1830)].
- 1980 *Teretia teres* (Forbes, 1844) – Bouchet & Warén, p. 81, figs 168, 229.
- 1984 *Teretia teres* (Reeve, 1844) – Fretter & Graham, p. 543, figs 373, 374.
- 1987 *Teretia teres* (Forbes, 1844) – Smriglio *et al.*, p. 384, pl. 1, fig. 15.
- 1988 *Teretia teres* (Reeve, 1844) – Graham, p. 462, fig. 194.

- 1996 *Teretia anceps* (Eichwald, 1830) – Vera-Peláez, p. 630, pl. 51, figs 1-10.
- 1997 *Teretia teres* (Reeve, 1844) – Chirli, p. 96, pl. 27, figs 11, 12.
- 2001 *Teretia teres* (Forbes, 1844) – Cachia *et al.*, p. 71, pl. 10, fig. 12.
- 2002 *Teretia anceps* (Eichwald, 1830) – Vera-Peláez, p. 223, pl. 14, figs K, L [non *Teretia anceps* (Eichwald, 1830)].
- 2003 *Teretia anceps* (Eichwald, 1830) – Brunetti & Vecchi, p. 52, pl. 2, figs 1-2, pl. 3, figs 1, 6 [non *Teretia anceps* (Eichwald, 1830)].
- 2003 *Teretia teres* (Forbes, 1844) – Brunetti & Vecchi, p. 52, pl. 2, figs 8, 9, pl. 3, fig. 2.
- 2010 *Teretia teres* (Forbes in Reeve, 1844) – Sosso & Dell'Angelo, p. 48, unnumbered fig. p. 64, middle row.
- 2011 *Teretia teres* (Forbes, 1844) – Hernández *et al.*, p. 232, pl. 79P-S, 80 U-V.
- 2011 *Teretia teres* (Forbes, 1844) – Chirli & Linse, p. 176, pl. 62, fig. 2.
- 2011 *Teretia anceps* (Eichwald, 1830) – Landau *et al.*, p. 35, pl. 18, fig. 7 [non *Teretia anceps* (Eichwald, 1830)].
- 2016 *Teretia teres* (Forbes, 1844) – Negri & Corselli, p. 68, figs 15m-p.
- 2017 *Teretia teres* (Forbes, 1844) – Horro & Rolán, p. 144, figs 1A-D, 2A-D.
- 2019 *Teretia teres* (Forbes, 1844) – Ortega & Gofas, p. 540, figs 23G-H.
- 2022 *Teretia teres* (Forbes, 1844) – J.D. Oliver *et al.*, p. 428, figs 40, 41, 43P.
- non 1879 *Pleurotoma teres?* Forbes – S.V. Wood, p. 18, pl. 2, fig. 7.
- non 1914 *Daphnella (Teretia) teres* (Forbes) – Cipolla, p. 158 [54], pl. 14 [3], fig. 5 5 [= *Teretia turritelloides* (Bellardi, 1847)].
- non 1992 *Teretia teres* (Forbes in Reeve, 1844) – Cavallo & Repetto, p. 146, fig. 408 [= *Teretia turritelloides* (Bellardi, 1847)].

Material and dimensions – Maximum height 10.5 mm, width 4.0 mm. **CO:** NHMW 22020/0171/0101 (2), 020/0171/0104-0105 (2), NHMW 2020/0171/0106 (10). **VC:** NHMW 2020/0171/0102 (1), NHMW 2020/0171/0103 (1). **EL:** NHMW 2020/0171/0635 (11).

Description – Shell medium sized, fragile, moderately broadly turritiform, with tall spire (apical angle 38.4°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture, last quarter whorl carinate (Estepona specimen; dp = 715 µm, hp = 1010 µm, dp/hp = 0.71). Teleoconch of up to 5.5 convex carinate whorls, with moderate width subsutural ramp, carinate at shoulder, weakly convex below, separated by narrowly impressed, linear suture. Sculpture on adapical third of subsutural ramp consisting of close-set, comma-shaped growth lines. Remaining sculpture of sharp elevated carinate cords; on first teleoconch

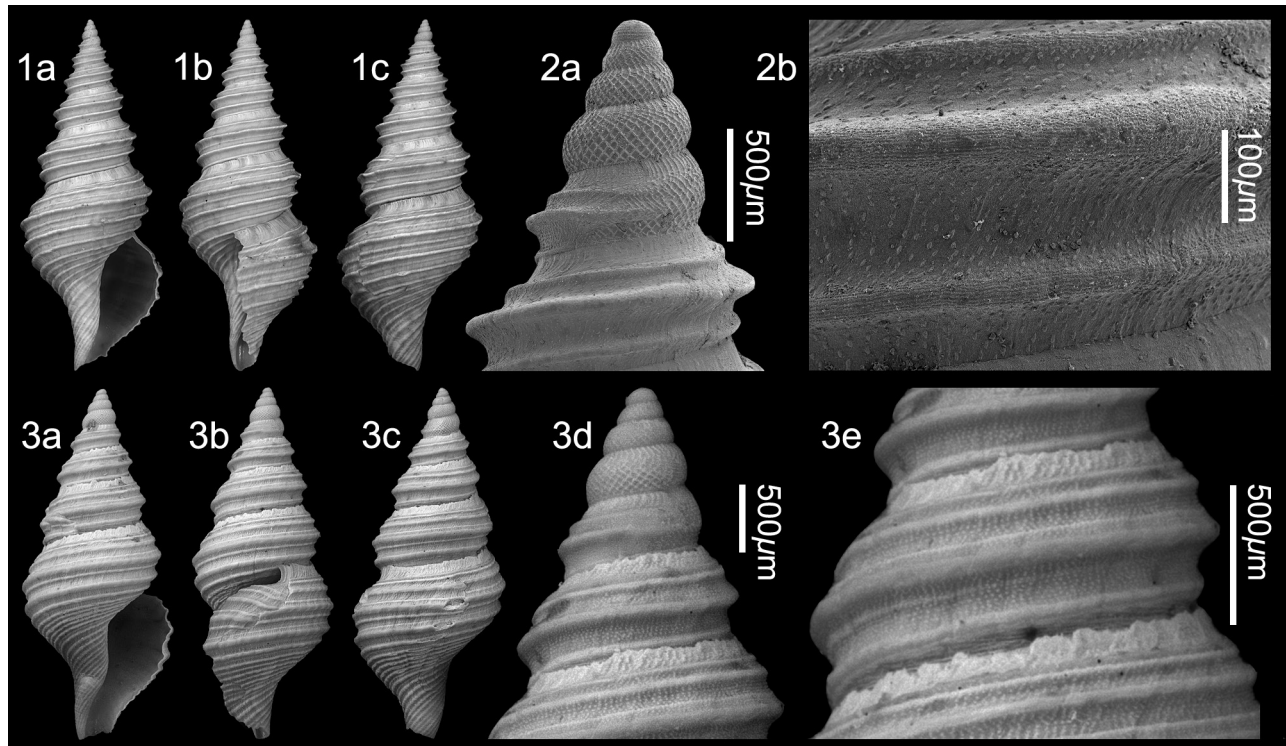


Plate 57. *Teretia teres* (Reeve, 1844); 1. NHMW 2020/0171/0104, height 8.5 mm, width 3.2 mm (digital images); 2. NHMW 2020/0171/0105, 2a, detail of protoconch, 2b, detail of teleoconch microsculpture (SEM image). Velerín conglomerates. 3. NHMW 2020/0171/0102, height 5.4 mm, width 2.3 mm, 3d, detail of protoconch, 3e, detail of teleoconch sculpture (digital image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

whorl three cords, placed just below and above suture, and more elevated cord mid-whorl; adapical and mid-cords closer-spaced. Abapically further cord develops, remaining in apposition with the abapical suture, single secondary thread intercalated between primary cords. Secondary cord develops between shoulder and next abapical cord on penultimate whorl. Microsculpture of scattered pustules. Last whorl about 56% of total height, with shape and sculpture as described above, rounded below weak shoulder carina, moderately constricted at base; sculpture of one primary over subsutural ramp, three mid whorl, all with single secondary thread intercalated, five further cords over base and about eight over fasciole, becoming more close-set abapically; base and fasciole not delimited. Aperture pyriform, 38% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus broad, moderately deep, reverse L-shaped; siphonal canal moderate length, bent slightly adaxially, tip incomplete. Columella smooth, broadly excavated in upper half, straight below, weakly twisted at fasciole. Columellar and parietal callus hardly developed, with spiral sculpture on venter extending into aperture, with only central portion smooth.

Discussion – Brunetti & Vecchi (2003) argued that *T. anceps* (Eichwald, 1830) was a fossil species that differed from the Upper Pliocene Piacenzian to present-day NE Atlantic and Mediterranean *T. teres* (Reeve, 1844) in being smaller sized, having a lower spire, 4-5 rounded spiral cords per whorls as opposed to 3-4 somewhat more

prominent lamellar cords in *T. teres* and in the absence of secondary spiral sculpture, whereas *T. teres* has 4-6 secondary cords per whorl (Brunetti & Vecchi, 2003). The surface of both these species is covered with micropustules and not smooth as described by Brunetti & Vecchi. This can be seen in their own figures (Brunetti & Vecchi, 2003, pl. 3, figs 1-2).

Hörnes (1854) specimens from the Paratethys of the Vienna Basin (Pl. 58, figs 1-4) show that the most consistent difference between *Teretia anceps* (Eichwald, 1830) and *T. teres* is the absence of secondary sculpture. It also tends to be slenderer than *T. teres*.

In present day specimens of *T. teres*, the secondary sculpture is highly irregular, but present in all shells seen. In Italian Pleistocene specimens at hand (NHMW coll.) the secondary sculpture is also evident, although we note that the Lower Pleistocene specimen illustrated by Chirli & Linse (2011, pl. 62, fig. 2) does not seem have secondary spirals. In Pliocene specimens it is more variable. Some specimens have well developed secondaries, and some have not (for Italian Pliocene specimens without secondary sculpture see Pavia, 1976, pl. 8, figs 25, 26; Brunetti & Vecchi, 2003, pl. 2, fig. 1; Sosso & dell'Angelo, 2010, unnumbered fig. p. 64 second row centre). This is also true in Estepona, where most specimens have the occasional secondary spiral, but a few do not. Regardless of the sculpture, the Pliocene to Pleistocene specimens discussed above tend to be broader than *T. anceps* from the Paratethys.

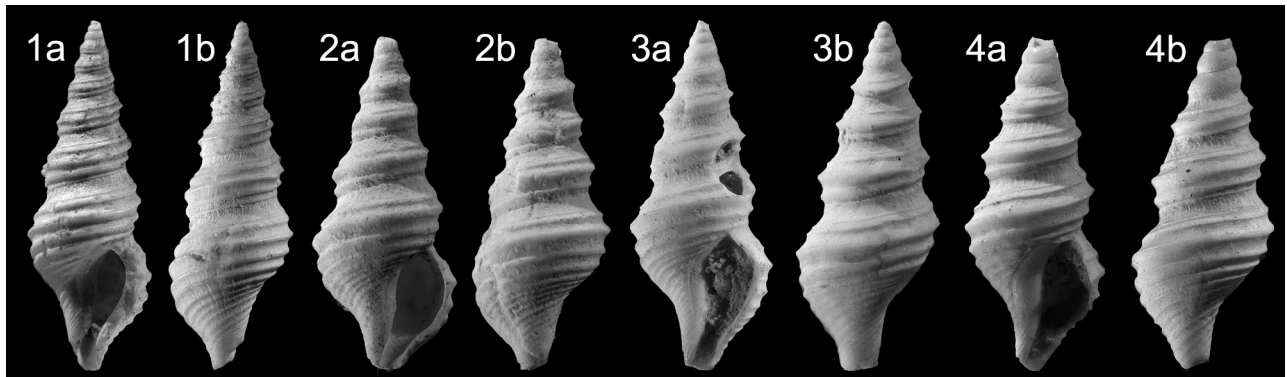


Plate 58. *Teretia anceps* (Eichwald, 1830); 1. NHMW 1855/0015/0148, height 4.4 mm, width 1.5 mm; 2. NHMW 1855/0015/0148, height 6.6 mm, width 3.0 mm; 3. NHMW 1863/0015/0733, height 7.5 mm, width 3.1 mm; 4. NHMW 1863/0015/0733, height 6.6 mm, width 2.9 mm (digital images, Mathias Harzhauser). 1 and 2 from Niederleis, 3 and 4 Niederleis and Bad Vöslau (mixed lot), Vienna Basin, Badenian, Middle Miocene. It is not clear which specimen was illustrated by Hörnes (1854, pl. 40, fig. 11).

It is possible that the predominantly Miocene *T. anceps* evolved into predominantly Pleistocene to present-day *T. teres*, with the progressively greater percentage of specimens acquiring secondary spiral sculpture. In the Pliocene most specimens have secondaries, and a few did not, or that they are two distinct species, *T. anceps* gradually replaced by *T. teres* during the Pliocene and Early Pleistocene. However, in view of the difference in width and the lack of correlation between the Miocene Paratethyan turritid assemblages and those from the Pliocene Mediterranean, we prefer to consider only the Paratethyan Miocene forms to represent *T. anceps* and the Mediterranean forms all represent a rather variable *T. teres* with secondary sculpture becoming more common over time. It is also possible that the extant specimens represent a species complex rather than a single taxon, as suggested by Horro & Rolán (2017, p. 145).

Bałuk (2003, p. 67) synonymised the Miocene North Sea Basin species *T. anceps* and *T. fusianiceps*. However, as pointed out by Janssen (1984, p. 328) there are constant differences in their shape and sculpture as well as in their microsculpture and they are here considered to be a distinct species.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Pavia, 1976; Brunetti & Vecchi, 2003). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Tabanelli & Vecchi, 2003; Sosso & Dell’Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (Tabanelli & Vecchi, 2003); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic, Scandinavia (Hubendick & Warén, 1973; Bouchet & Warén, 1980; Horro & Rolán, 2017), British Isles (Fretter & Graham 1984; Graham, 1988), Galicia, Spain (J.D. Oliver *et al.*, 2022), to Canary Islands (Hernández *et al.*, 2011), Mauritania (Horro & Rolán, 2017), western Mediterranean (Horro & Rolán, 2017; Ortega & Gofas, 2019), central Mediterranean (Bouchet & Warén, 1980; Smiriglio *et al.*, 1987; Negri & Corselli, 2016).

Teretia turritelloides (Bellardi, 1847)

Plate 59, fig. 1

- *1847 *Pleurotoma turritelloides* Bellardi, p. 71, pl. 4, fig. 5.
- 1877 *Homotoma turritelloides* Bell. – Bellardi, p. 36, pl. 8, fig. 29.
- 1904 *Teres anceps* (Eichw.) – Sacco, p. 54, pl. 14, figs 15-17 [*non Teretia anceps* (Eichwald, 1830)].
- 1910 *Daphnella (Teres) anceps* f. *turritelloides* Bell. – Cerulli-Irelli, p. 64 [256], pl. 6 [37], figs 11, 12.
- 1914 *Daphnella (Teretia) teres* (Forbes) – Cipolla, p. 158 [54], pl. 14 [3], fig. 5 5 [*non Teretia teres* (Reeve, 1844)].
- 1981 *Homotoma turritelloides* (Bellardi, 1847) – Ferrero Mortara *et al.*, p. 89, pl. 18, fig. 6.
- 1992 *Teretia teres* (Forbes in Reeve, 1844) – Cavallo & Repetto, p. 146, fig. 408 [*non Teretia teres* (Forbes, 1844)].
- 2003 *Teretia turritelloides* (Bellardi, 1847) – Brunetti & Vecchi, p. 52, pl. 2, figs 6, 7, pl. 3, fig. 3.

Material and dimensions – Height 7.7 mm, width 2.6 mm. **CO:** NHMW 2020/0171/0104 (1), NHMW 2020/0171/0682 (4).

Description – Shell small, relatively solid, slender turritiform, with tall, pagodiform spire (apical angle about 36°). Protoconch tall, conical multispiral, of 4.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture. Teleoconch of up to 5.5 angular whorls, with very broad, steeply sloping subsutural ramp, angled at shoulder carina placed at about one-third whorl height, concave below, separated by narrowly impressed, linear suture. Sculpture on adapical half of subsutural ramp consisting of close-set, comma-shaped growth lines. Remaining sculpture of cords; two on first whorl, adapical stronger, carinate, delimiting shoulder, abapical narrower, placed in apposition to suture. On second whorl, third weaker cord develops on subsutural ramp, placed close to shoulder carina. Surface abraded. Last whorl 54% of

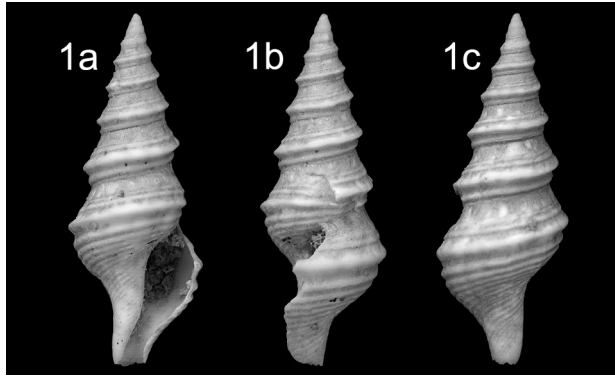


Plate 59. *Teretia turritelloides* (Bellardi, 1847); 1. NHMW 2020/0171/0104, height 7.7 mm, width 2.6 mm (digital image). Velerín conglomerates, Velerín, Estepona, Lower Pliocene, Upper Pliocene.

total height, with shape and sculpture as described above, shoulder strongly carinate, convex below, strongly constricted at base, with two weaker cords on adapical half of subsutural ramp, shoulder carina broad, elevated, about ten cords over base, weakening towards fasciole, further subobsolete cords over fasciole; base and fasciole not delimited. Aperture ovate, 39% of total height; outer lip thin (edge incomplete), without varix, smooth within; anal sinus broad, moderately deep, reverse L-shaped; siphonal canal moderate length, bent abaxially, hardly recurved, unnotched. Columella smooth, moderately broadly excavated in upper half, moderately twisted at fasciole. Columellar and parietal callus not thickened, well delimited, forming narrow indented rim.

Discussion – This species has been treated by some authors as a subspecies or form of *T. anceps* (Eichwald, 1830) (Cerulli-Irelli, 1910), or confused with that species (Cavallo & Repetto, 1992). Brunetti & Vecchi (2003, p. 56, tab. 1) summarised the differences between various Italian *Teretia* species, of which the most obvious difference is the strong and low-placed shoulder carina in *Teretia turritelloides* (Bellardi, 1847), with a narrower cord just above, whereas *T. anceps* and *T. teres* (Reeve, 1844) lack any shoulder carina. Brunetti & Vecchi noted that the surface was covered in micropustules, whereas that of *T. anceps* is smooth. Unfortunately, the Estepona specimens are worn and the teleoconch microsculpture is not preserved. *Teretia candela* Horro & Rolán, 2017 from the present-day Canary Islands and West Sahara is similar in profile, but the central carina is sharp instead of rounded and is not as prominent as it is in *T. turritelloides*. *Teretia hoisaeteri* Horro & Rolán, 2017 from present-day Angola, is more similar to *T. turritelloides*, but is squatter, the protoconch is broader, the central keel is not quite as prominent, and it lacks the comma-shaped axial riblets over the subsutural ramp.

Distribution – Middle Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); cen-

tral Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Cipolla, 1914; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

Genus *Thatcherina* Vera-Peláez, 1998

Type species – *Thatcherina carminis* Vera-Peláez, 1998, by original designation, Pliocene, Spain.

1998 *Thatcherina* Vera-Peláez, p. 60.

Note – Vera-Peláez (1998) erected this monotypic genus for *Thatcherina carminis* Vera-Peláez, 1998 from the deeper-water Estepona assemblages starting that it differed from *Thatcheria* Angas, 1877 in being smaller sized, having a protoconch totally covered by diagonally reticulated sculpture, whereas in *Thatcheria* only the first three whorls are diagonally reticulated, the last two protoconch whorls only have axial riblets, and having the anal sinus in reverse L-shape occupying one-third of the subsutural ramp, whereas in *Thatcheria* the sinus forms a continuous arc between the suture and shoulder (Vera-Peláez, 1998, p. 62). This last difference also separates the genus *Clinura* Bellardi, 1875 (see Charig, 1963). *Pleurotoma circumfossa* von Koenen, 1872 from the Middle Miocene North Sea Basin of Germany may also belong to the same genus. The entire protoconch is diagonally cancellate (see R. Janssen & Wienrich in Wienrich, 2007, pl. 115, fig. 5) and the sinus is like that of *Thatcherina carminis* Vera-Peláez, 1998.

***Thatcherina carminis* Vera-Peláez, 1998**

Plate 60, figs 1-3

*1998 *Thatcherina carminis* Vera-Peláez, p. 59, figs 2A-G, 3A-B.

2002 *Thatcherina carminis* Vera-Peláez, 1998 – Vera-Peláez, p. 235, pl. 8, fig. D, pl. 16, figs G, H, I.

Material and dimensions – Maximum height 18.7 mm, width 9.1 mm. VC: NHMW 2020/0171/0381-0383 (3), NHMW 2020/0171/0384 (1).

Description – Shell medium sized, fragile, broadly biconic-turritiform, with strongly pagodiform spire (apical angle 51.8–54.6°). Protoconch conical multispiral, of 3.5 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (dp = 680 µm, hp = 750 µm, dp/hp = 0.91). Junction with teleoconch marked by sinusigera. Teleoconch of up to 5.5 strongly carinate whorls, with very broad, weakly inclined, concave subsutural ramp, acutely angled at elevated, thickened shoulder cord, concave below, tapering inwards to superficial, linear suture. Sculpture on adapical half of subsutural ramp composed of close-set, comma-shaped growth lines ending abruptly mid-ramp; abapical half with fine spiral threads; below shoulder fine, close-set spiral threads of alternate strength. Entire surface covered in dense spiral rows of micropustules. Last whorl

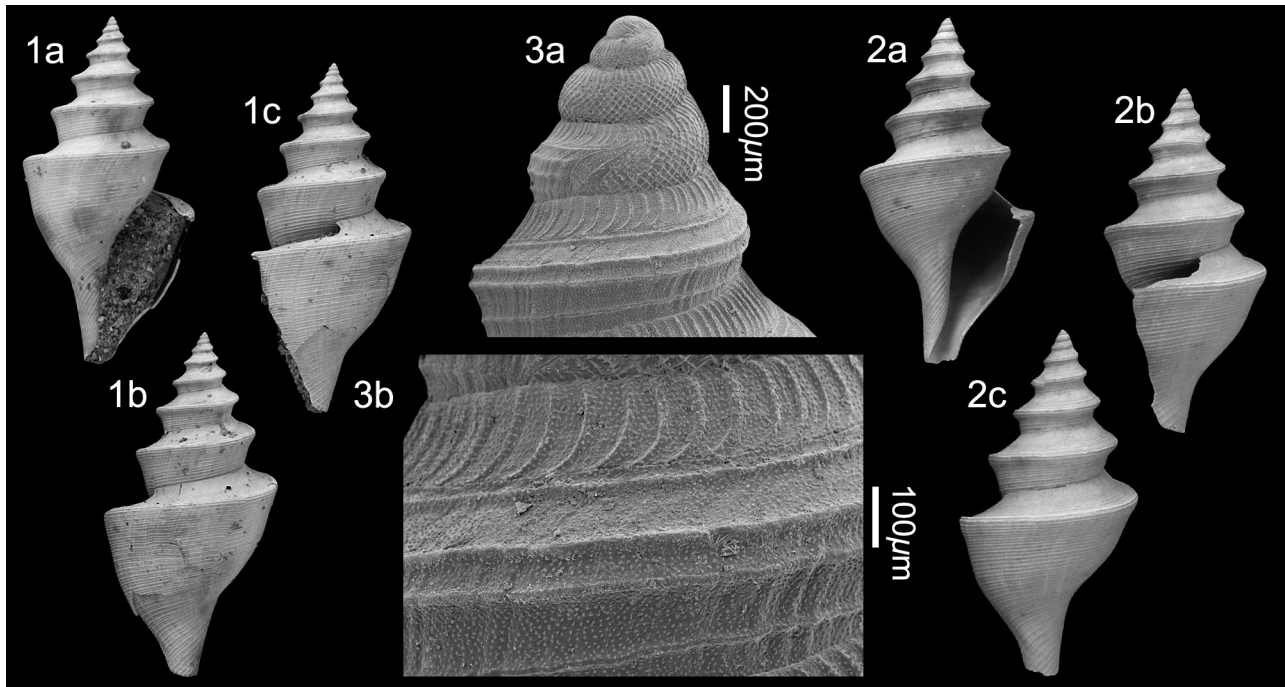


Plate 60. *Thatcherina carminis* Vera-Peláez, 1998; 1. NHMW 2020/0171/0381, height 18.7 mm, width 9.1 mm; 2. NHMW 2020/0171/0382, height 13.2 mm, width 6.9 mm (digital images); 3. NHMW 2020/0171/0383, 3a, detail of protoconch, 3b, detail or teleoconch microsculpture (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

broad, 66-67% of total height, with wide, concave subsutural ramp, acutely angled at elevated, high-placed shoulder cord, weakly convex below, moderately constricted at base; spirals strengthening and of equal strength over siphonal fasciole; base and fasciole not delimited. Aperture broad, subtrigonal, 49-50% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus moderately narrow, extremely deep reverse L-shape, occupying adapical half of ramp; siphonal canal moderate length, narrow, slightly bent adaxially, unnotched. Columella broadly and shallowly excavated mid-height, moderately twisted at fasciole. Columellar and parietal not developed.

Discussion – *Thatcherina carminis* Vera-Peláez, 1998 is impossible to confuse with any other *Estepona raphitomid*. It is uncommon and found only in the deeper-water assemblages of Parque Antena (type locality) and Velerín carretera (material at hand). There is little intraspecific variability; the paratype illustrated by Vera-Peláez (1998, figs 3A-B) has a slightly steeper subsutural ramp and slightly stronger spirals than the holotype (1998, figs 2A-G) and the specimens figured herein (Pl. 60, figs 1-2). *Thatcherina circumfossa* (von Koenen, 1872) from the Middle Miocene North Sea Basin of Germany differs in being smaller with a deeply concave canaliculate suture delimited by a more elevated keel-like carina.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

Genus *Xanthodaphne* Powell, 1942

Type species – *Pleurotoma membranacea* Watson, 1886, by original designation, present-day, New Zealand.

1942 *Xanthodaphne* Powell, p. 166.

***Xanthodaphne cf. pederzanii* Tabanelli & Bongiardino, 2018**

Plate 61, figs 1-3

cf. *2018 *Xanthodaphne pederzanii* Tabanelli & Bongiardino, p. 188, figs 1A-E.

Material and dimensions – Maximum height 7.6 mm, width 3.2 mm. VC: NHMW 2020/0171/0134-0136 (3), NHMW 2020/0171/0137 (2).

Description – Shell small, fragile, broadly fusiform, with medium height conical spire (apical angle 46.6-48.7°). Protoconch conical, multispiral, of 3.5-4.0 convex whorls, with small nucleus; post-nuclear whorls with fine, diagonally reticulated sculpture (dp = 550 μm, hp = 605 μm, dp/hp = 0.91). Junction with teleoconch marked by sinusigera. Teleoconch of up to four very weakly shouldered convex whorls, subsutural ramp slightly concave, poorly delimited, separated by narrowly impressed, linear suture. Sculpture of comma-shaped axial growth lines over subsutural ramp and irregular flattened cords separated by narrow grooves, cords below shoulder slightly wider. No microsculpture developed. Last whorl inflated, 69-

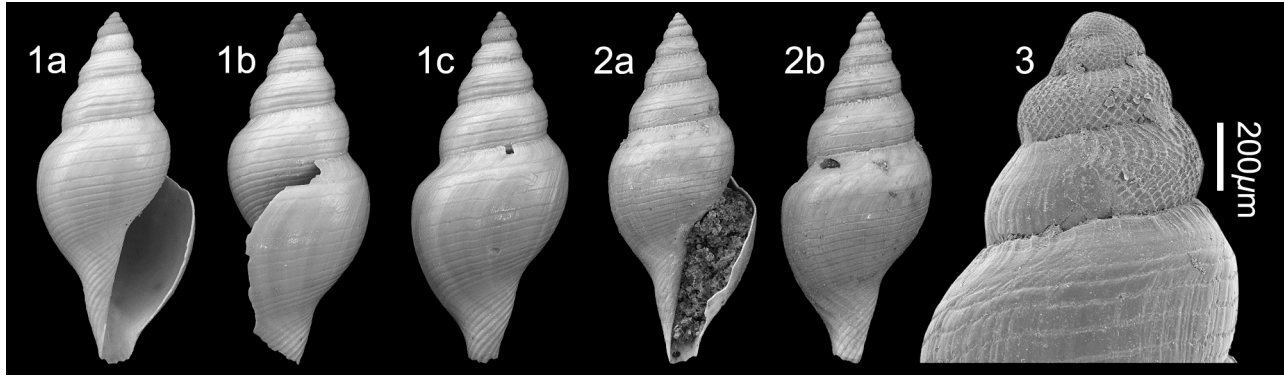


Plate 61. *Xanthodaphne* cf. *pederzanii* Tabanelli & Bongiardino, 2018; 1. NHMW 2020/0171/0134, height 7.6 mm, width 3.2 mm; 2. NHMW 2020/0171/0135, height 7.3 mm, width 3.0 mm (digital images); 2. NHMW 2020/0171/0136, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

70% of total height, slightly concave in subsutural area, convex below, moderately constricted at base; sculpture of 15–20 flattened cords, 4–5 cords mid-whorl broader, narrowing over base, about ten slightly raised rounded cords over fasciole; base and fasciole not delimited. Aperture subquadrate, 53% of total height; outer lip very thin, sharp edged, without varix, smooth within; anal sinus broad, deep, reverse L-shaped; siphonal moderate length, unnotched. Columella smooth, weakly excavated just above mid-height, straight and inclined abaxially below. Columellar and parietal callus not developed, with surface sculpture running into aperture.

Discussion – The specimens from Estepona are extremely similar, if not conspecific with *Xanthodaphne pederzanii* Tabanelli & Bongiardino, 2018, described from the Lower Pleistocene of Italy. The teleoconch sculpture is identical. It is placed in open taxonomy as it is larger than the Italian specimens (maximum height 7.6 mm vs holotype height 3.4 mm, *vide* Tabanelli & Bongiardino, 2018, p. 188), although the holotype at only two teleoconch whorls may not be fully adult. The paratype (2018, figs 1C–D) is clearly incomplete and would have been larger. The protoconch in the Italian specimens looks a little more pointed. These differences are probably not significant, but in the absence of a complete adult specimen from Italy we hesitate to synonymise the two. The extant NE Atlantic *X. heterogramma* (Odhner, 1960) is also closely similar, but according to the figure given by Bouchet & Warén (1980, fig. 136) it has more inflated whorls and the concave portion immediately below the suture is more evident. *Xanthodaphne bruneri* (Verrill, 1884) has more inflated whorls, a deeper anal sinus, and more numerous spirals cords that are not broader mid-whorl (see Bouchet & Warén, 1980, fig. 134).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Conclusions

In this paper we review the Raphitomidae of the Lower

Piacenzian, Upper Pliocene of Estepona, southern Spain. Sixty-two species are recorded representing 21 genera and subgenera, of which 12 species are described as new: *Clathromangelia acuticostata* nov. sp., *Clathromangelia mulderi* sp. nov., *Clathromangelia oliverioi* sp. nov., *Cyrellia clathrataeformis* nov. sp., *Cyrellia saldubensis* nov. sp., *Diaugasma mediterranea* nov. sp., *Microandonia minutissima* nov. sp., *Pleurotomella turrita* nov. sp., *Pleurotomella obesula* nov. sp., *Pseudodaphnella iberica* nov. sp., *Pseudodaphnella velerinensis* nov. sp., *Teretia inflatissima* nov. sp., and one genus *Microandonia* nov. gen.

This is almost double the 32 raphitomid species recorded by Vera-Peláez (2002). Most of his records are either confirmed or reattributed to different species herein. Four of Vera-Peláez's records are provisionally accepted but could not be confirmed: *Clathromangelia granum* (Philippi, 1844), *Gymnobela sphaera* (Vera-Peláez, 2002), *Pleurotomella antemnaensis* Vera-Peláez, 2002, and *Raphitoma pseudohystris* (Sykes, 1906).

The assemblage shows a relatively high level of endemism (23 species: 37%). Both shallow and deeper-water taxa are represented. The shallow water assemblage is similar at both genus and species level to that found in the tropical Mediterranean Pliocene of Italy [Mediterranean Plio-Pleistocene Molluscan Unit 1 (MPPMU1); for discussion on Pliocene Molluscan Units and renaming Raffi & Monegatti's (1993) MPMU to MPPMU; see Landau *et al.*, 2011, p. 47]. Of note is the first European record of the raphitomid genus *Pseudodaphnella* Boettger, 1895 found in the shallower facies in Estepona. Today this genus has a tropical Indo-Pacific distribution. The deeper-water assemblage is similar in generic composition to that recorded for the bathyal and abyssal northeastern Atlantic coast of Lusitania and West Africa (*e.g.*, Bouchet & Warén, 1980) but contains most of the endemic species.

From a stratigraphic standpoint, most of the species are relatively short-lived (Fig. 1). Only 11 (18%) occur today and 11 (18%) appeared already during the late Miocene. At species level, no association is found between the Este-

pona species and any of the Early to Middle Miocene assemblages of the European Atlantic Frontage, Paratethys or Proto-Mediterranean. Only from the Late Miocene there is an association between the Proto-Mediterranean and the Estepona assemblages (18%).

Most raphitomids in the Estepona assemblages have tall multispiral protoconchs with reticulated sculpture suggestive of planktotrophic development. If the best studied 'Raphitoma-like' lineages are considered, which are now classified into the genera *Cyrillia* Kobelt, 1905, *Leufroyia* Monterosato, 1884 and *Raphitoma* Bellardi, 1847, all 19 species confirmed in this work have planktotrophic-type protoconchs. Only one, *Raphitoma pseudohystrix* (Sykes, 1906), would have a paucispiral protoconch but its presence in Estepona is not confirmed. Høisæter (2016) reviewed the present-day species in the northern European waters off Norway and recorded six species, all of which have planktotrophic-type protoconchs. All nine raphitomid species reviewed by Rolán *et al.* (1998) from the tropical West African coasts also have multispiral protoconchs typical for planktotrophic development. In contrast, Giannuzzi-Savelli *et al.* (2018, p. 67), estimated about 30 species to occur in the Mediterranean, of which 25% have non-planktotrophic development, whilst the approximately 10 exclusively (or nearly exclusively) Atlantic species all have planktotrophic development. The situation in the Pliocene Mediterranean seems different, as to our knowledge no paucispiral species of *Cyrillia*, *Leufroyia* or *Raphitoma* have been reported. In contrast, Ceulemans *et al.* (2018, p. 107) discussed the abundance of 'Raphitoma' species in the Lower Pliocene Assemblage III deposits of northwestern France, where they recorded eight species, of which all but one had protoconchs suggesting non-planktotrophic development (of lecithotrophic types), and an even greater contrast is seen with the slightly older Assemblage I deposits of northwestern France in which Landau *et al.*, (2020, p. 55) where 14 of the 16 species had non-planktotrophic protoconchs. These French assemblages in the Mio-Pliocene Ligerian Bay are unusual as there is a predominance of non-planktotrophic developing species not only amongst the raphitomids, but across a wide range of other gastropod groups. We suggest that this was due to relative isolation of the Ligerian Bay from the open Atlantic. It is possible that a similar situation may be at work in the Mediterranean, and that non-planktotrophic raphitomids only evolved relatively recently since the Mediterranean was refilled following the Messinian Salinity Crisis. We note that Russini *et al.* (2020) presented some evidence that poecilogony might exist among present-day raphitomids of the genus *Raphitoma*, but as yet this has not been confirmed.

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Species	Geographical distribution					Stratigraphical distribution							
	Present-day					Miocene		Pliocene		Pleistocene		Hol	
	1	2	3	4	a/b	Lower	Middle	Upper	Lower	Upper	Lower		Upper
<i>Andonia bonellii</i> (Bellardi & Michelotti, 1841)		●	●		Ⓐ				■				
<i>Andonia wilhelminamariae</i> Landau & Mulder, 2020			●		Ⓜ			■	■				
<i>Clathromangelia acuticostata</i> nov. sp.			●		Ⓜ				■	■			
<i>Clathromangelia granum</i> (Philippi, 1844)			●		Ⓜ				■	■			
<i>Clathromangelia marinae</i> Oliverio, 1995			●		Ⓜ				■	■			
<i>Clathromangelia mulderi</i> nov. sp.			●		Ⓜ				■	■			
<i>Clathromangelia oliverioi</i> nov. sp.			●		Ⓜ				■	■			
<i>Clathromangelia tavianii</i> Oliverio, 1995			●		Ⓜ				■	■			
<i>Clinura calliope</i> (Brocchi, 1814)			●		Ⓜ				■	■			
<i>Cyrellia clathrataeformis</i> nov. sp.			●		Ⓜ				■	■			
<i>Cyrellia linearis</i> (Montagu, 1803)		●	●		Ⓐ				■	■			
<i>Cyrellia saldubensis</i> sp. nov.			●		Ⓜ				■	■			
<i>Daphnella (Paradaphne) romani</i> (Libassi, 1859)		●	●		Ⓐ				■	■			
<i>Daphnella</i> (s.l.) <i>malacitana</i> (Vera-Peláez, 2002)			●		Ⓜ				■	■			
<i>Diaugasma mediterranea</i> nov. sp.			●		Ⓜ				■	■			
<i>Favriella cipriani</i> (Hornung, 1920)			●		Ⓜ				■	■			
<i>Favriella tumidula</i> (Bellardi, 1877)			●		Ⓜ				■	■			
<i>Favriella weberi</i> (Hornung, 1920)			●		Ⓜ				■	■			
<i>Gymnobela brevis</i> (Bellardi, 1847)			●		Ⓜ				■	■			
<i>Gymnobela galerita</i> (Philippi, 1844)			●		Ⓜ				■	■			
<i>Gymnobela lozanoae</i> (Vera-Peláez, 2002)			●		Ⓜ				■	■			
<i>Gymnobela ovum</i> Vera-Peláez, 2002			●		Ⓜ				■	■			
<i>Gymnobela salinasi</i> (Calcara, 1841)			●		Ⓜ				■	■			

Figure 1. Geography, stratigraphy and distribution of species found in the Upper Pliocene Lower Piacenzian of the Estepona Basin, southern Spain. For present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan Province, 4 = Mauritanian-Senegalese Province (see Landau *et al.*, 2011, p. 49, text-fig. 8). For stratigraphic distribution black signifies Atlantic distribution (A), grey Mediterranean distribution (M).

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Species	Geographical distribution					Stratigraphical distribution							
	Present-day					Miocene		Pliocene		Pleistocene		Hol	
	1	2	3	4	o/□	Lower	Middle	Upper	Lower	Upper	Lower	Upper	
<i>Gymnobela sphaera</i> (Vera-Peláez, 2002)			●		(M)								
<i>Leufroyia concinna</i> (Scacchi, 1836)		●	●		(A)						■	■	■
<i>Leufroyia demoulinsi</i> (Bellardi, 1847)			●		(M)								
<i>Leufroyia erronea</i> Monterosato, 1884		●	●		(A)						■	■	■
<i>Leufroyia gradata</i> nov. sp.			●		(M)								
<i>Leufroyia inflata</i> (De Cristofori & Jan, 1832)		●	●		(A)								
<i>Leufroyia leufroyi</i> (Michaud, 1828)		●	●		(A)								
<i>Leufroyia montagui</i> (Bellardi, 1877)			●		(M)								
<i>Leufroyia stria</i> (Calcara, 1839)			●		(M)								
<i>Leufroyia</i> aff. <i>stria</i> (Calcara, 1839)			●		(M)								
<i>Lusitanops bermejensis</i> (Vera-Peláez, 2002)			●		(M)								
<i>Metuonella eufusinus</i> Vera-Peláez, 2002			●		(M)								
<i>Microandonia minutissima</i> nov. sp.			●		(M)								
<i>Pleurotomella antemnaensis</i> Vera-Peláez, 2002			●		(M)								
<i>Pleurotomella</i> cf. <i>gibbera</i> Bouchet & Warén, 1980			●		(M)								
<i>Pleurotomella obesula</i> nov. sp.			●		(M)								
<i>Pleurotomella tumens</i> (Bellardi, 1877)			●		(M)								
<i>Pleurotomella turrata</i> nov. sp.			●		(M)								
<i>Pseudodaphnella iberica</i> nov. sp.			●		(M)								
<i>Pseudodaphnella velerinensis</i> nov. sp.			●		(M)								
<i>Raphitoma contigua</i> (Monterosato, 1884)		●	●		(A)								
<i>Raphitoma echinata</i> (Brocchi, 1814) <i>sensu</i> AA		●	●		(A)								
<i>Raphitoma erinacea</i> (Bellardi, 1877)			●		(M)								
<i>Raphitoma hispidella</i> Püsateri & Giannuzzi-Savelli, 2019			●		(M)								
<i>Raphitoma hystrix</i> Bellardi, 1847			●		(M)								
<i>Raphitoma pseudohystrix</i> (Sykes, 1906)			●		(M)					?			
<i>Raphitoma pumila</i> (Monterosato, 1890)			●		(M)								
<i>Rimosodaphnella textile</i> (Brocchi, 1814)			●		(M)								

Figure 1, continued

Species	Geographical distribution					Stratigraphical distribution							
	Present-day					Miocene		Pliocene		Pleistocene		Hol	
	1	2	3	4	o/□	Lower	Middle	Upper	Lower	Upper	Lower		Upper
<i>Taranis circumflexa</i> (Hornung, 1920)			●		○								
<i>Teretia elegantissima</i> (Foresti, 1868)			●		○								
<i>Teretia inflatissima</i> nov. sp.			●		○								
<i>Teretia monterosatoi</i> (Cipolla, 1914)			●		○								
<i>Teretia</i> cf. <i>multicingula</i> (Seguenza, 1880)			●		○								
<i>Teretia pentacarinifera</i> Vera-Peláez, 2002			●		○								
<i>Teretia policarinarum</i> Vera-Peláez, 2002			●		○								
<i>Teretia teres</i> (Reeve, 1844)	●	●			○				■	■	■	■	■
<i>Teretia turritelloides</i> (Bellardi, 1847)			●		○		■	■					
<i>Thatcherina carminis</i> Vera-Peláez, 1998			●		○								
<i>Xanthodaphne</i> cf. <i>paderzanii</i> Tabanelli & Bongiardino, 2018			●		○								

Figure 1, continued

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