

The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 25: Mitroidea and Turbinelloidea (Neogastropoda)

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In this paper we continue to review the Mitroidea, family Mitridae Swainson, 1831 and Turbinelloidea, family Costellariidae MacDonald, 1860 of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. In the Mitridae 20 species are recorded representing four genera, of which one is described as new: *Episcomitra gonniae* nov. sp., and two are left in open nomenclature. *Episcomitra pliotenuis* nov. nom. is proposed for *Mitra tenuis* Bellardi, 1887, non Beyrich, 1854. This group is relatively thermophilic, and the assemblage of species is fairly typical for the tropical Pliocene Mediterranean-West African palaeobiogeographic province. No species survived to the present-day.

Within the Costellariidae ten species are recorded representing six genera, of which one is described as new: *Pusia ellenae* nov. sp., and one is left in open nomenclature. Again, the species present are typical for the palaeobiogeographic province. Somewhat less thermophilic, two species survive in the Mediterranean today.

KEY WORDS: southern Spain, Upper Pliocene, Gastropoda, Mitridae, Turbinelloidea, new species

Introduction

In this paper we continue the revision of the diverse Pliocene assemblage of Estepona in south-western Spain and describe the superfamily Mitroidea Swainson, 1831. The Mediterranean Neogene Mitroidea were first monographed by Bellardi (1850), followed by a more detailed description of the superfamily in Bellardi (1887a, 1887b, 1888). Sacco first described (1890) and then illustrated (1904) some of the varieties described, but not figured by Bellardi. Until today, this remains the standard text on central Mediterranean (Italian) Miocene-Pliocene Mitroidea. Ferrero Mortara *et al.* (1981) published an extremely useful illustrated catalogue of the Bellardi & Sacco Collection in the Museo Regionale di Scienze naturali de Torino (Italy) offering quality photographs of the type material described by those authors that was still present in the collections. However, apart from Davoli's (2000) revision of the Upper Miocene Mitroidea from Montegibbio, no other familial revisions have been attempted. For the Pliocene, Mitroidea were discussed as part of the overall assemblage in works such as Ruggieri *et al.* (1959), Pelosio (1967),

Cavallo & Repetto (1992), and Chirli (2002) *inter alia*. These works accepted Bellardi's species offering little discussion, and none can be considered in depth critical revisions of the family.

Cernohorsky (1970, 1976, 1991), in his revision of the Mitridae of the World, discussed many extinct taxa, but he considered "...the majority of species described by Bellardi are probable synonyms and cannot be considered to constitute recognised taxa (1976, p. 278). This view was repeated "Taxa proposed for extinct species undoubtedly contain a high percentage of synonyms in view of the numerous names proposed by Bellardi, 1887, for species forms from the Mio-Pliocene deposits of Italy" (1976, p. 305) and again "...the majority [of *Mitra* species] having been described by Bellardi. His so-called "species" are mostly individual, ecological and developmental forms of previously described and well-known species....The number of described immature and juvenile individuals of species is unusually high in Bellardi's work" (1976, p. 374). As discussed by Harzhauser & Landau (2021a, p. 4), Cernohorsky's statements were based on literature surveys and not material-based revisions. Moreover, he followed a 'lumping' approach,

which at least for extant taxa, is not supported by molecular data (*i.e.* Fedosov *et al.*, 2017). In addition, the broad genus concept of ‘*Mitra*’ as proposed by Cernohorsky (1970, 1976, 1991) is not supported by molecular data, expressed pointedly as the “collapse of *Mitra*” by Fedosov *et al.* (2018).

Whilst some of Bellardi’s taxa may well eventually be synonymised, his species are usually based on careful and detailed comparison of shell characters and should not be discarded lightly. More recent revisions of other groups of Italian fossil species such as the Buccinoidea Rafinesque, 1815 (Brunetti & Della Bella, 2014, 2016) or Cancellarioidea Forbes & Hanley, 1851 (Brunetti *et al.*, 2008, 2009, 2011) have tended to re-establish some of Bellardi’s species previously synonymised rather than find new synonymies. Similarly, in our revision of the Mitridae Swainson, 1831 (Harzhauser & Landau, 2021a) and Costellariidae MacDonald, 1860 (Harzhauser & Landau, 2021b) of the Miocene Paratethys Sea, we found that in the historical literature diversity was overlooked rather than exaggerated.

It is clear that a detailed revision of the Miocene and Pliocene Proto-/Mediterranean Mitridae is long overdue. Unfortunately, the Estepona material is not suitable for such a revision.

In the Estepona assemblages almost all the Mitroidea are found in the shallower water assemblage of Velerín conglomerates, and to a lesser extent in the El Lobillo assemblage. Very few are found in the deeper water deposits of Velerín carretera. Almost all the mitrid specimens from the shallower water assemblages are worn to a greater or lesser degree, the protoconch is invariably not preserved, and the early teleoconch whorls, and most of the teleoconch surface, are abraded. Moreover, compared to other groups, the material is not abundant. The relative scarcity of specimens and their worn state would suggest some degree of transport for most mitrids before deposition. The majority of extant species live in shallow-water of the intertidal zone (Cernohorsky, 1976, p. 273), so why they should be worn whilst other groups inhabiting similar ecological niches are not, is unclear.

Very little is known on the presence of these groups in the Iberian Pliocene. A few records exist for the Atlantic Mondego Basin of central west Portugal (Silva, 2001), the Guadalquivir Basin (González Delgado, 1992; Ruiz Muñoz *et al.*, 1997; Landau *et al.*, 2011), and the Pliocene of Barcelona, NE Spain (Martinell, 1979) as part of an overall description of those assemblages, but between them they record less than half a dozen species.

In this work we have attempted to match shell characters to Bellardi’s species and have adopted a rather conservative approach. No synonymies of Bellardi’s taxa are suggested based on the Spanish material and about one-third of the mitrid specimens remain unidentified due to their poor conservation. It is very likely that further species are present in the assemblage that will become recognised as better preserved material becomes available.

Age of the deposits

Prior to 2013 the age of the deposits was stated as Late Zanclean (late Early Pliocene) (for list of papers giving Zanclean age see Landau & Micali, 2021, p. 160) following Guerra-Merchán *et al.* (2002). In our later works we have dated the assemblages as earliest Piacenzian, early Late Pliocene, an age corroborated by the assemblage of Euthecosomata (Janssen, 2004). Either way, they form part of the Mediterranean ecostratigraphic unit MPPMU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al.*, 2011, text-fig. 9). Ultra violet light did not enhance colour pattern in any specimens from Estepona.

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL; 1997–2020) and by Henk Mulder between 2008–2023, to whom 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, p. 4, text-fig. 1). The material is housed in the Natural History Museum Vienna (NHMW) and Naturalis Biodiversity Center (RGM).

A comprehensive and critical chresonymy and distribution is given for each species, concentrating on fossil records, in which only illustrated records are included. The descriptions for each species are based on the Estepona material.

For the Mitridae we follow Harzhauser & Landau (2021a). In the descriptions we categorise the shells as: small (SL < 20.0 mm), medium-sized (20–40 mm), moderately large (40.1–60 mm) and large (SL > 60 mm). For the statistical analysis of the morphometric data, we evaluated aperture length (AL), aperture width (AW), aperture height (AH), and last whorl height (LWH) to derive following ratios (Fig. 2): SL/MD, AH/SL and AL/AW. The SL/MD ratio is an expression of slenderness of the shell. To be objective in the descriptions we define shell shapes of the Mitridae as follows: broad (SL/MD 3.0–3.5), slender (SL/MD > 3.5). The relative width of the aperture is calculated as aperture length (AL) versus aperture width (AW). Apertures are described as narrow (AL/AW ≥ 5.8), moderately narrow (AL/AW = < 4.0). As measurement for the relative length of the siphonal canal we calculated aperture height (AH) versus siphonal length (S). For pragmatic reasons siphonal length (S) was measured starting from the crest of the third columellar fold because this is a homologous point in all specimens, whereas the abapical fourth fold (which would be the conchologically more correct point) is missing in some species and is very weak in some other species. The siphonal canal length is categorised as follows: long (AH/S < 2.1), moderately long (AH/S = 2.1–<2.5), moderately short (AH/S = 2.5–2.9), short (AH/S ≥ 3.0) (see Harzhauser & Landau, 2021a, p. 6, fig. 2).

For the Costellariidae we follow Harzhauser & Landau (2021b). Shell size; small ($SL \leq 6.0$ mm), medium-sized (6.1-10.0 mm), moderately large (10.1-20.0 mm) and large ($SL \geq 20.1$ mm). For the statistical analysis of the morphometric data, we evaluated aperture length (AL), aperture width (AW), aperture height (AH), and last whorl height (LWH) to derive following ratios (Fig. 2): SL/MD, AH/SL and AL/AW. The SL/MD ratio is an expression of slenderness of the shell. To be objective in the descriptions we define shell shapes of Paratethyan Costellariidae as follows: broad ($SL/MD \leq 2.4$), moderately broad, ($SL/MD = 2.5-2.6$), moderately slender ($SL/MD = 2.7-3.1$), slender ($SL/MD \geq 3.2$). The relative width of the aperture is calculated as aperture length (AL) versus aperture width (AW). Apertures are described as narrow ($AL/AW \geq 5.1$), moderately narrow ($AL/AW = 4.0-4.0$) and wide ($AL/AW \leq 3.9$). As measurement for the relative length of the siphonal canal we calculated aperture height (AH) versus siphonal length (S). For pragmatic reasons siphonal length (S) was measured starting from the crest of third columellar fold because this is a homologous point in all specimens, whereas the abapical fourth fold (which would be the conchologically more correct point) is missing in some species and is very weak in some other species. The siphonal canal length is categorized as follows: long ($AH/S \leq 2.1$), moderately long ($AH/S = 2.2-2.4$), moderately short ($AH/S = 2.5-2.9$), short ($AH/S \geq 3.0$) (see Harzhauser & Landau, 2021b, p. 7, fig. 2).

Abbreviations:

CO: Velerín conglomerates; **VC:** Velerín carretera;
EL: El Lobillo; see Landau *et al.* (2003, p. 4, text-fig. 1).
NHMW: Natural History Museum Vienna (Austria).
RGM: Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

Systematic Palaeontology

Superfamily Mitroidea Swainson, 1831
 Family Mitridae Swainson, 1831
 Subfamily Imbricatariinae Troschel, 1867
 Genus *Cancilla* Swainson, 1840

Type species (by subsequent designation by Hermannsen, 1846) – *Tiara isabella* Swainson, 1831, present-day, Indo-Pacific.

1840 *Cancilla* Swainson, p. 320.

Cancilla alligata (Defrance in de Blainville, 1825) Plate 1, figs 1-4

- 1814 *Voluta striatula* Brocchi, p. 318, pl. 4, fig. 8 (*non* Schröter, 1804; *nec* *Mitra striatula* Lamarck, 1811).
 *1825 *Mitra alligata* Defrance in Blainville, p. 494.
 1850 *Mitra striatula* Brocc. – Bellardi, p. 13, pl. 1, fig. 23.

- 1880 *Mitra striatula* Brocchi – Fontannes, p. 86, pl. 6, figs 7, 8.
 1887a *Mitra alligata* Defr. – Bellardi, p. 72, pl. 4, fig. 35.
 1904 *Mitra alligata* var. *aequopersulcata* Sacco, p. 83, pl. 18, figs 43, 44.
 1904 *Mitra alligata* var. *quatuorsulcatula* Sacco, p. 83, pl. 18, fig. 45.
 1955 *Mitra* (*Scabricula*) (*Cancilla*) *scrobiculata* var. *striatula* (Brocchi 1814) – Rossi Ronchetti, p. 248, fig. 132.
 1959 *Mitra* (*Scabricula*) *alligata* (Defrance) – Ruggieri *et al.*, p. 82, pl. 19, fig. 119.
 1974 *Mitra* (*Tiara*) *alligata* (Defrance, 1825) – Malatesta, p. 358, pl. 29, fig. 3.
 1975 *Mitra striatula* (Brocchi) – Fekih, p. 131, pl. 39, fig. 4.
 1976 *Mitra* (*Tiara*) *alligata* Defrance – Pavia, p. 113, pl. 7, fig. 17.
 1978 *Mitra striatula* Brocchi, 1814 – Pinna & Spezia, p. 171, pl. 67, fig. 4.
 1979 *Mitra* (*Tiara*) *alligata* Defrance – Martinell, p. 62, pl. 1, fig. 3.
 1988 *Mitra* (*Tiara*) *alligata* Defrance – Chirli, p. 22, pl. 8, fig. 17.
 1991 *Cancilla alligata* (Defrance in Blainville, 1824 [*sic*]) – Cernohorsky, p. 35, pl. 25, figs 6, 7.
 1992 *Cancilla alligata* Defrance, 1824 [*sic*] – Cavallo & Repetto, p. 119, fig. 302.
 1992 *Mitra* (*Tiara*) *alligata* (Defrance, 1824 [*sic*]) – González Delgado, p. 11, pl. 1, figs 1, 2.
 1997 *Mitra alligata* Defrance – Ruiz Muñoz *et al.*, p. 180, pl. 37, figs 7, 8.
 2001 *Cancilla alligata* Defrance, 1824 [*sic*] – Silva, p. 487, pl. 22, figs 10, 11.
 2002 *Cancilla alligata* (Defrance, 1824 [*sic*]) – Chirli, p. 43, pl. 21, figs 3-9.
 2011 *Cancilla alligata* (Defrance in Blainville, 1825) – Landau *et al.*, p. 29, pl. 15, fig.
 ?2018 *Cancilla alligata* Defrance in Blainville, 1825 [*sic*] – Brunetti & Cresti, p. 82, fig. 311.
 non 1852 *Mitra striatula* Brocc. – Hörnes, p. 102, pl. 10, figs 19–21 [= *Cancilla nanostriatula* Harzhauser & Landau, 2021a].
 non 1880 *Mitra* (*Nebularia*) *striatula* Brocchi – Hörnes & Auinger, p. 80, pl. 9, figs 20a-b [= *Cancilla suballigata* Bellardi, 1887].
 non 1973 *Mitra* (*Tiara*) *striatula* (Brocchi) 1814 – Bohn-Havas, p. 1117, pl. 9, fig. 5 [= *Fraudiziba* sp.].

Material and dimensions – Maximum height 32.6 mm, width 8.7 mm. **CO:** NHMW 2024/0042/0035-0038 (4), 2024/0042/0034 (10).

Description – Medium sized, solid, slender fusiform shell, with moderately high spire, and relatively low last whorl; apical angle 30-32°. Protoconch missing in all specimens. Teleoconch up to eight weakly convex whorls, with periphery at abapical suture, separated by moderately incised suture. Sculpture consisting of flat-

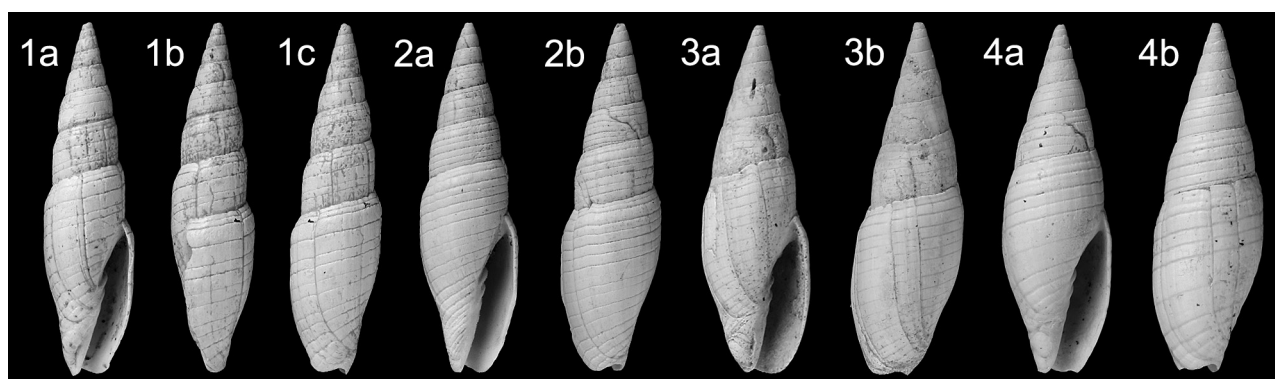


Plate 1. *Cancilla alligata* (Defrance in de Blainville, 1825); 1. NHMW 2024/0042/0035, height 32.6 mm, width 8.4 mm; 2. NHMW 2024/0042/0036, height 27.3 mm, width 7.6 mm; 3. NHMW 2024/0042/0037, height 24.3 mm, width 7.6 mm; 4. NHMW 2024/0042/0038, height 24.6 mm, width 7.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

tened spiral cords separated by narrow punctate grooves, three on early teleoconch whorls, increasing to 5-7 on penultimate whorl, cords of irregular width. Axial sculpture restricted to strong collabral growth halts interrupting cords. Last whorl 58-62% of total height, slender, shoulder obsolete or almost so, subcylindrical to weakly convex, with moderately constricted base; about 12-15 flattened cords of irregular width, some subdivided by shallower punctate grooves in some specimens; fasciole narrow, rounded, moderately well delimited from base by grooves. Aperture narrow, elongate; outer lip thin; anal sinus marked by shallow V-shaped notch; siphonal canal moderately long, twisted, with incised siphonal notch. Columellar callus narrow, indented over medial edge of base. Columella bearing 4-5 folds, weakening and increasingly oblique abapically. Colour pattern preserved consisting of narrow orange lines in the grooves on last whorl.

Discussion – As discussed by Harzhauser & Landau (2021a, p. 60) *Voluta striatula* Brocchi, 1814 is a primary homonym of *Voluta striatula* Schröter, 1804 (Schröter 1804, p. 37) and a secondary homonym of *Mitra striatula* Lamarck, 1811 (Lamarck 1811, p. 210). Therefore, Defrance in Blainville (1825: 494) introduced *Mitra alligata* as new name. Obviously, Potiez & Michaud (1838, p. 497) were unaware of Defrance's name and introduced *Mitra brocchii* as new name for the same species. *Mitra striosa*, mentioned by Sismonda (1842, p. 41) and Hörnes (1852, p. 103) as replacement names for *Voluta striatula* Brocchi, is a *nomen nudum* and refers to a label name in the Museo Regionale di Scienze Naturali, Torino written by Franco Andrea Bonelli (1784-1830). Therefore, the valid name for the Pliocene species is *Cancilla alligata* (Defrance in Blainville, 1825).

Bellardi (1887a) included this species in a group of species about 15-20 mm in height, characterised by their relatively tall spired and low last whorls, and relatively strongly twisted columella and constricted base. Within this group it is most similar to *C. suballigata* (Bellardi, 1887), described from the Tortonian of Stazzano (Italy) but also present in the Middle Miocene Paratethys

(Harzhauser & Landau, 2021a, p. 60), but differs in being slenderer with a proportionally higher spire.

Cancilla alligata is somewhat variable; some specimens have a weak rounded shoulder placed high, whilst in others the shoulder is obsolete. Spiral sculpture is also highly variable the cords wide in some specimens, in others subdivided by further weaker punctate grooves. All Estepona specimens have four well-developed columellar folds, with a subobsolete fifth abapical fold in some specimens. *Cancilla altavillensis* Ruggieri, Bruno & Curti, 1959 from the Upper Pliocene of Altavilla, Italy, originally described as a subspecies of *C. alligata*, was said to differ in being smaller, broader, with a more regularly conical spire, shallower suture, and with fewer spiral cords. That species was again illustrated in Brunetti & Cresti (2018, fig. 309) from the Pliocene of Tuscany. Although variable, none of the Estepona specimens are as broad or have a spire as regularly conical. We therefore separate Ruggieri *et al.*'s taxon at full species rank as did Brunetti & Cresti. We are uncertain whether the specimen illustrated as *C. alligata* by Brunetti & Cresti (2018, fig. 311) is that species. It is larger than any specimen from Estepona at 45 mm in height and the spire is slenderer.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1992; Ruiz Muñoz *et al.*, 1997; Landau *et al.*, 2011); western Mediterranean, NE Spain (Martinell, 1979), Roussillon Basin, France (Fontannes, 1880), Tunisia (Fekih, 1975); central Mediterranean, Italy (Bellardi, 1887a; Ruggieri *et al.*, 1959; Pavia, 1976; Chirli, 1988, 2002). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887a; Sacco, 1904; Ruggieri *et al.*, 1959; Malatesta, 1974; Cavallo & Repetto, 1992).

***Cancilla bonellii* (Bellardi, 1850)**

Plate 2, figs 1-3

*1850 *Mitra Bonellii* Bellardi, p. 13, pl. 1, fig. 21.

1887a *Mitra Bonellii* Bell. – Bellardi, p. 76, pl. 4, fig. 19.

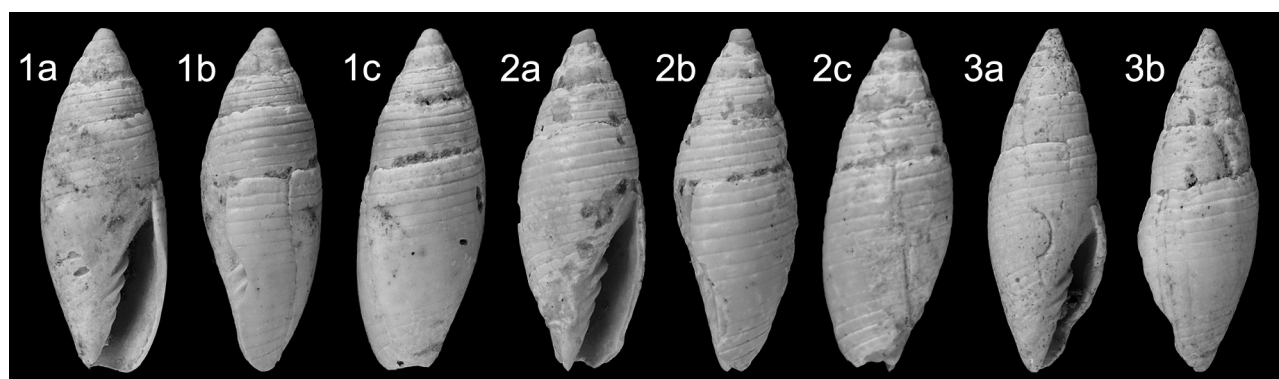


Plate 2. *Cancilla bonellii* (Bellardi, 1850); 1. NHMW 2024/0042/0064, height 11.2 mm, width 4.1 mm; 2. NHMW 2024/0042/0065, height 11.7 mm, width 4.4 mm; 3. NHMW 2024/0042/0066, height 13.8 mm, width 4.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

- 1890 *Mitra Bonellii* var. *angustoacuta* Sacco, p. 251 (= var A of Bellardi, 1887a).
 1904 *Mitra Bonellii* var. *angustoacuta* Sacco, p. 83, pl. 18, fig. 46.
 1959 *Mitra bonellii* Bellardi – Ruggieri *et al.*, p. 87, pl. 18, fig. 110.
 1981 *Mitra bonellii* Bellardi, 1850 – Ferrero Mortara *et al.*, p. 160, pl. 49, fig. 4.
 1997 *Mitra (Tiara) bonellii* Bellardi, 1850 – Bałuk, p. 28, pl. 11, fig. 9.
 2000 *Cancilla (Ziba) bonellii* (Bellardi, 1887) – Davoli, p. 192, pl. 3, fig. 8.
 2002 *Cancilla (Ziba) bonellii* (Bellardi, 1850) – Chirli, p. 47, pl. 23, figs 3-8.
 2011 *Cancilla bonellii* (Bellardi, 1850) – Chirli & Linse, p. 143, pl. 48, fig. 4.
 2021a *Episcomitra bonellii* (Bellardi, 1850) – Harzhauer & Landau, p. 10.

Material and dimensions – Maximum height 13.8 mm, width 4.7 mm. **CO:** NHMW 2024/0042/0064-0065 (2), NHMW 2024/0042/0066 (1).

Description – Small sized, solid, slender biconic-fusiform shell with relatively short spire; apical angle initially 52-61°, later 36-39°. Protoconch unknown. Teleoconch up to five weakly convex whorls, with periphery at abapical suture, separated by superficially incised suture. Sculpture consisting of regular flattened spiral cords separated by narrow grooves, five on third teleoconch whorl, increasing to 6-7 on penultimate whorl. Last whorl 66-72% of total height, slender, subcylindrical, bearing flattened cords along entire surface; fasciole hardly developed. Aperture narrow, elongate; posterior sinus marked by narrow V-shaped notch; outer lip thin, smooth within; siphonal canal very short, open, with shallow siphonal notch. Columellar callus narrow, poorly delimited, indented over medial edge of base. Columella bearing four strong oblique folds, weakening abapically.

Discussion – The specimens from Estepona are slightly smaller than those from Italy (13.7-17.6 mm height; *fide*

Chirli, 2002), but otherwise agree with Italian specimens. In his species description Chirli (2002, p. 47) noted that three columellar folds were well developed with a fourth abapically hardly visible. However, this is not reflected in the specimens illustrated in which the fourth fold is clearly developed in all specimens (2002, pl. 23, figs 3, 5-8), as is the case with the Estepona specimens. For comparison see *Cancilla dignota* (Bellardi, 1887) below.

This is one of the few Mitridae in the Estepona assemblages with a relatively long geological history, from the Middle Miocene of the Paratethys, to the Upper Miocene central Proto-Mediterranean, where it is present until the end of the Pliocene. Its Paratethyan record is based on a single report by Bałuk (1997) which Harzhauer & Landau (2021a) were not able to support with further Paratethyan occurrences. Nevertheless, Bałuk's record seems to represent that species and was accepted.

Distribution – Middle Miocene: Paratethys, Poland (Bałuk, 1997). Upper Miocene: central Proto-Mediterranean, Italy (Davoli, 2000). Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1850, 1887a; Ruggieri *et al.*, 1959; Ferrero Mortara *et al.*, 1981). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Cancilla dignota (Bellardi, 1887)

Plate 3, figs 1-4

- *1887a *Mitra dignota* Bellardi, p. 77, pl. 4, fig. 20.
 1890 *Mitra dignota* var. *subasulcata* Sacco, p. 251 (= var A of Bellardi, 1887a).
 1890 *Mitra dignota* var. *convexoparva* Sacco, p. 251 (= var B of Bellardi, 1887a).
 1904 *Mitra dignota* var. *subasulcata* Sacco, p. 83.
 1904 *Mitra dignota* var. *convexoparva* Sacco, p. 83, pl. 18, figs 47, 48.
 1981 *Mitra dignota* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 160, pl. 49, fig. 2.

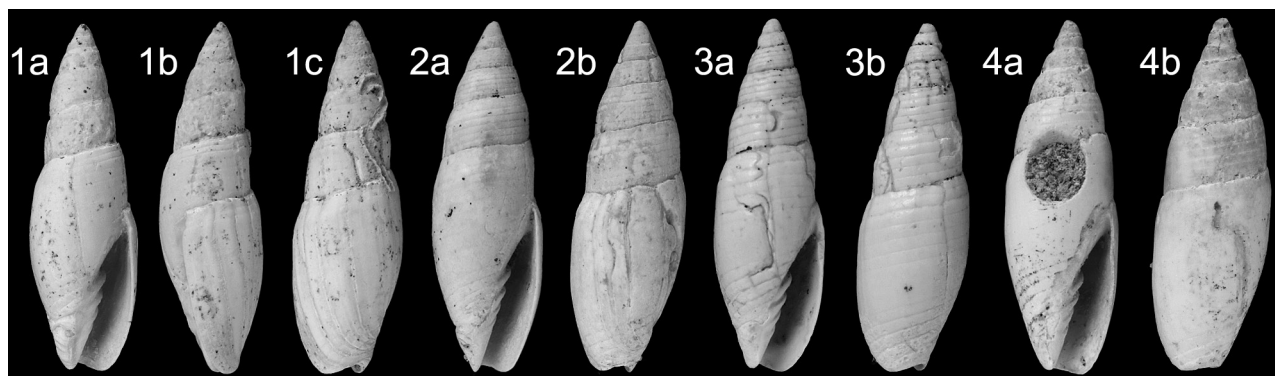


Plate 3. *Cancilla dignota* (Bellardi, 1887); 1. NHMW 2024/0042/0026, height 18.1 mm, width 5.7 mm; 2. NHMW 2024/0042/0027, height 17.1 mm, width 5.8 mm; 3. NHMW 2024/0042/0028, height 17.9 mm, width 5.7 mm; 4. NHMW 2024/0042/0029, height 16.1 mm, width 5.2 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2002 *Cancilla* (Ziba) *dignota* (Bellardi, 1887) – Chirli, p. 48, pl. 23, figs 9-12, pl. 24, figs 1-3.

Material and dimensions – Maximum height 23.3 mm, width 7.1 mm. **CO:** NHMW 2024/0042/0026-0028 (3), 2024/0042/0021 (10).

Description – Small sized, solid, slender fusiform shell; apical angle initially approx. 50°, later approx. 35°. Protoconch unknown. Teleoconch up to seven weakly convex whorls, with periphery at abapical suture, separated by weakly incised suture. Sculpture consisting of regular flattened spiral cords separated by narrow grooves, five on fourth teleoconch whorl, increasing to 6-7 on penultimate whorl. Axial sculpture restricted to strong collabral growth halts interrupting cords. Last whorl 63-65% of total height, slender, subcylindrical, hardly constricted at base; 3-6 cords in subsutural area weakening abapically, mid-whorl smooth, base with 4-6 cords, strengthening towards fasciole; fasciole flattened, poorly delimited from base. Aperture narrow, elongate; posterior sinus marked by shallow V-shaped notch; outer lip thin; siphonal canal short, open, with incised siphonal notch. Columellar callus narrow, poorly delimited, indented over medial edge of base. Columella bearing four strong oblique folds in lower half, weakening abapically.

Discussion – The Estepona specimens are slightly variable in slenderness and in the strength of the spiral cords on the last whorl. In all but one of the Estepona specimens the cords are obsolete mid-whorl. The columellar folds are strongly developed in all specimens. We note that Chirli (2002, p. 48) counted five folds in his Italian specimens, whereas almost all the Estepona specimens have four, and one of the larger ones also has five.

Bellardi (1887a, p. 75) included *Mitra dignota* Bellardi, 1887 in his '37^a Serie' which he considered difficult to phrase in words what these species had in common, but they all had the whorl surface covered in narrow cords, the columellar lip depressed, and the columella short, almost truncated. *Cancilla bonellii* (Bellardi, 1850) from

the Upper Pliocene of Italy (syntype illustrated by Ferrero Mortara *et al.*, 1981, pl. 49, fig. 2) that also occurs in the Estepona assemblages, differs in being smaller, squatter, with a shorter spire, and the spiral cords on the last whorl are more strongly developed. *Cancilla interposita* (Bellardi, 1850) (holotype illustrated by Ferrero Mortara *et al.*, 1981, pl. 49, fig. 3), from the same Upper Pliocene Italian deposits as *C. dignota*, differs in having an unusually short last whorl in relation to the spire. Bellardi (1887a, p. 77) described it as exceedingly rare. The taxon seems to have been erected based on a single specimen, and we do not exclude this being a specimen of *C. dignota* with an abnormally short last whorl. *Cancilla zanolensis* (Bellardi, 1887) (holotype illustrated by Ferrero Mortara *et al.*, 1981, pl. 49, fig. 6) is another member of this group, squatter than *C. dignota*, with a lower spire, extremely similar to *C. bonellii* in profile and sculpture. It was said to differ from that species in being smaller (13 mm vs. 16 mm height; *fide* Bellardi, 1887a), the spire longer and more acute, the suture deeper, and the spiral cords slightly more crowded. We have not seen these specimens but suspect they may represent a single species based on the holotypes illustrated by Ferrero Mortara *et al.* (1981). The last two species included in '37^a Serie' by Bellardi are *E. optabilis* (Bellardi, 1887) from the Middle Miocene and *C. praecedens* (Bellardi, 1887) from the Upper Miocene. Both differ from *C. dignota* in being squatter.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887a; Sacco, 1904; Ferrero Mortara *et al.*, 1981).

***Cancilla planicostata* (Bellardi, 1887)**

Plate 4, fig. 1

1880 *Mitra* (*Nebularia*) *scrobiculata* Brocc. – Hoernes & Auinger, p. 80, pl. 9, fig. 17 [*non Cancilla scrobiculata* (Brocchi, 1814)].

- 1887a *Mitra exarata* Bellardi, p. 84, pl. 4, fig. 53 [non A. Adams, 1853].
- * 1887b *Mitra planicostata* Bellardi, p. 5, pl. 2, fig. 9.
- 1890 *Cancilla planicostata* var. *bifidocostata* Sacco, p. 252 (= var. A Bellardi, 1887b).
- 1890 *Cancilla planicostata* var. *lingusticocontorta* Sacco, p. 252 (= var. B Bellardi, 1887b).
- 1904 *Cancilla planicostata* var. *bifidocostata* Sacc. – Sacco, p. 84, pl. 18, fig. 54.
- 1904 *Cancilla planicostata* var. *lingusticocontorta* Sacc. – Sacco, p. 84, pl. 18, fig. 55.
- 1958 *Mitra (Cancilla) scrobiculata* var. *karamanensis* Erünal-Erentöz, p. 82, pl. 12, fig. 18.
- 1960 *Mitra (Tiara) grateloupi* d'Orbigny, 1852 – Kojumdgieva in Kojumdgieva & Strachimirov, p. 157, pl. 42, fig. 1 [non d'Orbigny, 1852].
- 1981 *Mitra exarata* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 162, pl. 50, fig. 1.
- 1981 *Mitra planicostata* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 162, pl. 50, fig. 2.
- 1992 *Cancilla planicostata* Bellardi, 1887 [sic] – Cavallo & Repetto, p. 118, fig. 303.
- 1998 *Mitraria (Tiara) grateloupi* d'Orbigny – Schultz, p. 70, pl. 28, fig. 9 [non d'Orbigny, 1852].
- 2000 *Cancilla planicostata* (Bellardi, 1887) – Davoli, p. 187, pl. 4, figs 6, 7.
- 2002 *Cancilla planicostata* (Bellardi, 1887) – Chirli, p. 45, pl. 22, figs 10, 11.
- 2008 *Cancilla planicostata* (Bellardi, 1887) – Chirli & Richard, p. 52, pl. 10, fig. 1.
- 2013 *Cancilla planicostata* (Bellardi, 1887) – Landau *et al.*, p. 211, pl. 33, figs 4-8, pl. 80, fig. 7.
- 2018 *Cancilla planicostata* (Bellardi, 1887) – Brunetti & Cresti, p. 82, fig. 312.
- 2021a *Cancilla planicostata* (Bellardi, 1887) – Harzhauser & Landau, p. 54, figs 14E₁-E₂, F₁-F₂, G₁-G₂, H, 7I₁-I₂, J₁-J₂.

Material and dimensions – Height 39.0 mm, width 10.7 mm. **EL:** NHMW 2024/0042/0067 (1).

Description – Shell medium sized, slender fusiform with narrowly incised suture; apical angle initially 40°, later 32°. Protoconch not preserved. Teleoconch of seven whorls; spire whorls initially almost straight sided, slightly convex abapically, with periphery at abapical suture. Surface of first three teleoconch whorls abraded. Fourth whorl with seven rounded spiral cords with flattened tops, separated by narrow punctate grooves. Last whorl elongate, 64% of total height, weakly convex, slowly contracting with shallow concavity at base, bearing twenty spiral cords crossed by relatively strong crowded axial growth lines; fasciole moderately developed, weakly rounded, poorly delimited from base. Aperture moderately narrow; outer lip thin, smooth within; anal sinus marked by narrow V-shaped notch; siphonal canal long, moderately narrow, distinctly twisted, with deep siphonal notch. Columellar callus narrow, thin, sharply delimited. Columella with three oblique folds placed mid-aperture, weakening abapically.

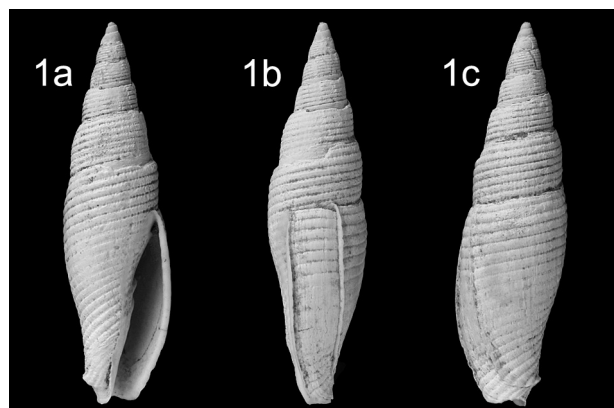


Plate 4. *Cancilla planicostata* (Bellardi, 1887); 1. NHMW 2024/0042/0067, height 39.0 mm, width 10.7 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – *Cancilla planicostata* (Bellardi, 1887) is represented by a single relatively well preserved specimen from the shallower water El Lobillo assemblage. Size is in the middle of the range given by Harzhauser & Landau (31.1-45.7 mm; 2021a, p. 54) for Paratethyan specimens and Landau *et al.* (30.8-42.4 mm; 2013, pl. 33, figs 4-8) for Middle Miocene specimens from Turkey. The protoconch is not preserved in the Estepona material but is high conical of about three weakly convex whorls (Harzhauser & Landau, 2021a). The colour pattern of axial flammules illustrated by Landau *et al.* (2013, pl. 80, fig. 7) for Middle Miocene specimens from the Karaman Basin of Turkey and Harzhauser & Landau (2021a) for Paratethyan specimens is not preserved in the Estepona material, nor enhanced under UV light. For full discussion and comparison with congeners, see Landau *et al.* (2013, p. 211). In the Estepona assemblages it is most similar to *C. transiens* (Bellardi, 1887), but in that species the spiral cords are flatter and tend to become subobsolete on at least the central portion of the last whorl, whereas in *C. planicostata* they remain strongly developed along the entire last whorl.

Distribution – Middle Miocene: Paratethys, Austria (Schultz, 1998; Harzhauser & Landau, 2021a), Romania (Hoernes & Auinger, 1880; Harzhauser & Landau, 2021a), Bulgaria (Kojumdgieva in Kojumdgieva & Strachimirov, 1960). Middle Miocene: western Proto-Mediterranean, Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.*, 2013); central Proto-Mediterranean, Italy (Bellardi, 1887a). Upper Miocene: central Proto-Mediterranean, Italy (Davoli, 2000). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887b; Sacco, 1904; Chirli, 2002; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1904; Cavallo & Repetto, 1992).

***Cancilla scrobiculata* (Brocchi, 1814)**

Plate 5, fig. 1

- * 1814 *Voluta scrobiculata* Brocchi, p. 317, pl. 4, fig. 3.
 1850 *Mitra scrobiculata* Brocc. – Bellardi, p. 16, pl. 2, figs 5-9.
 1880 *Mitra scrobiculata* var. *massoti* Fontannes, p. 84, pl. 6, fig. 6.
 1887b *Mitra scrobiculata* Brocc. – Bellardi, p. 7, pl. 2, fig. 19, pl. 5, fig. 11.
 1890 *Cancilla scrobiculata* var. *ligusticosulcata* Sacco, p. 253 (= var. A of Bellardi, 1887a).
 1890 *Cancilla scrobiculata* var. *laevigatoangusta* Sacco, p. 253 (= var. B of Bellardi, 1887a).
 1904 *Cancilla scrobiculata* var. *ligusticosulcata* Sacc. – Sacco, p. 84, pl. 19, fig. 3.
 1904 *Cancilla scrobiculata* var. *laevigatoangusta* Sacc. – Sacco, p. 84.
 1933 *Mitra scrobiculata* Br. – Ravetta, p. 125, pl. 1, figs 1-15.
 1955 *Mitra (Scabricula) (Cancilla) scrobiculata* (Brocchi 1814) – Rossi Ronchetti, p. 246, fig. 131.
 1959 *Mitra (Scabricula) scrobiculata* (Brocchi) – Ruggieri *et al.*, p. 81, pl. 18, figs 107, 108.
 1967 *Mitra (Tiara) scrobiculata* (Brocchi) – Pelosio, p. 147, pl. 42, figs 10-12.
 1973 *Mitra (Mitra) scrobiculata* (Brocchi) – Caprotti & Vescovi, p. 170, pl. 2, fig. 16.
 1974 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Malatesta, p. 363, pl. 29, fig. 7.
 1975 *Mitra scrobiculata* (Brocchi) – Fekih, p. 131, pl. 39, fig. 3.
 1976 *Mitra scrobiculata* (Brocchi) – Caprotti, p. 11, pl. 16, fig. 16.
 1978 *Voluta scrobiculata* Brocchi, 1814 – Pinna & Spezia, p. 170, pl. 66, fig. 2.
 1979 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Martinell, p. 61, pl. 1, figs 1, 2.
 1991 *Cancilla scrobiculata scrobiculata* (Brocchi, 1814) – Cernohorsky (*partim*), p. 33, pl. 25, figs 1-4.
 1992 *Cancilla scrobiculata* (Brocchi, 1814) – Cavallo & Repetto, p. 121, fig. 304.
 2002 *Cancilla scrobiculata* (Brocchi, 1814) – Chirli, p. 45, pl. 22, figs 1-4.
 2008 *Cancilla scrobiculata* (Brocchi, 1814) – Chirli & Richard, p. 52, pl. 10, figs 2, 3.
 2011 *Cancilla scrobiculata* (Brocchi, 1814) – Landau *et al.*, p. 29, pl. 15, fig. 4.
 2018 *Cancilla scrobiculata* (Brocchi, 1814) – Brunetti & Cresti, p. 82, fig. 313.
 non 1852 *Mitra scrobiculata* Brocc. – Hörnes (*pars*), p. 100, pl. 10, fig. 15 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1852 *Mitra scrobiculata* Brocc. – Hörnes (*pars*), p. 100, pl. 10, fig. 16 [= *Cancilla exornata* (Bellardi, 1887)].
 non 1852 *Mitra scrobiculata* Brocc. – Hörnes (*pars*), p. 100, pl. 10, fig. 17 [= *Domiporta turpis* Harzhauser & Landau, 2021a].
 non 1852 *Mitra scrobiculata* Brocc. – Hörnes (*pars*), p. 100, pl. 10, fig. 18 [= *Domiporta austrogallica* (Mayer-Eymar, 1898)].
 ?non 1866 *Mitra scrobiculata* Brocc. – Pereira da Costa, p. 68, pl. 12, fig. 13.
 non 1880 *Mitra (Nebularia) scrobiculata* Brocc. – Hoernes & Auinger (*pars*), p. 80, pl. 9, fig. 17 [= *Cancilla planicostata* (Bellardi, 1887)].
 non 1880 *Mitra (Nebularia) scrobiculata* Brocc. – Hoernes & Auinger (*pars*), p. 80, pl. 9, figs 18-19 [= *Nebularia soliphila* Harzhauser & Landau, 2021a].
 non 1911 *Mitra (Cancilla) scrobiculata* Brocc. var. – Friedberg, p. 16, pl. 1, fig. 9 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1954 *Mitra (Nebularia) scrobiculata* Brocc. – Csepregy-Meznerics, p. 46, pl. 5, figs 24, 27-28 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1959 *Mitra scrobiculata* Brocc. – Eremija, pl. 1, fig. 4 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1961 *Mitra scrobiculata* Brocc. – Florei, p. 686, pl. 9, fig. 68 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1966 *Mitra (Nebularia) scrobiculata* Brocchi, 1814 – Strausz (*pars*), p. 365, pl. 26, figs 6, 7 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1966 *Mitra (Nebularia) scrobiculata* Brocchi, 1814 – Strausz (*pars*), p. 365, pl. 26, fig. 8 [= *Cancilla exornata* (Bellardi, 1887)].
 non 1972 *Mitra (Nebularia) scrobiculata* Br. – Csepregy-Meznerics, p. 30, pl. 14, figs 11, 12 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1973 *Mitra (Tiara) scrobiculata* Brocchi – Bohn-Havas, p. 1059, pl. 6, fig. 6, pl. 10, fig. 2 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1982 *Mitra (Nebularia) scrobiculata* (Brocchi, 1814) – Švagrovský, p. 397, pl. 4, fig. 2 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1984 *Mitra (Cancilla) scrobiculata* (Brocchi, 1814) – Ruggieri & Davoli, p. 62, pl. 3, fig. 1 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1985 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Atanacković, p. 162, pl. 36, figs 11, 12 [= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 1997 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Bałuk, p. 28, pl. 7, fig. 9 [?= *Cancilla praescrobiculata* (Toldo, 1889)].
 non 2010 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Caze *et al.*, p. 33, fig. 5C1-C2 [= *Domiporta amoena* Harzhauser & Landau, 2021a].
 non 2014 *Mitra (Tiara) scrobiculata* (Brocchi, 1814) – Popa *et al.*, p. 15, pl. 4, fig. 7 [= *Cancilla praescrobiculata* (Toldo, 1889)].

Material and dimensions – Height 60.0 mm, width 13.4 mm (incomplete; restored height ~ 70 mm). **CO:** NHMW 2024/0042/0068 (1).

Description – Shell large, slender fusiform with moderately incised suture; apical angle initially 36°, later 26°. Protoconch and surface of earliest teleoconch whorls not preserved. Teleoconch of eight whorls, surface of

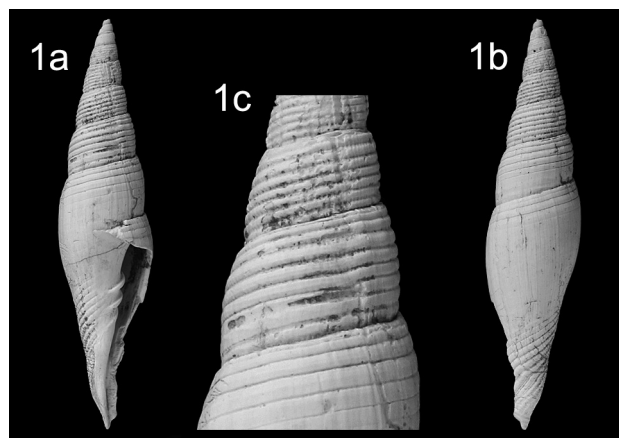


Plate 5. *Cancilla scrobiculata* (Brocchi, 1814); 1. NHMW 2024/0042/0068, height 60.0 mm, width 13.4 mm, 1c, detail of sculpture mid-whorls. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

only last five whorls preserved. Spire whorls very weakly convex with periphery at abapical suture. Sculpture of eight regular flattened spiral cords, initially separated by fine grooves, abapically spiral interspaces widen slightly with close set lamellar growth lines in spiral interspaces. Last whorl slender, subcylindrical, weakly constricting at base; sculpture of fine spiral cords, well developed in subsutural area, base and fasciole, obsolete mid-whorl, interspaces again narrowed to fine grooves, axial growth lines not evident in interspaces; fasciole poorly developed. Aperture elongate; outer lip incomplete; anal sinus and siphonal canal incomplete. Columella bearing four oblique folds weakening abapically. Columellar callus thickened abapically, very narrow bordering fasciole, thinning and indistinct abapically.

Discussion – *Cancilla scrobiculata* (Brocchi, 1814) is the largest of the Pliocene Mediterranean *Cancilla* species. Sculpture, slenderness, apical angle and the number of columellar folds is variable, which was extensively discussed by Ravetta (1933) and Pelosio (1967). Unfortunately, the species is extremely uncommon in the Estepona assemblages, and the only specimen at hand is incomplete, which does not allow us to add much useful information to the discussions put forward by those authors, except to say that the Estepona specimen has the spiral sculpture obsolete mid-whorl on the last whorl, similar to one of the specimens illustrated by Pelosio (1967, pl. 42, fig. 11) and Chirli (2002, pl. 22, figs 1, 2). In the distribution we have not included the Upper Miocene record of Pereira da Costa (1866) which is based on a small shell and is unlikely to be conspecific.

Cancilla praescrobiculata (Toldo, 1889), widespread in the Middle and Upper Miocene Paratethys and Proto-Mediterranean Sea, is considered the Miocene ancestor of the Pliocene *C. scrobiculata* by Toldo (1889), Davoli (2000) and Landau *et al.* (2013). In summary, *C. praescrobiculata* differs from *C. scrobiculata* in having the

intermediate whorls with 5–6 irregular spiral cords, separated by interspaces which are widest adapically, narrowing abapically, whereas in the Pliocene shells the cords are more regularly spaced, separated by narrow grooves of equal width (Pl. 5, fig. 1c), in *C. scrobiculata* the spiral sculpture becomes attenuated on the last adult whorl, whereas it is consistently stronger in the Miocene form, in *C. praescrobiculata* the adapical four columellar folds are strong and unequally developed, with a weaker fifth fold abapically, whereas in *C. scrobiculata* only the adapical two folds are strongly developed, and lastly the siphonal fasciole is twisted to the left in the Miocene form but not in the Pliocene one. For further discussion on differences between the species see Landau *et al.* (2013, p. 212).

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011); western Mediterranean, NE Spain (Martinell, 1979), Roussillon Basin, France (Fontannes, 1880), Tunisia (Fekih, 1975); central Mediterranean, Italy (Bellardi, 1887b; Sacco, 1904; Pelosio, 1967; Chirli, 2002; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Ruggieri *et al.*, 1959; Malatesta, 1974; Caprotti & Vescovi, 1973; Caprotti, 1976; Cavallo & Repetto, 1992).

***Cancilla* aff. *sismondai* (Michelotti, 1847)**

Plate 6, fig. 1

- aff. *1847 *Mitra Sismondai* Michelotti, p. 317.
- aff. 1967 *Mitra (Tiara) sismondiae* Michelotti – Pelosio, p. 148, pl. 43, figs 1a,b, 2, 13.
- aff. 1968 *Mitra (Tiara) sismondiae* Michelotti, 1847 – Robba, p. 562, pl. 43, fig. 2.
- aff. 1992 *Cancilla sismondai* Michelotti, 1847 [sic] – Cavallo & Repetto, p. 120, fig. 305.
- aff. 2000 *Cancilla sismondai* (Michelotti, 1847) – Davoli, p. 190, pl. 6, figs 19–22.

Material and dimensions – Height 34.6 mm, width 13.0 mm (incomplete; restored height ~ 45 mm). CO: NHMW 2024/0042/0057 (1).

Description – Shell moderately large, moderately slender fusiform with narrowly incised suture. Protoconch and earliest teleoconch whorls not preserved. Fragment with four teleoconch whorls, surface of only last two whorls preserved. Spire whorls very weakly convex with periphery at abapical suture. Sculpture of fine regular spiral cords and close set lamellar growth lines most visible in spiral interspaces, giving surface finely cancellate appearance. Last whorl subcylindrical, regularly constricting at base; sculpture of fine spiral cords and lamellar growth lines covering entire surface; fasciole poorly developed. Aperture elongate; outer lip incomplete, smooth within; anal sinus hardly developed, siphonal canal incomplete. Columella bearing four oblique

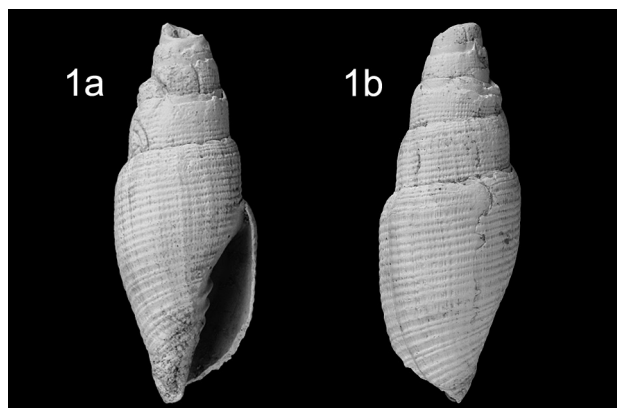


Plate 6. *Cancilla* aff. *sismondai* (Michelotti, 1847); 1. NHMW 2024/0042/0057, height 34.6 mm, width 13.0 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

folds weakening abapically. Columellar callus slightly thickened abapically, thinning abapically, indented in parietal area.

Discussion – Unfortunately, this species is represented in the Estepona assemblages by a single incomplete specimen, missing the apex and early teleoconch whorls, outer lip and end of the siphonal canal. Nevertheless, it differs from all other Estepona mitrids in its sculpture composed of fine regular cords and close-set, lamellar growth lines that give the surface a finely cancellate appearance. It belongs to the *Cancilla sismondai* (Michelotti, 1847) species group that has been reported from the Middle Miocene Paratethys and the Upper Miocene to Lower Pliocene Mediterranean. However, Harzhauser & Landau (2021a, p. 60) suggested that Mediterranean Pliocene records did not represent that species and differed in their larger, more elongate shell and a more delicate and uniform spiral sculpture. The Estepona specimen is about the same size as specimens of *C. sismondai* from the Miocene but does indeed have very regular spiral sculpture. The main difference between the Estepona specimen and Miocene specimens illustrated by authors as *C. sismondai* is that the two whorls preserved are subcylindrical, forming a telescopic spire, more similar to the Italian Pliocene specimens illustrated by Pelosio (1967, pl. 43, figs 1a,b, 2, 13), but with even more gradate whorls. Paratethyan Miocene specimens illustrated by Harzhauser & Landau (2021a) as *C. sismondai* are not conspecific; they have far less cylindrical whorls. The species was originally described from the Upper Miocene of Italy. Unfortunately, the type material was destroyed during World War II (Manni, 2005). Pelosio (1967) considered *Mitra altilis* (Bellardi, 1887) described from the Lower Pliocene of Italy (for holotype see Ferrero Mortara *et al.*, 1981, pl. 43, fig. 7) a form of *M. sismondai*, but that species is even more unlike the Estepona specimen in having an inflated last whorl and is unlikely to be a form of *C. sismondai*. The specimen illustrated as *Cancilla sismondai* by Cavallo & Repetto

(1992, fig. 305) is similar in sculpture to the Estepona specimen, but again has more regularly convex whorls, especially the last whorl is not subcylindrical. The Estepona species probably represents yet another species in the *C. sismondai* group, but with the single incomplete specimen available we hesitate to erect a new taxon. For full chresonymy of *C. sismondai*, see Harzhauser & Landau (2021a, p. 59).

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

Cancilla laevigatobrevis (Sacco, 1904)

Plate 7, figs 1-4

- 1887b *Mitra transiens* var. A Bellardi, p. 6 [not pl. 2, fig. 10 = *Cancilla transiens* (Bellardi, 1887)].
- 1887b *Mitra fusulus* Cocc. – Bellardi, p. 16, pl. 4, fig. 55 (non Cocconi, 1873).
- *1890 *Mitra transiens* var. *laevigatobrevis* Sacco, p. 253 (= var. A Bellardi, 1887b).
- 1904 *Mitra (Cancilla) transiens* var. *laevigatobrevis* Sacc. – Sacco, p. 84, pl. 19, fig. 1.
- 1974 *Mitra (Tiara) fusulus* Cocconi, 1873 – Malatesta, p. 361, pl. 29, fig. 12.
- 1974 *Mitra (Tiara) transiens* Bellardi, 1887 – Malatesta, p. 364, pl. 29, fig. 11 [non *Cancilla transiens* (Bellardi, 1887)].
- 1992 *Ziba fusulus* (Cocconi, 1873) – Cavallo & Repetto, p. 118, fig. 301)
- 2002 *Cancilla fusulus* (Cocconi, 1873) – Chirli, p. 44, pl. 22, figs 5–9.
- 2002 *Cancilla transiens* (Bellardi, 1887) – Chirli, p. 47, pl. 23, figs 1, 2 [non *Cancilla transiens* (Bellardi, 1887)].
- 2010 *Mitra fusulus* Cocconi, 1873 – Sosso & Dell'Angelo, p. 42, 59 unnumbered fig. top row right.

Material and dimensions – Maximum height 53.5 mm, width 14.4 mm. **CO:** NHMW 2024/0042/0030-0033 (4), 2024/0042/0085 (8).

Description – Shell moderately large, slender fusiform with narrowly incised suture; apical angle initially approx. 39°, later 27°. Protoconch not preserved. Teleoconch of up to nine tall, weakly convex whorls, with periphery at abapical suture, bearing six spiral cords separated by narrow punctate grooves. First 2-3 whorls lower, slightly more convex, whorls increasing in height from fourth whorl. Suture weakly impressed. Abapically cords broaden, flatten and weaken, especially on abapical half of later spire whorls. Last whorl elongate, approx. 63% of total height, slightly flattened in subsutural area, weakly and broadly convex mid-whorl, slowly contracting with shallow concavity at base; 1-3 very weak broad, flattened spirals separated by shallow grooves persisting in subsutural area and up to ten equally weak cords over fasciole; mid-whorl and base smooth; fasciole weakly rounded, poorly delimited from base. Aperture moder-

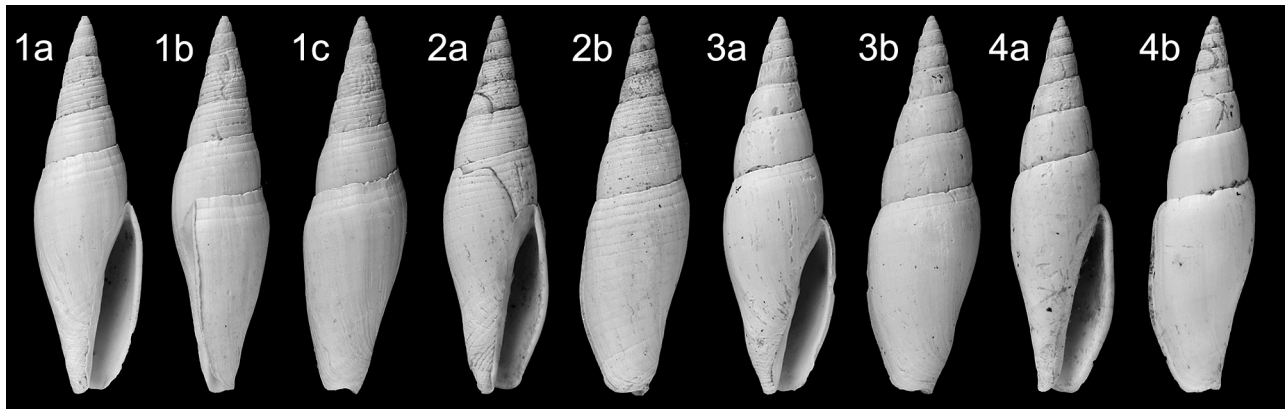


Plate 7. *Cancilla laevigatobrevis* (Sacco, 1904); 1. NHMW 2024/0042/0030, height 47.6 mm, width 13.1 mm; 2. NHMW 2024/0042/0031, height 42.3 mm, width 11.4 mm; 3. NHMW 2024/0042/0032, height 43.6 mm, width 12.5 mm; 4. NHMW 2024/0042/0033, height 40.7 mm, width 11.2 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ately narrow. Outer lip thin, almost straight, edge narrowly everted. Columellar callus narrow, thin, sharply delimited, bearing four oblique folds, weakening abapically, fourth fold subobsolete. Siphonal canal moderately long, moderately wide, weakly twisted, with deep siphonal notch.

Discussion – Bellardi (1887b) grouped a series of ‘*Mitra*’ species characterised by their tall, slender shells, axial and spiral sculpture and four columellar folds in which the early whorls including the nucleus were very small and pointed and the whorls increased in height from the fourth or fifth whorl (1887b, p. 3, ‘43^a Serie’). Three Italian Pliocene species were included in this group; *M. colligens* Bellardi, 1887, *M. planicostata* Bellardi, 1887, and *M. transiens* Bellardi, 1877. Unfortunately, the protoconch is missing and the earliest teleoconch whorl is abraded in the Estepona material, but the earliest teleoconch whorls show a progressive increase in whorl height over the first 3–4 whorls preserved.

This group was placed in the genus *Cancilla* Swainson, 1840 by Harzhauser & Landau (2021a) based on their slender elongate shell, high aperture, long siphonal canal, hardly constricted base, spiral sculpture that covers most of the surface, and by the absence of axial sculpture or at most restricted to the earliest teleoconch whorls.

The Estepona specimens are conspecific with what authors have called *Mitra fusulus* Cocconi, 1873. In our opinion, these specimens probably do not represent Cocconi’s species that is based on an incomplete or juvenile specimen with a lower spire (Cocconi, 1873, pl. 11, figs 17, 18). Bellardi (1887b, pl. 4, fig. 55) discussed the difficulty in interpreting Cocconi’s species and figured a shell as *M. fusulus* that is, in our opinion, conspecific with the Estepona specimens. Bellardi (1887b) described *Mitra transiens* from the Upper Pliocene of Italy that differs from the Estepona specimens in having spiral sculpture along the entire last whorl (for syntype see Ferrero Mortara *et al.*, pl. 50, fig. 12). In his discussion he described a variety with part of the last whorl smooth, later

formally named var. *laevigatobrevis* by Sacco (1890) and illustrated by that author (1904). This seems to be the form found in Estepona. The specimen illustrated as *Ziba fusulus* by Cavallo & Repetto (1992, fig. 301) is identical to the Estepona specimens. Sculpture is somewhat variable, in most specimens from Estepona a few weak cords persist in the subsutural area and base of the last whorl smooth (Pl. 7, figs 1, 3), although occasional specimens are completely smooth (Pl. 7, fig. 4), whilst at the opposite extreme, some specimens have cords persisting along almost the entire last whorl (Pl. 7, fig. 2), but never along the entire last whorl as in *C. transiens*. The specimen illustrated by Brunetti & Cresti (2018, fig. 314) as *Ziba fusulus* is not conspecific with the Estepona species.

Therefore, in summary, we consider *Mitra fusulus* Cocconi, 1873 a *species inquirenda*, most records in the literature referring to that species can be ascribed to *Cancilla laevigatobrevis* (Sacco, 1904), a species similar to *C. transiens* (Bellardi, 1887), but differing in having spiral sculpture that does not cover the entire last whorl. It is possible that they represent extreme sculptural morphotypes of a single species, but based on the Estepona material, we prefer to keep them separate.

Cancilla colligens is immediately separated from *C. laevigatobrevis* by its larger size (up to 78 mm; *fide* Bellardi, 1887b, p. 5) and finely cancellate sculpture (see Ferrero Mortara *et al.*, 1981, pl. 50, fig. 10 for syntype). *Cancilla planicostata* differs in having more numerous spiral cords that do not weaken on later whorls; the entire last whorl spirally sculptured (see Ferrero Mortara *et al.*, 1981, pl. 50, fig. 2 for syntype).

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887b; Sacco, 1904; Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Cavallo & Repetto, 1992; Malatesta, 1974; Sosso & Dell’Angelo, 2010).

Subfamily Mitrinae Swainson, 1831
Genus *Episcomitra* Monterosato, 1917

Type species (by monotypy) – *Mitra zonata* Marryat, 1818, present-day, Mediterranean.

1917 *Episcomitra* Monterosato, p. 26.

Note – For generic discussion see Landau *et al.* (2013, p. 209) and Harzhauser & Landau (2021a, p. 8).

***Episcomitra addita* (Bellardi, 1887)**

Plate 8, fig. 1

- *1887a *Mitra addita* Bellardi, p. 28, pl. 1, fig. 25.
- 1975 *Mitra addita* Bellardi – Fekih, p. 132, pl. 39, fig. 10.
- 1981 *Mitra addita* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 150, pl. 42, fig. 10.
- 2002 *Mitra addita* Bellardi, 1887 – Chirli, p. 29, pl. 15, figs 1-6.

Material and dimensions – Height 56.5 mm, width 20.3 mm.
CO: NHMW 2024/0042/0054 (1).

Description – Shell large, solid, moderately broad fusiform, with moderate height spire; apical angle initially 48°, later 38°. Protoconch unknown. Teleoconch of six relatively low, very weakly convex whorls, with periphery at abapical suture; suture moderately shallow, narrowly impressed. Spire whorls smooth. Last whorl 69% of total height, barrel-shaped, weakly convex with maximum width just above mid-whorl, regularly attenuated below, hardly constricted at base, base smooth; fasciole very strongly developed, raised and flattened, sharply delimited from base, bordering well developed pseudumbilical chink. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short (incomplete). Columellar callus moderately thickened

in lower half, bordering narrow pseudumbilical chink, sharply delimited, thinning in parietal area. Columella bearing five oblique folds, weakening abapically, fifth subobsolete.

Discussion – Bellardi (1887a, p. 27) placed *Mitra addita* in his '13^a Serie' characterised by having a relatively tall, subcylindrical last whorl, more than half the total height, smooth surface, and 4-6 columellar folds. The holotype was figured by Ferrero Mortara *et al.* (1981, pl. 42, fig. 10). Within this group he placed seven species from the Pliocene of Italy. Of these, only three are large shelled like *Episcomitra addita*. *Episcomitra submarginata* (Bellardi, 1887) (for syntype see Ferrero Mortara *et al.*, 1981, pl. 43, fig. 3) is slenderer, with a taller spire and a narrower apical angle, the whorls are more convex, the outer lip is more produced adapically (damaged in the Estepona specimen), the columellar folds are weaker, and the columella is less strongly twisted at the siphonal canal, the fasciole weaker not forming a pseudumbilical chink. *Episcomitra inedita* (Bellardi, 1887) (for syntype see Ferrero Mortara *et al.*, 1981, pl. 43, fig. 1) is taller spired, the last whorl is less cylindrical, the outer lip is thinner, the fasciole weaker bearing weak spiral grooves.

In Estepona this species is represented by a single specimen missing the adapical tip of the outer lip. Nevertheless, it is similar to specimens illustrated by Chirli (2002, pl. 15, figs 1-6) from the Lower Pliocene of Tuscany (Italy), especially in being relatively thick shelled, having a subcylindrical last whorl, and developing a strong siphonal fasciole.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002); western Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887a; Ferrero Mortara *et al.*, 1981).

***Episcomitra astensis* (Bellardi, 1850)**

Plate 9, figs 1-3

- *1850 *Mitra astensis* Bellardi, p. 8, pl. 1, figs 11, ?12.
- 1887a *Mitra astensis* Bell. – Bellardi, p. 21, pl. 1, fig. 18.
- 1890 *Mitra astensis* var. *apertoventrosa* Sacco, p. 247 (= var. A Bellardi, 1887a).
- 1890 *Mitra astensis* var. *acutolonga* Sacco, p. 247 (= var. B Bellardi, 1887a).
- 1904 *Mitra (Cancilla) astensis* var. *apertoventrosa* Sacco, p. 81, pl. 18, figs 12, 13.
- 1904 *Mitra (Cancilla) astensis* var. *acutolonga* Sacco, p. 81, pl. 18, fig. 14.
- 1911 *Mitra astensis* Bell. – Cerulli-Irelli, p. 234 [284], pl. 21 [38], figs 15, 16.
- 1960 *Mitra (Mitra) astensis* Bellardi, 1850 – Malatesta, p. 175, pl. 9, fig. 2.
- 1974 *Mitra (Mitra) astensis* Bellardi, 1850 – Malatesta, p. 353, pl. 29, fig. 15, ?17.
- 1975 *Mitra astensis* Bellardi – Fekih, p. 132, pl. 39, fig. 5.

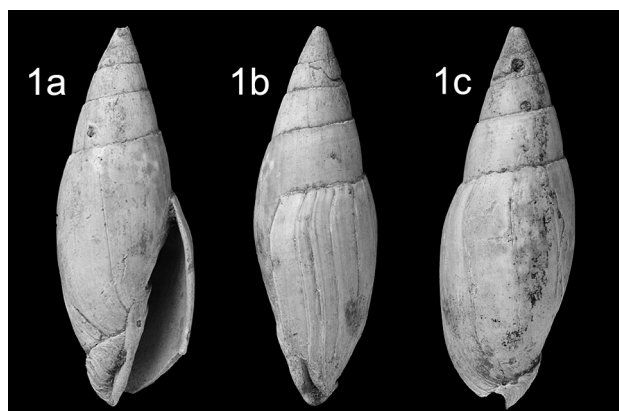


Plate 8. *Episcomitra addita* (Bellardi, 1887); 1. NHMW 2024/0042/0054, height 56.5 mm, width 20.3 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1981 *Mitra astensis* Bellardi, 1850 – Ferrero Mortara *et al.*, p. 148, pl. 42, fig. 4.

Material and dimensions – Maximum height 54.7 mm, width 19.8 mm. **CO:** NHMW 2024/0042/0052-0053 (2), 2024/0042/0086 (1), 2024/0042/0087 (1).

Description – Shell moderately large to large, solid, moderately broad fusiform, with moderate height spire; apical angle initially approx. 39°, later 36°. Protoconch unknown. Teleoconch of up to seven relatively low, very weakly convex whorls, with periphery at abapical suture; suture moderately shallow, narrowly impressed. Spire whorls smooth. Last whorl 64-68% of total height, weakly convex with maximum width mid-whorl, regularly attenuated below, hardly constricted at base, base smooth or with very weak spirals; fasciole well developed, delimited from base by ridge. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short, wide, slightly twisted with deep siphonal notch. Columellar callus moderately thickened in lower half, bordering narrow pseudumbilical chink, sharply delimited, thinning in parietal area. Columella bearing five oblique folds, weakening abapically, fifth subobsolete.

Discussion – Bellardi (1887a, p. 20) included only *Episcomitra astensis* (Bellardi, 1850) in his '11^a Serie', which he characterised as including larger shells than his '10^a Serie', with a relatively low last whorl, the relatively wide apical angle of the later teleoconch whorls, and the relatively short almost truncated columella, convex whorls and the absence of sculpture on the spire whorls. It is superficially similar to some of the species placed by Bellardi in '8^a Serie', like *E. atava* (Bellardi, 1887), but all members of that group have spiral grooves on the early teleoconch whorls.

Distribution – Lower Pliocene: western Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediter-

anean, Italy (Bellardi, 1887a; Malatesta, 1974). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Malatesta, 1960).

Episcomitra atava (Bellardi, 1887)

Plate 10, figs 1-3

- *1887a *Mitra atava* Bellardi, p. 15, pl. 1, fig. 12.
- 1911 *Mitra atava* Bell. – Cerulli-Irelli, p. 234 [284], pl. 21 [38], fig. 18.
- 1974 *Mitra (Mitra) atava* Bellardi, 1887 – Malatesta, p. 354, pl. 29, fig. 5.
- 1981 *Mitra atava* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 147, pl. 41, fig. 3.
- 2002 *Mitra atava* Bellardi, 1887 – Chirli (*partim?*), p. 32, pl. 16, figs 9, 10 (?).

Material and dimensions – Maximum height 58.8 mm, width 19.1 mm. **CO:** NHMW 2024/0042/0088-0090 (3), NHMW 2024/0042/0091 (2).

Description – Shell moderately large, solid, moderately broad fusiform, with relatively high spire; apical angle 32-36°. Protoconch unknown. Teleoconch of up to seven relatively tall, very weakly convex whorls, with periphery at abapical suture; suture shallow, narrowly impressed. Sculpture on early whorls of very fine, narrow, shallow grooves that fade on later whorls. Last whorl approx. 64% of total height, weakly convex with maximum width mid-whorl, regularly attenuated below, not constricted at base, base bearing numerous very weak, narrow spiral cords; fasciole poorly developed, weakly delimited from base. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short, wide, not twisted with deep siphonal notch. Columellar callus moderately thickened in lower half, weakly expanded over basal area closing pseudumbilicus or leaving narrow chink, sharply delimited, thinning in parietal area to a thin callus wash in most specimen. Columella bearing five oblique folds, weakening abapically, fifth subobsolete.

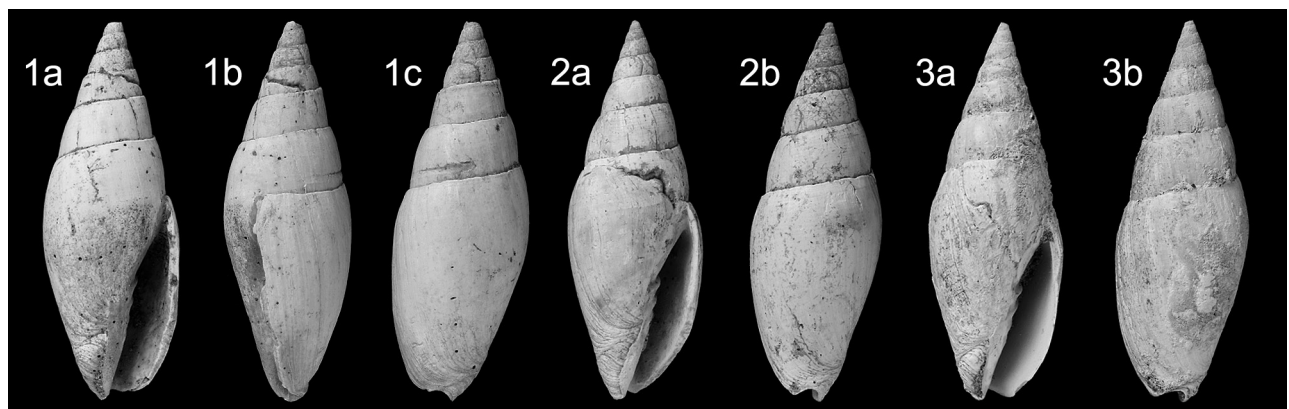


Plate 9. *Episcomitra astensis* (Bellardi, 1850); 1. NHMW 2024/0042/0054, height 54.7 mm, width 19.8 mm; 2. NHMW 2024/0042/0053, height 53.1 mm, width 18.7 mm; 3. NHMW 2024/0042/0052, height 49.9 mm, width 17.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

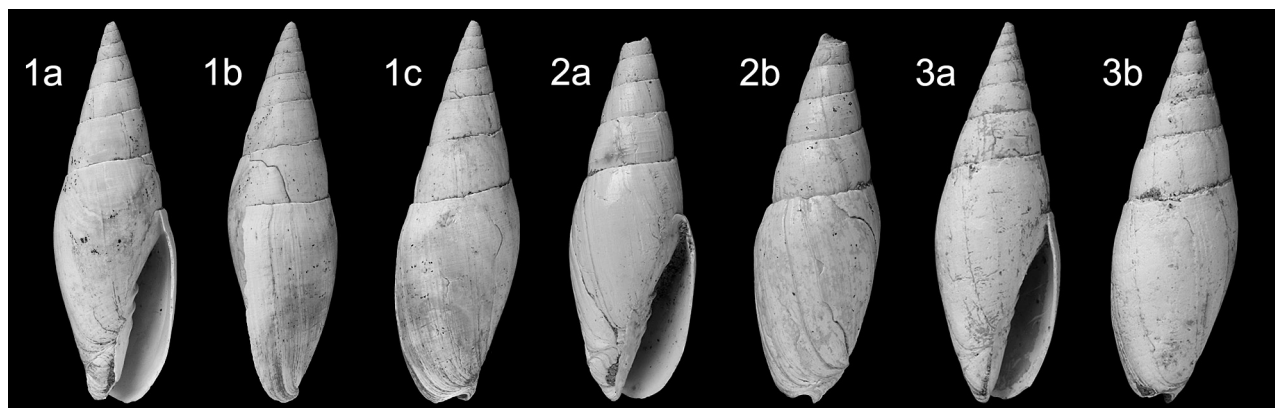


Plate 10. *Episcomitra atava* (Bellardi, 1887); 1. NHMW 2024/0042/0088, height 58.3 mm, width 18.4 mm; 2. NHMW 2024/0042/0089, height 57.4 mm, width 20.2 mm; 3. NHMW 2024/0042/0090, height 50.6 mm, width 16.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – Bellardi (1887a) placed this species in his ‘8^a Serie’ together with other Pliocene species *E. turricula* (De Cristofori & Jan, 1832), *E. pliocenica* (Bellardi, 1887), and *E. tracta* (Bellardi, 1887). Based on material from Tuscany identified by Chirli (2002, p. 32), he suggested that *E. atava* might be a form of *E. turricula*. However, if our interpretation of Bellardi’s species is correct, and based on the Estepona material, the two species are different. As noted by Bellardi (1887, p. 15) *E. atava* is slenderer, with a taller, more pointed spire, the spire whorls are flattened and not weakly shouldered as in *E. turricula*, the last whorl is about half the total height, and the aperture is narrower. Bellardi also noted that there were fewer spiral grooves on the early whorls. This is not the case in the Estepona specimens that have more numerous grooves, but they are weaker, and they disappear earlier in ontogeny than in *E. turricula*. *Episcomitra pliocenica* and *E. tracta* are much larger species.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887a; Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Malatesta, 1974). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911)

***Episcomitra gonniae* nov. sp.**

Plate 11, fig. 1

ZooBank registration – urn:lsid:zoobank.org:act:CAF20282-06BA-44DC-816A-422E69A72D17

Type material – Holotype NHMW 2023/0323/0102, height 13.9 mm, width 6.1 mm.

Other material – Known from holotype only.

Type locality – El Lobillo, Estepona, Spain.

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

Etymology – Name after Gonnée Mulder, sister of Henk Mulder who has so kindly made his collection available to us throughout this series and donated specimens generously. *Episcomitra*, gender feminine.

Diagnosis – *Episcomitra* species of small size, with squat, ovate profile, low cyrtocoid spire, teleoconch of four smooth whorls, spire whorls convex, last whorl barrel-shaped, weak spirals over fasciole, four columellar folds.

Description – Shell small, subcylindrical-fusiform, with low cyrtocoid spire and barrel-shaped last whorl; apical angle initially 78°, later 45°. Protoconch unknown. Teleoconch of four whorls separated by moderately deeply impressed suture. Spire whorls smooth, low, convex, with periphery at abapical suture. Last whorl subcylindrical, 75% of total height, weakly constricted at base; base bearing three weak cords; fasciole broad, flattened, moderately developed and delimited from base. Aperture moderately broad elongate; outer lip incomplete, smooth within; anal sinus hardly developed; siphonal canal very short, notched at tip. Columellar callus narrow, sharply delimited, continuous with thinner parietal callus. Columella bearing four prominent oblique folds, weakening abapically.

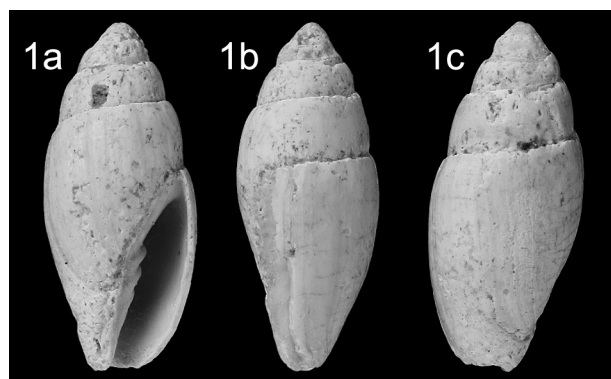


Plate 11. *Episcomitra gonniae* nov. sp.; 1. **Holotype** NHMW 2024/0042/0102, height 13.9 mm, width 6.1 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – Unfortunately, this species is represented by a single somewhat abraded specimen, but its characters are quite distinctive and unlike any other known European Neogene mitrid. Despite its small size, it seems to be fully adult. In profile it is most like *Episcomitra doliolum* (Bellardi, 1887) from the Upper Miocene Tortonian of Stazzano (Italy) (for syntype see Ferrero Mortara *et al.*, pl. 41, fig. 8). However, at 31 mm height, that species is more than double the size and the apical angle is somewhat narrower than in the *Estepona* species. The fasciole is also more developed forming a small pseudoumbilical chink in *E. doliolum*, absent in the *Estepona* species. *Episcomitra indicata* (Bellardi, 1887), also from the Stazzano assemblage, is more similar in size (19 mm height), is also low spired and has a subcylindrical last whorl but differs in having the spire whorls more gradate and the last whorl is evenly subcylindrical mid-whorl and not weakly convex as in the *Estepona* species. The Mediterranean Pliocene *Episcomitra obesa* (Foresti, 1868) that also occurs in the *Estepona* assemblage is also a low-spired species, but broader, with a more inflated last whorl.

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

Episcomitra obesa (Foresti, 1868)

Plate 12, fig. 1

- *1868 *Mitra obesa* Foresti, p. 42.
- 1999 *Mitra obesa* Foresti, 1868 – Forli *et al.*, p. 119, pl. 4, figs 6, 7.
- 2002 *Mitra obesa* Foresti, 1868 – Chirli, p. 36, pl. 18, figs 4, 5.

Material and dimensions – Height 20.3 mm, width 9.9 mm.
CO: NHMW 2024/0042/0039 (1).

Description – Shell medium sized, ovate-fusiform, with low cyrtocoid spire and inflated last whorl; apical angle initially 71°, later 66°. Protoconch unknown. Teleoconch of five whorls separated by shallowly impressed suture. Spire whorls low, convex, with periphery at abapical suture, bearing fine indistinct spiral cords separated by shallow grooves, (first whorl surface abraded) six on second whorl, 12 on third, weakening further abapically. Last whorl globose, 76% of total height, broadly convex, weakly constricted at base, slightly stronger spiral cords over base; fasciole narrow, rounded, poorly developed. Aperture short, moderately broad elongate; outer lip incomplete, smooth within; anal sinus hardly developed; siphonal canal short (tip incomplete). Columellar callus narrow, sharply delimited, continuous with thinner indented parietal callus. Columella bearing three prominent oblique folds mid-aperture, weakening abapically.

Discussion – This species has seldom been illustrated or discussed. It was not included in the classic monographs of the family by Bellardi (1887a, b, 1888) nor Sacco (1904). The first illustration is that of Forli *et al.* (1999,

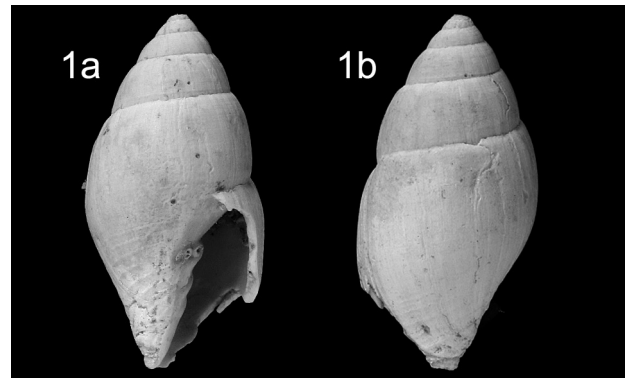


Plate 12. *Episcomitra obesa* (Foresti, 1868); 1. NHMW 2024/0042/0039, height 20.3 mm, width 9.9 mm. Velerín conglomerates, Velerín, *Estepona*, Lower Piacenzian, Upper Pliocene.

pl. 4, figs 6, 7) recorded from the Lower Pliocene of Tuscany (Italy). The Italian specimen illustrated compares closely to the single specimen from *Estepona* in size and profile, and although their description states the surface is “*liscia* [smooth]” (1999, p. 119) fine spiral sculpture can be seen in their photographs similar to that seen in the *Estepona* specimen. The authors describe four columellar folds, although only three can be clearly seen. The only other record is that of Chirli (2002, pl. 18, figs 4, 5). It is based on the same specimen, as a hole on the dorsal side of the penultimate whorl matches exactly. Chirli does describe the fine spiral sculpture. Again, although he describes four columellar folds, only three are evident. It is not uncommon in this family for the abapical fold to be obsolete or almost so. We consider them conspecific. *Episcomitra obesa* (Foresti, 1868) seems to be an extremely uncommon species both in Italy and *Estepona* and all specimens illustrated are incomplete. Forli *et al.* (1999) associated it with clayey deposits. The single specimen from *Estepona* comes from the storm deposits of Velerín conglomerates. No ecological implications can be made.

Distribution – Lower Pliocene: central Mediterranean, Italy (Foresti, 1868; Forli *et al.*, 1999; Chirli, 2002). Upper Pliocene: western Mediterranean, *Estepona* Basin (this paper).

Episcomitra pliocenica (Bellardi, 1887)

Plate 13, figs 1-3

- *1887a *Mitra pliocenica* Bellardi, p. 17, pl. 2, fig. 17.
- 1981 *Mitra pliocenica* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 148, pl. 41, fig. 7.
- non 2002 *Mitra pliocenica* Bellardi, 1887 – Chirli, p. 37, pl. 18, figs 6-10.

Material and dimensions – Maximum height 88.9 mm (incomplete, reconstructed height ~ 96 mm), width 27.9 mm.
CO: NHMW 2024/0042/0046-0048 (3).

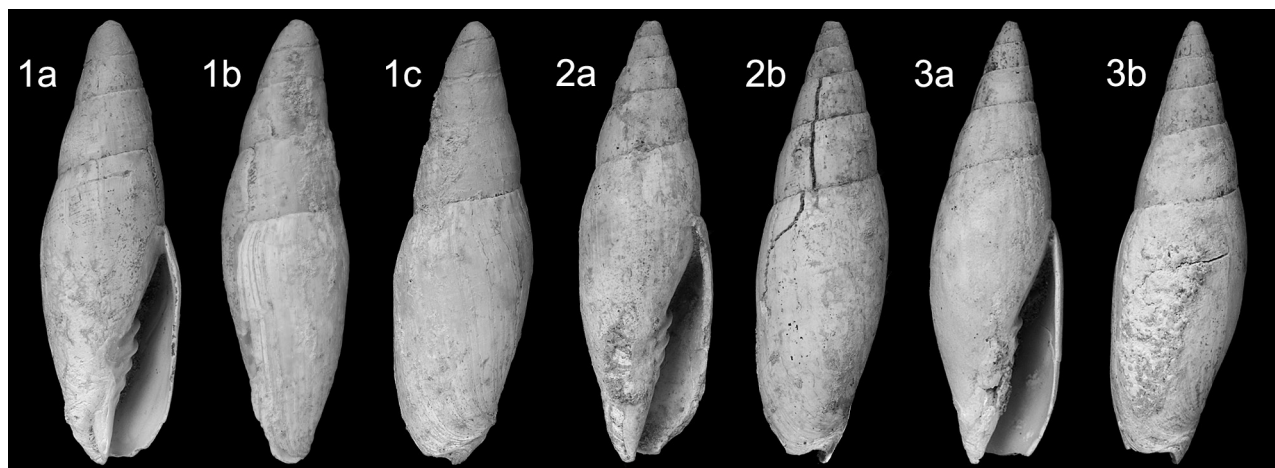


Plate 13. *Episcomitra pliocenica* (Bellardi, 1887); 1. NHMW 2024/0042/0046, height 88.9 mm, width 27.9 mm; 2. NHMW 2024/0042/0047, height 87.6 mm, width 26.5 mm; 3. NHMW 2024/0042/0048, height 72.6 mm, width 21.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell very large, solid, slender fusiform, with relatively high spire and last whorl; apical angle initially 49°, later 25–30°. Protoconch unknown. Up to six teleoconch whorls preserved (earliest whorls abraded). Spire whorls tall, convex, with periphery at abapical suture; suture moderately shallow, narrowly impressed. Surface covered in very fine, subobsolete spiral threads (abraded over most of the surface in all specimens). Last whorl low, approx. 69% of total height, slightly weakly and broadly convex, hardly at base, with cords over base; fasciole moderately developed, rounded, poorly delimited from base. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short, wide, not twisted with deep siphonal notch. Columellar callus strongly thickened in lower half, expanded over basal area closing pseudumbilicus, sharply delimited, thinning in parietal area. Columella bearing five prominent oblique folds, weakening abapically.

Discussion – Bellardi (1887a) placed *Mitra pliocenica* Bellardi, 1887 in his ‘8^a Serie’ characterised by species in which the last whorl is taller than the spire, the last whorl is regularly attenuated abapically and hardly constricted at the base, the aperture is relatively wide anteriorly and almost truncated, and the columella is straight, the margin very broad and deep. In this group only two species reach a size of about 100 mm height: *Episcomitra pliocenica* and *E. tracta* (Bellardi, 1887), both from the Upper Pliocene of Italy. Judging from Bellardi’s descriptions and the illustration of the syntypes in Ferrero Mortara *et al.* (1981, pl. 41, fig. 7 and 9), the main difference seems to be the shape of the whorls, which are more barrel shaped in *E. tracta* and separated by a slightly deeper suture. The last whorl is subcylindrical rather than convex and slightly inflated at the periphery as in *E. pliocenica*. The profile of the Estepona specimens resembles more closely that of *E. pliocenica*, although the specimens are slightly less inflated at the periphery of the last whorl. We have excluded from the synonymy specimens illustrated as *M. pliocenica*

by Chirli (2002, pl. 18, figs 6–10). The specimens seem to be fully adult, but less than half the size of adult *E. pliocenica* (maximum 47 mm height vs. 95–100 mm) and their spire is more regularly conical.

Another Italian Pliocene species, *Episcomitra turricula* (de Cristofori & Jan, 1832), was also placed in this group by Bellardi. That species differs from *M. pliocenica* in only reaching half the maximum adult size (42–47 mm height; *vide* Bellardi, 1887a; Chirli, 2002), is relatively stouter in profile, with whorls that are slightly shouldered just below the suture.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887a).

***Episcomitra pliotenuis* nov. nom.**

Plate 14, fig. 1

*1887a *Mitra tenuis* Bellardi, p. 79, pl. 4, fig. 50 (*non* Beyrich, 1854).

1981 *Mitra tenuis* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 161, pl. 49, fig. 5 (*non* Beyrich, 1854).

Material and dimensions – Height 32.4 mm, width 9.6 mm. **CO:** NHMW 2024/0042/0063 (1).

Description – Shell medium sized, slender fusiform with high spire and slender last whorl; apical angle initially 36°, later 33°. Protoconch unknown. Teleoconch of up to seven weakly convex whorls increasing in height abapically, with periphery at abapical suture; suture shallow, narrowly impressed. Surface mostly smooth, with occasional extremely fine spiral thread. Last whorl 61% of total height, subcylindrical below, hardly constricted at base, with few subobsolete spiral cords over base; fasciole moderately developed, weakly rounded. Aperture narrowly elongate; outer lip thin, weakly flared abapically,

smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short and wide, not twisted with moderately shallow siphonal notch. Columellar callus moderately wide and thickened, sharply delimited, continuous with parietal callus. Columella straight, bearing four prominent oblique folds weakening abapically, subobsolete fifth fold, indented in parietal area.

Discussion – *Mitra tenuis* Bellardi, 1887a is a junior primary homonym of *Mitra tenuis* Beyrich, 1854, and the name *Episcomitra pliotenuis* nov. nom. is proposed herein as a replacement name.

Episcomitra pliotenuis (Bellardi, 1887) is the slenderest mitrid in the Estepona assemblages. Bellardi (1887a, p. 77) placed this species in his ‘38ª Serie’ characterised by their elongated slender profile, smooth surface except for microscopic spirals, narrow aperture, slightly expanded abapically, and the inner lip indented or compressed. Bellardi did not specify the number of columellar folds, but the Estepona specimen has four well developed folds and an indistinct fifth. The Spanish specimen differs slightly from the syntype illustrated by Ferrero Mortara *et al.* (1981, pl. 49, fig. 5) in having the columella straighter and not slightly bent to the left.

Within this series it is most similar to *Episcomitra junior* (Bellardi, 1887) from the Upper Pliocene of Italy, but that species is larger shelled (57 mm vs. 35 mm; *fide* Bellardi, 1887a), with a shorter, broader spire, with fewer whorls despite being larger, the last whorl and aperture are relatively longer, and the aperture is slightly wider anteriorly. The last Pliocene member of the series, *Episcomitra arcta* (Bellardi, 1887) (syntype see Ferrero Mortara *et al.*, 1981, pl. 49, fig. 7), is also larger shelled (42 mm) and possibly slightly more twisted at the fasciole, although this aspect may be artefactual to the outer lip being broken back. Bellardi did not compare this species to the other Pliocene species in the series and a critical revision is required.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887a). Upper Pliocene: western Mediterranean, Estepona Basin (this paper).

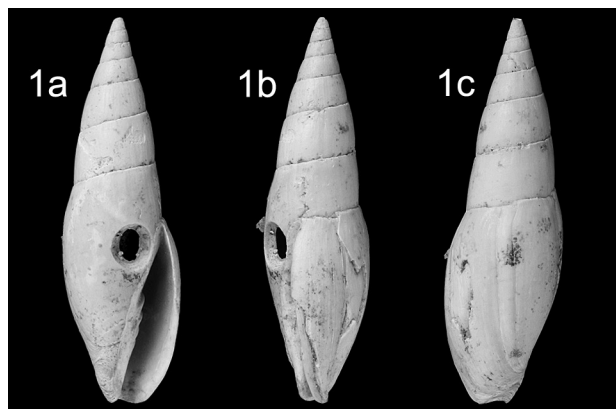


Plate 14. *Episcomitra pliotenuis* nov. nom.; 1. NHMW 2024/0042/0063, height 32.4 mm, width 9.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Episcomitra subestriata (Bellardi, 1887)

Plate 15, figs 1-2

- *1887a *Mitra subestriata* Bellardi, p. 35, pl. 1, fig. 34.
- 1981 *Mitra subestriata* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 152, pl. 43, fig. 8.
- 2002 *Mitra subestriata* Bellardi, 1887 – Chirli, p. 38, pl. 19, figs 7-12.
- 2011 *Mitra subestriata* Bellardi, 1887 – Chirli & Linse, p. 141, pl. 48, fig. 1.

Material and dimensions – Maximum height 46.6 mm, width 14.3 mm. **CO:** NHMW 2024/0042/0072-0073 (2).

Description – Shell moderately large, solid, moderately slender fusiform, with relatively high narrowly conical spire; apical angle 32-37°. Protoconch unknown. Teleoconch of up to seven very weakly convex whorls, with periphery at abapical suture; suture shallow, narrowly impressed. Sculpture of very fine, irregular spiral cords on early teleoconch whorls, weakening towards abapical half of whorl and subobsolete on penultimate whorl. Last whorl approx. 66% of total height, evenly subcylindrical, hardly constricted at base, bearing a few subobsolete spiral cords just below suture and over fasciole; fasciole weakly developed, slightly rounded, moderately delimited from base. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short, wide, not twisted with deep siphonal notch. Columellar callus narrow, moderately thickened in lower half, sharply delimited, thinning and weakly indented in parietal area. Columella bearing 4 or 5 prominent oblique folds, weakening abapically.

Discussion – Two specimens from Estepona are ascribed to *Episcomitra subestriata* (Bellardi, 1887). They agree fairly well in profile with the syntype illustrated by Ferrero Mortara *et al.* (1981, pl. 43, fig. 8) and specimens from Tuscany illustrated by Chirli (2002, pl. 19, figs 7-12), and with the fine, irregular, non-punctate spiral sculpture on the spire whorls described by Bellardi (1887a, p. 35). The original description notes five columellar folds. One of the Estepona specimens has five, the other four. However, the folds can vary by one in some mitrid species, as they usually decrease in strength abapically so that the last fold is obsolete or almost so in some specimens (Chirli, 2002; Harzhauser & Landau, 2021).

Bellardi (1887a) placed this species in his ‘14ª Serie’, a relatively large group characterised by having the sort of irregular fine spiral sculpture on the spire whorls described above. This group included several Pliocene species including *Episcomitra obesata* (Bellardi, 1887) which is immediately separated by its broader form and more rounded spire whorls, and *E. altilis* (Bellardi, 1887) that differs in its strongly inflated last whorl. The last of the group, *E. decipiens* (Bellardi, 1887) is closely similar to *E. subestriata*. Comparing the syntypes illustrated by Ferrero Mortara *et al.* (1981, pl. 44, fig. 1) *E. decipiens* has a slightly more deeply impressed suture and possibly

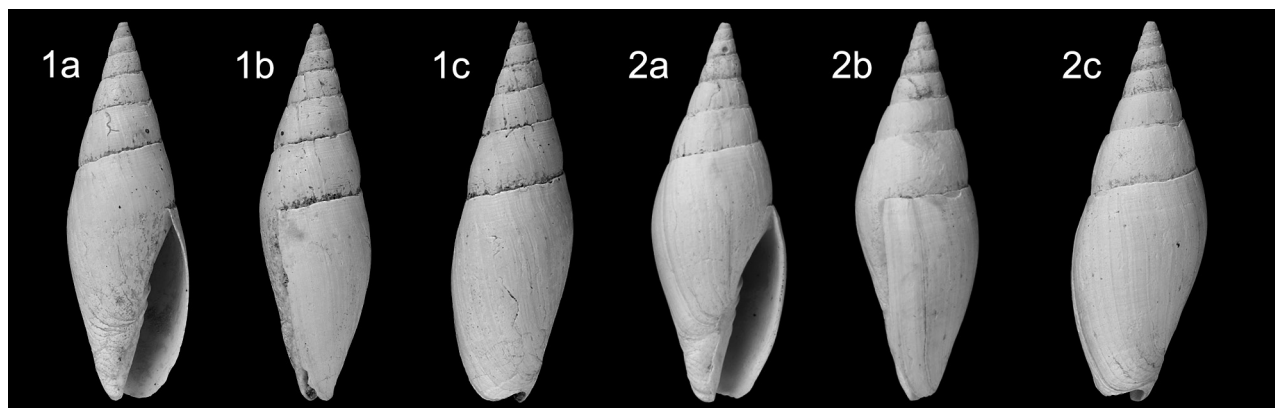


Plate 15. *Episcomitra subestriata* (Bellardi, 1887); 1. NHMW 2024/0042/0072, height 46.6 mm, width 14.3 mm; 2. NHMW 2024/0042/0073, height 42.1 mm, width 14.3 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

narrower spire. A revision of Italian material would be needed to verify if they are indeed distinct species. In any case, the suture in the Estepona specimens is very shallow, similar to the syntype of *E. subestriata*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887a; Ferrero Mortara *et al.*, 1981; Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Episcomitra turricula (de Cristofori & Jan, 1832)

Plate 16, figs 1-3

- *1832 *Mitra turricula* de Cristofori & Jan, p. 14.
- 1887a *Mitra turricula* Jan – Bellardi, p. 15, pl. 1, fig. 13.
- 1890 *Mitra turricula* var. *minutisulcata* Sacco, p. 246 (= var. A Bellardi, 1887a).
- 1890 *Mitra turricula* var. *labiatorima* Sacco, p. 246 (= var. B Bellardi, 1887a).
- 1904 *Mitra turricula* var. *minutisulcata* Sacc. – Sacco, p. 81, pl. 18, fig. 5.
- 1904 *Mitra turricula* var. *labiatorima* Sacc. – Sacco, p. 81, pl. 18, fig. 6.
- 1911 *Mitra turricula* Jan – Cerulli-Irelli, p. 234 [284], pl. 21 [38], fig. 17.
- 1959 *Mitra turricula* Jan – Ruggieri *et al.*, p. 84, pl. 19, fig. 118.
- 1967 *Mitra (Mitra) turricula* Jan, 1832 – Palla, p. 989, pl. 74, fig. 8.
- 1971 *Mitra turricula* De Cristofori & Jan, 1832 – Pinna, p. 434, pl. 77, fig. 5.
- 1974 *Mitra (Mitra) turricula* Jan, 1832 – Malatesta, p. 357, pl. 29, fig. 14.
- 1978 *Mitra turricula* De Cristofori & Jan, 1832 – Pinna & Spezia, p. 144, pl. 22, fig. 4.
- 2002 *Mitra turricola* [sic] De Cristofori & Jan, 1832 – Chirli, p. 39, pl. 20, figs 1-4.
- 2011 *Episcomitra fusiformis* (Brocchi, 1814) – Landau *et al.*, p. 29, pl. 15, fig. 2 [*non Episcomitra fusiformis* (Brocchi, 1814)].

- 2011 *Mitra turricola* [sic] De Cristofori & Jan, 1832 – Chirli & Linse, p. 142, pl. 48, fig. 2.

Material and dimensions – Maximum height 53.2 mm, width 18.7 mm. **CO:** NHMW 2024/0042/0049-0051 (3), NHMW 2024/0042/0092 (2).

Description – Shell moderately large, solid, moderately broad fusiform, with relatively high somewhat gradate spire; apical angle approx. 37°. Protoconch unknown. Teleoconch of up to seven weakly convex whorls, with periphery at abapical suture; suture moderately shallow, narrowly impressed. Sculpture on early whorls of about 6 narrow, shallow punctate grooves that fade on later whorls. Last three whorls slightly shouldered just below suture. Last whorl 65-69% of total height, weakly shouldered just below suture, regularly attenuated below, weakly constricted at base, base bearing numerous weak, narrow spiral cords; fasciole moderately developed, rounded, sharply delimited from base by raised ridge. Aperture long, moderately narrow elongate; outer lip thin, smooth within; anal sinus very narrow V-shaped notch; siphonal canal moderately short, wide, not twisted with deep siphonal notch. Columellar callus strongly thickened in lower half, weakly expanded over basal area closing pseudumbilicus or leaving narrow chink, sharply delimited, thinning in parietal area. Columella bearing five prominent oblique folds, weakening abapically.

Discussion – Chirli (2002, p. 40) discussed the differences between *E. turricula* (de Cristofori & Jan, 1832) and *E. fusiformis* (Brocchi, 1814), two species similar in that they both have shouldered late teleoconch whorls. In summary, based on the lectotypes of the two species illustrated by Pinna & Spezia (1978), he concluded that *E. turricula* differed from *E. fusiformis* in: 1) having a squatter shell with gradate rather than conical spire, 2) lower, more strongly shouldered whorls, 3) shorter last whorl adapically fusiform rather than subcylindrical, 4) punctate spiral grooves more prominent, 5) SH/MD: *E. turricula* = 2.8, *E. fusiformis* = 3.5; SL/LWH: *E. turricula* = 1.55, *E. fusiformis* = 1.67. For further discussion, see Chirli (2002, p. 40).

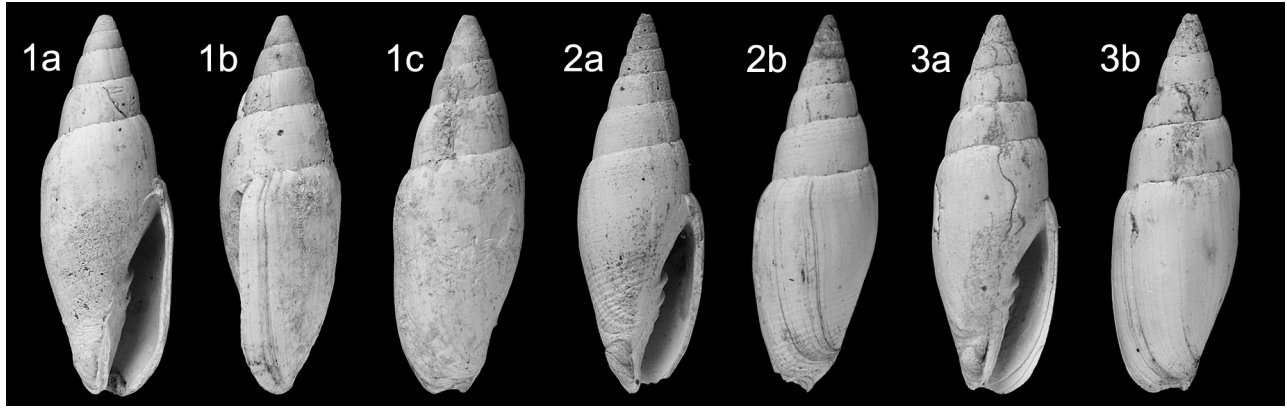


Plate 16. *Episcomitra turricula* (de Cristofori & Jan, 1832); 1. NHMW 2024/0042/0049, height 53.2 mm, width 18.7 mm; 2. NHMW 2024/0042/0050, height 49.8 mm, width 16.7 mm; 3. NHMW 2024/0042/0051, height 40.5 mm, width 13.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

As discussed in the introduction, the Estepona Mitridae material is not always easy to interpret due to its rather poor state of preservation, however, these specimens agree with *M. turricula*. Bellardi (1887a) placed this species in his '8ª Serie' together with *E. atava* (Bellardi, 1887) that differs in being slenderer with a higher spire and non-shouldered whorls, and *E. pliocenica* (Bellardi, 1887) and *E. tracta* (Bellardi, 1887) which are much larger species with a more expanded columellar callus and slightly wider aperture abapically.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (de Cristofori & Jan, 1832; Bellardi, 1887a; Sacco, 1904). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Ruggieri *et al.*, 1959; Palla, 1967; Malatesta, 1974); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Episcomitra sp.

Plate 17, figs 1-2

Material and dimensions – Height 27.4 mm, width 10.1 mm. CO: NHMW 2024/0042/0074-0075 (2), NHMW 2024/0042/0076 (1).

Description – Shell medium sized, slender fusiform with conical spire; apical angle 36-41°. Protoconch unknown. Six very weakly convex teleoconch whorls with periphery at abapical suture; suture moderately shallow, narrowly impressed. Surface bearing extremely fine and irregular spiral threads visible only under magnification. Last whorl smooth, 64% of total height, slightly inflated and roundly angled mid-whorl, weakly constricted at base; fasciole not developed. Aperture short, moderately broad elongate; outer lip thin; anal sinus very narrow V-shaped notch; siphonal canal short, wide, not twisted with shallow siphonal notch. Columellar callus narrow,

weakly thickened, sharply delimited, continuous with slightly thinner parietal callus. Columella bearing four oblique folds mid-aperture, weakening abapically.

Discussion – This species is characterised by its rather small size, almost completely smooth surface, except for microscopic spiral threads seen only under magnification, and the last whorl which is roundly angled mid-whorl at the level of the insertion of the outer lip. It is similar to specimens identified herein as *Episcomitra subestriata* (Bellardi, 1887), but smaller sized (maximum height 27.4 mm vs. 46.5 mm), and the last whorl is more constricted at the base. *Episcomitra interiecta* (Bellardi, 1887) from the Upper Miocene of Italy (for syntype see Ferrero Mortara *et al.*, 1981, pl. 44, fig. 2) is also similar, but larger, and the outer lip is flared adapically overhanging the tip of the columella. *Isara nigra* (Gmelin, 1791) from the present-day coast of West Africa is similar in profile but has well developed cords over the base and fasciole. We cannot match this species to any of the myriads of forms described by Bellardi. However, in view of the scarcity of specimens and the rather worn state of all of them, we refrain from formally describing it.

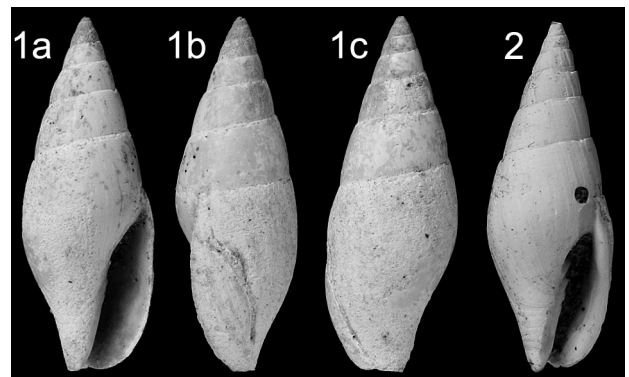


Plate 17. *Episcomitra* sp.; 1. NHMW 2024/0042/0074, height 27.4 mm, width 10.1 mm; 2. NHMW 2024/0042/0075, height 25.5 mm, width 9.0 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

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

Genus *Fraudiziba* Harzhauser & Landau, 2021a

Type species (by original designation) – *Ziba paratethyca* Harzhauser & Landau, 2021a, Middle Miocene, Paratethys Sea.

2021a *Fraudiziba* Harzhauser & Landau, p. 33.

***Fraudiziba concava* (Bellardi, 1887)**

Plate 18, figs 1-2

*1887a *Mitra concava* Bellardi, p. 67, pl. 4, fig. 45.

Material and dimensions – Maximum height 22.6 mm, width 9.0 mm. CO: NHMW 2024/0042/0055-0056 (2).

Description – Shell medium-sized, broad to moderately broad, solid; apical angle 45°. Protoconch unknown. Teleoconch of six whorls. Early teleoconch whorls weakly convex, high-placed, rounded shoulder developed on penultimate whorl. Suture of early teleoconch whorls incised, faintly canaliculate, deeper impressed on late whorls. Last whorl high, 69% of total height, bulging shoulder placed just below suture, subcylindrical to slightly concave to weakly inflated at periphery, slowly contracting below. Aperture moderately narrow; outer lip incomplete; anal sinus marked by narrow V-shaped notch; siphonal canal moderately short, wide, straight, with relatively shallow siphonal notch. Columella straight, with four oblique folds, decreasing in strength abapically. Columellar callus narrow, thin, extending from adapical columellar fold to tip of siphonal canal, moderately delimited from base, small poorly delimited parietal pad, callus between adapical columellar fold and parietal pad not developed. Shell surface smooth except for very weak spiral cords on fasciole.

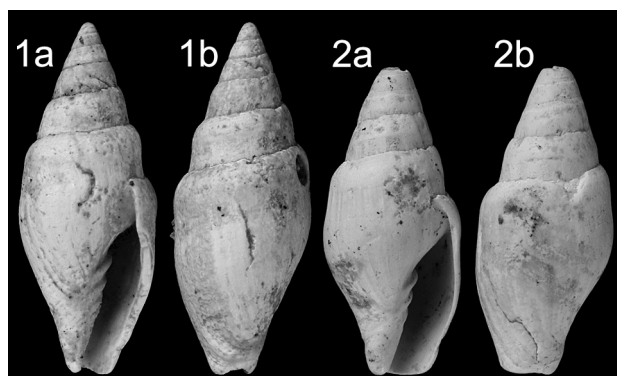


Plate 18. *Fraudiziba concava* (Bellardi, 1887); 1. NHMW 2024/0042/0055, height 22.6 mm, width 9.0 mm; 2. NHMW 2024/0042/0056, height 20.3 mm, width 9.1 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – Harzhauser & Landau (2021a, p. 33) erected the genus *Fraudiziba* for European Neogene mitrid species characterised by their medium size, moderately slender to moderately broad fusiform shell, paucispiral protoconch, smooth early teleoconch whorls, subcylindrical later teleoconch whorls with rounded or angled shoulder, and spiral sculpture of flat spiral cords separated by narrow, partly punctate spiral grooves. The genus is also characterised by a colour pattern of large subquadrate dots on shoulder and spiral rows of dots and/or dashes on the last whorl. Those authors included the Lower Pliocene Italian *Mitra concava* Bellardi, 1887 in the genus *Fraudiziba*. Unfortunately, the type seems to be lost, as it was not illustrated by Ferrero Mortara *et al.* (1981), nevertheless, the two specimens from Estepona closely resemble the original figure of Bellardi (1887a, pl. 4, fig. 45). The protoconch and colour pattern are not preserved in the Spanish material. *Fraudiziba concava* seems to be extremely uncommon. It seems to have been based on a single specimen from Italy, and we have not seen it referred to subsequently in the literature. In Estepona it is also uncommon, represented by two specimens.

Fraudiziba goniophora (Bellardi, 1850), *F. protracta* (Bellardi, 1887) and *F. subcarinata* (Bellardi, 1887) from the Upper Miocene of Italy all differ in having the shoulder placed lower. *Fraudiziba protensa* (Bellardi, 1887) from the Lower Miocene of Italy is closely similar, but has a higher, slenderer last whorl and the concavity between the shoulder and mid-whorl inflated portions of the last whorl is less concave. Of the Middle Miocene Paratethys *Fraudiziba* species *F. paratethyca* Harzhauser & Landau 2021 is probably the most similar, but that is a slenderer species with a higher spire.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887a). Upper Pliocene: western Mediterranean, Estepona Basin (this paper).

Subfamily Isarinae Fedosov, Herrmann, Kantor & Bouchet, 2018

Genus *Isara* H. Adams & A. Adams, 1853

Type species (by subsequent designation Cossmann, 1899): *Mitra bulimoides* Reeve, 1845 [= *M. glabra* Swainson, 1821]. Present-day, Indo-West Pacific.

1853 *Isara* H. Adams & A. Adams, p. 171.

Note – As discussed by Fedosov *et al.* (2018) it is impossible to separate *Episcomitra* Monterosato, 1917 and *Isara* H. Adams & A. Adams, 1853 based on conchological features alone. Therefore, some of the species placed herein in *Episcomitra* might belong to *Isara*. Herein, we place *Mitra aperta* Bellardi, 1887 and *Mitra ulivii* Chirli, 2002 in *Isara*, as they are morphologically closely similar to the present-day *Isara cornea* (Lamarck, 1811).

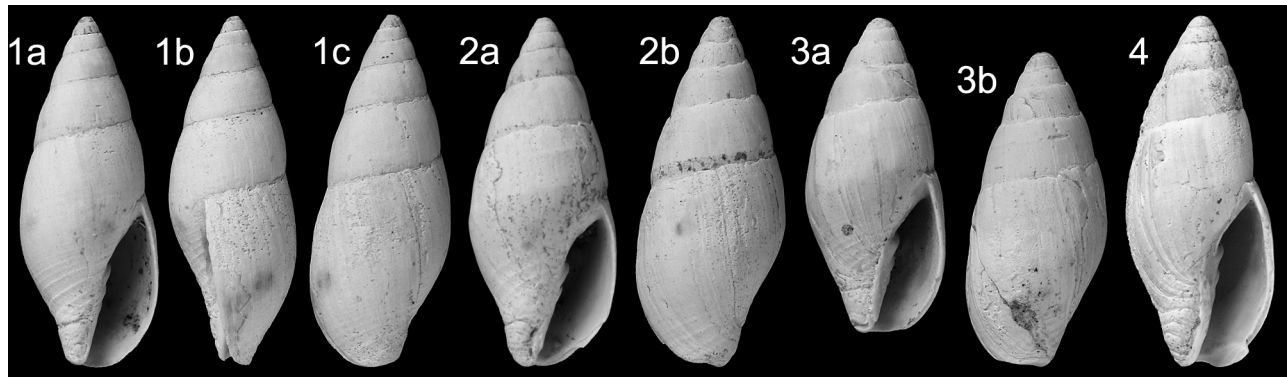


Plate 19. *Isara aperta* (Bellardi, 1850); 1. NHMW 2024/0042/0058, height 25.3 mm, width 9.6 mm; 2. NHMW 2024/0042/0059, height 26.7 mm, width 11.1 mm; 3. NHMW 2024/0042/0060, height 21.6 mm, width 9.4 mm; 4. NHMW 2024/0042/0061, height 25.5 mm, width 10.1 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Isara aperta (Bellardi, 1850)

Plate 19, figs 1-4

- *1850 *Mitra aperta* Bellardi, p. 9, pl. 1, fig. 13.
- 1887a *Mitra aperta* Bell. – Bellardi, p. 42, pl. 3, fig. 19.
- 1890 *Mitra aperta* var. *subturritolonga* Sacco, p. 248 (= var. A Bellardi, 1887a).
- 1904 *Mitra aperta* var. *subturritolonga* Sacco, p. 82, pl. 18, fig. 25.
- 1981 *Mitra aperta* Bellardi, 1850 – Ferrero Mortara *et al.*, p. 153, pl. 45, fig. 14.
- non 1852 *Mitra aperta* Bell. – Hörnes, p. 97, pl. 10, figs 1-3 [= *Isara hoernesii* (Mayer, 1864)].
- non 1957 *Mitra aperta* Bellardi – Pavlovsky, p. 53, pl. 1, figs 10a, b [= *Isara hoernesii* (Mayer, 1864)].
- non 2002 *Mitra aperta* Bellardi, 1850 – Chirli, p. 31, pl. 16, figs 1-6.

Material and dimensions – Maximum height 26.8 mm, width 11.0 mm. **CO:** NHMW 2024/0042/0058-0061 (2), 2024/0042/0062 (6).

Description – Shell medium sized, relatively solid, moderately broad fusiform, with moderate height spire; apical angle initially 50-55°, later 39-42°. Protoconch unknown. Teleoconch of up to five relatively low, weakly convex whorls, with periphery at abapical suture; suture shallow, narrowly impressed. Early teleoconch whorls with very fine spiral grooves visible only under magnification that fade on third whorl. Last whorl 67-71% of total height, broadly convex with maximum width mid-whorl, weakly constricted at base, base with very weak spirals; fasciole weak to hardly developed; bordering narrow pseudoumbilical chink in some specimens. Aperture long, moderately broad elongate; outer lip thin, smooth within; anal sinus shallow V-shaped notch; siphonal canal short, wide, straight, with shallow siphonal notch. Columellar callus narrow, moderately thickened in lower half, sharply delimited, thinning in parietal area. Columella bearing four oblique folds, weakening abapically.

Discussion – *Isara aperta* (Bellardi, 1850) is one of the most abundant and variable mitrid species in the Estepo-na assemblages. Many of the specimens closely resemble the syntype from the Upper Pliocene of Italy figured by Ferrero Mortara *et al.* (1981, p. 45, fig. 14) in being rather squat (Pl. 6, fig. 4), whilst other represent the more elongated variety named *Mitra aperta* var. *subturritolonga* Sacco, 1904 (Pl. 6, fig. 1). The fasciole is also rather variable; almost absent in most specimens, but weakly rounded bordering a narrow pseudoumbilical groove in some (Pl. 6, figs 2, 4). The spiral grooves on the earliest teleoconch whorls are finer than in most of its congeners and visible only under magnification. This was already highlighted by Bellardi “*Superficies laevis, vix in primis anfractibus sub lente passim minutissime transverse sulcata:...* [surface smooth, except for the first whorls that are minutely transversely striate visible only under a lens]” (1887a, p. 42).

In our opinion, the Italian Pliocene specimens illustrated by Chirli (2002, pl. 16, figs 1-6) do not represent this species. Compared to the lectotype of *I. aperta*, they have a markedly deeper suture, almost narrowly canaliculate (2002, pl. 16, figs 3, 4), whereas in the syntype the suture is very shallow, the cords over the base are far stronger than in *I. aperta*, and the profile of the last whorl in Chirli’s specimens is more regularly subcylindrical.

Paratethyan records of this species represent *Isara hoernesii* (Mayer, 1864) that differs in its broader profile and stronger sculpture on the early spire whorls and over the base (see Harzhauser & Landau, 2021a, p. 46).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887a; Ferrero Mortara *et al.*, 1981).

Isara ulivii (Chirli, 2002)

Plate 20, figs 1-3

- *2002 *Mitra ulivii* Chirli, p. 41, pl. 20, figs 5-12.
- 2011 *Mitra ulivii* Chirli, 2002 – Chirli & Linse, p. 142, pl. 48, fig. 3.

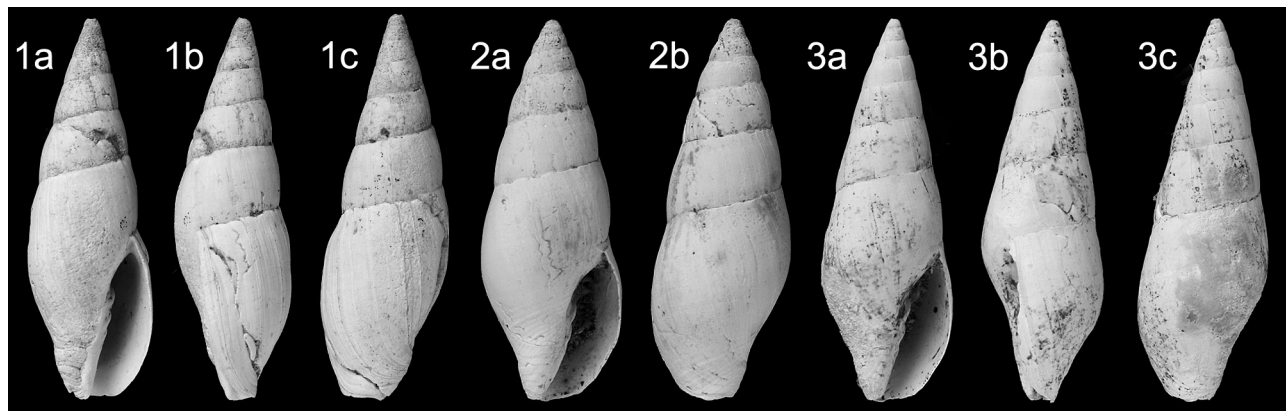


Plate 20. *Isara ulivii* (Chirli, 2002); 1. NHMW 2024/0042/0069, height 37.6 mm, width 12.0 mm; 2. NHMW 2024/0042/0070, height 33.0 mm, width 11.8 mm; 3. NHMW 2024/0042/0071, height 32.9 mm, width 10.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Material and dimensions –Maximum height 37.6 mm, width 12.0 mm. **CO:** NHMW 2024/0042/0069–0071 (3), 2024/0042/0093 (2).

Description – Shell medium sized, slender fusiform with high spire and low last whorl; apical angle initially 36–43°, later 25–33°. Protoconch unknown. Eight weakly convex teleoconch whorls with periphery at abapical suture; suture shallow, narrowly impressed. Surface smooth, except for suggestion of extremely faint subsutural grooves just visible on 4th and 5th whorls (surface somewhat abraded). Last whorl low, approx. 60% of total height, slightly narrowly depressed in subsutural area, weakly convex to sub-cylindrical below, weakly constricted at base, with few subobsolete spiral cords over base; fasciole moderately developed, flattened. Aperture short, moderately broad elongate; outer lip thin; anal sinus very narrow V-shaped notch; siphonal canal short, wide, not twisted with moderately deep siphonal notch. Columellar callus moderately wide and thickened, sharply delimited, continuous with slightly thinner parietal callus. Columella bearing four prominent oblique folds mid-aperture, weakening abapically.

Discussion – This species is characterised by its very slender fusiform profile, with a relatively high spire and short last whorl, the siphonal canal is very short, almost truncated resulting in a relatively short aperture for the genus. We have tentatively ascribed it to *Isara ulivii* (Chirli, 2002) from the Lower Pliocene of Italy. Most shell characters agree with the original description of that species, except spiral cords are more prominent on the early teleoconch whorls and a little more strongly developed over the base in the Italian specimens. The surface is somewhat abraded in the Estepona shell, nevertheless, a suggestion of spiral sculpture can be seen. It differs from *Isara aperta* (Bellardi, 1850) in its slenderer profile and taller spire. For further comparison with other mitrids, see Chirli (2002, p. 41).

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediter-

anean, Estepona Basin (this paper). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Superfamily Turbinelloidea Swainson, 1835 (authorship ascribed to Rafinesque, 1815 in Harzhauser & Landau, 2021b, p. 8 was a *lapsus*)

Family Costellariidae MacDonald, 1860

Genus *Bellardithala* Harzhauser & Landau, 2021b

Type species (by typification of replacement name) – *Voluta obsoleta* Brocchi, 1814, Pliocene, Italy.

1888 *Micromitra* Bellardi, p. 5. Type species (by original designation): *Voluta obsoleta* Brocchi, 1814, Pliocene, Italy.

2021b *Bellardithala* Harzhauser & Landau, p. 14.

***Bellardithala obsoleta* (Brocchi, 1814)**

Plate 21, figs 1–3

*1814 *Voluta obsoleta* Brocchi, p. 646, pl. 15, fig. 30.

1850 *Mitra obsoleta* Brocch. – Bellardi, p. 28, pl. 2, fig. 29.

1880 *Mitra obsoleta* Brocchi – Fontannes, p. 87, pl. 6, fig. 9.

1888 *Micromitra pusilla* Bellardi p. 8, pl. 6, fig. 48.

1888 *Micromitra obsoleta* (Brocch.) – Bellardi, p. 8, pl. 6, fig. 49.

1888 *Micromitra mangeliaeformis* Bellardi, p. 9, pl. 6, fig. 50.

1890 *Micromitra obsoleta* var. *angustolonga* Sacco, p. 258 (= var. A of Bellardi, 1888).

1890 *Micromitra obsoleta* var. *elatocostata* Sacco, p. 258 (= var. B of Bellardi, 1888).

1904 *Thala obsoleta* var. *angustolonga* Sacco, p. 88, pl. 19, fig. 24.

1904 *Thala obsoleta* var. *elatocostata* Sacco, p. 88, pl. 19, fig. 25.

- 1955 *Pusia (Pusia) (Pusia) obsoleta* (Brocchi 1814) – Rossi Ronchetti, p. 243, fig. 129.
- 1978 *Voluta obsoleta* Brocchi, 1814 – Pinna & Spezia, p. 169, pl. 68, fig. 2.
- 1981 *Micromitra mangeliaeformis* Bellardi, 1888 – Ferrero Mortara *et al.*, p. 172, pl. 54, fig. 3.
- 1981 *Micromitra pusilla* Bellardi, 1888 – Ferrero Mortara *et al.*, p. 172, pl. 54, fig. 6.
- 1983 *Thala obsoleta* (Brocchi, 1814) – Giannuzzi-Savelli & Reina, p. 233, text-fig. 2.
- 1992 *Thala mangeliaeformis* (Bellardi, 1888) – Cavallo & Repetto, p. 120, fig. 310.
- 2000 *Thala obsoleta* (Brocchi, 1814) – Davoli, p. 210, pl. 7, fig. 10, pl. 8, figs 1, 2.
- 2002 *Thala obsoleta* (Brocchi, 1814) – Chirli, p. 56, pl. 28, figs 5-12.
- 2011 *Thala obsoleta* (Brocchi, 1814) – Landau *et al.*, 29, pl. 15, fig. 6.
- 2013 *Thala obsoleta* (Brocchi, 1814) – Landau *et al.*, 218, pl. 34, fig. 18-19.
- 2023 *Bellardithala obsoleta* (Brocchi, 1814) – Sacchetti *et al.*, p. 77, pl. 5, figs H₁-H₂.
- non 1852 *Mitra obsoleta* Bronn [*sic*] – Hörnes, p. 110, pl. 10, fig. 32 [= *Bellardithala kovaci* Harzhauser & Landau, 2021b].
- non 1997 *Thala obsoleta* (Brocchi, 1814) – Bařuk, p. 39, pl. 11, fig. 2 [= *Bellardithala kovaci* Harzhauser & Landau, 2021b].

Material and dimensions – Maximum height 8.3 mm, width 2.9 mm. **CO:** NHMW 2024/0042/0095-0097 (3), 2024/0042/0098 (3). **EL:** NHMW 2024/0042/0099 (4).

Description – Shell medium-sized, moderately slender fusiform with weakly cyrtoconoid spire and narrowly incised suture. Protoconch tall, multispiral, of about 3.5 whorls (surface abraded). Teleoconch of 4.5 weakly convex whorls, with periphery at abapical suture on first two whorls. Penultimate whorl somewhat inflated with periphery in abapical third. Sculpture on first two whorls of orthocone to weakly opisthocline axial ribs, about 18 on second whorl, separated by narrower interspaces, crossed

by very fine spiral cords only visible in axial interspaces. Later teleoconch whorls with densely spaced axial ribs separated by very narrow interspaces, crossed by numerous fine spiral cords. Subsutural spiral cord only slightly wider. Last whorl weakly convex, 61-65% of total height, with weakly constricted base; sculpture tends to become obscure, flattened cords, obscurely beaded in some specimens, subobsolete mid-whorl in some specimens. Fasciole weak, bearing weak spiral cords. Aperture elongate, moderately narrow, with indistinct anal sinus. Columellar callus narrow. Columella with four columellar folds, weakening abapically. Outer lip only weakly thickened, with about ten delicate denticles within. Siphonal canal wide, moderately long, straight, shallowly notched at tip.

Discussion – Harzhauser & Landau (2021b, p. 14) erected the name *Bellardithala* as replacement name for *Micromitra* Bellardi, 1888 *non* Meek (1873, p. 479). For discussion and comparison with congeners see Landau *et al.* (2013, p. 218) and Harzhauser & Landau (2021b, p. 18-20).

Distribution – Middle Miocene: Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (Bellardi, 1888; Davoli, 2000). Lower Pliocene: Atlantic, Santa Maria Island, Azores (Sacchetti *et al.*, 2023), Guadalquivir Basin, Spain (Landau *et al.* 2011); western Mediterranean, NE Spain (NHMW coll.), Rousillon Basin, France (Fontannes, 1880). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Cavallo & Repetto, 1992).

Genus *Ebenomitra* Monterosato, 1917

Type species (by subsequent designation Coan, 1966) – *Mitra ebenus* Lamarck, 1811, present-day, Mediterranean.

1917 *Ebenomitra* Monterosato, 1917, p. 24.

Note – Fedosov *et al.* (2017) concluded that all present-day Mediterranean species formed a single monophyletic group, for which they used *Ebenomitra* Monterosato,

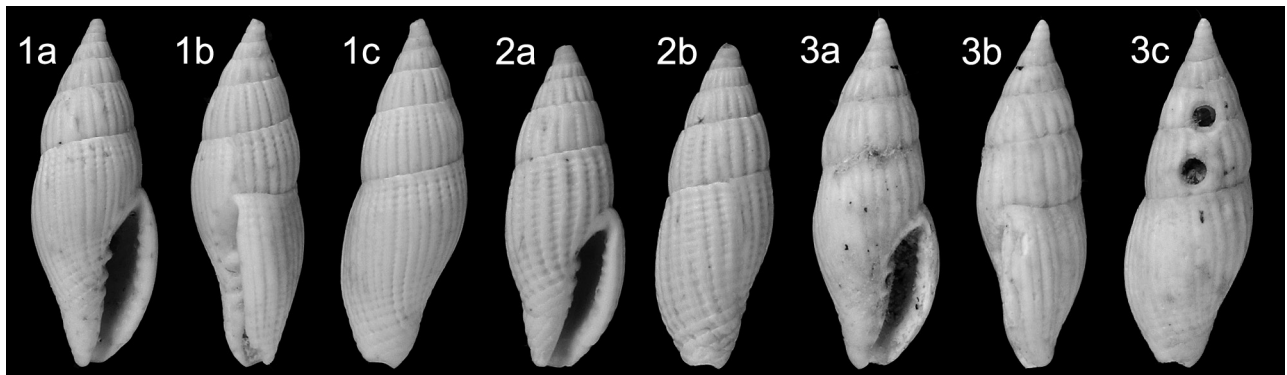


Plate 21. *Bellardithala obsoleta* (Brocchi, 1814); 1. NHMW 2024/0042/0095, height 8.3 mm, width 2.9 mm; 2. NHMW 2024/0042/0096, height 5.8 mm, width 2.3 mm; 3. NHMW 2024/0042/0018, height 8.3 mm, width 2.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1917 as a subgenus of *Pusia* Swainson, 1840. This group was characterised by having a paucispiral protoconch, indicative of non-planktotrophic larval development, a character they considered unique among species of *Pusia* (Fedosov *et al.*, 2017, p. 601). In contrast, in the genus *Vexillum* Röding, 1798, the protoconch is described as ‘tall, conical, whitish or brown, translucent, with three or more evenly convex glossy whorls’ (Fedosov *et al.*, 2017, p. 617). Today *Ebenomitra* does not occur further north than the Mediterranean, but in the warmer Miocene its range extended along the European Atlantic frontage at least to NW France and there are sporadic records in the Pliocene North Sea Basin (Wood, 1857; Harmer, 1918; Marquet, 1997, 1998). Here we follow Harzhauser & Landau (2021b, p. 28) in using *Ebenomitra* at full genus rank.

***Ebenomitra ebenus* (Lamarck, 1811)**

Plate 22, figs 1-4; Plate 23, figs 1-4

- *1811 *Mitra ebenus* Lamarck, p. 216.
- 1811 *Mitra plumbea* Lamarck, p. 220.
- 1826 *Mitra buplicata* Risso, p. 242.
- 1826 *Mitra cornicula* Risso, p. 242 (*non* Lamarck, 1811).
- 1826 *Mitra littoralis* Risso, p. 243.
- 1826 *Mitra costulata* Risso, p. 246.
- 1826 *Mitra Defranci* Payraudeau, p. 166, pl. 8, fig. 22.
- 1830 *Mitra cornicularis* O.G. Costa, p. 71.
- 1836 *Mitra caffra* Scacchi, p. 10.
- 1847 *Mitra Carna* Nardo, p. 48.
- 1853 *Mitra cordierii* Maravigna, p. 137.
- 1857 *Mitra ebenus* Lam. – Wood, p. 310, pl. 31, fig. 7.
- 1868 *Mitra ebenus* var. *costata* Weinkauff, p. 25.
- 1868 *Mitra ebenus* var. *laevigata* Weinkauff, p. 25.
- 1886 *Mitra ebenina* Locard, p. 104, 539.
- 1886 *Mitra congesta* Locard, p. 105, 540.
- 1890 *Mitra gracilis* Locard, p. 109.
- 1890 *Mitra Servaini* Locard, p. 109.
- 1891 *Mitra Bourguignati* Locard, p. 48.
- 1891 *Mitra subpyramidella* Locard, p. 48.
- 1891 *Mitra plicatuliformis* Locard, p. 49.
- 1900 *Turricula (Uromitra) ebenus* var. *nigra* Pallary, p. 264.
- 1903 *Mitra tunetana* Pallary, p. 8, pl. 1, figs 8, 9.
- 1912 *Uromitra Blanci* Pallary, p. 20, pl. 1, figs 54, 55.
- 1918 *Mitra ebenus* Lamarck – Harmer, p. 310, pl. 33, fig. 4.
- 1959 *Pusia (Pusia) ebenus* (Lamarck) – Ruggieri *et al.*, p. 78, pl. 9, fig. 50.
- 1960 *Vexillum (Vexillum) ebenus* (Lamarck, 1811) – Matalista, p. 178, pl. 9, fig. 8.
- 1965 *Pusia (Pusia) ebenus* (Lamk.) – Ruggieri & Greco, p. 53, pl. 9, fig. 6.
- 1982 *Fuscomitra (Ebenomitra) ebenus haifensis* Nord-sieck, p. 232, pl. 81, n. 83.60a.
- 1982 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Gian-nuzzi Savelli, p. 96, fig. 29, 31bis, 31ter.
- 1987 *Mitra (Ebenomitra) ebenus* Lamarck 1811 – Cuerda Barceló, p. 28, figs 7, 8.

- 1995 *Mitra ebenus* Lk. – Della Bella & Tabanelli, p. 293, fig. B (protoconch).
- 1997 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Marquet, p. 99, pl. 8, fig. 7.
- 1998 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Marquet, p. 154, fig. 128.
- 2002 *Vexillum ebenus* (Lamarck, 1811) – Chirli, p. 49, pl. 24, figs 9-12, pl. 25, figs 1-6.
- 2003 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Gian-nuzzi-Savelli *et al.*, p. 264, figs 652-667.
- 2011 *Vexillum ebenus* (Lamarck, 1811) – Landau *et al.*, p. 29, pl. 15, fig. 5.
- 2011 *Vexillum ebenus* (Lamarck, 1811) – Chirli & Linse, p. 138, pl. 46, fig. 5, pl. 47, fig. 1.
- 2011 *Vexillum ebenus* (Lamarck, 1811) – Hernández *et al.*, p. 203, pl. 63, figs Q-R.
- non* 1852 *Mitra ebenus* Lam. – Hörnes, p. 109, pl. 10, figs 11-13 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1880 *Mitra (Volutomitra) ebenus* Lamk. – Hoernes & Auinger, p. 82, pl. 7, figs 10-12, 14 [= *Ebenomitra leucozona* (Andrzejowski, 1830)], pl. 7, fig. 13 [= *Ebenomitra pseudopyramidella* (Boettger, 1906)], pl. 9, figs 22-25 [= *Pusia avellanella* (Boettger, 1906)].
- non* 1911 *Turricula ebenus* Lam. – Friedberg, p. 18, pl. 1, figs 10-11 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1954 *Mitra ebenus* Lamarck – Csepregy-Meznerics, p. 46, pl. 6, figs 6, 7 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1966 *Mitra (Pusia) ebenus* Lamarck – Strausz, p. 366, pl. 26, fig. 5, figs 3-5 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1973 *Mitra (Pusia) ebenus* Lamarck, 1811 – Nicorici & Sagatovici, p. 173, pl. 27, figs 16, 17 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1982 *Mitra (Ebenomitra) ebenus ebenus* Lamarck, 1811 – Švagrovský, p. 397, pl. 4, fig. 3 [= *Ebenomitra leucozona* (Andrzejowski, 1830)].
- non* 1992 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Cavallo & Repetto, p. 120, fig. 307 [= *Vexillum pyramidellum* (Brocchi, 1814)].

‘Smoother form’

Material and dimensions – Maximum height 20.9 mm, width 8.0 mm. **EL:** NHMW 2024/0042/0016-0019 (4), 2024/0042/0020 (11).

Description – Shell moderately large, solid, broadly biconic, with moderately high spire; apical angle initially 47-57°, later approx. 40°. Protoconch paucispiral, with low nucleus and about two moderately convex whorls (height: 525 µm, diameter: 710 µm). Transition to teleoconch marked by change in colour. Teleoconch of up to seven weakly convex whorls, with periphery at abapical suture, separated by moderately shallowly impressed linear to shallowly undulating suture. Early teleoconch whorls smooth, last 2-3 whorls smooth in some specimens, with irregular axial

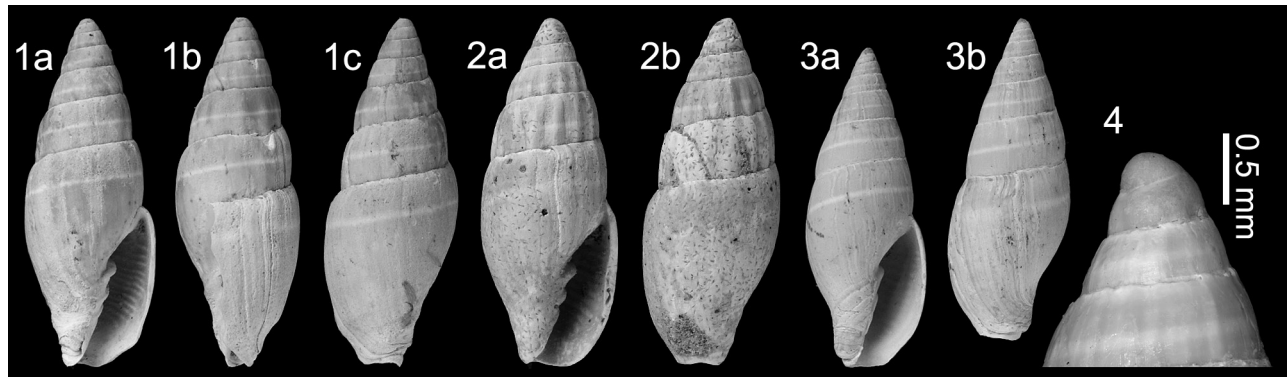


Plate 22. *Ebenomitra ebenus* (Lamarck, 1811), 'smoother form'; 1. NHMW 2024/0042/0017, height 21.2 mm, width 7.8 mm; 2. NHMW 2024/0042/0016, height 20.8 mm, width 8.0 mm; 3. NHMW 2024/0042/0018, height 16.8 mm, width 6.0 mm; 4. NHMW 2024/0042/0019 (juvenile), detail of protoconch. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

folds and growth halts in some, or with about 12 low axial ribs that fade on the last whorl in others. Last whorl 63-65% of total height, barrel-shaped to faintly convex, moderately constricted at base; fasciole bearing four cords extending from columellar folds. Aperture wide, with narrow, V-shaped anal canal; outer lip thin, weakly lyrate within; siphonal canal moderately short, slightly bent to left, with shallow siphonal notch. Columella bearing three oblique folds in most specimens, adapical most prominent, sharp, weakening abapically, fourth subobsolete fold occasionally present. Columellar callus slightly thickened, sharply delimited, thinning and indented in parietal area. Colour pattern preserved consisting of orange-brown background and narrow white band placed mid-whorl on spire whorls and midway between adapical suture and insertion of outer lip on last whorl.

'Ribbed form'

Material and dimensions – Maximum height 14.9 mm, width 5.4 mm. **CO:** NHMW 2024/0042/0022-0025 (4), 2024/0042/0005 (3).

Description – Shell moderately large, solid, broadly biconic, with moderately high gradate spire; apical angle initially 55-60°, later 33-42°. Protoconch not preserved.

Teleoconch of up to six weakly convex whorls, with periphery at abapical suture, separated by moderately impressed suture. Sculpture of straight, orthocline rounded ribs extending between sutures, ten on first teleoconch whorl, 16 on penultimate whorl, wider than their interspaces. Spiral sculpture reduced to very fine threads visible only on magnification and tangential light. Last whorl 61-65% of total height, barrel-shaped to faintly convex, moderately constricted at base; axials fading over base and last half whorl; fasciole bearing four cords extending from columellar folds. Aperture wide, with shallow, V-shaped anal canal; outer lip thin, irregularly lyrate within; siphonal canal moderately short, slightly bent to left, with shallow siphonal notch. Columella bearing four oblique folds, adapical most prominent, sharp, weakening abapically. Columellar callus hardly thickened, indented onto medial margin of venter, sharply delimited. Colour pattern preserved consisting of orange-brown background and narrow white band placed mid-whorl on spire whorls and midway between adapical suture and insertion of outer lip on last whorl.

Discussion – This species group has been problematic, both in the fossil and extant faunas. The number of synonyms listed in the chresonymy reflects the huge variability

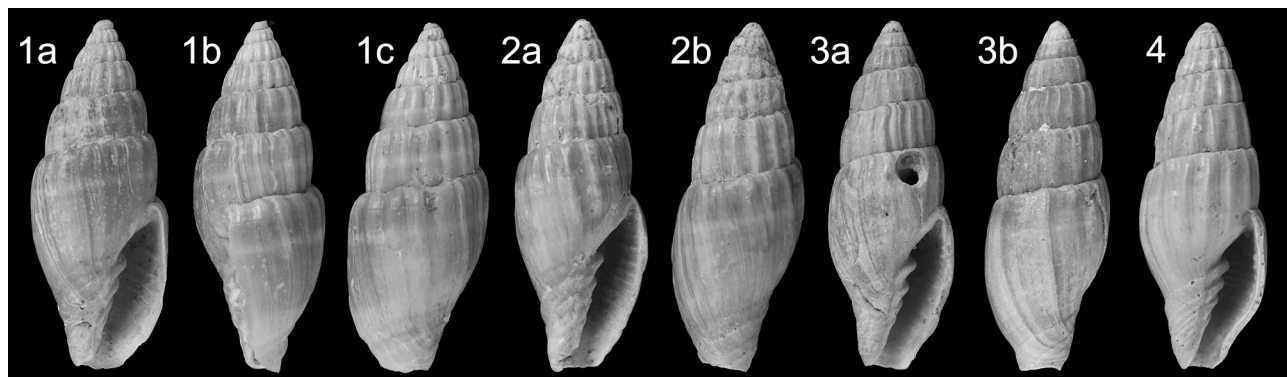


Plate 23. *Ebenomitra ebenus* (Lamarck, 1811), 'ribbed form'; 1. NHMW 2024/0042/0022, height 14.9 mm, width 5.4 mm; 2. NHMW 2024/0042/0023, height 13.9 mm, width 5.5 mm; 3. NHMW 2024/0042/0024, height 13.2 mm, width 4.7 mm; 4. NHMW 2024/0042/0025, height 13.3 mm, width 4.9 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

seen in living shells and numerous authors working on fossil material have confused *Mitra ebenus* Lamarck, 1811, *Mitra leucozona* Andrzejowski 1830, *Voluta pyramidella* Brocchi, 1814 and *Voluta plicatula* Brocchi, 1814.

To summarise, Brocchi's two taxa are different forms of a single species with a multispiral protoconch and should be placed in the genus *Vexillum* Röding, 1798, with the name *Vexillum pyramidellum* (Brocchi, 1814) having priority.

The *Mitra ebenus* species group is more problematic. Both Lamarck and Andrzejowski's species have a paucispiral protoconch and are placed in the genus/subgenus *Ebenomitra* Monterosato, 1917. According to Glibert (1952, p. 361), *Ebenomitra ebenus* differed in having four columellar folds as opposed to three in *E. leucozona*, and the colour pattern, which is often preserved in both species, consists of a single narrow white spiral band on the last whorl in *E. ebenus*, whereas *E. leucozona* has two broader white spiral bands. However, as noted by Landau *et al.* (2013, p. 215) and Harzhauser & Landau (2021b, p. 30), some Paratethyan Middle Miocene specimens have a weak or subobsolete fourth abapical fold. Bellardi (1887b, p. 52-55, pl. 6, figs 7-13) separated Italian Pliocene specimens as *Uromitra eoebenus* Bellardi, 1887 and described six different forms in the Pliocene, all of which were then given varietal names by Sacco (1904, p. 86). According to Bellardi, the Pliocene species differed from extant specimens in 1) being larger, 2) spire composed of a greater number of whorls, and almost always inflated in the middle, 3) the early teleoconch whorls always lack axial ribs, regardless of whether the later adult whorls are axially sculptured or entirely smooth. Based on Pliocene specimens from San Gimignano (Siena, Italy) we recognise the *eoebenus* form coexisting with the *ebenus* morphotype. The *eoebenus* morphotype does not occur in Estepona. Therefore, we provisionally consider it separate at full species level coexisting in the Italian Pliocene with *E. ebenus*.

The Estepona material shows a similar range of variability for *E. ebenus* as illustrated by Giannuzzi-Savelli *et al.* (2003, figs 652-667). Some specimens are entirely smooth (Pl. 22, fig. 3), have smooth last 2-3 whorls (Pl. 22, fig. 1), or have only the last whorl smooth (Pl. 22, fig. 2). In others, axial ribs are developed on all whorls (Pl. 23, figs 1-3). The number of columellar folds is usually four, although the abapical one is subobsolete in some specimens. The entirely ribbed form (Pl. 23, figs 1-3) is usually smaller than the 'smoother' form. For these reasons we present the two 'forms' on separate plates.

Distribution – Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1857; Harmer, 1918), Katendijk Formation, Belgium (Marquet, 1997, 1998); central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1918); Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011). western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Ruggieri *et al.*, 1959). Lower Pleistocene: central Mediterranean, Italy (Malatesta, 1960); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Upper Pleistocene: western Mediterrane-

an, Balearic Islands (Cuerda Barceló, 1987). Present-day: Atlantic coasts of West Africa, Canaries, Mediterranean (Giannuzzi Savelli, 1982; Giannuzzi-Savelli *et al.*, 2003; Hernández *et al.*, 2011).

***Ebenomitra ellenae* nov. sp.**

Plate 24, figs 1-4

ZooBank registration – urn:lsid:zoobank.org:act:79285076-0260-4434-91E6-3D3885639ABF

Type material – Holotype NHMW 2023/0323/0040, height 23.8 mm, width 11.4 mm; paratype 1 NHMW 2023/0323/0041, height 16.4 mm, width 8.5 mm; paratype 2 NHMW 2012/0197/0042 height 17.5 mm, width 8.9 mm; paratype 3 NHMW 2023/0323/0043, height 19.2 mm, width 8.6 mm; paratype 4 NHMW 2023/0323/0044 (only last whorl preserved), height 19.2 mm, width 10.5 mm; paratype 5 RGM.1404375, height 13.7 mm, width 6.9 mm.

Other material – Maximum height 23.8 mm, width 11.4 mm. **CO:** NHMW 2023/0323/0045 (1).

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

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

Etymology – Name after Ellen Mulder, sister of Henk Mulder who has so kindly made his collection available to us throughout this series and donated specimens generously. *Ebenomitra*, gender feminine.

Diagnosis – *Ebenomitra* species with ovate profile, relatively low spire, teleoconch of five smooth whorls, no spirals on base of fasciole, outer lip with narrow, elevated axial ridge followed by axial concavity some distance behind peristome.

Description – Shell medium sized, ovate-fusiform, with relatively low cyrtocoid spire and high last whorl; apical angle 64-66°. Protoconch unknown. Teleoconch of five smooth whorls separated by shallowly impressed suture. Spire whorls low, convex, with periphery at abapical suture. Last whorl ovate, approx. 76% of total height, broadly convex, weakly constricted at base; fasciole narrow, rounded, poorly developed. Aperture short, moderately broad elongate. Outer lip thin, smooth edged, with weak, narrow, rounded, axial ridge placed some distance behind peristome running from position of anal denticle, fading abapically towards outer border of siphonal canal, ridge bordered internally by axial concavity roughly equal in width to the ridge. Anal sinus marked by V-shaped notch; siphonal canal short, notched at tip. Columellar callus narrow, sharply delimited, continuous with thinner indented parietal callus. Columella bearing four prominent oblique folds occupying entire columellar

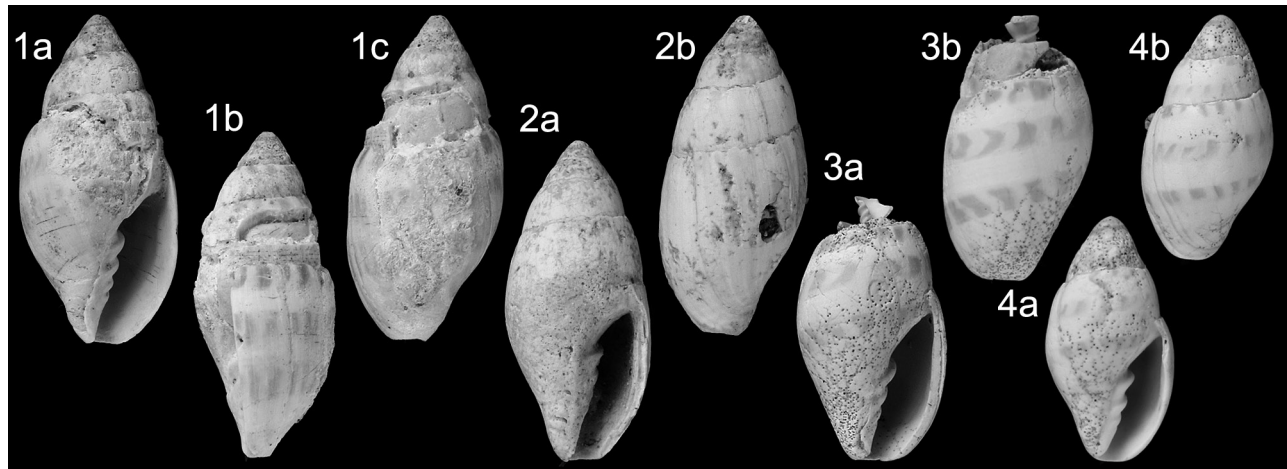


Plate 24. *Ebenomitra ellenae* nov. sp.; 1. **Holotype** NHMW 2023/0323/0040, height 23.8 mm, width 11.4 mm; 2. **Paratype 3** NHMW 2023/0323/0043, height 19.2 mm, width 8.6 mm; 3. **Paratype 4** NHMW 2023/0323/0044, height 19.3 mm, width 10.5 mm; 4. **Paratype 1** NHMW 2023/0323/0041, height 16.4 mm, width 8.5 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

length, weakening abapically. Colour pattern preserved of two bands of orange subquadratic blotches placed just below and above suture on spire whorls, four bands on last whorl, blotches mid-whorl chevron shaped.

Discussion – We have placed this species in the genus *Ebenomitra* Monterosato, 1917 as it is similar in profile and colour pattern to some forms of the present-day Mediterranean *Pusia granum* (Forbes, 1844) (see Giannuzzi-Savelli *et al.*, 2003, figs 680, 681) and *P. zebrina* (d'Orbigny, 1840) from the Canary Islands (see Hernández *et al.*, 2011, pl. 63, fig. L). Fedosov *et al.* (2017) placed '*Pusia*' *granum* in *Ebenomitra* and in their ongoing phylogenetic study on the Costellariidae, '*Pusia*' *granum* was sequenced, and appeared to be a part of the *Ebenomitra* clade (Alexander Fedosov personal communication BL; 08/2024).

Ebenomitra ellenae nov. sp. is superficially similar to several Italian Neogene species such as *Mitra brevis* Bellardi, 1887 and *M. doliolum* Bellardi, 1887, both from the Upper Miocene of Italy, in being ovate in profile with a low spire. It differs from both of these in not having any spiral sculpture even on the earliest teleoconch whorls and in having a very characteristic colour pattern preserved consisting of four bands of axially elongated subquadratic orange blotches. *Ebenomitra ellenae* also displays an unusual apertural feature: an elevated rounded ridge some distance behind the peristome in a position in which one might find a row of denticles in other gastropods, but the ridge is low and uninterrupted, and bordered internally by a shallow groove of roughly equal width. Superficially similar to *Episcomitra obesa* (Forsati, 1868), it differs in having a less inflated last whorl, lacking the fine spiral sculpture seen in that species, and the colour pattern.

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

Ebenomitra frumentum (Bellardi, 1887)

Plate 25, figs 1-3

- *1887b *Uromitra frumentum* Bellardi, p. 60, pl. 6, fig. 25.
- 1959 *Pusia* (*Pusia*) *tricolor savignyi* Payr. – Ruggieri *et al.*, p. 77, pl. 9, fig. 53 [*non Ebenomitra savignyi* (Payraudeau, 1826)].
- 1981 *Uromitra frumentum* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 170, pl. 53, fig. 5.
- 2002 *Vexillum frumentum* (Bellardi, 1887) – Chirli, p. 51, pl. 25, figs 9-12, pl. 26, figs 1-6.
- 2011 *Vexillum frumentum* (Bellardi, 1887) – Chirli & Linse, p. 138, pl. 47, fig. 2.

Material and dimensions – Maximum height 10.2 mm, width 3.7 mm. **CO:** NHMW 2024/0042/0094 (86). **EL:** NHMW 2024/0042/0006-0008 (3), 2024/0042/0009 (10).

Description – Shell small, solid, fusiform, with conical spire; apical angle approx. 43°. Protoconch paucispiral, of 1.5 smooth convex whorls with elevated nucleus (height: 560 μ m, diameter: 640 μ m). Transition to teleoconch marked by change in colour and lustre. Teleoconch of up to six convex whorls with periphery at abapical suture, separated by moderately impressed undulating suture. Sculpture of 10-12 low, rounded, straight orthocline ribs, slightly narrower than their interspaces, extending between sutures. Spiral sculpture restricted to extremely fine subobsolete threads just visible under magnification and oblique lighting. Penultimate and preceding whorl somewhat inflated compared to earlier teleoconch whorls. Last whorl approx. 60% of total height, subcylindrical, flat-sided, moderately constricted at base; fasciole flattened, poorly delimited from base, bearing 4-6 flattened cords. Aperture wide, with shallow, narrow anal canal; outer lip thin, bearing short lirae starting some distance behind peristome and not extending deep within aperture. Siphonal canal short, straight or bent weakly to

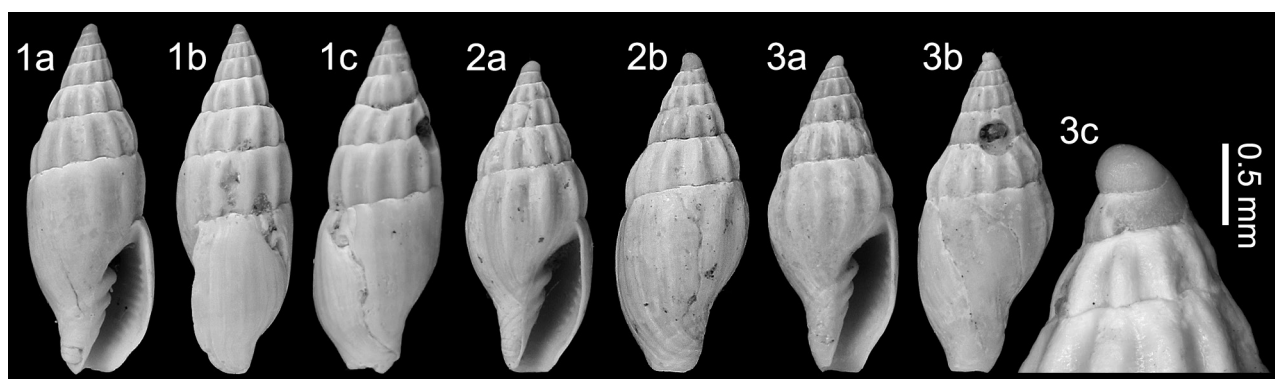


Plate 25. *Ebenomitra frumentum* (Bellardi, 1887); 1. NHMW 2024/0042/0006, height 9.8 mm, width 3.4 mm; 2. NHMW 2024/0042/0008, height 7.9 mm, width 3.2 mm; 3. NHMW 2024/0042/0007, height 8.6 mm, width 3.5 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

left, unnotched at tip. Columella with three oblique folds, weakening abapically, subobsolete fourth fold in some specimens. No colour pattern preserved.

Discussion – *Ebenomitra frumentum* (Bellardi, 1887) differs from *Ebenomitra savignyi* (Payraudeau, 1826) in its smaller size, more slender fusiform profile, and weaker axial ribs. Chirli (2002, p. 52) stressed that the two could be reliably separated based on their colour pattern on the last whorl; two fine reddish lines in *E. frumentum*, the lower placed at the level of the insertion of the outer lip, vs. a white band in *E. savignyi* placed along the periphery. Strangely, no colour pattern is preserved in any of the specimens of *E. frumentum* from Estepona, whereas it is preserved in specimens of *E. savignyi*. The specimen illustrated by Ruggieri *et al.* (1959, pl. 9, fig. 53) as *Pusia (Pusia) tricolor savignyi* has the low ribs and cylindrical last whorl we associate with *E. frumentum*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Bellardi, 1887b; Ruggieri *et al.*, 1959). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

***Ebenomitra savignyi* (Payraudeau, 1826)**

Plate 26, figs 1-2

- *1826 *Mitra Savignyi* Payraudeau, p. 166, pl. 8, fig. 23-25.
- 1982 *Vexillum (Pusia) savignyi* (Payraudeau, 1826) – Giannuzzi Savelli, p. 107, fig. 38, 40, 40bis.
- ?1992 *Vexillum (Pusia) savignyi* (Payraudeau, 1826) – Cavallo & Repetto, p. 120, fig. 309 (poorly preserved).
- 2003 *Vexillum (Pusia) savignyi* (Payraudeau, 1826) – Giannuzzi-Savelli *et al.*, p. 266, figs 668-670.

non 1959 *Pusia (Pusia) tricolor savignyi* Payr. – Ruggieri *et al.*, p. 77, pl. 9, fig. 53 [= *Ebenomitra frumentum* (Bellardi, 1887)]

Material and dimensions – Maximum height 11.5 mm, width 5.1 mm. **CO:** NHMW 2024/0042/0010-0011 (2), 2024/0042/0012 (3).

Description – Shell small, solid, broadly fusiform, with conical spire; apical angle 52-58°. Protoconch not preserved. Teleoconch of up to five convex weakly shouldered whorls with periphery at abapical suture, separated by weakly impressed shallowly undulating suture. Sculpture of eleven rounded, orthocone ribs, narrower than their interspaces, weakening over subsutural ramp. Last whorl 65-67% of total height, convex, moderately constricted at base; fasciole flattened, sharply delimited by cord developed as continuation of adapical columellar fold. Aperture wide; anal canal narrow; outer lip thin, bearing short lirae starting some distance behind peristome and not extending deep within aperture in some specimens, smooth in others. Siphonal canal moderately short, unnotched at tip. Columella with three oblique folds, weakening abapically. Colour pattern preserved consisting of broad white band over background orange placed mid-way between adapical suture and level of insertion of outer lip.

Discussion – We attribute a few specimens to the extant Mediterranean *Ebenomitra savignyi* (Payraudeau, 1826) that share the characteristic white colour band over darker orange/brown (Giannuzzi Savelli, 1982; Giannuzzi-Savelli *et al.*, 2003). It differs from *Ebenomitra frumentum* (Bellardi, 1887) in being larger, broader, and the ribs are stronger, but fade over the subsutural ramp, which is not developed in *E. frumentum*.

Fossil records for this species are scarce. The specimen figured by Cavallo & Repetto, fig. 309) is too poorly preserved to be certain of the identification but is probably correct. Bellardi (1887b, p. 60) suggested *E. savignyi* might have evolved from *E. frumentum*, but both seem to co-exist in the Estepona assemblages.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Cavallo & Repetto, 1992). Present-day: southern

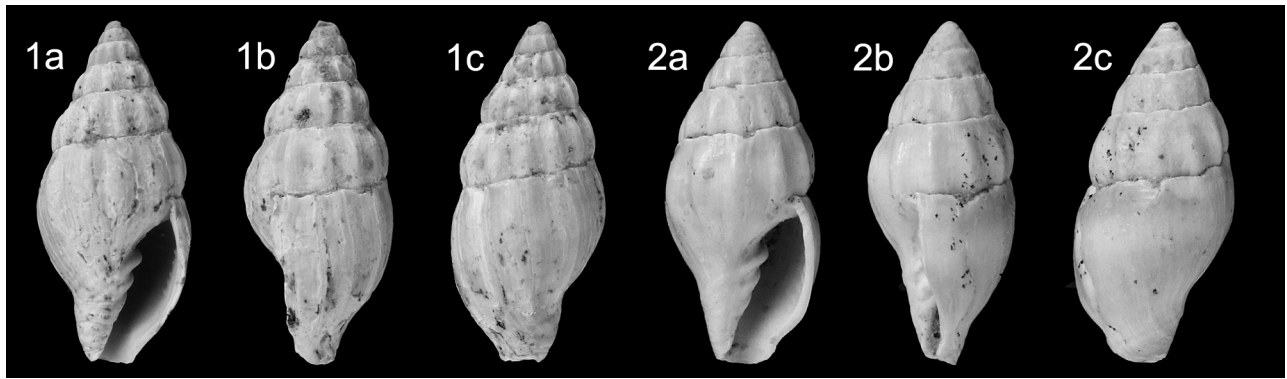


Plate 26. *Ebenomitra savignyi* (Payraudeau, 1826); 1. NHMW 2024/0042/0010, height 11.5 mm, width 5.1 mm; 2. NHMW 2024/0042/0011, height 10.6 mm, width 4.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Iberian Atlantic coast, western and central Mediterranean (Giannuzzi Savelli, 1982; Giannuzzi-Savelli *et al.*, 2003).

Genus *Fedosovia* Harzhauser & Landau, 2021

Type species (by original designation) – *Mitra* (*Callithea*) *fuchsi* Hoernes & Auinger, 1880, Middle Miocene, Paratethys.

2021b *Fedosovia* Harzhauser & Landau, p. 34.

***Fedosovia multigranosa* (Vera-Peláez, 2002)**

Plate 27, figs 1-3

- *2002 *Anarithma?* *multigranosa* Vera-Peláez, p. 196, figs 2S-U.
- 2018 *Morula nodulosa* (C.B. Adams, 1845) – Brunetti, p. 316, fig. 4 [*non Clarendontella nodulosa* (C.B. Adams, 1845)].
- 2022 *Fedosovia multigranosa* (Vera-Peláez, 2002) – Landau & Harzhauser, p. 140, pl. 24, fig. 1.

Material and dimensions – Maximum height 8.7 mm, width 3.7 mm. **VC:** NHMW 2020/0171/0002 (1), NHMW 2024/0042/0013-0014 (2), NHMW 2024/0042/0015 (2).

Description – Shell very small, moderately broad to moderately slender fusiform; apical angle approx. 48°. Protoconch paucispiral, low conical, 1.25 smooth, convex whorls with raised nucleus (height: 610 μ m, diameter: 560 μ m). Teleoconch boundary marked by beginning of axial sculpture. Teleoconch of up on 4.5 whorls, separated by shallow suture. First two teleoconch whorls almost flat-sided, later weakly convex; first whorl with about 14 prosocline axial ribs, slightly wider than their interspaces, second whorl three spiral cords, fourth mostly covered by succeeding whorl at abapical suture, cords beaded at axial intersections. On penultimate whorl third spiral cord splits to form five rows of beads. Axial and spiral interspaces very narrow, resulting in densely spaced, pillow-like, subquadrate beads. Last whorl 73% of total height, convex mid-whorl, moderately constricted at base, bearing about 14 beaded cords formed by splitting of spirals; siphonal fasciole relatively long, weakly rounded, bearing about six narrower beaded cords. Aperture ovate, moderately narrow; anal sinus not developed; outer lip thin (incomplete in all specimens), smooth within. Columellar

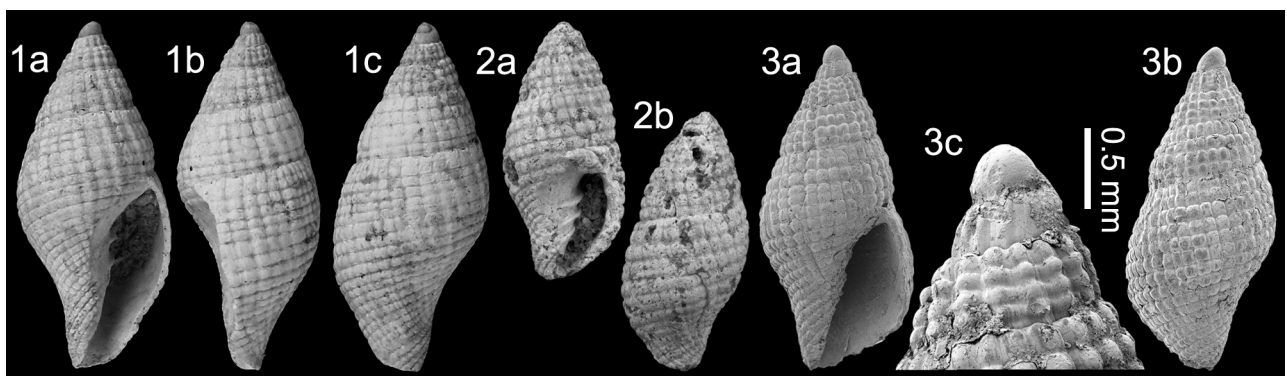


Plate 27. *Fedosovia multigranosa* (Vera-Peláez, 2002); 1. NHMW 2024/0042/0013, height 8.7 mm, width 3.7 mm; 2. NHMW 2020/0171/0002, height 6.3 mm, width 2.9 mm (digital images); 3. NHMW 2024/0042/0014, height 5.6 mm, width 2.6 mm, 3c, detail of protoconch (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

callus not thickened, marked by moderately broad indented rim over medial border of venter, bearing three columellar folds; adapical two folds very prominent, abapical weaker. Siphonal canal moderately long, narrow, straight or slightly bent to the left, unnotched at tip.

Discussion – This species was described within the genus *Anarithma* Iredale, 1916, now placed in the family Mitromorphidae Casey, 1904. Whilst mitromorphid turrids do have columellar folds, they are not as strong or as sharp as those seen in this species. Moreover, the teleoconch sculpture seen in the Estepona species of rows of squarish beads is different from that seen in some species of *Anarithma*, in which small tubercles are developed at the sculptural intersections. In our opinion, the Estepona shell should be placed in the family Costellariidae MacDonald, 1860. It is highly reminiscent in sculpture to members of the genus *Fedosovia* Harzhauser & Landau, 2021, although smaller shelled than the Miocene Paratethyan *F. fuchsi* (Hoernes & Auinger, 1880). The genus *Fedosovia* differs from other costellariid genera by the combination of a peculiar ‘pillow-like’ sculpture and a paucispiral protoconch (as opposed to *Ebenomitra*, which has a paucispiral protoconch, but lacks the peculiar sculpture). The protoconch is paucispiral (Pl. 27, fig. 3), similar to that of the Paratethyan species (see Harzhauser & Landau, 2021, fig. 4G). Since Landau & Harzhauser (2022) further specimens were found misplaced in the NHMW collection, nevertheless, it is a rare species associated with the deeper water Velerín carretera assemblage.

It has also been reported in the Italian Upper Pleistocene. Brunetti (2018, fig. 4) illustrated it as *Morula nodulosa* (C.B. Adams, 1845). This specimen is not an Eraglataxinae but represents *F. multigranosa*. Brunetti (2018, p. 316) described three columellar folds, which are not clearly seen in his figure.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (Vera-Peláez, 2002; Landau & Harzhauser, 2022). Upper Pleistocene: central Mediterranean, Sardinia (Brunetti, 2018).

Genus *Uromitra* Bellardi, 1887b

Type species (by subsequent designation, Harris, 1897) – *Uromitra antegressa* Bellardi, 1887, Neogene, Italy.

- 1887b *Uromitra* Bellardi, p. 23. Cossmann (1899, p. 168) subsequently invalidly designated as type species *Voluta cupressina* Brocchi, 1814 (also an originally included species).
- 1965 *Tosapusia* Azuma, p. 56. Type species (by monotypy): *Mitropifex isaoi* Kuroda & Sakurai in Kuroda, 1959, present-day, Indo-West Pacific.

Note – Harzhauser & Landau (2021b, p. 57) suggested placement of a group of European costellariids that had historically been placed in the genus *Vexillum* Röding, 1798 into *Tosapusia* Azuma, 1965. This group that in-

cluded *Voluta cupressina* Brocchi, 1814 from the Mediterranean Pliocene and *Mitra neudorfensis* Schaffer, 1898 and *Vexillum pseudocupressinum* Bafuk, 1997 from the Middle Miocene Paratethys, differed from *Vexillum* in having a longer unnotched siphonal canal and straight axial ribs, as opposed to arcuate and undulating in *Vexillum* (Fedosov *et al.*, 2017). Moreover, the preference for offshore settings of all three species is consistent with the deep water habitat of extant *Tosapusia* species.

However, in their enthusiasm to adapt fossil taxonomy to modern molecular phylogenetics, they missed that Bellardi (1887b) had already given a name to this group of costellariids. The group assigned by Harzhauser & Landau (2021b) corresponds to Bellardi’s ‘1^a Serie’ of *Uromitra* species characterised as including “*relatively elongated slender shells, with a very acute spire composed of numerous whorls, reticulated surface pattern, strongly twisted columella, ending in a relatively long siphonal canal set obliquely to the main shell axis* [loosely translated from Italian]” (Bellardi, 1887b, p. 23). Species included were: *Uromitra antegressa* Bellardi, 1887, *U. antemissa* Bellardi, 1887, *U. belliata* Bellardi, 1887, *U. paucicostata* Bellardi, 1887 from the Italian Miocene, and *Voluta cupressina* Brocchi, 1814 from the Pliocene. Harris (1897, p. 124) designated the Lower Miocene *U. antegressa* as type species, which is unfortunate, as the specimen illustrated is incomplete and it was not refigured by Ferrero Mortara *et al.* (1981). Cossmann’s (1899, p. 168) designation of *Voluta cupressina* as type for *Uromitra* would have been more appropriate, however, it is invalid. Therefore, if Harzhauser & Landau’s (2021b) generic concept is correct, *Tosapusia* Azuma, 1965 is a junior subjective synonym of *Uromitra* Bellardi, 1887b. How many of Bellardi’s ‘Serie’ correspond to this generic concept needs to be reviewed with Italian Miocene material, but probably Bellardi’s ‘1-10^a Serie’ are *Uromitra* (Bellardi, 1888, pl. 5, figs 21-45). His ‘11^a Serie’ is considered to represent *Vexillum* Röding, 1798 (see under *V. recticosta*).

Uromitra cupressina (Brocchi, 1814)

Plate 28, figs 1-3

- *1814 *Voluta cupressina* Brocchi, p. 319, pl. 4, fig. 6.
- 1847 *Mitra elegans* Michelotti, p. 314, pl. 13, figs 12, 13 (*non* Reeve, 1845).
- 1850 *Mitra cupressina* Brocc. – Bellardi, p. 19, pl. 2, figs 15, 16.
- 1887b *Uromitra cupressina* Bell. [*sic*] – Bellardi, p. 26, pl. 5, fig. 25.
- 1899 *Uromitra cupressina* Br. – Cossmann, p. 168, pl. 8, fig. 32.
- 1904 *Uromitra cupressina* var. *reticulomarginata* Sacco, p. 85 (= var. A of Bellardi 1887b).
- 1904 *Uromitra cupressina* var. *subrectosuturata* Sacco, p. 85 (= var. B of Bellardi 1887b).
- 1955 *Vexillum* (*Vexillum*) *cupressinum* (Brocchi 1814) – Rossi Ronchetti, p. 244, fig. 130.
- 1960 *Vexillum* (*Uromitra*) *cupressinum* (Brocchi, 1814) – Malatesta, p. 181, pl. 9, fig. 7.

- 1967 *Vexillum (Uromitra) cupressinum* (Brocchi) – Pelosio, p. 46 [146], pl. 42, figs 7, 8.
- 1967 *Vexillum (Uromitra) cupressinum* (Brocchi, 1814) f. *reticulomarginata* (Sacco) – Pelosio, p. 46, pl. 42, fig. 9.
- 1969 *Vexillum (Uromitra) cupressinum* (Brocchi) – Mastroilli, p. 120, pl. 8, fig. 20.
- 1974 *Vexillum cupressinum* (Brocchi) – Caprotti, p. 30, pl. 3, fig. 10.
- 1974 *Uromitra cupressina* (Brocchi, 1814) – Malatesta, p. 367, pl. 29, fig. 4.
- 1978 *Voluta cupressina* Brocchi, 1814 – Pinna & Spezia, p. 168, pl. 61, fig. 4.
- 1992 *Vexillum (Costellaria) cupressinum* (Brocchi, 1814) – Cavallo & Repetto, p. 120, fig. 306.
- 2000 *Vexillum (Uromitra) cupressinum* (Brocchi, 1814) – Davoli, p. 203, pl. 6, figs 15-18.
- 2002 *Vexillum (Uromitra) cupressinum* (Brocchi, 1814) – Chirli, p. 55, pl. 27, figs 9-12, pl. 28, figs 1-4.
- 2008 *Vexillum cupressinum* (Brocchi, 1814) – Chirli & Richard, p. 53, pl. 10, figs 5, 6.
- 2011 *Uromitra cupressina* (Brocchi, 1814) – Chirli & Linse, p. 137, pl. 46, fig. 4.
- 2013 *Costellaria cupressina* (Brocchi, 1814) – Landau et al., p. 217, pl. 34, fig. 13.
- 2018 *Vexillum cupressinum* (Brocchi, 1814) – Brunetti & Cresti, p. 82, fig. 315.
- non 1852 *Mitra cupressina* Brocc. – Hörnes, p. 104, pl. 10, figs 25-27 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1880 *Mitra (Callithea) cupressina* Brocc. – Hoernes & Auinger, p. 86, pl. 10, fig. 10 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1908 *Mitra (Callithea) cupressina* Brocc. – Schaffer, p. 100, pl. 10, fig. 19 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1911 *Turricula (Uromitra) cupressina* Brocc. – Friedberg, p. 29, pl. 1, fig. 22 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1928 *Turricula cupressina* Brocc. – Friedberg, p. 580, pl. 37, fig. 29 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1960 *Vexillum (Uromitra) cupressinum* (Brocchi, 1814) – Kojumdgieva in Kojumdgieva & Strachimirov, p. 161, pl. 42, fig. 12 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1961 *Vexillum (Uromitra) cupressinum* Brocc. – Florei, p. 686, pl. 9, fig. 69 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1966 *Mitra (Vexillum) cupressina* Brocchi, 1814 – Strausz, p. 369, pl. 25, figs 4, 5 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1972 *Vexillum (Vexillum) cupressinum* Brocchi – Csepregy-Meznerics, p. 30, pl. 14, fig. 7 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 1998 *Vexillum (Uromitra) cupressinum* (Brocchi) – Schultz, p. 70, pl. 28, fig. 6 [*Uromitra pseudocupressina* (Bałuk, 1997)].
- non 2007 *Vexillum (Uromitra) cupressianum* [sic] (Brocchi) – Tiță, p. 548, fig. 5c [*Uromitra pseudocupressina* (Bałuk, 1997)].

Material and dimensions – Maximum height 13.8 mm, width 4.0 mm. VC: NHMW 2024/0042/0001-0003 (3), 2024/0042/0004 (1).

Description – Shell small, slender fusiform, with moderately incised suture; apical angle 34-37°. Protoconch high conical, of 3.5 smooth, convex whorls (height: 920 μ m, diameter: 620 μ m). Teleoconch of up to six weakly convex to subcylindrical whorls. Sculpture on first teleoconch whorl about 12 opisthocline axial ribs crossed by single subsutural cord beading ribs to give weakly coronate appearance at adapical suture. Abapically number of primary cords increases to six on penultimate whorl, with occasional secondaries intercalated in some interspaces in some specimens. Subsutural cord remains slightly stronger and wider spaced than the rest of the cords. Number of axial ribs extremely variable, between 12-22 on penultimate whorl, the cords variably forming small tubercles over the intersections. Last whorl 58 % of total height, moderately convex, moderately contracted at base; siphonal fasciole broad, rounded, sharply delimited from base, bearing four strong spiral cords that are continuations

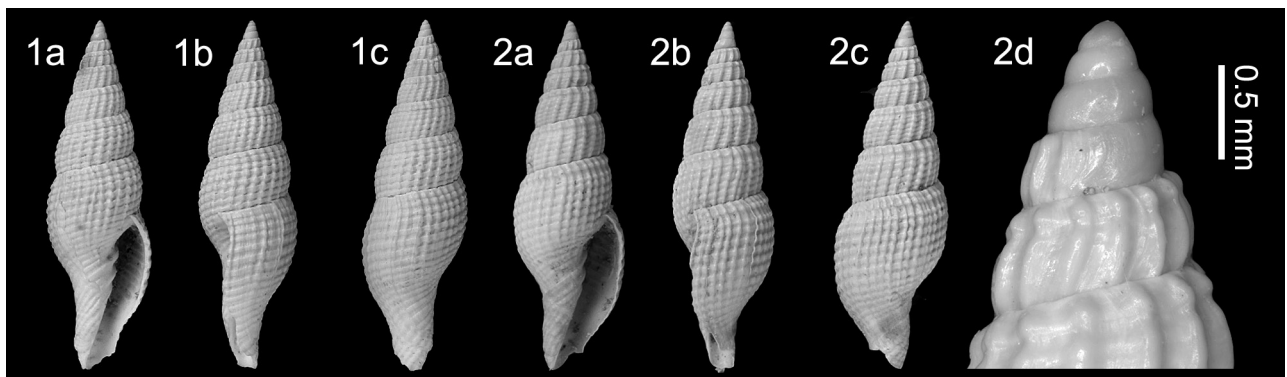


Plate 28. *Uromitra cupressina* (Brocchi, 1814); 1. NHMW 2024/0042/0001, height 14.0 mm, width 3.9 mm; 2. NHMW 2024/0042/0002, height 11.6 mm, width 3.5 mm; 3. NHMW 2024/0042/0003, height 9.8 mm, width 3.3 mm. Velerin carretera, Velerin, Estepona, Lower Piacenzian, Upper Pliocene.

of the columellar folds. Aperture narrow, elongate; outer lip thin, bearing delicate lirae deep within aperture; siphonal canal long, moderately narrow, straight, unnotched. Columella strongly twisted at fasciole, bearing four prominent, elevated, sharp folds weakening abapically. Columellar callus weakly delimited, not thickened.

Discussion – The protoconch and earliest teleoconch whorls in *Uromitra cupressina* (Brocchi, 1814) show little intraspecific variability. However, with ontogeny the number of axial ribs on later whorls is highly variable resulting in two main morphotypes; one with finely reticulated sculpture, axials weakly predominant, with small tubercles developed at the intersections where the cords cross the ribs; this is var. *reticulomarginata* Sacco, 1904. The second with strongly predominant and widely spaced axial ribs, the cords slightly swollen over the ribs, but not tubercular; var. *subrectosuturata* Sacco, 1904. These two morphotypes occur together in the deeper water assemblage of Velerín carretera. They have also been recognised co-occurring in the Italian Pliocene (Bellardi, 1887b; Pelosio, 1967; Chirli, 2002).

Harzhauser & Landau (2021b, p. 59) adopted a stricter species concept than that of Landau *et al.* (2013, p. 218) and considered the Paratethyan records a separate species, *Uromitra pseudocupressina* (Bafuk, 1997). The Paratethyan species differs in having a higher number of axial ribs (especially on early spire whorls), the spiral cords are more numerous and not swollen over the ribs (not forming tubercles), separated by more numerous narrower grooves visible in the axial interspaces in *U. pseudocupressina* (see Harzhauser & Landau, 2021, figs 19E–H).

Distribution – Middle Miocene: Proto-Mediterranean (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: central Proto-Mediterranean (Michelotti, 1847; Bellardi, 1850, 1887b; Davoli, 2000). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887b; Pelosio, 1967; Caprotti, 1974; Chirli, 2002; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Malatesta, 1960); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Genus *Vexillum* Röding, 1798

Type species (by subsequent designation by Woodring, 1928) – *Vexillum plicatum* Röding, 1798 (= *Voluta plicaria* Linnaeus, 1758), present-day, Indo-Pacific.

1798 *Vexillum* Röding, p. 138.

For generic synonymy see Harzhauser & Landau (2021b) and Fedosov *et al.* (2017).

Vexillum nitidum (Bellardi, 1887)

Plate 29, fig. 1

*1887b *Uromitra nitida* Bellardi, p. 45, pl. 5, fig. 49.

1981 *Uromitra nitida* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 167, pl. 52, fig. 18.

1992 *Vexillum (Uromitra) nitidum* (Bellardi, 1887) – Cavallo & Repetto, p. 120, fig. 308.

2002 *Vexillum nitidum* (Bellardi, 1887) – Chirli, p. 52, pl. 26, figs 7–9.

2018 *Vexillum nitidum* (Bellardi, 1887) – Brunetti & Cresti, p. 82, fig. 316.

non 2021b *Vexillum nitidum* (Schaffer, 1898) [non Bellardi, 1887] – Harzhauser & Landau, p. 52, fig. 18B.

Material and dimensions – Height 21.0 mm, width 7.6 mm. VC: NHMW 2024/0042/0084 (1).

Description – Shell large, solid, moderately slender fusiform, with mid-height, regularly conical spire; apical angle initially 47°, later 30°. Protoconch not preserved. Teleoconch of up to seven low, weakly convex to subcylindrical whorls, separated by moderately impressed suture. Axial sculpture of about 16 low, narrow, straight orthocline ribs, about ½–⅓ width of their interspaces continuing strongly developed to outer lip. Fine spiral threads cover entire surface visible only under magnification. Last whorl 60% of total height, broadly convex, moderately constricted at base; fasciole flattened, poorly developed. Aperture elongate, moderately narrow; outer lip thin edged, bearing about ten short lirae starting some distance behind peristome; anal canal narrow, shallow V-shaped; siphonal canal moderately long, slightly bent to left, very shallowly notched at tip. Columella straight, bearing four oblique folds, weakening abapically. Columellar callus weakly thickened abapically, narrowly discontinuous above adapical fold, indented in parietal region.

Discussion – Bellardi grouped together a series of *Uromitra* Bellardi, 1877 species with straight axial ribs that where weakly coronate at the adapical suture, lack of spiral sculpture, except for the weakest, almost im-

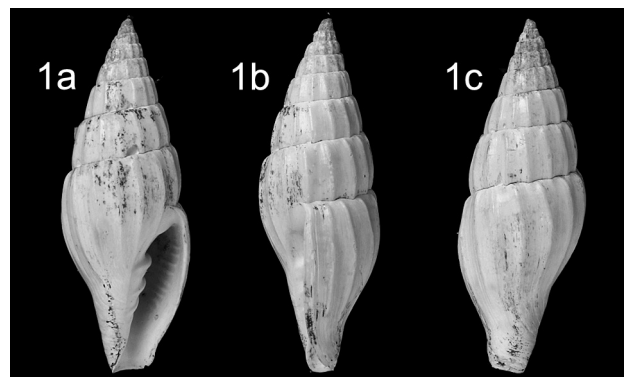


Plate 29. *Vexillum nitidum* (Bellardi, 1887); 1. NHMW 2024/0042/0084, height 21.0 mm, width 7.6 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

perceptible, spiral threads or grooves, and a short almost straight columella, weakly bent to the left (1887b, p. 43, '11^a Serie'). In this group he included *Uromitra recticostata* [sic] (Bellardi, 1850) (unnecessary emendation of his earlier name *recticosta*), *U. soror* Bellardi, 1877, *U. crebricostata* Bellardi, 1887, and *U. nitida* Bellardi, 1877 (see Ferrero Mortara *et al.*, 1981, pl. 52 figs 15-18 for types). Herein, these species are all placed in *Vexillum*.

Vexillum recticosta differs in being smaller, with a somewhat gradate rather than regularly conical spire, the last whorl is more strongly constricted at the base, the axial ribs are more numerous and lower, not as sharp. *Vexillum soror* and *V. crebricostatum* have more numerous ribs. This species seems to be uncommon in the Italian Pliocene (Bellardi, 1887b, p. 45) and associated with sandy clays (Chirli, 2002, p. 52). In Estepona the only specimen at hand comes from the deeper water assemblage of Velerin carretera.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Bellardi, 1887b). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887b; Ferrero Mortara *et al.*, 1981; Cavallo & Repetto, 1992; Chirli, 2002; Brunetti & Cresti 2018). Upper Pliocene: western Mediterranean, Estepona Basin (this paper).

***Vexillum pyramidellum* (Brocchi, 1814)**

Plate 30, figs 1-3

- *1814 *Voluta pyramidella* Brocchi, p. 318, pl. 4, fig. 5.
- 1814 *Voluta plicatula* Brocchi, p. 318, pl. 4, fig. 7.
- 1887b *Uromitra pyramidella* (Brocc.) – Bellardi, p. 46, pl. 5, fig. 51.
- 1887b *Uromitra plicatula* (Brocc.) – Bellardi, p. 49, pl. 5, figs 54-56.
- 1904 *Uromitra pyramidella* var. *miostriata* Sacc., Sacco, p. 85, pl. 19, fig. 13.
- 1911 *Mitra (Uromitra) pyramidella* Br. – Cerulli-Irelli, p. 287, pl. 38, fig. 23.
- 1911 *Mitra (Uromitra) plicatula* Br. – Cerulli-Irelli, p. 287, pl. 38, fig. 24-29.
- 1955 *Pusia (Pusia) (Pusia) ebenus* var. *pyramidella* (Brocchi 1814) – Rossi Ronchetti, p. 239, fig. 127.
- 1955 *Pusia (Pusia) (Pusia) ebenus* var. *plicatula* (Brocchi 1814) – Rossi Ronchetti, p. 241, fig. 128.
- 1959 *Pusia (Pusia) pyramidella* (Brocchi) – Ruggieri *et al.*, p. 79, pl. 19, fig. 116.
- 1959 *Pusia (Pusia) plicatula* (Brocchi) – Ruggieri *et al.*, p. 80, pl. 17, fig. 106.
- 1964 *Vexillum (Uromitra) plicatulum* (Brocchi 1814) – Anderson, p. 262, pl. 26, fig. 200.
- 1967 *Pusia (Pusia) plicatula* (Brocchi) – Pelosio, p. 45, pl. 42, figs 4-6.
- 1974 *Pusia (Pusia) plicatula* (Brocchi) – Caprotti, p. 30, pl. 3, fig. 11.
- 1974 *Vexillum (Ebenomitra) pyramidella* (Brocchi 1814) – Malatesta, p. 366, pl. 29, fig. 1.
- 1974 *Vexillum (Ebenomitra) ebenus plicatula* (Brocchi 1814) – Malatesta, p. 366, pl. 29, fig. 2.
- 1976 *Pusia pyramidella* (Brocchi, 1814) – Caprotti, p. 11, pl. 16, fig. 18.
- 1978 *Voluta pyramidella* Brocchi, 1814 – Pinna & Spezia, p. 170, pl. 65, fig. 2.
- 1978 *Voluta plicatula* Brocchi, 1814 – Pinna & Spezia, p. 170, pl. 67, fig. 2.
- 1984 *Vexillum (Uromitra) plicatulum* (Brocchi, 1814) – A.W. Janssen, p. 267, pl. 67, fig. 9.
- 1992 *Vexillum (Pusia) ebenus* (Lamarck, 1811) – Cavallo & Repetto, p. 120, fig. 307 [*non Ebenomitra ebenus* (Lamarck, 1811)].
- 1995 *Voluta pyramidella* Br. – Della Bella & Tabanelli, p. 293, fig A.
- 2000 *Vexillum (Uromitra) aff. V. (U.) plicatulum* (Brocchi, 1814) – Davoli, p. 206, pl. 6, figs 1-6.
- 2002 *Vexillum pyramidellum* (Brocchi, 1814) – Chirli, p. 53, pl. 27, figs 10-12, pl. 27, figs 1-8.
- 2007 *Vexillum (Uromitra) plicatulum* (Brocchi, 1814) – Wienrich, p. 654, pl. 137, fig. 2.
- 2010 *Vexillum ebenus pyramidella* (Brocchi, 1814) – Sosso & dell'Angelo, p. 42, p. 59 unnumbered figure centre middle row.
- 2011 *Vexillum pyramidellum* (Brocchi, 1814) – Chirli & Linse, p. 139, pl. 47, fig. 3.
- 2017 *Pusia pyramidella* (Brocchi, 1814) – Büyükmeriç *et al.*, p. 7, 9, fig. 5G (named as *Vexillum ebens* [sic] *pyramidella* on plate text).
- 2018 *Vexillum plicatulus* (Brocchi, 1814) – Brunetti & Cresti, p. 82, fig. 317.
- non* 1852 *Mitra pyramidella* Brocc. – Hörnes (*pars*), p. 107, pl. 10, fig. 28 [= *Vexillum badensis* (Hoernes & Auinger, 1880)].
- non* 1852 *Mitra pyramidella* Brocc. – Hörnes (*pars*), p. 107, pl. 10, fig. 29 [= *Vexillum transalpinum* Harzhauser & Landau, 2021b].
- non* 1911 *Turricula plicatula* Brocc. – Friedberg, p. 28, pl. 1, fig. 20 [= *Vexillum transalpinum* Harzhauser & Landau, 2021b].
- non* 1954 *Vexillum (Costellaria) plicatulum* (Brocchi) – Csepregy-Meznerics, p. 45, pl. 5, fig. 26 [?= *Vexillum transalpinum* Harzhauser & Landau, 2021b].
- non* 1958 *Vexillum (Vexillum) plicatula* (Brocchi) – Erőnal-Erentöz, p. 78, pl. 12, figs 6-12 [= *Vexillum transalpinum* Harzhauser & Landau, 2021b].
- non* 1966 *Mitra (Vexillum) aff. plicatula* Brocchi, 1814 – Strausz, p. 368, pl. 26, figs 1-2 [?= *Vexillum transalpinum* Harzhauser & Landau, 2021b].
- non* 2013 *Pusia pyramidella* (Brocchi, 1814) – Landau *et al.*, p. 215, pl. 34, figs 7-9, pl. 68, fig. 9 [= *Vexillum transalpinum* Harzhauser & Landau, 2021b].

Material and dimensions – Maximum height 34.3 mm, width 10.6 mm. **CO:** NHMW 2024/0042/0077-0079 (3), 2024/0042/0080 (10). **EL:** 2024/0042/0100 (3). **PA:** 2024/0042/0083 (1).

Description – Shell large, solid, moderately slender fusiform, with moderately high, slightly gradate conical spire; apical angle 31-40°. Protoconch poorly preserved,

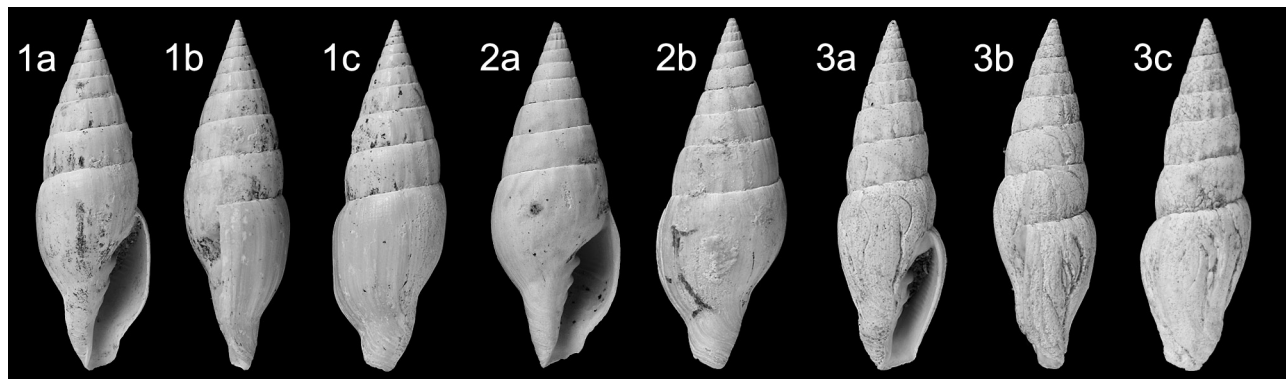


Plate 30. *Vexillum pyramidellum* (Brocchi, 1814); 1. NHMW 2024/0042/0077, height 34.0 mm, width 10.8 mm; 2. NHMW 2024/0042/0078, height 29.8 mm, width 10.8 mm; 3. NHMW 2024/0042/0079, height 32.4 mm, width 9.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

but multispiral. Teleoconch of up to ten weakly convex to subcylindrical whorls, separated by impressed suture. Axial sculpture extremely variable, about 14 low, orthocline ribs, roughly equal in width to their interspaces, in most specimens weakening to obsolete on last two whorls. Fine spiral threads cover entire surface visible only under magnification. Last whorl 53–57% of total height, moderately convex to subcylindrical, constricted at base; fasciole broadly rounded, poorly delimited from base. Aperture elongate, moderately narrow; outer lip thin edged, very weakly lirate, lirae starting deep within aperture; anal canal narrow, shallow V-shaped; siphonal canal moderate length, slightly bent to right, very shallowly notched at tip. Columella straight, bearing four oblique folds, weakening abapically. Columellar callus weakly thickened abapically, narrowly discontinuous above adapical fold with slightly thickened parietal pad.

Discussion – Most authors have placed this species in the genus *Vexillum* Röding, 1798. However, it differs from members of that genus in lacking ribs on mid-spire whorls (but rather broad and low folds), having an unnotched siphonal canal, and a rather short aperture. The shell shape and sculpture are reminiscent of members of the genus *Protoelongata* Herrmann, Stossier & R. Salisbury, 2014 [type species *Protoelongata dekkersi* (Herrmann, Stossier & R. Salisbury, 2014), present-day, Philippines], but this is an Indo-Pacific genus. With some hesitation we provisionally maintain the species in *Vexillum*.

Della Bella & Tabanelli (1995) concluded that *Voluta pyramidella* Brocchi, 1814 and *Voluta plicatula* Brocchi, 1814 were different forms of a single species, the name *Vexillum pyramidellum* having priority. The teleoconch of *Ebenomitra ebenus* (Lamarck, 1811) is similar, but the protoconch differs in being paucispiral, character of the genus *Ebenomitra* Monterosato, 1917, whereas *Vexillum pyramidellum* has a multispiral protoconch, character of the genus *Vexillum* Röding, 1798.

Although *Vexillum pyramidellum* is highly variable in profile and sculpture (see e.g., Chirli, pl. 27, figs 10–12, pl. 27, figs 1–8), the Estepona specimens are less variable,

all having relatively weak axial ribs on early teleoconch whorls that become obsolete or weaken on the last two whorls in most specimens.

In view of the variability seen in Pliocene specimens of this species, Landau *et al.* (2013) adopted a wide species concept that did not stand up to critical review when Middle Miocene Paratethyan material was re-examined. Harzhauser & Landau (2021b) considered most of the Paratethyan records to represent *Vexillum transalpinum* Harzhauser & Landau, 2021b that, although also variable in shape and sculpture, differed from Brocchi's species in that the axial sculpture is never completely reduced on penultimate and last whorls, as is typical for Pliocene specimens of *V. pyramidellum*. We have provisionally kept in the synonymy the rather poorly preserved specimens from the Miocene North Sea Basin recorded by Anderson (1964, pl. 26, fig. 200), Janssen (1984, pl. 67, fig. 9) and Wienrich (2007, pl. 137, fig. 2), although better preserved material may demonstrate these to represent a separate species within the *V. pyramidellum* species group.

For further discussion see under *V. cf. recticosta* (Bellardi, 1850) below.

Distribution – Lower-Middle Miocene: North Sea Basin (late Burdigalian-Langhian): Germany (Anderson, 1964; Wienrich, 2007), Netherlands (A.W. Janssen, 1984). Upper Miocene: Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Bellardi, 1887; Davoli, 2000). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1887b; Pelosio, 1967; Chirli, 2002; Brunetti & Cresti, 2018); eastern Mediterranean (Büyükmeriç *et al.*, 2017). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellardi, 1887; Ruggieri *et al.*, 1959; Caprotti, 1974, 1976; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & dell'Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Della Bella & Tabanelli, 1995); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

***Vexillum cf. recticosta* (Bellardi, 1850)**

Plate 31, figs 1-2

- cf. *1850 *Mitra recticosta* Bellardi, p. 22, pl. 2, fig. 19.
 cf. 1887b *Uromitra recticostata* [sic] Bell. – Bellardi, p. 43.
 cf. 1968 *Vexillum* (*Uromitra*) *recticosta* (Bellardi, 1850) – Robba, p. 557, pl. 42, fig. 9.
 cf. 1981 *Uromitra recticosta* Bellardi, 1850 – Ferrero Mortara *et al.*, p. 166, pl. 52, fig. 15.
- non 1852 *Mitra recticosta* Bell – Hörnes, p. 106, pl. 10, fig. 31 [= *Pusia schafferi* (Meznerics, 1933)].
 non 1880 *Mitra* (*Costellaria*) *recticosta* Bell. – Hoernes & Auinger, p. 85, pl. 10, figs 5-8 [= *Pusia pseudo-recticosta* (Boettger, 1906)].

Material and dimensions – Maximum height 33.1 mm, width 11.0 mm. **CO:** NHMW 2024/0042/0081-0082 (2). **VC:** NHMW 2024/0042/0101 (4).

Description – Shell large, solid, moderately broad fusiform, with moderately high conical spire; early spire weakly gradate; apical angle 36-39°. Protoconch not preserved. Teleoconch of up to ten low subcylindrical whorls, separated by deeply impressed, very narrowly canaliculate suture. Axial sculpture of about 12 straight, narrow, widely spaced orthocline ribs, slightly produced apically making suture weakly coronate. Extremely faint spiral grooves cover entire surface, abraded in most specimens. Last whorl relatively short, 50-56% of total height, weakly convex, moderately constricted at base; fasciole weakly rounded, weakly delimited from base by shallow neck. Aperture elongate, moderately narrow; anal canal marked by faint narrow groove; outer lip thin, with 11-13 lirae starting some distance behind peristome, extending deep within aperture. Columella relatively short, bearing four folds, increasingly oblique and weakening abapically. Columellar callus indistinct in abapical half, poorly delimited, slightly thickened in parietal region. Siphonal canal moderately short, almost straight, slightly bent to left, with wide, shallow siphonal notch.

Discussion – The Estepona specimen is closely similar to *V. recticosta* in sculpture, having low spire whorls and a short last whorl. However, it is twice the size of *V. recticosta* (13.0-19.0 mm; *fide* Bellardi, 1887b; Robba, 1968) and the spire is higher. It may represent a gerontic specimen, but with the material available we are unsure, and leave it in open nomenclature.

Vexillum soror (Bellardi, 1877), also from the Lower Pliocene of Italy differs from *V. recticosta* in being slenderer with more numerous axial ribs. *Vexillum crebricostatum* from the Upper Miocene of Italy is broad like *V. recticosta* but has more numerous axial ribs like *V. soror*. *Vexillum nitidum* from the Upper Miocene-Lower Pliocene of Italy is larger shelled (25 mm vs. 19 mm; *fide* Bellardi, 1887b), the spire is regularly conical, not gradate, the whorls slightly more convex, the axial ribs fewer and weaker, and the last whorl is less constricted at the base.

Another species that must be compared is *Vexillum bifarium* (Bellardi, 1887). This was placed together with *V. pyramidellum* (Brocchi, 1814) in ‘12^a Serie’ that, according to Bellardi, had no characters that clearly separated these species from species in his ‘Series 11’, but included species with a spire higher than the last whorl, more or less constricted anteriorly, and the surface entirely covered in irregular axial ribs; the early teleoconch whorls are ribbed in all species in ‘11^a Serie’ except for *V. eobenus* (Bellardi, 1887). If *V. bifarium* is indeed a valid species and not just an extreme form of *V. pyramidellum*, the syntype illustrated by Ferrero Mortara *et al.* (1981, pl. 52, fig. 19) differs in having more numerous ribs. Specimens illustrated by Chirli (2002, pl. 52, figs 4-8) are problematic. Some show close-set ribs (pl. 52, figs 4-6), whilst one specimen has lower, broader, sub-obsolete ribs, similar to one specimen from the Rio del Padron locality in Estepona that we consider an extreme form of *V. pyramidellum*. These *Vexillum* species in Bellardi’s ‘11^a e 12^a Serie’ require revision based on Italian specimens.

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

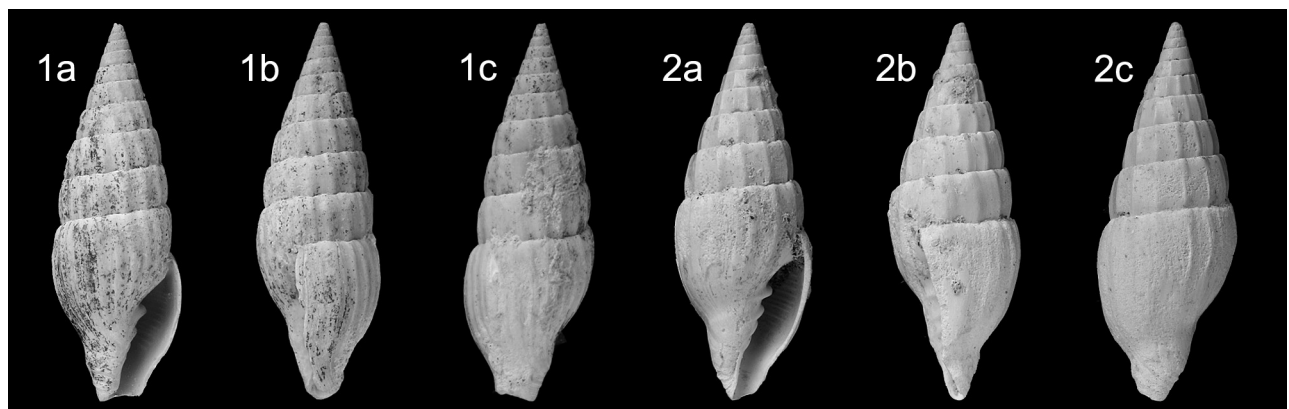


Plate 31. *Vexillum cf. recticosta* (Bellardi, 1850); 1. NHMW 2024/0042/0081, height 33.1 mm, width 11.0 mm; 2. NHMW 2024/0042/0082, height 32.3 mm, width 11.5 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion

In the superfamily Mitroidea only Mitridae Swainson, 1831 are represented in the Estepona assemblages, and in the Turbinelloidea only Costellariidae MacDonald, 1860.

Mitridae

In this superfamily 20 species are recorded representing four genera, of which one species is described as new: *Episcomitra gonniae* nov. sp., and two are left in open nomenclature. This is a vast increase from the 3-4 species previously known from the Iberian Pliocene. Moreover, this is likely to be an underestimate in diversity bearing in mind that a large amount of material was too poorly preserved to identify to species level. It is, nevertheless, clear that the Pliocene Mediterranean has a rich and diversified mitrid assemblage that did not survive the cooling events during the Pliocene. Loss of diversity seems to have been more gradual than in other more thermophilic groups, as most of the species are present in both the Early and Late Pliocene, and six species survived until the end of the Early Pleistocene (see Figure 1). None of the Pliocene mitrid species survive today in the Mediterranean where only three species occur (Giannuzzi-Savelli *et al.*, 2003).

Costellariidae

The Costellariidae are represented by ten species representing five genera, of which one species is described as new: *Ebenomitra ellenae* nov. sp., and one is left in open nomenclature. This group is possibly less thermophilic, two species survive in the Mediterranean today, although all seem to represent the genus *Ebenomitra* (of species figured in Giannuzzi-Savelli *et al.*, 2003). *Bellardithala*, *Fedovsovia*, *Uromitra* and *Vexillum* do not occur in the Mediterranean today (Figure 1).

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References

- Adams, A. 1853. Description of fifty-two new species of the genus *Mitra*, from the Cumington collection. *Proceedings of the Zoological Society of London* (1851) 19: 132-141.
- Adams, C.B. 1845. Specierum novarum conchyliorum, in Jamaica repertorium, synopsis. *Proceedings of the Boston Society of Natural History* 2: 1-17.
- Adams, H. & Adams, A. 1853-1858. *The Genera of Recent Mollusca; Arranged According to Their Organization*. Parts 1 & 2. John van Voorst, London, 484 & 660 pp. [published in parts, Part 1: pp. 1-256, pls 1-32 (1853) + 257-484 (1854), Part 2: pp. 1-284, pls 33-96 (1855) + 285-412, pls 97-112 (1856) + 413-540, pls 113-128 (1857) + 541-660, pls 129-138 (1858).
- Anderson, H.J. 1964. Die miocäne Reinbek-Stufe in Nord- und Westdeutschland und ihre Mollusken-Fauna. *Fortschritte in der Geologie von Rheinland und Westfalen* 14: 31-368.
- Andrzejowski, A. 1830. Notice sur quelques coquilles fossiles de Volhynie, Podolie etc. *Bulletin de la Société Impériale des Naturalistes de Moscou* 2: 90-104.
- Atanacković, M.A. 1985. Mekusci Morskog Miocena Bosne. *Geologija Bosne I Hercegovine, Fosilna Fauna I Flora* 1: 1-308.
- Azuma, M. 1965. On the radulae of the family Vexillidae. *Venus* 24(1): 53-57.
- Bałuk, W. 1997. Middle Miocene (Badenian) gastropods from Korytnica, Poland, 3. *Acta Geologica Polonica* 47: 1-75.
- Bellardi, L. 1850. Monografia delle mitre fossili del Piemonte. *Memorie della Reale Accademia delle Scienze di Torino* 2(11): 357-390.
- Bellardi, L. 1887a. I molluschi dei terreni terziarii del Piemonte e della Liguria, 5(a). Mitridae. *Memorie della Reale Accademia delle Scienze di Torino* (2)38 (1888): 79-166 (reprint 85 pp.) (January 15, 1887).
- Bellardi, L. 1887b. I molluschi dei terreni terziarii del Piemonte e della Liguria, 5(b). Mitridae (continuazione). *Memorie della Reale Accademia delle Scienze di Torino* (2)38 (1888): 257-327 (reprint 72 pp.) (June 1, 1887).
- Bellardi, L. 1888. I molluschi dei terreni terziarii del Piemonte e della Liguria, 5(c). Mitridae (fine). *Memorie della Reale Accademia delle Scienze di Torino* (2)39 (1889): 145-194 (reprint 52 pp.) (September 20, 1888).
- Beyrich, E. 1853-1856. Die Conchylien des norddeutschen Tertiärgeländes. *Zeitschrift der Deutschen Geologischen Gesellschaft* 5: 273-358, pls. 4-8 (1853); 6: 408-500, 726-781, pls. 9-18 (1854); 8: 21-88, 553-588, pls. 16-28 (1856).
- Boettger, O. 1906-1907. Zur Kenntnis der Fauna der mittelmiozänen Schichten von Kőstěj im Krassó-Szörényer Komitat. Gasteropoden und Anneliden, 3. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt* 54/55: i-viii, 1-99 (1906); 101-244 (1907).
- Bohn-Havas, M. 1973. Tortonische Molluskenfauna des östlichen Mecsek-Gebirges. *Magyar Állami Földtani Intézet évkönyve* 53: 947-1161.
- Brocchi, G. 1814. *Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente*, 1-2. Milano (Stamperia Reale): 1-240 (1); 241-712 (2), 16 pls.
- Brunetti, M.M. 2018. Two new records of fossil gastropods from the Italian upper Pleistocene. *Biodiversity Journal* 9(4): 315-318.

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).

Species	Geographical distribution					Stratigraphical distribution								
						Miocene			Pliocene		Pleistocene		Hol	
	Lower	Middle	Upper	Lower	Upper	Lower	Upper							
Mitroidea Swainson, 1831	1	2	3	4	5/6									
Cancilla alligata (Defrance in de Blainville, 1825)		●	●	●	A M					■	■			
Cancilla bonellii (Bellardi, 1850)				●	M				■	■	■	■		
Cancilla dignota (Bellardi, 1887)				●	M					■	■			
Cancilla planicostata (Bellardi, 1887)				●	M		■	■	■	■	■			
Cancilla scrobiculata (Brocchi, 1814)			●	●	A M				■	■				
Cancilla aff. sismondai (Michelotti, 1847)				●	M					■				
Cancilla laevigatobrevis (Sacco, 1904)				●	M					■	■			
Episcomitra addita (Bellardi, 1887)				●	M					■	■			
Episcomitra astensis (Bellardi, 1850)				●	M					■	■	■	■	
Episcomitra atava (Bellardi, 1887)				●	M					■	■	■	■	
Episcomitra gonnieae nov. sp.				●	M					■	■			
Episcomitra obesa (Foresti, 1868)				●	M					■	■	■	■	
Episcomitra pliocenica (Bellardi, 1887)				●	M						■			
Episcomitra pliotenuis nov. nom.				●	M					■	■			
Episcomitra subestriata (Bellardi, 1887)				●	M					■	■	■	■	
Episcomitra turricula (de Cristofori & Jan, 1832)		●		●	M					■	■	■	■	
Episcomitra sp.				●	M						■			
Fraudiziba concava (Bellardi, 1887)				●	M					■	■			
Isara aperta (Bellardi, 1850)		●		●	M						■			
Isara ulivii (Chirli, 2002)				●	M					■	■	■	■	
Turbinelloidea Swainson, 1835														
Bellardithala obsoleta (Brocchi, 1814)			●	●	A M		■	■		■	■			
Ebenomitra ebenus (Lamarck, 1811)	●	●	●	●	A M					■	■	■	■	
Ebenomitra ellenae nov. sp.				●	M						■			
Ebenomitra frumentum (Bellardi, 1887)				●	M					■	■	■	■	
Ebenomitra savignyi (Payraudeau, 1826)			●	●	A M						■	■	■	■
Fedosovia multigranosa (Vera-Peláez, 2002)				●	M						■	■	■	
Uromitra cupressina (Brocchi, 1814)				●	M		■	■	■	■	■			
Vexillum nitidum (Bellardi, 1887)				●	M			■	■	■	■			
Vexillum pyramidellum (Brocchi, 1814)	●			●	A M	■	■	■				■	■	
Vexillum cf. recticosta (Bellardi, 1850)				●	M						■			

- Brunetti, M.M. & Cresti, M. 2018. *I fossili di Orciano Pisano* [The fossils of Orciano Pisano]. Atlante iconografico [An Iconographic Atlas]: 1-232. Edizioni Danaus, Palermo.
- Brunetti, M.M. & Della Bella, G. 2014. La famiglia Buccinidae Rafinesque, 1815 nel Plio-Pleistocene italiano: i genere *Aplus* De Gregorio, 1884, *Engina* Gray, 1839 e *Gemophos* Olsson & Harbison, 1953 (Gastropoda). *Bollettino Malacologico* 40: 11-32.
- Brunetti, M.M. & Della Bella, G. 2016. Revisioni di alcuni generi della famiglia Buccinidae Rafinesque, 1815 nel Plio-Pleistocene del Bacino Mediterraneo, con descrizione di tre nuove specie. *Bollettino Malacologico* 52: 3-37.
- Brunetti, M.M., Della Bella, G., Forli, M. & Vecchi, G. 2008. La famiglia Cancellariidae Gray, J.E., 1853 nel Pliocene italiano: note sui generi *Scalptia* Jousseume, 1887, *Tribia* Jousseume, 1887, *Contortia* Sacco, 1894, *Trigonostoma* Blainville, 1827 e *Aneurystoma* Cossmann, 1899 (Gastropoda), con descrizione di una nuova specie. *Bollettino Malacologico* 44 (5-8): 51-69.
- Brunetti, M.M., Della Bella G., Forli, M. & Vecchi, G. 2009. La famiglia Cancellariidae Forbes & Hanley, 1851 nel Plio-Pleistocene italiano: i generi *Bonellitia*, *Pseudobabylonella* n. gen., *Admete* e *Cancellicula* Tabanelli, 2008, con descrizione di tre nuove specie. *Bollettino Malacologico* 45 (2): 55-81.
- Brunetti, M.M., Della Bella, G., Forli, M. & Vecchi, G. 2011. La famiglia Cancellariidae Forbes & Hanley, 1851 nel Plio-Pleistocene italiano: note sui generi *Bivetiella*, *Sveltia*, *Calcarata*, *Solatia*, *Trigonostoma* e *Brocchinia* (Gastropoda). *Bollettino Malacologico* 47 (2): 85-130.
- Büyükeriç, Y., Tekin, E., Herece, E., Sözeri, K., Akça, N. & Varol, B. 2017. Early Pliocene molluscs from the easternmost Mediterranean region (SE Turkey): biostratigraphic, ecostratigraphic, and palaeobiogeographic implications. *Turkish Journal of Earth Sciences* 26: 1-25.
- Caprotti, E. 1974. Molluschi del Tabianiano (Pliocene inferiore) della Val d'Arda. Loro connessioni temporali e spaziali. *Conchiglie* 10: 1-47.
- Caprotti, E. 1976. Malacofauna dello stratotipo piacentino (Pliocene de Castell'Arquato). *Conchiglie* 12: 1-56.
- Caprotti, E. & Vescovi, M. 1973. Neogastropoda ed Euthyneura dello stratotipo piacentino (Castell'Arquato, Piacenza). *Natura, Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 64: 156-193.
- Casey, T.L. 1904. Notes on the Pleurotomidae with descriptions of some new genera and species. *Transactions of the Academy of Science of St. Louis* 14: 123-170.
- Cavallo, O. & Repetto, G. 1992. Conchiglie fossili del Roero. Atlante iconografico. *Associazione Naturalistica Piemontese Memorie (Associazione Amici del Museo 'Federico Eusebio')* 2: 1-251.
- Caze, B., Saint Martin, J.-P., Merle, D. & Saint Martin, S. 2010. Intérêt des motifs colourés résiduels des coquilles de mollusques pour la valorisation des sites paléontologiques et des collections: l'exemple du Badénien de Roumanie. In: Saint Martin, J.-P., Saint Martin, S., Oaic, G., Seghedi, A. & Grigorescu, D. (Eds.), *Le patrimoine paléontologique*, GeoEco Mar, Bucarest, pp. 27-38.
- Cernohorsky, W.O. 1970. Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). *Bulletin of the Auckland Museum* 8: 1-190.
- Cernohorsky, W.O. 1976. The Mitridae of the World. Part I. The subfamily Mitrinae. *Indo-Pacific Mollusca* 3(17): 273-528.
- Cernohorsky, W.O. 1991. The Mitridae of the World. Part 2. The Subfamily Mitrinae concluded and Subfamilies Imbricariinae and Cyndromitridinae. *Monographs of Marine Mollusca* 4: 1-164.
- Cerulli-Irelli, S. 1911. Fauna malacologica mariana, 5. Cancellariidae, Marginellidae, Mitridae, Fusidae, Chrysodomidae, Buccinidae, Nassidae, Columbelloidae, Muricidae, Tritonidae, Cassididae, Cypraeidae, Chenopodidae. *Paleontographia Italica* 17: 280-325.
- Chirli, C. 1988. *Malacofauna pliocenica di Poggibonsi, Cava delle Piaggiole*. Poggibonsi (Lalli Ed.): 1-89.
- Chirli, C. 2002. *Malacofauna Pliocenica Toscana, 3. Superfamiglia Muricoidea-Cancellarioidea*. Firenze (C. Chirli): 92 pp., 37 pls.
- Chirli, C. & Linse, U. 2011. *The Pleistocene marine Gastropods of Rhodes Island (Greece)*. Grafiche PDB, Tavarnelle V.P. Firenze: 262 pp, 90 pls.
- Chirli, C. & Richard, C. 2008. *Les mollusques plaisanciens de la Côte d'Azur*. Tavarnelle (C. Chirli): 128 pp.
- Cocconi, G. 1873. Enumerazione sistematica dei molluschi miocenici e pliocenici delle provincie di Parma e di Piacenza. *Memorie della Accademia delle Scienze dell'Instuto di Bologna* ser. 3, 3: 409-776, 11 pls.
- Coan, E. 1966. Nomenclatural units in the gastropod family Mitridae. *Veliger* 9, 127-137.
- Costa, O.G. 1830 [1829]. *Catalogo sistematico e ragionato de' testacei delle Due Sicilie*. Tipografia della Minerva, Napoli, pp. 1-8, i-cxxxii, pl. 1-3.
- Cossmann, M. 1899. *Essais de paléoconchologie comparée*, 3. Paris (Cossmann): 201 pp., 8 pls.
- Cristofori, J. de & Jan, G. 1832. *Catalogus in IV sectiones divisus rerum naturalium in Museo Exstantium Josephi de Christofori et Georgio Jan Plurinum Acad. Scient. et Societ. Nat. Cur. Sodalium ecc. Sectio II. Pars I. Conchylia fossilia ex formatione telluris tertiaria in collection nostra exstantia*. Parma (Carmignani): 16 pp.
- Csepregy-Meznerics, I. 1954. A Keletcsérháti Helvétii és Tortonai fauna. *Annales Instituti Geologici Publici Hungarici* 41: 1-185.
- Csepregy-Meznerics, I. 1972. La faune tortonienne-inferieure des gisements tufiques de la Montagne de Bükk: Gastropodes, 2. *Az Egri Múzeum Évkönyve (Annales Musei Agriensis)* 8-9 (1970-1971): 26-46.
- Cuerda Barceló, J. 1987. *Molluscos marinos y salobres del Pleistoceno Balear*. Palma de Mallorca (Publ. Caja de Baleares 'Sa Nostra'): 421 pp.
- Davoli, F. 2000. I gasteropodi mitriformi del Tortoniano di Montegibbio (Subappennino modenese). *Bollettino della Società Paleontologica Italiana* 39: 165-215.
- Defrance, M. 1825. Mitre, *Mitra*. In: Blainville, M. de (Ed.), *Mollusques, Vers et Zoophytes*. In: Cuvier, F. (Ed.), *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des differens etres de la nature, consideres soit en eux-memes. d'apres l'etat actuel de nos connais sciences, soit relativement a l'utilite qu'en peuvent retirer la medicine, l'agriculture, le commerce et les arts. Suive d'une biographie des plus celebres naturalistes*. 31. Levrault, Le Normant, Paris, Strasbourg: pp. 480-494.

- Della Bella, G. & Tabanelli, C. 1995. Qualche considerazione su *Mitra ebenus* Lk., *Voluta plicatula* Br., *Voluta pyramida* Br. (Mollusca, Gastropoda, Costellariidae). *Bollettino Malacologico* 30: 293-296.
- Eremija, M. 1959. Paläontologische Neuigkeiten aus Neogenschichten südlich vor der Stadt Glin (Croatien). *Annales Géologiques de la Péninsule Balkanique* 26: 185-193.
- Erünał-Erentöz, L. 1958. Mollusques du Néogène des Bassins de Karaman, Adana et Hatay (Turquie). Première these, 1ère partie. *Publications de l'Institut d'Étude et de Recherches Minières de Turquie* (C)4: 1-232.
- Fedosov, A.E., Puillandre, N., Herrmann, M., Dgebuadze, P. & Bouchet, P. 2017. Phylogeny, systematics, and evolution of the family Costellariidae (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society* 179: 541-626.
- Fedosov, A., Puillandre, N., Herrmann, M., Kantor, Yu., Oliverio, M., Dgebuadze, P., Modica, M.V. & Bouchet, P. 2018. The collapse of *Mitra*: molecular systematics and morphology of the Mitridae (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society* 183: 253-337.
- Fekih, M. 1975. Paleocologie du Pliocène marin au nord de la Tunisie. *Annales des Mines et de la Géologie* 27: 1-195.
- Ferrero Mortara, E., Montefameglio, L., Pavia, G. & Tampieri, R. 1981. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco. Parte I. *Museo Regionale di Scienze Naturali* Catalogo 6: 1-327.
- Florei, N. 1961. Contribuții la cunoașterea faunei miocene de la Zorlentul-Mare (Banat). *Studii Si Cercetari de Geologie* 6: 667-698.
- Fontannes, F. 1879-1880. *Les invertébrés du bassin tertiaire du Sud-Est de la France. Les mollusques pliocènes de la Vallée du Rhône et du Roussillon. I. Gastéropodes des formations marines et saumâtres*. Paris (Georg, Lyon & F. Savy): viii + 276 pp., 12 pls (pp. 1-76 published in 1879, remainder in 1880).
- Forbes, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology. *Reports of the British Association for the Advancement of Science for 1843*: 130-193.
- Forbes, E. & Hanley, S.C.T. 1848-1853. *A history of British Mollusca and their shells*. London, van Voorst. 4 vols., 2064 pp., 203 pls. Vol. 1: i-xxxx [May 1, 1853], 1-478 [Jan.-Dec. 1848], 479-486 [May 1, 1853]; Vol. 2: i-viii [May 1, 1853], 1-480 [Jan.-Dec. 1849], 481-557 [Jan.-Feb. 1850]; Vol. 3: i-x [May 1, 1853], 1-320 [Mar.-Dec. 1850], 321-616 [Jan.-Sep. 1851]; Vol. 4: i-vi [May 1, 1853], 1-280 [Jan.-Dec. 1852], 281-302 [May 1, 1853]; pl. A-W, AA-ZZ, AAA-ZZZ, pl. 1-114F [dates uncertain].
- Foresti, L. 1868. Catalogo dei molluschi fossili pliocenici delle colline bolognesi. *Memorie della Accademia delle Scienze dell'Istituto di Bologna* (2)7: 99 pp.
- Forli, M., Dell' Angelo, B. & Taviani, M. 1999. Molluschi del Pliocene inferiore toscano: la sezione Montenero (Grosseto). *Bollettino Malacologico* 34: 109-122.
- Friedberg, W. 1911-28. Mięczaki miocenne ziem Polskich (Mollusca Miocaenica Poloniae), 1. Ślimaki i łódkonogi, 1. Gastropoda et Scaphopoda. Lwow (Muzeum Imienia Dzieduszyckich): 631 pp. (issued in parts: 1, 1-112, pls 1-5 (1911); 2, 113-240, pls 6-14 (1912); 3, 241-360, pls 15-20 (1914); 4, 361-440, pls 21-26 (1923); 5, 441-631, pls 27-38 (1928). Reprinted 1951-55 with slightly different title and pagination, Warszawa (Wydawnictwa Geologiczne).
- Giannuzzi Savelli, R. 1982. La Superfamiglia Mitroidea nel Mediterraneo. *Lavori S.I.M.* 21: 67-116.
- Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A. & Ebreo, C. 2003. *Atlante delle conchiglie marine del Mediterraneo, vol. 4 (Neogastropoda: Muricoidea)*. Evolver, Roma. 298 pp.
- Giannuzzi-Savelli, R. & Reina, M. 1983. *Thala obsoleta* (Brocchi, 1814) nel Pliocene di Altavilla ed alcune considerazioni evolutive e paleoecologiche sul genere. *Bollettino Malacologico* 19: 227-236.
- Glibert, M. 1952. Gastropodes du Miocène moyen du Bassin de la Loire, 2. *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* 2(46): 241-450.
- Gmelin, J.F. 1791. Vermes. In: Gmelin J.F. (Ed.) *Caroli a Linnaei Systema Naturae per Regna Tria Naturae*, Ed. 13. Tome 1(6). G.E. Beer, Lipsiae [Leipzig]. pp. 3021-3910. *Systema Naturae. Linnaeus (ed.). Ed. 13. 1: pars. 6*.
- González Delgado, J.A. 1992. Estudio sistemático de los gasterópodos del Plioceno de Huelva (SW de España), 5. Neogastropoda (Volutacea, Conacea). *Studia Geologica Salamanticensia* 28: 7-69.
- Guerra-Merchán, A., Serrano, A. & Ramallo, D., 2002. Evolución sedimentaria y paleogeográfica pliocena del borde septentrional de la cuenca de Alborán en el área de Estepona (provincia de Málaga, Cordillera Bética). *Pliocénica* 2: 31-43.
- Harmer, F.W. 1914-1918. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's monograph of the Crag Mollusca, 1. *Monographs of the Palaeontographical Society* 1(1): 1-200 (1914); 1(2): 201-302 (1915), 1(3): 303-461 (1918), 1(4): 463-483 (1919), 2(1): 485-652 (1920), 2(2): 653-704 (1921), 2(3): 705-856 (1923), 2(4): 857-900 (1925).
- Harris, G.F. 1897. *Catalogue of the Tertiary Mollusca in the department of geology, British Museum (Natural History), 1. The Australasian tertiary Mollusca*. London [British Museum (Natural History)]: 407 pp.
- Harzhauser, M. & Landau, B. 2021a. The Mitridae (Gastropoda: Neogastropoda) of the Miocene Paratethys Sea. *Zootaxa* 4983(1): 1-72.
- Harzhauser, M. & Landau, B. 2021b. An overlooked diversity – the Costellariidae (Gastropoda: Neogastropoda) of the Miocene Paratethys Sea. *Zootaxa* 4982(1): 1-70.
- Hernández, J.M., Rolán, E., Swinnen, F., Gómez, R. & Pérez, J.M. 2011. *Moluscos y conchas marinas de Canarias*. ConchBooks, Hackenheim. 716 pp.
- Herrmann, M., Stossier, G. & Salisbury, R.A. 2014. A new subgenus including three new species of the genus *Vexillum* (Gastropoda: Costellariidae) from the central Indo-Pacific with remarks on *Vexillum (Pusia) semicostatum* (Anton, 1838). *Contributions to Natural History* 24: 1-55.
- Herrmannsen, A.N. 1846. *Indicis Generum Malacozoorum primordia*. Fischer, Cassel, 1, pp. 155.
- Hörnes, M. 1851-1870. Die fossilen Mollusken des Tertiär Beckens von Wien. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 3-4: 1-42, pl. 1-5 (1851), 43-208, pl. 6-20 (1852), 209-296, pl. 21-32 (1853), 297-382, pl. 33-40 (1854), 383-460, pl. 41-45 (1855), 461-736, pl. 46-52 (1856) (3); 1-479, pls 1-85 (1870) (4).

- Hoernes, R. & Auinger, M. 1879-91. Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 12: 1-382, 50 pls. Published in parts: 1-52, pls 1-6 (1879); 53-112, pls 7-12 (1880); 113-152, pls 13-16 (1882); 153-192, pls 17-22 (1884); 193-232, pls 23-28 (1885); 233-282, pls 29-36 (1890); 283-330, pls 37-42 (1891); 331-382, pls 43-50 (1891).
- Iredale, T. 1916. On some new and old molluscan names. *Proceedings of the Malacological Society of London* 12(1): 27-37.
- Janssen, A.W. 1984. *Mollusken uit het Mioceen van Winterswijk-Miste. Een inventarisatie, met beschrijvingen en afbeeldingen van alle aangetroffen soorten*. Amsterdam (Koninklijke Nederlandse Natuurhistorische Vereniging, Nederlandse Geologische Vereniging & Rijkmuseum van Geologie en Mineralogie): 451 pp.
- Janssen, A.W. 2004. Holoplanktonic molluscan assemblages (Gastropoda, Heteropoda, Thecosomata) from the Pliocene of Estepona (Spain, Malaga). *Palaeontos* 5: 103-131.
- Kojumdzieva, E.M. & Strachimirov, B. 1960. *Les fossiles de Bulgarie, 7. Tortonien*. Académie des Sciences de Bulgarie, Sofia: 317 pp.
- Kuroda, T. 1958-1959. Descriptions of new species of marine shells from Japan. *Venus* 20(4): 317-335 [Text, issued 30 Nov. 1959], pl. 20-12 [issued 1958].
- Lamarck, J.B.P.A. de M. 1811 ["1810"]. [Suite de la détermination des espèces de Mollusques Testacés.] Genre *Volute* et *Mitre*. *Annales du Muséum d'Histoire Naturelle* 17: 54-80, 145-222 [published 1811].
- Landau, B.M. & Harzhauser, M. 2022. The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 15: Borsoniidae, Clathurellidae, Mitromorphidae, Pseudomelatomidae (Gastropoda, Conoidea). *Cainozoic Research* 22: 103-156.
- Landau, B.M., Harzhauser, M., İslamoğlu, Y. & Silva, C.M. da 2013. Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research* 11-13: 3-584.
- Landau, B.M., Marquet, R. & Grigis, M. 2003. The early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 1: Vetigastropoda. *Palaeontos* 3: 1-87, pls 1-19.
- Landau, B.M. & Micali, P. 2021. The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 13: Murchisonelloidea and Pyramidelloidea. *Cainozoic Research* 21(2): 159-351.
- Landau, B., Silva, C.M. da & Mayoral, E. 2011. The lower Pliocene gastropods of the Huelva Sands Formation, Guadalquivir Basin, southwestern Spain. *Palaeofocus* 4: 1-90.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 1. Editio decima, reformata*. Holmiae (Laurentii Salvii): 824 pp. [facsimile reprint, British Museum (Natural History), 1956].
- Locard, A. 1886. *Prodrome de malacologie française. Catalogue général des mollusques vivants de France. Mollusques marins*. Lyon: H. Georg & Paris: Baillière. x + 778 pp.
- Locard, A. 1890. Notices conchyliologiques. X. Les Mitres des côtes de France. *L'Echange* 6(62): 109-110.
- Locard, A. 1891. Les coquilles marines des côtes de France. *Annales de la Société Linnéenne de Lyon* 37: 1-385 [Published 31 October 1891; also published by Baillière as a book in 1892].
- MacDonald, J.D. 1860. Further observations on the metamorphosis of Gastropoda, and the affinities of certain genera, with an attempted distribution of the principal families of the order. *Transactions of the Linnean Society of London* 23(1): 69-81.
- Malatesta, A. 1960. Malacofauna pleistocenica di Grammichele (Sicilia). *Memorie per Servire alla Carta Geologica d'Italia* 12: 1-196.
- Malatesta, A. 1974. Malacofauna pliocenica Umbra. *Memorie per Servire alla Carta Geologica d'Italia* 13: 1-498.
- Manni, R. 2005. The non-isocrinid crinoids of the Michelotti Collection. *Bollettino della Società Paleontologica Italiana* 44: 211-218.
- Maravigna, C. 1853. Descrizione di alcune nuove o poco conosciute specie di conchiglie siciliane. *Atti dell'Accademia Gioenia di Scienze Naturali* (2)8: 121-140.
- Marquet, R. 1997. Pliocene gastropod faunas from Kallo (Oost-Vlaanderen, Belgium), 3-4. Caenogastropoda: Aporrhaidae to Muricidae (3); Buccinidae to Helicidae (4). *Contributions to Tertiary and Quaternary Geology* 34: 69-149.
- Marquet, R. 1998. *De Pliocene gastropodenfauna van Kallo (Oost-Vlaanderen, België)*. Antwerpen (Belgische Vereniging voor Paleontologie v.z.w.): 1-246.
- Marryat, F. 1818. Descriptions of two new shells. *Transactions of the Linnean Society of London* 12: 336-339.
- Martinell, J. 1979 [1978]. Volutacea del plioceno del Empordà (Girona). *Acta Geológica Hispánica* 13(2): 61-69.
- Mastrorilli, V. 1969. I molluschi del Pliocene ligure nella collezione dell'Istituto di Geologia dell'Università di Genova, e i microfossili delle formazioni che li ricettavano, 1. I reperti provenienti dalle marne di Genova. *Atti dell'Istituto di Geologia dell'Università di Genova* 7: 85-228.
- Mayer, K. 1864. *Die Tertiär-Fauna der Azoren und Madeiren. Systematisches Verzeichniss der fossilen Reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten*. Published by the author, Zürich: vi + 107 pp.
- Mayer-Eymar, K. 1898. Systematisches Verzeichnis der Fauna des unteren Saharianum (marines Quartaer) der Umgegend von Kairo, nebst Beschreibung der neuen Arten. *Palaeontographica* 30: 61-90.
- Meek, F.B. 1873. Descriptions of new species of fossils. *Sixth Annual Report of the U.S. Geological and Geographical Survey of the Territories embracing portions of Montana, Idaho, Wyoming, and Utah; being a report of progress of the explorations for the year 1872, 1873*: 479-518.
- Meznerics, I. 1933. Die Minutien der tortonischen Ablagerungen von Steinabrunn in Niederösterreich. *Annalen des Naturhistorischen Museums Wien* 46: 319-359.
- Michelotti, G. 1847. Description des fossiles des terrains miocènes de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem* (2)3: 408 pp. Also as: Ouvrage publié par la société Hollandaise des Sciences, et accompagné d'un atlas de 17 planches. Leiden (A. Arns & Compie): 408 pp.
- Monegatti, P. & Raffi, S. 2001. Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. *Palaeogeography Palaeoclimatology Palaeoecology* 165: 171-193.

- Monterosato, T. di 1917. Molluschi delle coste cirenaiche raccolti dall'Ing. Camillo Crema. *Memorie Reale Comitato Talassografico Italiano* 107: 1-14.
- Nardo, G.D. 1847. *Sinonimia Moderna delle Specie Registrate nell'Opera Intitolata: Descrizione de' Crostacei, de' Testacei e de' Pesci che Abitano le Lagune e Golfo Veneto Rappresentati in Figure, a Chiaro-scuro ed a Colori dall'Abate Stefano Chiareghini* Ven. Clodiense. Antonelli: Venezia. xi + 128 pp.
- Nicorici, E. & Sagatovici, A. 1973. Studiul faunei badenian – superioara de la Minisul de Sus (bazinul Zarand). *Anuarul Institutului de Geologie a României* 40: 111-194.
- Nordsieck, F. 1982. *Die Europäischen Meeres-Gehäuseschnecken (Prosobranchia). Vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer. 2., Völlig Neubearbeitete und Erweiterte Auflage.* Gustav Fischer Verlag, Stuttgart, xii + 539 pp.
- Orbigny, A.D. d'. 1836-1842. *Mollusques, Echinodermes, Foraminifères et Polypiers recueillis aux Iles Canaries par MM. Webb et Berthelot.* In: Barker-Webb, P. & Berthelot, S. (eds) *Histoire naturelle des Iles Canaries*, volume 2(2): 117 pp., pls 1-7, 7B. pp. 1-24 [Aug. 1839], 25-48 [Sept. 1839], 49-72 [Oct-1839], 73-104 [Jan. 1840], 105-136 [Mar. 1840], 137-143 [Apr. 1840], 145-152 [Aug. 1842]; pl. 1 [Jul. 1836], 2 [Dec. 1836], 3 [May 1842], 4-5 [June 1840], 7 [May 1842], 6, 7B [Aug. 1842]. Paris: Bèthune.
- Palla, P. 1967. Gasteropodi pliocenici della Bassa Val d'Elsa (Toscana Occidentale). *Rivista Italiana di Paleontologia e Stratigrafia* 73: 931-1020.
- Pallary, P. 1900. Coquilles marines du littoral du département d'Oran. *Journal de Conchyliologie* 48(3): 211-422.
- Pallary, P. 1903. Addition à la faune conchyliologique de la Méditerranée. *Annales du Musée d'Histoire naturelle de Marseille, Zoologie* 8: 4-16, plate 1. Marseille.
- Pallary, P. 1912. Sur la faune de l'ancienne lagune de Tunis. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 4(9): 215-228, 1 unnumbered plate.
- Pavia, G. 1976. I molluschi del Pliocene inferiore di Monteu Roero (Alba, Italia NW). *Bollettino della Società Paleontologica Italiana* 14: 99-175.
- Pavlovsky, M. 1957. Prilog Poznavanju Miocenskih Gastropoda Zapresic-Brijega Kraj Samobora. *Geološki vjesnik* 10: 51-55.
- Payraudeau, B.C. 1826. *Catalogue descriptif et méthodique des annélides et des mollusques de l'île de Corse; avec huit planches représentant quatre-vingt-huit espèces, dont soixante-huit nouvelles.* Imprimerie de J. Tastu, Paris, vii + 218 pp., pls. 1-8.
- Pelosio, G. 1967. La malacofauna dello stratotipo del Tabianiano (Pliocene inferiore) de Tabiano Bagni (Parma). *Bollettino della Società Paleontologica Italiana* 5: 101-183.
- Pereira da Costa, F.A. 1866-1867. Molluscos fosseis. Gasteropodes dos depositos terciarios de Portugal. *Memória Comissão Geologica de Portugal* 4(1): 1-116 (1866); (2): 117-252 (1867).
- Pinna, G. 1971. I tipi delle specie di Gasteropodi terziari istituite da Guisepe De Cristofori e Giorgio Jan nel 1832 conservate nelle collezioni del Museo Civico di Storia Naturale di Milano. *Atti della Società Italiana di Scienze Naturali Museo Civico di Storia Naturale di Milano* 112(4): 421-446.
- Pinna, G. & Spezia, L. 1978. Catalogo dei tipi del Museo Civico di Storia Naturale di Milano, 5. I tipi dei Gasteropodi fossili. *Atti della Società Italiana di Scienze naturali Museo Civico di Storia naturale* 119: 125-180.
- Popa, M.V., Duma, A. & Săplăcan, A. 2014. Badenian gastropods from the collections of the Mureș County Museum. *Analele Stiintifice ale Universitatii 'Al. I. Cuza' din Iasi Seria Geologie* 60: 5-30.
- Potiez, V.L.V. & Michaud, A.L.G. 1838. In: *Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai.* Tome premier. Baillière, Paris and London, pp. 1-36 + 1-560 + 1-56 (atlas), pls. 1-37.
- Raffi, S. & Monegatti, P. 1993. Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climatic-oceanographic and stratigraphic inferences. *Ciências da Terra* 12: 45-50.
- Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés.* Palermo (Rafinesque): 223 pp.
- Ravetta, E. 1933. Sulla variabilità della *Mitra scrobiculata* Br. *Rivista italiana di Paleontologia* 39: 125-128, 1 pl.
- Reeve, L.A. 1844-1845. Monograph of the genus *Mitra*. In: *Conchologia Iconica, or, illustrations of the shells of molluscular animals*, vol. 2, pl. 1-39 and unpaginated text. L. Reeve & Co., London. [stated dates: pl. 1-7, August 1844; pl. 8-15, September 1844; pl. 16-19, October 1844; pl. 20-23, November 1844; pl. 24-27, December 1844; pl. 28-29, January 1845; pl. 30 imprinted March 1844, presumably March 1845; pl. 31-39, March 1845].
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Tome quatrième.* Levraut, Paris, vii + 439 pp., pls 1-12.
- Robba, E. 1968. Molluschi del Tortoniano-tipo (Piemonte). *Rivista Italiana di Paleontologia e Stratigrafia* 74: 457-646.
- Röding, P.F. 1798. *Museum Boltenianum, sive catalogus cimeliorum e tribus regnis naturae quae olim colligera Joa. Fried. Bolten, M.D.p.d. per XL annos proto physicus Hamburgensis, 2. Conchylia sive Testacea univalvia, Bivalvia et multivalvia.* Hamburgi (Johan. Christi. Trappii): 199 pp.
- Rossi Ronchetti, C. 1955. I tipi della 'Conchiologia Fossile Sub apennina' di G. Brocchi, 2. Gastropodi, Scafopodi. *Rivista Italiana di Paleontologia e Stratigrafia* Memorie 5: 91-343.
- Ruggieri, G., Bruno, F. & Curti, G. 1959. La malacofauna pliocenica di Altavilla (Palermo), 1. *Atti dell'Accademia di Scienze Lettere e Arti di Palermo* 18: 1-97.
- Ruggieri, G. & Davoli, F. 1984. Malacofauna di Casa Nova Calise (Sogliano, Forlì). *Palaeontographia Italica* 73 (nuova serie 43): 41-85.
- Ruggieri, G. & Greco, A. 1965. Studi geologici e paleontologici su Capo Milazzo con particolare riguardo al Milazziano. *Geologica Romana* 4: 41-88.
- Ruiz Muñoz, F., González-Regalado Montero, M.L. & Redondo Sanz, J.L. 1997. *Guía de fósiles del sur de la provincia de Huelva.* Diputación Provincial de Huelva (Imprenta Diputación): 204 pp.
- Sacchetti, C., Landau, B. & Ávila, S.P. 2023. The Lower Pliocene marine gastropods of Santa Maria Island, Azores: Taxonomy and palaeobiogeographic implications. *Zootaxa* 5295(1): 1-150.

- Sacco, F. 1890. Catalogo paleontologico del bacino terziario del Piemonte. *Bollettino della Società Geologica Italiana* 9: 185-340.
- Sacco, F. 1904. *I Molluschi dei terreni terziari del Piemonte e della Liguria*, 30. Aggiunte e correzioni (con 1400 figure). *Considerazioni generali. Indice generale dell'opera*. Torino (C. Clausen: 203 + xxxvi pp., 31 pls.
- Scacchi, A. 1836. *Catalogus conchyliorum Regni Neapolitani*. Neapoli [Naples]: Typis Filiatre-Sebetii. 18 p., 1 pl.
- Schaffer, F. 1898. Der marine Tegel von Theben-Neudorf in Ungarn. *Jahrbuch der k.k. Geologischen Reichsanstalt* 47: 533-548.
- Schaffer, F.X. 1908. *Geologischer Führer für Exkursionen im inneralpinen Wienerbecken*, 2. Teil nebst einer Einführung in die Kenntnis seiner Faunen. Berlin (Verlag Gebrüder Borntraeger): 157 pp.
- Schröter, J.S. 1804. Neue Conchylienarten und Abänderungen, Anmerkungen und Berichtigungen nach dem Linnéischen System der XII. Ausgabe. (Fortsetzung). *Archiv für Zoologie und Zootomie* 4: 7-44.
- Schultz, O. 1998. *Tertiärfossilien Österreichs, Wirbellose, niedere Wirbeltiere und marine Säugetiere; schöne, interessante, häufige und wichtige Makrofossilien aus den Beständen des Naturhistorischen Museums Wien und Privatsammlungen; eine Bilddokumentation*. Wien (Golschneck-Verlag): 159 pp.
- Silva, C.M. da 2001. *Gastropodes pliocénicos marinhos de Portugal: sistemática, paleoecologia, paleobiologia, paleogeografia*. Dissertação de doutoramento. Faculdade de Ciências da Universidade de Lisboa, Lisboa: 747 pp. (unpublished).
- Sismonda, E. 1842. *Synopsis methodica animalium invertebratorum pedemontii fossilium*. Augustae Taurinorum Typis Regiis. Torino, 44 pp.
- Sosso, M. & Dell'Angelo, B. 2010. *I fossili del Rio Torsero*. Prato (Editing Marginalia, Cartotecnica Beusi srl): 95 pp.
- Strausz, L. 1966. *Die Miozän-Mediterranen Gastropoden ungarns*. Budapest (Akadémiai Kiadó): 692 pp.
- Švagrovský, J. 1982. Gastropoda, Prosobranchia. Teil 2. Neogastropoda des oberen Badenians von Borský Mikuláš (NO-Teil des Wiener Beckens) und ihre stratigraphische Bedeutung. *Geologický Zborník; Geologica Carpathica* 33/4: 383-435.
- Swainson, W. 1821. *Exotic conchology; or figures and descriptions of rare, beautiful, or undescribed shells*. W. Wood, J. & A. Arch, London: 39 pp., 48 pls.
- Swainson, W. 1829-1833. *Zoological Illustrations, or original figures and descriptions of new, rare, or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranged according to their apparent affinities*. Second series. Baldwin & Cradock, London. pl. 1-30 [1829] pl. 31-45 [1830] pl. 46-85 [1831] pl. 86-96 [1832] pl. 97-136 [1833].
- Swainson, W. 1835. *The elements of modern conchology*. Baldwin & Cradock, London, 62 pp.
- Swainson, W. 1840. *A treatise on malacology or shells and shell-fish*. Longman, London: viii + 419 pp.
- Toldo, G. 1889. Mitridae del Miocene superiore di Montegibbio. *Bollettino della Società Malacologica Italiana* 14: 144-150.
- Troschel, F.H. 1867. *Das Gebiss der Schnecken, zur Begründung einer natürlichen Classification*. Nicolai, Berlin, 2: 49-96.
- Vera-Peláez, J.L. 2002. Revisión de la familia Turridae, excepto Clavatulinae (Gastropoda, Prosobranchia) en el Plioceno de las cuencas de Málaga y Vélez Málaga (Málaga, S España) con la descripción de 26 especies nuevas. *Pliocénica, Publicaciones del Museo Municipal Paleontológico de Estepona* 2: 176-262.
- Weinkauff, H.C. 1867. *Die Conchylien des Mittelmeeres, ihre geographische und geologische Verbreitung*. T. Fischer, Cassel Vol. 1: pp. XIX + 307 [1867], Vol. 2: pp. VI + 512 [1868].
- Wienrich, G. 2007. *Die Fauna des marinen Miozäns von Kevelaer (Niederrhein), 4. Gastropoda ab Mitridae*. (Turridae by Janssen, R. & Wienrich, G.). Leiden (Backhuys Publishers BV): 640-954.
- Wood, S.V. 1851-1857. A monograph of the Crag Mollusca with descriptions of shells from the Upper Tertiaries of the British Isles, 2. Bivalves. *Monographs of the Paleontographical Society*: 1-150, pl. 1-12 (1851) 151-216, pl. 13-20 (1853) 217-342, pl. 21-31 (1857).
- Woodring, W.P. 1928. *Miocene mollusks from Bowden, Jamaica*, 2. *Gastropods and discussion of results*. Washington (Carnegie Institution of Washington, DC): 564 pp.