The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 24: Dolicholatiridae and Fasciolariidae (Neogastropoda, Buccinoidea)

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In this paper we continue to review the Buccinoidea of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain, with the description of the families Dolicholatiridae and Fasciolariidae. One species within the Dolicholatiridae is described: *Dolicholatirus alboranensis* nov. sp., and 13 within the Fasciolariidae, representing seven genera, of which one is new: *Tarantinaea micalii* nov. sp., and one is left in open nomenclature.
This group is relatively thermophilic, and the assemblage of species is fairly typical for the tropical Pliocene Mediterranean-West African palaeobiogeographic province. The family Dolicholatiridae is reported in the Pliocene European assemblages and is another example of the relict Miocene taxa present in the Pliocene of Estepona.

Key words: southern Spain, Upper Pliocene, Gastropoda, Dolicholatiridae, Fasciolariidae, Buccinoidea, new species

Introduction

The Fasciolariidae are one of the few families in the Estepona assemblages that have already been monographed in part by Muñiz Solís (1998) who covered the Fasciolariinae and Peristerniinae. In his work he recognised eight species, leaving two in open nomenclature. Fasciolariidae have also been recorded from other Pliocene Iberian assemblages; the Atlantic Mondego Basin of central west Portugal (Silva, 2001), and the Guadalquivir Basin (González-Delgado, 1989; Ruiz Muñoz *et al*., 1997; Landau *et al*., 2013; Brunetti, 2022), as part of an overall description of those assemblages. This paper revises the previous identifications and almost doubles the number of species recognised in the Iberian Pliocene.

Age of 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 MPP-MU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al*., 2011, text-fig. 9).

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.
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.

In the descriptions we follow Harzhauser *et al*. (2024, p. 6, fig. 1) and categorize the shells as: small (SL < 25.0 mm), medium-sized (25–60 mm), large (>60–100 mm) and very large (SL > 100 mm). We evaluated aperture length (AL), aperture width (AW), aperture height (AH), and last whorl height (LWH) to derive following ratios: 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 Paratethyan Fasciolariidae as follows: broad (SL/MD <2.3), moderately slender (SL/MD = 2.3–2.4), slender (SL/MD = >2.4–2.9) and very slender (SL/MD >2.9). The relative width of the aperture is calculated as aperture length (AL) versus aperture width (AW). Apertures are described as narrow (AL/AW ≥ 3.5) and moderately wide (AL/AW = <3. 5). As measurement for the relative length of the siphonal canal we calculated aperture length (AL) versus siphonal length (S). The siphonal canal length is categorized as follows: extraordinarily long (AL/S <1.6), moderately long (AH/S = >1.6-1.9) and moderately short (AL/S ≥2.0). Terminology follows Couto & Simone (2019): small (SL < 20.0 mm), medium-sized (20–60 mm), large (>60–100 mm) and very large (SL > 100 mm). We evaluated aperture length (AL), aperture width (AW), aperture height (AH), and last whorl height (LWH). Inner lip denticles numbered D1-D7, where D1 = the anal denticle.

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

Subclass Caenogastropoda
Order Neogastropoda
Superfamily Buccinoidea Rafinesque, 1815
Family Dolicholatiridae Kantor, Fedosov, Kosyan, Puillandre, Sorokin, Kano, R. Clark & Bouchet, 2021
Genus *Dolicholatirus* Bellardi, 1884

Type species (by subsequent designation, Cossmann, 1901) – *Turbinella bronni* Michelotti, 1847, Miocene, Italy.

1884 *Dolicholatirus* Bellardi, p. 38.
1901 *Dolicholathyrus* Cossmann, p. 22. Unjustified emendation of *Dolicholatirus* Bellardi, 1884, also spelled *Dolicholatyrus* Cossmann, 1901, p. 23 and *Dolycholathyrus* Cossmann, 1902, p. 56.

***Dolicholatirus alboranensis* nov. sp.**
Plate 1, figs 1-3

1998 *Dolicholatirus bronni* (Michelotti, 1847) – Muñiz Solís, p. 3, pl. 1, figs E-F.

ZooBank registration – urn:lsid:zoobank.org:act:5241E787-A740-4FDE-82FE-06F56041CB1E

Type material – Holotype NHMW 2023/0323/0073, height 26.9 mm, width 8.1 mm; paratype 1 NHMW 2023/0323/0074, height 25.1 mm, width 7.4 mm; paratype 2 NHMW 2023/0323/0125, height 24.8 mm, width 6.6 mm; paratype 3 NHMW 2023/0323/0126, height 25.5 mm, width 7.8 mm; paratype 4 NHMW 2023/0323/0127, height 23.5 mm, width 6.6 mm; paratype 5 NHMW 2023/0323/0128, height 24.4 mm, width 6.9 mm. **Velerín conglomerates**. Paratype 6 NHMW 2023/0323/0076, height 24.1 mm, width 5.8 mm. **Velerín carretera**.

Other material – Maximum height 26.9 mm, width 8.1 mm. **CO**: NHMW 2023/0323/0075 (5). **EL:** NHMW 2023/0323/0077 (2).

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

Type stratum – unnamed beds lower Piacenzian, Upper Pliocene.

Etymology – Named after the Alboran Sea, where it occurred in the Pliocene. *Dolicholatirus,* gender masculine.

Diagnosis – *Dolicholatirus* species of medium size, small, smooth, depressed paucispiral protoconch of one whorl, slender teleoconch of up to seven convex whorls with narrow, slightly concave subsutural area, seven axial ribs, siphonal fasciole smooth or with fine threads, no columellar folds.

Description – Shell medium-sized, very slender fusiform, with tall spire and extremely long siphonal canal; apical angle about 34°. Protoconch small, paucispiral, of just over one depressed whorl. Junction with teleoconch delimited by beginning of spiral sculpture. Teleoconch of seven convex whorls, somewhat swollen in their abapical half, separated by moderately deeply impressed, shallowly undulating suture. Sculpture on first teleoconch whorl of three spiral cords overrunning close-set axial ribs slightly broader than the cords forming reticulated pattern. Second whorl with four spiral cords; axials broaden and become wider spaced. Subsequent whorls with seven broad, rounded, orthocline ribs, wider than their interspaces, weakening over subsutural ramp, crossed by 6-7 fine spiral cords of subequal strength, slightly finer over subsutural ramp. Arcuate growth lines forming finely reticulated pattern most notable just below suture and in spiral interspaces. Last whorl about 63% of total height, subsutural ramp steep, slightly concave, poorly delimited by rounded shoulder, evenly convex mid-whorl, moderately constricted at base, fasciole very long, poorly delimited; axial and spiral sculpture strongest at periphery, weakening over base, fasciole with very faint close-set spirals to almost smooth. Aperture moderately wide. Columella weakly excavated in upper third, slightly angled at transition to siphonal canal. Columellar callus very nar-

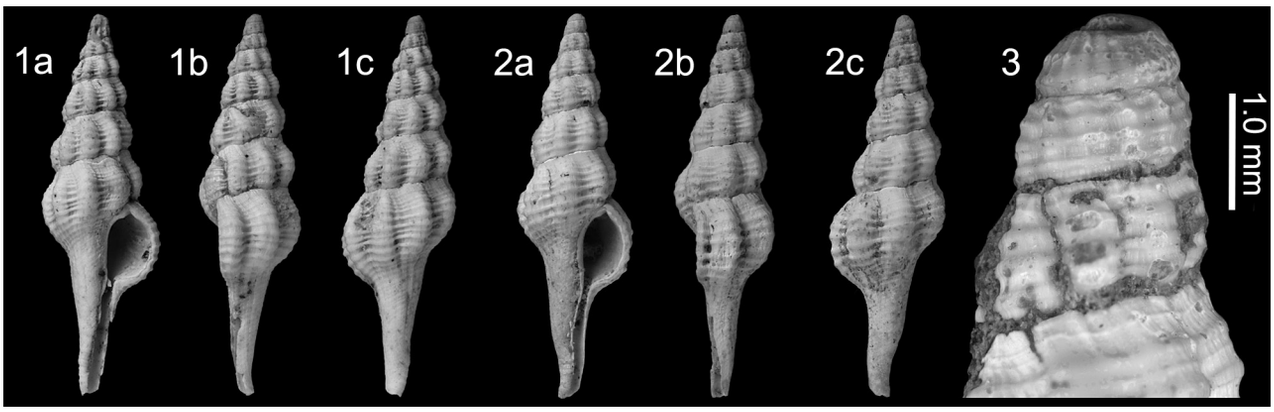

Plate 1. *Dolicholatirus alboranensis* nov. sp.; 1. **Holotype** NHMW 2023/0323/0073, height 26.9 mm, width 8.1 mm; 2. **Paratype 1** NHMW 2023/0323/0074, height 25.1 mm, width 7.4 mm. Velerín conglomerates. 3, **Paratype 6** NHMW 2023/0323/0076, height 24.1 mm, width 5.8 mm, detail of protoconch. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

row, sharply delimited, smooth, except for small parietal denticle. Anal canal narrowly incised, small. Outer lip slightly thickened by terminal varix, smooth or weakly lirate within. Siphonal canal very long, narrow, straight, tip slightly bent.

Discussion – This species from Estepona was identified as *Dolicholatirus bronni* (Michelotti, 1847) by Muñiz Solís (1998, p. 3, pl. 1, figs E-F). *Turbinella bronni* was figured by Michelotti (1847, pl. 10, fig. 15) without accompanying description, originally described from the Upper Miocene Tortonian of Italy.

The Estepona specimens differ from those described and figured by Bellardi (1884, 39, pl. 2, figs 13, 14) in having only seven axial ribs as opposed to eight and the spiral cords seem weaker over the ribs and stronger in the axial interspaces than in the Italian species. The axial ribs are aligned vertically in the specimen illustrated by Bellardi, whereas in the Estepona specimens they are aligned vertically in a clockwise direction or in some specimens, offset in others; this seems to be a variable character. More importantly, there are no columellar folds, whereas Bellardi (1884, p. 38) described two columellar folds in his generic characterisation. This is an unexpected character of the Estepona species which is, in all other features, typical for the genus.

In the Estepona specimens the columella is slightly twisted at the junction of the siphonal canal, but there are no folds even deep within the aperture. *Dolicholatirus bronni* has a less constricted base and weaker neck, the siphonal canal has very prominent primary and secondary cords unlike *Dolicholatirus alboranensis* nov. sp. that has an almost smooth siphonal canal, at most bearing close-set fine spiral threads. Lastly, the Estepona species has a slightly concave subsutural ramp, whereas the whorls in *D. bronni* are regularly convex.

The protoconch is a little abraded but is small and consists of one depressed whorl. We have examined the protoconch of other *Dolicholitarus* species at hand from both the European [*D. gaasensis* Vergneau, 1965] and Tropical American Neogene [*D. exilis* (Gabb, 1873), *D. pauli* (McGinty, 1955)] and they all have a smooth, paucispiral protoconch.

As far as we are aware, this is the only record for *Dolicholitarus* in the European Pliocene.

Dolicholatirus is a thermophilic genus today found in the tropical Pacific and western Atlantic but does not occur in the eastern Atlantic. It managed to survive in the westernmost Mediterranean Alboran Sea during the tropical Pliocene MPPMU1 (of Raffi, & Monegatti, 1993; Monegatti & Raffi, 2001), and is another example of relict groups that survived in the Pliocene of Estepona but did not extend their range further into the Pliocene Mediterranean (see Landau *et al*., 2003, p. 72; 2004, p. 87: 2007, p. 64).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (Muñiz Solís, 1998).

Family Fasciolariidae Gray, 1853
Subfamily Fasciolariinae Gray, 1853
Genus *Aurantilaria* Snyder, Vermeij & Lyons, 2012

Type species (by original designation) – *Fasciolaria aurantiaca* Lamarck, 1816, present-day, *Fasciolaria aurantiaca* Lamarck, 1816, present-day, Caribbean.

2012 *Aurantilaria* Snyder, Vermeij & Lyons, p. 44.

***Aurantilaria tarbelliana* (Grateloup, 1845)**
Plate 2, figs 1-3

*1845 *Fasciolaria Tarbelliana* Grateloup, pl. 23, fig. 14.
1854 *Fasciolaria Tarbelliana* Grat. – Hörnes, p. 298, pl. 33, figs 1-4.
1867 *Fasciolaria Tarbelliana* Grat. – Pereira da Costa, p. 187, pl. 22, figs 3-9, pl. 23, fig. 1a, b.
1885 [*Fasciolaria tarbelliana*] var. *andella* De Greg. – De Gregorio, p. 49 [*nov. nom. pro. Fasciolaria tarbelliana sensu* Hörnes 1854: pl. 33, figs 2, 3].

1890 *Fasciolaria tarbelliana* Grat. (Varietas *inermis*) – Hoernes & Auinger, p. 262, pl. 30, fig. 5 [*non Fasciolaria inermis* Jonas, 1846].
1890 *Fasciolaria tarbelliana* Grateloup (Varietas *nodosa*) – Hoernes & Auinger, p. 262, pl. 30, figs 6, 7.
1901 *Fasciolaria* (*Pleuroploca*) *Tarbelliana* Grat. – Cossmann, p. 39, plate captions, pl. 2, fig. 7.
1904 *Pleuroploca tarbelliana* (Grat.) – Sacco, p. 28, pl. 8, fig. 14.
1904 *Pleuroploca tarbelliana* var. *tauroventrosa* Sacco, p. 28, pl. 8, fig. 15.
1904 *Pleuroploca tarbelliana* var. *taurocostulatissima* Sacco, p. 28, pl. 8, fig. 16.
1904 *Pleuroploca tarbelliana* var. *dertomagna* Sacco, p. 28, pl. 8, fig. 17.
1928 *Fasciolaria (Pleuroploca*) *tarbelliana* Grateloup – Peyrot, p. 71, pl. 7, figs 12, 13.
1928 *Fasciolaria* (*Pleuroploca*) *tarbelliana* mut. *praecedens* Peyrot, p. 73, pl. 7, figs 14, 15.
1935 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grat. – Montanaro, p. 62, pl. 4, fig. 17.
1935 *Fasciolaria* (*Pleuroploca*) *tarbelliana* mut. *praecendens* Peyr. – Montanaro, p. 63, pl. 4, fig. 17.
1950 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Gratelup [*sic*] – Csepreghy-Meznerics, p. 56, pl. 2, fig. 15.
1954 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grat. – Strausz, p. 30, pl. 4, fig. 99a, pl. 5, fig. 99b.
1955 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grat. – Korobkov, plate captions, pl. 94, fig. 15.
1960 *Fasciolaria* (*Pleuroploca*) *tarbelliana* (Grateloup 1840 [*sic*]) – Kojumdgieva in Kojumdgieva & Strachimirov (*partim*), p. 187, pl. 45, figs 16a, b.
1962 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grateloup – Strausz, p. 80, pl. 28, figs 14, 15, pl. 29, fig. 1.
1963 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grat. – Venzo & Pelosio, p. 110, pl. 38, figs 22, 23.
1966 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grateloup, 1840 [*sic*] – Strausz, p. 353, pl. 28, figs 14, 15, pl. 29, fig. 1.
1989 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grateloup, 1840 [*sic*] – González-Delgado, p. 295, pl. 6, figs 1, 2.
1994 *Fasciolaria* (*Pleuroploca*) *tarbelliana nodosa* Hoernes, Auinger, 1890 – Nikolov, p. 53, pl. 3, figs 1, 2, pl. 4, figs 1-6.
1995 *Fasciolaria tarbelliana* Grateloup, 1840 [*sic*]– Bałuk, p. 248, pl. 36, figs 3-5.
1997 *Fasciolaria tarbelliana* Grateloup – Ruiz Muñoz *et al*., p. 64, pl. 37, figs 3, 4.
1998 *Pleuroploca tarbelliana* (Grateloup, 1840 [*sic*]) – Muñiz Solís, p. 2, pl. 1, figs A-D.
2011 *Pleuroploca tarbelliana* (Grateloup, 1840 [*sic*]) – Landau *et al*., p. 28, pl. 14, figs 3, 4.
2011 *Fasciolaria* (*Pleuroploca*) *tarbelliana* Grateloup, 1840 [*sic*] – Caprotti, p. 58, figs 3I, L.
2013 *Aurantilaria tarbelliana* (Grateloup, 1845) – Landau *et al*., p. 197, pl. 31, fig. 1.
2014 *Pleuroploca tarbelliana* (Grateloup, 1840 [*sic*]) – Tabanelli, p. 9, pl. 1, figs 1, 2.
2019 *Aurantilaria tarbelliana* (Grateloup, 1845) – Cárdenas *et al.*, p. 212, fig. 6a.
2021 *Aurantilaria tarbelliana* (Grateloup, 1845) – Lozouet, p. 13, pl. 15, figs 4-6.
2022 *Aurantilaria tarbelliana* (Grateloup, 1845) – Kovács, p. 75, figs 36-38.
2022 *Pleuroploca tarbelliana* (Grateloup, 1840 [*sic*]) – Brunetti, p. 60, fig. 108.
2024 *Aurantilaria tarbelliana* (Grateloup, 1845) – Harzhauser *et al*. p. 14, figs 2B, 6A-E.

non 1960 *Fasciolaria* (*Pleuroploca*) *tarbelliana* – Kojumdgieva in Kojumdgieva & Strachimirov (*partim*): 187, pl. 45, fig. 13 [= *Hemipolygona lynchi* (de Basterot, 1825)].

Material and dimensions – Maximum height 155.0 mm, width 60.5 mm. **CO**: NHMW 2023/0323/0078-0080 (3), NHMW 2023/0323/0081 (4).

Description – Shell very large, moderately slender fusiform of up to seven teleoconch whorls; apical angle ~43°. Protoconch not preserved. First two teleoconch whorls weakly convex with periphery close above abapical suture; later whorls weakly shouldered with shallow, concave sutural ramp and very narrow subsutural collar. Sculpture of eight broad axial ribs, separated by wider interspaces. Spiral sculpture of two spiral cords on subsutural collar, very weak, narrow cords on subsutural ramp, slightly stronger cords below of roughly alternating strength; shoulder cord slightly strengthened. Axial ribs reduced to blunt or slightly pointed nodes along shoulder. Last whorl attaining ~68-70% of total height, with broad sutural ramp, weakly angled to roundly shouldered, moderately convex below; spiral sculpture often subobsolete along periphery; shoulder smooth or with small nodes; base moderately convex, strongly constricted, bearing slightly stronger cords; fasciole relatively narrow, rounded, with prominent growth lines, delimited by narrow chink from columellar callus. Aperture moderately wide, pyriform. Columellar callus forming broad rim along siphonal canal, adhered above. Columella moderately and broadly excavated with three strongly oblique columellar folds deep inside aperture, adapical fold weaker, abapical fold marking slightly angled transition to siphonal canal, folds not visible in aperture in fully-grown specimens. Anal canal small, narrowly incised. Outer lip thin, with numerous thin lirae extending deep within aperture. Siphonal canal moderately short, narrow, slightly deflected to the left.

Discussion – Aurantilaria tarbelliana (Grateloup, 1845) is a remarkably long-lived and widely distributed species in the European Neogene, especially for a species with a paucispiral protoconch (see Harzhauser *et al*., 2024, fig. 2B). It is also remarkably variable, with both tuberculate (Pl. 2, figs 2, 3) and smooth (Pl. 2, fig. 1) forms occurring in Estepona. Loss of tubercles does not seem to be a gerontic character, as some of the smaller specimens from Estepona have already lost their tubercles at a

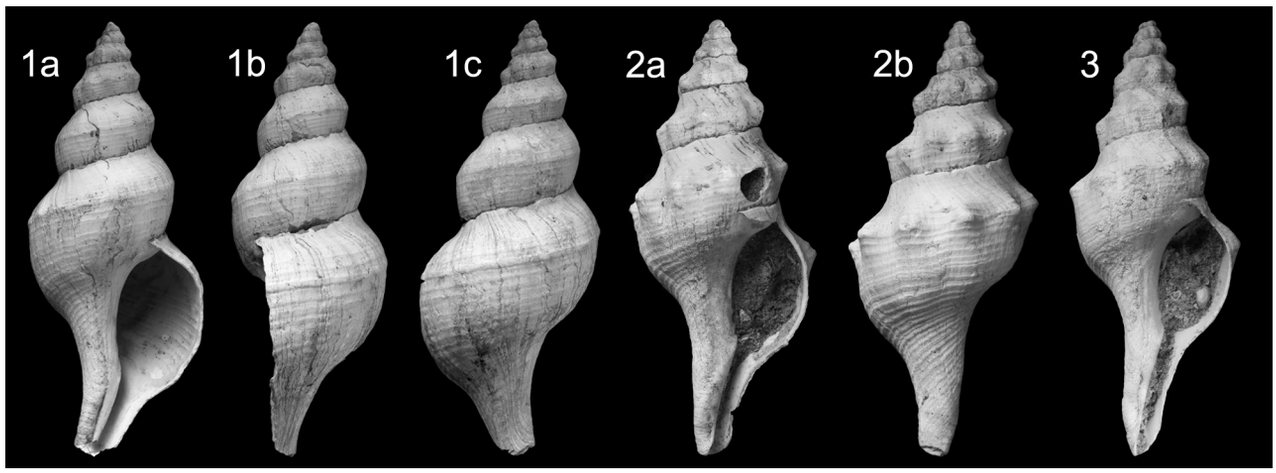

Plate 2. *Aurantilaria tarbelliana* (Grateloup, 1845); 1. NHMW 2023/0323/0078, height 155.0 mm, width 60.5 mm; 2. NHMW 2023/0323/0079, height 96.1 mm, width 43.2 mm; 3. NHMW 2023/0323/0080, height 125.5 mm, width 48.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

smaller size than some of the tuberculate specimens. This species has only been found in the Velerín conglomerates assemblage. For further discussion see Landau *et al*. (2013, p. 197) and Harzhauser *et al*. (2024, p. 15).
Landau *et al*. (2013) noted that at the time the species had only been recorded from the Pliocene westernmost Mediterranean Alboran Sea (Muñiz Solís, 1998) and adjacent Atlantic Guadalquivir Basin (González-Delgado, 1989; Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011). However, Tabanelli (2014, p. 9, pl. 1, figs 1, 2) recorded specimens from the Piacenzian Pliocene of "Croara" from the Scarabelli collection in the Musei Civici di Imola. The two specimens illustrated by that author are relatively small (48 mm and 29 mm) and have much stronger nodes developed at the shoulder. Nevertheless, they fit within the extraordinary variability currently accepted for the species (Landau *et al*., 2013, p. 197; Harzhauser *et al*. 2024, p. 14).

Distribution – Lower Miocene: Atlantic, Burdigalian, Aquitaine Basin, France (Grateloup, 1845; Lozouet, 2021). Middle Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1928); Paratethys, Austria (Hoernes & Auinger, 1890), Czech Republic (Hoernes & Auinger, 1890), Bulgaria (Kojumdgieva in Kojumdgieva & Strachimirov, 1960; Nikolov, 1994), Hungary (Strausz, 1966; Kovács, 2022), Poland (Bałuk, 1995), Romania (Hoernes & Auinger, 1890); eastern Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Tortonian, Atlantic, Algarve Basin, Cacela, Portugal (Pereira da Costa, 1867), Guadalquivir Basin (Cárdenas *et al*., 2019); central Proto-Mediterranean, Italy (Sacco, 1904; Montanaro, 1935; Venzo & Pelosio, 1963; Caprotti, 2011). Lower Pliocene, Atlantic, Guadalquivir Basin (González-Delgado, 1989; Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Muñiz Solís, 1998), central Mediterranean, Italy (Tabanelli, 2014).

Subfamily Fusininae Wrigley, 1927
Genus *Angustifusus* Vermeij & Snyder, 2018

Type species (by original designation) – *Fusus vindobonensis* Hoernes & Auinger, 1890, Middle Miocene, Austria.

2018 *Angustifusus* Vermeij & Snyder, p. 71.

***Angustifusus longiroster* (Brocchi, 1814)**
Plate 3, figs 1-3

*1814 *Murex logiroster* Brocchi, p. 418, pl. 8, fig. 7.
1872 *Fusus longiroster* Defr. [*sic*] – d'Ancona, p. 120, pl. 15, fig. 2.
1876 *Fusus longiroster* var. *aequicingulata* Foresti, p. 17.
1879 *Fusus longiroster* Brocchi – Fontannes, p. 14, pl. 2, fig. 9.
1901 *Fusus longiroster* (Brocchi) – Cossmann, p. 10, pl. 1, fig. 7.
1904 *Fusus longiroster* (Br.) – Sacco, p. 24, pl. 7, figs 5, 6.
1904 *Fusus longiroster* (Brocchi) – Grabau, p. 52, pl. 6, figs 1-3.
1904 *Fusus inaequicostatus* Bellardi – Grabau, p. 54, pl. 6, figs 5-7 (*non* Bellardi, 1873).
1911 *Fusus longiroster* Br. – Cerulli-Irelli, p. 238 [288], pl. 21 [38], figs 30-36.
?1914 *Fusus longiroster* (Brocchi) – Harmer, p. 173, pl. 14, fig. 23.
1950 *Fusus longiroster* (Brocchi) – Ruggieri, p. 74, pl. 2, fig. 14.
1955 *Fusus* (*Fusus*) *longiroster* (Brocchi 1814) – Rossi Ronchetti, p. 234, fig. 124.
1959 *Fusinus longiroster* (Brocchi) – Ruggieri *et al*., p. 67, pl. 14, fig. 86, pl. 17, figs 100a, b.
1960 *Fusinus* (*Fusinus*) *longiroster* (Brocchi, 1814) – Malatesta, p. 171, pl. 9, fig. 1.

1967 *Fusinus* (*Fusinus*) *longiroster* (Brocchi) – Pelosio, p. 144 [44], pl. 41, fig. 18, pl. 42, figs 1, 2.
1969 *Fusinus* (*Fusinus*) *longiroster* (Brocchi) – Mastrorilli, p. 119, pl. 8, fig. 19.
1974 *Fusinus* (*Fusinus*) *longiroster* (Brocchi, 1814) – Malatesta, p. 349, pl. 28, fig. 2.
1976 *Fusinus longiroster* (Brocchi) – Caprotti, p. 11, pl. 16, fig. 13.
1978 *Murex longiroster* Brocchi, 1814 – Pinna & Spezia, p. 151, pl. 37, fig. 4.
1992 *Fusinus* (*Fusinus*) *longiroster* (Brocchi, 1814) – Cavallo & Repetto, p. 102, fig. 235.
1997 *Fusinus longiroster* (Brocchi, 1814) – Marquet, p. 95, pl. 8, fig. 2.
1998 *Fusinus longiroster* (Brocchi, 1814) – Marquet, p. 141, fig. 115.
2000 *Fusinus longiroster* (Brocchi, 1814) – Chirli, p. 120, pl. 48, figs 10, 11, pl. 49, figs 1-3.
?2001 *Fusinus* (*Fusinus*) cf. *longiroster* (Brocchi, 1814) – Silva, p. 455, pl. 21, fig. 3.
2008 *Fusinus longiroster* (Brocchi, 1814) – Chirli & Richard, p. 50, pl. 9, figs 8, 9.
2010 *Fusinus longiroster* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 40, p. 57 unnumbered fig. bottom row right.
?2011 *Fusus longiroster* (Brocchi, 1814) – Caprotti, p. 59, figs 4C, D (incomplete specimen).
2011 *Fusinus longiroster* (Brocchi, 1814) – Chirli & Linse, p. 152, pl. 51, fig. 3.
2014 *Fusinus longiroster* (Brocchi, 1814) – Tabanelli, p. 27, pl. 6, figs 2, 10, pl. 7, figs 1, 2.
2018 *Fusinus longiroster* (Brocchi, 1814) – Brunetti & Cresti, p. 76, fig. 277.

non 1853 *Fusus longirostris* [*sic*] Brocchi – Hörnes, p. 293, pl. 32, figs 5–7 [= *Angustifusus hoessii* (Naumann, 1852)].

Material and dimensions – Maximum height 109.6 mm, width 29.6 mm. **CO**: NHMW 2023/0323/0082-0083 (2), NHMW 2023/0323/0084 (1), NHMW 2023/0323/0088 (1).

Description – Shell very large, very slender fusiform, of up to seven convex teleoconch whorls; apical angle 37-39°. Protoconch not preserved. Early teleoconch whorls shouldered above mid-whorl with concave subsutural ramp, sculptured by seven broad axial ribs, wider than their interspaces, fading over subsutural ramp; two prominent spirals on earliest whorls; very weak secondary and tertiary spirals appear on subsutural ramp, stronger between primaries below shoulder. Suture weakly impressed. Later whorls with narrow concave sutural ramp, shoulder rounded, convex below; axial ribs broaden, weaken and fade out around fifth teleoconch whorl; spirals increasing to about five primary cords on penultimate whorl, with one secondary cord flanked by one tertiary thread on each side in interspaces. Last whorl high, attaining ~69-71% of total height, weakly shouldered, rapidly constricted at base with regular spiral sculpture of numerous delicate cords of primary to tertiary strength, no axial sculpture except weak axial growth lines and occasional stronger growth halts; fasciole not developed. Aperture small, moderately wide, ovate pyriform. Columellar callus forming thin, narrow rim, moderately delimited from siphonal canal, adherent in parietal area. Columella smooth except for weak parietal fold, shallowly excavated, weakly twisted at siphonal canal. Anal canal poorly developed. Outer lip thin, smooth, attached distinctly below periphery of last whorl. Siphonal canal extraordinarily long, slender, straight, narrow.

Discussion – *Angustifusus longiroster* (Brocchi, 1814) is a very characteristic species, with its slender fusiform shape, broad ribs on early teleoconch whorls that disappear with ontogeny to leave only weak spiral sculpture on the last 1-2 whorls, small aperture, and very long narrowly open siphonal canal. Juvenile material is not available from Estepona and the protoconch is not preserved, but a specimen illustrated by Tabanelli (2014, pl. 7, figs 1, 2) shows the protoconch to be paucispiral with a bulbous first whorl, typical of non-planktotrophic development. Sculpture on the first teleoconch whorls consist of two prominent spirals placed mid-whorl, with the third spiral developing on the subsutural ramp on the second teleoconch whorl. Late teleoconch whorls can be rather variable in profile, from regularly convex (Pl. 3, fig. 2) to shouldered (Pl. 3, fig. 1), which in some cases can be extreme (see Tabanelli, 2014, pl. 6, fig. 10). Montanaro (1935, p. 55, pl. 4, fig. 4) described a small specimen from the Tortonian Upper Miocene of Montegibbio as *Fusus longiroster*? var. *excellens*. It represents a juvenile fasciolariid and is excluded from the chresonymy and distribution.
Angustifusus pachyrostratus (Ruggieri, 1950), described from the Upper Pliocene of Italy and extends into the Lower Pleistocene Calabrian (Tabanelli, 2014, p. 28), is most like *A. longiroster*, but differs in its smaller adult size, in having axial ribs that persist through ontogeny to the outer lip, having a more pronounced shoulder, and a broader siphonal fasciole.
Grabau (1904, p. 54, pl. 4, fig. 4) described *Fusus castelarquatensis* from the Pliocene of Castelarquato (Italy). It differs from *A. longiroster* in that the axial sculpture disappears even earlier in ontogeny, leaving more teleoconch whorls with only fine spiral sculpture. Judging from the type illustration the suture is shallower resulting in the abapical half of the whorl being less convex, and the siphonal canal is shorter. We have not seen this species that seems to have been based on a single specimen and can give no information on its intraspecific variability. Grabau considered one of the specimens illustrated by Hörnes (1853, pl. 32, fig. 5) to represent *Angustifusus castelarquatensis*, however the Austrian specimens represent *Angustifusus hoessii* (Naumann, 1852).
Angustifusus hoessii from the Middle Miocene Paratethys is immediately separated by its multispiral protoconch and much narrower fasciole. Like *A. longiroster* (Brocchi, 1814), adult specimens vary enormously in profile

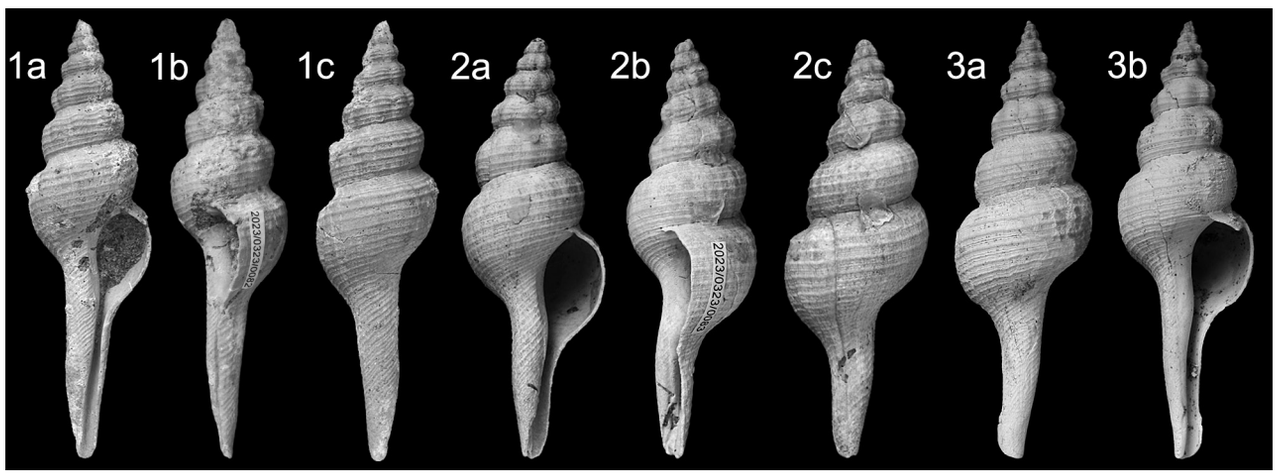

Plate 3. *Angustifusus longiroster* (Brocchi, 1814); 1. NHMW 2023/0323/0082, 109.6 mm, width 29.6 mm; 2. NHMW 2023/0323/0083, height 84.9 mm, width 29.9 mm; 3. NHMW 2023/0323/0088, height 86.3 mm, width 25.4 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

and sculpture (see Harzhauser *et al*., 2024, figs 14A-F). The type species, *A. vindobonensis* (Hoernes & Auinger, 1890), also from the Middle Miocene Paratethys is even slenderer than *A. longiroster*, has a stronger shoulder on late teleoconch whorls in most specimens, and spiral sculpture is weaker, usually obsolete on the last two whorls (see Harzhauser *et al*., 2024, figs 15A-D). That species also has a larger protoconch of 2.5 whorls.
Angustifusus longiroster is uncommon in the Estepona assemblages and found only in the shallower water assemblage of Velerín conglomerates.

Distribution – Upper Miocene: Tortonian, central Proto-Mediterranean, Italy (Montanaro, 1935; Caprotti, 2011). Lower Pliocene: western Mediterranean, Roussillon Basin, France (Fontannes, 1879; Cossmann, 1901); central Mediterranean, Italy (Pelosio, 1967; Chirli, 2000; Tabanelli, 2014; Brunetti & Cresti, 2018). Upper Pliocene: North Sea Basin: Oorderen Member, Belgium (Marquet, 1997, 1998); Atlantic: ?Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al*., 1959; Mastrorilli, 1969; Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Tabanelli, 2014). Pliocene (indeterminate): ?Irish Sea: Isle of Man (Harmer, 1914). Lower Pleistocene. Central Mediterranean, Italy (Cerulli-Irelli, 1911; Ruggieri, 1950; Malatesta, 1960; Tabanelli, 2014); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Genus *Apertifusus* Vermeij & Snyder, 2018

Type species (by original designation) – *Fusus meyeri* Dunker, 1869, present-day, West Africa.

2018 *Apertifusus* Vermeij & Snyder, p. 67.

***Apertifusus clavatus* (Brocchi, 1814)**
Plate 4, fig. 1

*1814 *Murex clavatus* Brocchi, p. 418, pl. 8, fig. 2.
1872 *Fusus clavatus* Bast. [*sic*] – d'Ancona (*pars*), p. 239, pl. 14, fig. 3 [not pl. 15, fig. 1 = *Apertifusus etruscus* (Pecchioli, 1862)].
1904 *Streptochetus*? *clavatus* (Br.) – Sacco, p. 25, pl. 7, figs 8, 9.
1904 *Fusus clavatus* (Brocchi) – Grabau, p. 57, pl. 8, fig. 15.
1955 *Fusus* (*Fusus*) *clavatus* (Brocchi 1814) – Rossi Ronchetti, p. 236, fig. 125.
1959 *Fusinus clavatus* (Brocchi) – Ruggieri *et al*., p. 68, pl. 15, fig. 87, pl. 16, fig. 96.
1974 *Fusinus* (*Fusinus*) *clavatus* (Brocchi, 1814) – Malatesta, p. 347, pl. 28, fig. 9.
1978 *Murex clavatus* Brocchi, 1814 – Pinna & Spezia, p. 146, pl. 32, fig. 4.
1988 *Fusinus clavatus* (Brocchi, 1814) – Chirli, p. 21, pl. 8, fig. 13.
1989 *Fusinus* (*Gracilipurpura*) *clavatus* (Brocchi, 1814) – González-Delgado, p. 297, pl. 6, figs 3-5.
2000 *Fusinus clavatus* (Brocchi, 1814) – Chirli, p. 116, pl. 46, figs 6-10.
2010 *Fusinus clavatus* (Brocchi, 1814) – Sosso & Dell' Angelo, p. 40, p. 57 unnumbered fig. middle row centre.
2011 *Fusinus clavatus* (Brocchi, 1814) – Landau *et al*., p. 28, pl. 14, fig. 6.
2014 *Fusinus etruscus* (Pecchioli, 1862) – Tabanelli, p. 26, pl. 7, fig. 3 [*non Apertifusus etruscus* (Pecchioli, 1862)].
2022 *Fusinus etruscus* Pecchioli, 1864 [*sic*] – Brunetti, p. 60, fig. 109 [*non Apertifusus etruscus* (Pecchioli, 1862)].

non 1852 [*Fusus*] *clavatus* – Naumann, plate captions, pl. 70, fig. 9 [= *Eurolatirus zahlbruckneri* (Quenstedt, 1884)].

non 1958 *Fusus clavatus* (Brocchi) – Erünal-Erentöz, p. 71, pl. 11, fig. 10 [= *Eurolatirus zahlbruckneri* (Quenstedt, 1884)].

non 1975 *Fusus clavatus* (Brocchi) – Fekih, p. 111, pl. 33, fig. 6 [*non Apertifusus etruscus* (Pecchioli, 1862)]

non 2011 *Fusus clavatus* (Brocchi, 1814) – Caprotti, p. 59, figs 4A, B [= turrid].

Material and dimensions – Height 91.8 mm, width 27.9 mm. **EL**: NHMW 2023/0323/0090 (1).

Description – Shell very large, very slender fusiform, of up to eight convex teleoconch whorls, swollen in abapical half; apical angle 35°. Protoconch not preserved. Early teleoconch whorls weakly convex, sculptured by seven broad axial ribs, crossed by five spiral cords (surface somewhat abraded). Narrow concave subsutural area develops from third whorl, with narrow infrasutural cord, two further slightly weaker cords over ramp, three cords below; shoulder not developed. Fourth cord appears above abapical suture on fourth whorl and single fine secondary thread intercalated below shoulder between primaries. Suture relatively shallow, narrowly impressed, shallowly undulating. Abapically number of ribs increases, about 16 on penultimate whorl; ribs broaden, flatten and become subobsolete on last whorl. Close-set axial growth lines give surface weakly and finely reticulated appearance. Last whorl high, attaining 70% of total height, slightly concave in subsutural area, convex mid-whorl, moderately constricted at base, with regular spiral sculpture of alternating strength, axial sculpture subobsolete, except weak growth lines and occasional stronger growth halts; fasciole not developed. Aperture moderately small, narrow elongate-ovate. Columellar callus thickened forming narrow rim, strongly delimited and detached from siphonal canal, adherent in parietal area. Columella smooth, shallowly excavated, weakly twisted at siphonal canal. Anal canal marked by small V-shaped notch. Outer lip thin, attached distinctly below periphery of last whorl, bearing nine weak lirae starting a short distance behind peristome. Siphonal canal moderately long, slender, narrow, twisted, shallowly notched at tip.

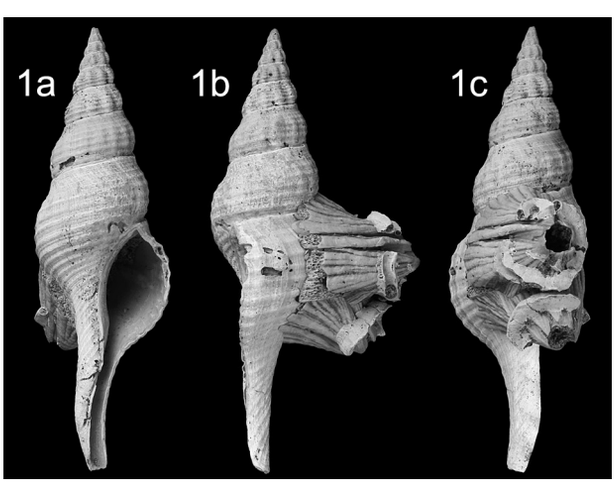

Plate 4. *Apertifusus clavatus* (Brocchi, 1814); 1. NHMW 2023/0323/0090, 91.8 mm, width 27.9 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – Two closely similar species have been described from the Italian Pliocene; *Murex clavatus* Brocchi, 1814 and *Fusus etruscus* Pecchioli, 1862. According to Bellardi, *Fusus etruscus* differed from *F. clavatus* in having "*fewer, wider, obtuse cords overrunning nodular ribs: which are more numerous (15-16), less obtuse, and more oblique* [translated from Latin]" (1873, p. 136). In his discussion (1873, p. 137) he stressed the narrower, more depressed posterior part of the whorls [subsutural ramp], deeper suture, and more prominent axial ribs. These differences are seen in the specimens of *F. clavatus* and *F. etruscus* illustrated by Sacco (1904, pl. 7, figs 7-11 and 12 respectively). A similarly strongly ribbed specimen was illustrated as *F. etruscus* by Chirli (2000, pl. 47, fig. 118). The type specimen illustrated by Pecchioli (1862) has strong ribs, but the shoulder knobs are not as strong as those seen in the specimens of Sacco and Chirli. We note that the specimens illustrated as *F. etruscus* by authors are all large (*e.g.*, 108 mm-180 mm height; Chirli, 2000) compared to *F. clavatus* (*e.g.*, 61-69 mm height; Chirli, 2000).

Both species occur in the Estepona deposits where they are both uncommon. Based on the Spanish material, *Apertifusus clavatus* is much smaller than *A. etruscus* (91.8 mm vs. 160.0 mm), the apical angle is narrower, the suture shallower, and the sculpture of axial ribs finer, whereas *A. etruscus* has more convex whorls and coarsely rugose axial sculpture. The ribs in the Estepona specimen are not as elevated as in the holotype of *A. clavatus* but based on specimens of *A. clavatus* from the Lower Pliocene Guadalquivir Basin of southwestern Spain this feature is variable. Some Italian specimens of *A. etruscus* have strong shoulder knobs (*e.g.*, Sacco, 1904, pl. 7, fig. 12; Chirli, 2000, pl. 47, figs 4-6) that do not occur in the Estepona ones. However, the type illustrated by Pecchioli (1862, unnumbered pl. and fig.) does not have shoulder knobs either. Like *Aurantilaria tarbelliana* (Grateloup, 1845), the presence or absence of shoulder knobs seems a variable character.

In Estepona only one specimen is at hand from the El Lobillo assemblage. It has two large balanids attached to the dorsum.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin (González-Delgado, 1989; Landau *et al*., 2011; Brunetti, 2022); central Mediterranean, Italy (Chirli, 1988, 2000). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al*., 1959; Malatesta, 1974; Sosso & Dell'Angelo, 2010; Tabanelli, 2014).

Apertifusus etruscus (Pecchioli, 1862)

Plate 5, figs 1-3

1862 *Fusus etruscus* Pecchioli, p. 4, pl. and fig. unnumbered.

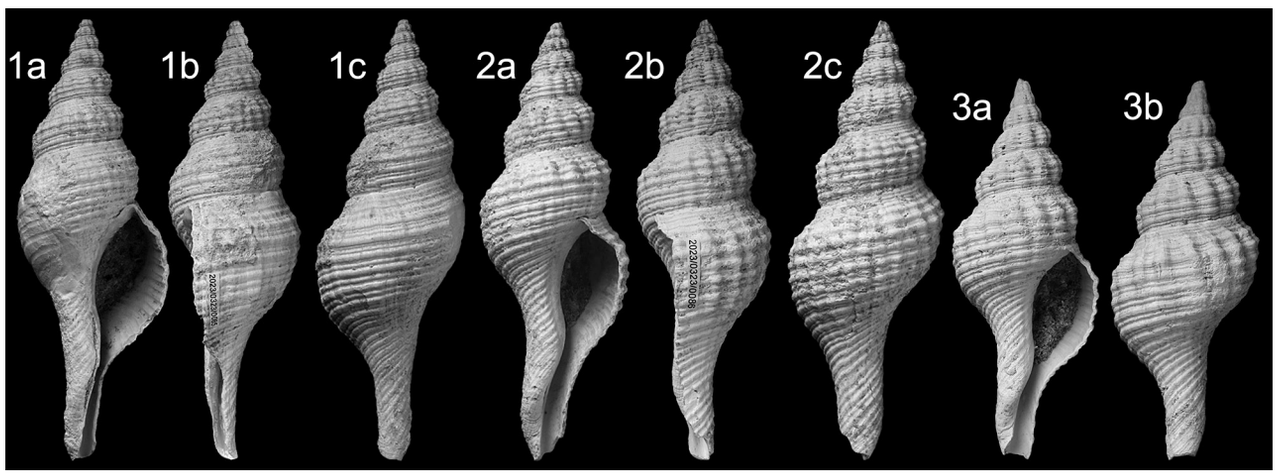

Plate 5. *Apertifusus etruscus* (Pecchioli, 1862); 1. NHMW 2023/0323/0085, 160.0 mm, width 55.0 mm (small area of repair apertural view left side of shell); 2. NHMW 2023/0323/0086, height 125.9 mm, width 43.8 mm; 3. NHMW 2023/0323/0089, height 75.6 mm, width 28.3 mm (subadult). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1867 *Fusus Etruscus* Pecchioli – Pereira da Costa, p. 180, pl. 21, fig. 4.
1872 *Fusus clavatus* Bast. [*sic*] – d'Ancona (*pars*), p. 239, pl. 15, fig. 1 [not pl. 14, fig. 3 = *Apertifusus clavatus* (D'Ancona, 1872)].
1904 *Streptochetus*? *clavatus* var. *magnicostata* Sacco, p. 25, pl. 7, figs 10, 11.
1904 *Streptochetus*? *etruscus* var. *ligustica* Sacco, p. 25, pl. 7, fig. 12 (?13).
1904 *Fusus etruscus* Pecchioli – Grabau, p. 57, pl. 8, fig. 14.
1959 *Fusinus clavatus etruscus* Pecchioli [*sic*] – Ruggieri *et al*., p. 69, pl. 17, figs 104, 105.
1975 *Fusus clavatus* (Brocchi) – Fekih, p. 111, pl. 33, fig. 6 [*non Apertifusus clavatus* (Brocchi, 1814)]
2000 *Fusinus etruscus* (Pecchioli, 1862) –Chirli, p. 118, pl. 47, figs 4-6.

non 1872 *Fasciolaria etrusca* D'Anc. [*sic*] – d'Ancona, p. 201, pl. 12, figs 1, 2 [= *Tarantinaea danconai* (Pecchioli, 1864)].
non 2014 *Fusinus etruscus* (Pecchioli, 1862) – Tabanelli, p. 26, pl. 7, fig. 3 [= *Apertifusus clavatus* (Brocchi, 1814)].
non 2022 *Fusinus etruscus* Pecchioli, 1864 [*sic*] – Brunetti, p. 60, fig. 109 [= *Apertifusus clavatus* (Brocchi, 1814)].

Material and dimensions – Maximum height 160.0 mm, width 55.0 mm. **CO**: NHMW 2023/0323/0085-0086 (2), NHMW 2023/0323/0087 (2 + 1 fragment last whorl), NHMW 2023/0323/0089 (1 subadult).

Description – Shell very large, slender fusiform, of up to seven convex teleoconch whorls, swollen in abapical half; apical angle 40-44°. Protoconch not preserved. Early teleoconch whorls weakly convex, sculptured by nine broad axial ribs, crossed by five spiral cords (surface of first three whorls somewhat abraded). Narrow concave subsutural area develops from third whorl, with narrow infrasutural cord, three cords below; shoulder rounded. Fourth cord appears above abapical suture on fourth whorl and single fine secondary thread intercalated between all primaries. Suture moderately deep, impressed, shallowly undulating. Abapically number of ribs increases, about 13-15 on penultimate whorl; ribs continue relatively well developed to aperture. Close-set axial growth lines give surface finely reticulated appearance. Last whorl high, attaining 70-71% of total height, concave in subsutural area, rounded at shoulder, convex below, moderately constricted at base, with regular spiral sculpture of alternating strength, axial sculpture giving surface rugose appearance. Aperture moderate size, moderately narrow, elongate-ovate. Columellar callus moderately thickened forming narrow rim, strongly delimited and detached from siphonal canal, adherent in parietal area. Columella shallowly excavated, weakly twisted at siphonal canal, bearing a few weak folds in parietal area and slightly stronger parietal fold. Anal canal marked by V-shaped notch. Outer lip thin, attached distinctly below periphery of last whorl, bearing about 18 narrow lirae roughly arranged in pairs, starting just behind peristome. Siphonal canal moderately short, slender, narrow, twisted, shallowly notched at tip.

Discussion – See above under *Apertifusus clavatus* (Brocchi, 1814). Apart from the differences highlighted under the previous species, we note that the lirae within the outer lip are roughly arranged in pairs. This can also be seen in the specimens illustrated by D'Ancona (1872, pl. 15, fig. 1b), Sacco (1904, pl. 7, fig. 12), Ruggieri *et al*. (1959, fig. 104) and Chirli (2000, pl. 47, fig. 5). In *A. clavatus* the lirae are weaker and not as clearly arranged in pairs, although there is a tendency in some specimens.

Distribution – Upper Miocene: Tortonian, Algarve Basin, Cacela, Portugal (Pereira da Costa, 1867). Lower Pliocene: western Mediterranean, Tunisia (Fekih, 1975);

central Mediterranean, Italy (Chirli, 2000). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al*., 1959).

Genus *Parvofusus* Tabanelli, 2014

Type species (by original designation) – *Fusus lamellosus* Borson, 1821, Pliocene, Italy.

2014 *Parvofusus* Tabanelli, p. 32.

***Parvofusus lamellosus* (Borson, 1821)**
Plate 6, figs 1-3

*1821 *Fusus lamellosus* Borson, p. 317, pl. 1, fig. 14.
1847 *Fusus lamellosus* Borson – Michelotti, p. 271, pl. 9, fig. 14.
1872 *Fusus lamellosus* Borson – d'Ancona, p. 127, pl. 15, fig. 4.
1873 *Fusus lamellosus* Bors. – Bellardi, p. 142, pl. 9, fig. 17.
1901 *Fusus* (*Aptyxis*) *lamellosus* (Borson) – Cossmann, p. 16, text-fig. 6, pl. 1, fig. 3.
1935 *Fusinus* (*Aptyxis*) *lamellosus*? Bors. cfr. *pulchellus* Phil. – Montanaro, p. 55, pl. 4, fig. 10.
1959 *Fusinus lamellosus* (Borson) – Ruggieri *et al*., p. 72, pl. 17, fig. 103.
1967 *Fusinus* (*Aptyxis*) *lamellosus* (Borson) – Pelosio, p. 143 [43], pl. 41, figs 16, 17.
1973 *Fusinus* (*Aptyxis*) *lamellosus* (Borson) – Caprotti & Vescovi, p. 169, pl. 2, fig. 12.
1976 *Fusinus lamellosus* (Borson) – Caprotti, p. 11, pl. 16, fig. 12.
1992 *Fusinus* (*Fusinus*) *lamellosus* (Borson, 1821) – Cavallo & Repetto, p. 102, fig. 234.
1994 *Fusinus lamellosus* (Borson, 1821) – Tabanelli & Segurini, p. 11, pl. 2, fig. 4.
2010 *Fusinus lamellosus* (Borson, 1821) – Sosso & Dell' Angelo, p. 40, p. 57 unnumbered fig. middle row right.
2014 *Parvofusus lamellosus* (Borson, 1821) – Tabanelli, p. 33, pl. 5, figs 3-5.

non 1836 *Fusus lamellosus* Philippi, p. 204, pl. 11, fig. 30 [= *Hirtomurex squamosus* (Bivona e Berardi, 1838)].
non 1853 *Fusus lamellosus* Borson – Hörnes, p. 853, pl. 31, figs 16a–b [= *Takashius vinculum* Harzhauser, Landau & Vermeij, 2024].
non 1873 *Fusus lamellosus* Bors. – Bellardi, p. 142, pl. 9, fig. 17 [= *Takashius vinculum* Harzhauser, Landau & Vermeij, 2024].
non 1954 *Fusus lamellosus* Borson – Csepreghy-Meznerics, p. 44, pl. 5, fig. 25 [= *Fraudifusinus crispoides* (Kittl, 1887)].
non 1960 *Fusus* (*Aptyxis*) *lamellosus* Borson 1821 – Kojumdgieva in Kojumdgieva & Strachimirov, p. 190, pl. 46, figs 13a-b [= *Takashius vinculum* Harzhauser, Landau & Vermeij, 2024].
non 1966 *Fusus* (*Aptyxis*) *lamellosus* – Strausz, p. 344, pl. 26, fig. 19 [= *Fraudifusinus crispoides* (Kittl, 1887)].
non 1972 *Fusus lamellosus* (Hoernes et Auinger) – Csepreghy-Meznerics, p. 30, pl. 13, fig. 3 [= *Takashius vinculum* Harzhauser, Landau & Vermeij, 2024].
non 2000 *Fusinus lamellosus* (Borson, 1821) – Chirli, p. 119, pl. 48, figs 1-9 [*Takashius ligusticus* (Bellardi, 1884).
non 2014 *Fusinus lamellosus* – Popa *et al.* pl. 3, fig. 7 [= *Fraudifusinus crispoides* (Kittl, 1887)].

Material and dimensions – Maximum height 20.4 mm, width 7.4 mm. **EL**: NHMW 2023/0323/0091-0093 (3), NHMW 2023/0323/0094 (12).

Description – Shell small, slender fusiform, of up to seven teleoconch whorls; apical angle 37-40°. Protoconch dome-shaped, multispiral, of 3.5 smooth, convex whorls. Junction with teleoconch delimited by prosocline scar. Teleoconch whorls convex, separated by deeply impressed undulating suture. Sculpture of strong, elevated cords overrunning 8-10 rounded ribs extending between sutures,

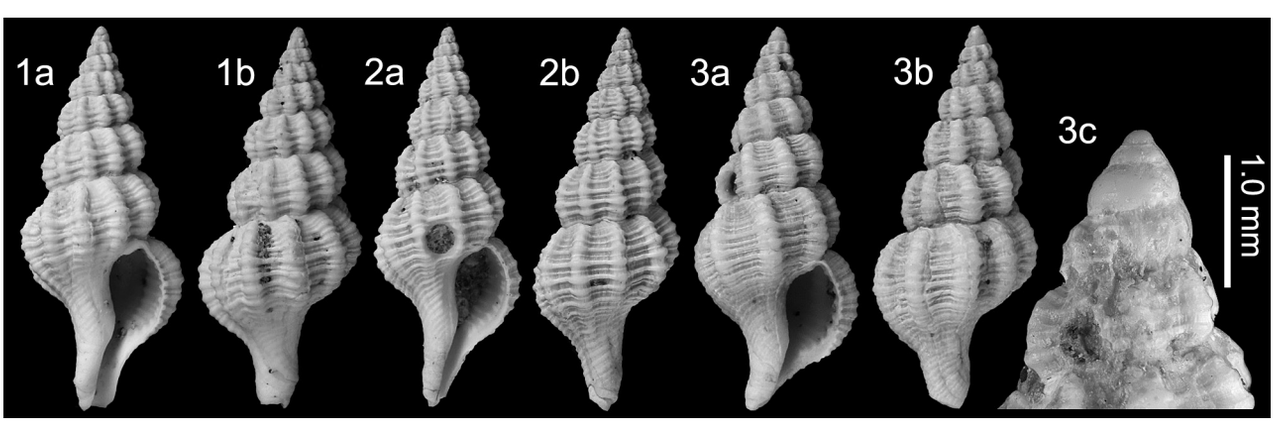

Plate 6. *Parvofusus lamellosus* (Borson, 1821); 1. NHMW 2023/0323/0091, height 19.0 mm, width 7.6 mm; 2. NHMW 2023/0323/0092, height 20.4 mm, width 7.4 mm: 3. NHMW 2023/0323/0093, height 15.2 mm, width 6.1 mm, 3c, detail of protoconch. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

roughly half width of their interspaces; cords very slightly swollen over ribs. On later whorls 2-3 weaker cords develop in subsutural area, secondary thread intercalated between primaries on penultimate whorl. Last whorl 57-59% of total height, strongly convex, with 9-11 axial ribs continuing over base, weakening over fasciole, secondary cords intercalated between primaries; base strongly constricted with prominent primary and secondary spiral cords; indistinct fasciole. Aperture moderately wide pyriform. Columellar callus forming narrow rim, sharply delimited from base. Columella moderately excavated in upper half, smooth, moderately twisted at fasciole. Anal canal wide, accentuated by weak parietal denticle. Outer lip thickened by terminal varix with prominent lirae extending deep within aperture. Siphonal canal moderately short, moderately narrow, deflected to the left.

Discussion – For discussion, see *Takashius ligusticus* (Bellardi, 1884).

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Bellardi, 1873; Michelotti, 1847; Montanaro, 1935). Lower Pliocene: western Mediterranean, Roussillon Basin, France (Cossmann, 1901); central Mediterranean, Italy (Pelosio, 1967; Tabanelli, 2014). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Ruggieri *et al*., 1959; Caprotti & Vescovi, 1973; Caprotti, 1976; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Tabanelli, 2014). Lower Pleistocene: central Mediterranean, Italy (Tabanelli, 2014).

Genus *Pseudofusus* Monterosato, 1884

Type species (by subsequent designation by Crosse, 1885) – *Murex rostratus* Olivi, 1792, present-day, Mediterranean.

1884 *Pseudofusus* Monterosato, p. 117.
2017 *Aegeofusinus* Russo, p. 64. Type species (by original designation): *Fusinus margaritae* Buzzurro & Russo, 2007, present-day, Mediterranean.
2018 *Gracilipurpura sensu* Vermeij & Snyder, p. 71 not Jousseaume, 1880, p. 335; see Fassio *et al*., 2022, p. 633.

Note – Vermeij & Snyder (2018, p. 71) tentatively synonymised *Carinofusus* Ceulemans, Landau & Van Dingenen, 2014 (type species *Clavella neogenica* Cossmann, 1901, Pliocene, NW France) with *Gracilipurpura* (*Pseudofusus*) saying the type species represented an extreme variation. That is an understatement to say the least. *Carinofusus* loses its axial sculpture completely early in ontogeny, spiral sculpture is very weak, it has an extremely strong shoulder carina without nodes, the terminal callus is not developed, and two parietal folds as opposed to a denticle. Considering this species a highly derived *Pseudofusus* is conjectural as there is no *Pseudofusus* species approximating the shell features of *Carinofusus*. We remove it from the synonymy of *Pseudofusus*.

***Pseudofusus affinis* (Bronn, 1831)**
Plate 7, figs 1-3

*1831 *Fusus affinis* Bronn, p. 39.
1872 *Fusus affinis* Bronn – d'Ancona, p. 251, pl. 14, fig. 5.
2000 *Fusinus affinis* (Bronn, 1831) – Chirli, p. 115, pl. 45, figs 1-6.

Material and dimensions – Maximum height 36.8 mm, width 13.4 mm. **CO**: NHMW 2023/0323/0097-0099 (3), NHMW 2023/0323/0100 (5). **EL**: NHMW 2023/0323/0101 (11).

Description – Shell medium sized, slender fusiform shell of up to seven teleoconch whorls; apical angle 39-41°. Protoconch paucispiral, conical of two moderately convex whorls, with prosocline axial riblets on last quarter protoconch whorl. Junction with teleoconch marked by scar. Early teleoconch whorls convex, weakly shouldered mid-whorl, with three spiral cords, abapical slightly weaker, overrunning eight rounded axial ribs, roughly

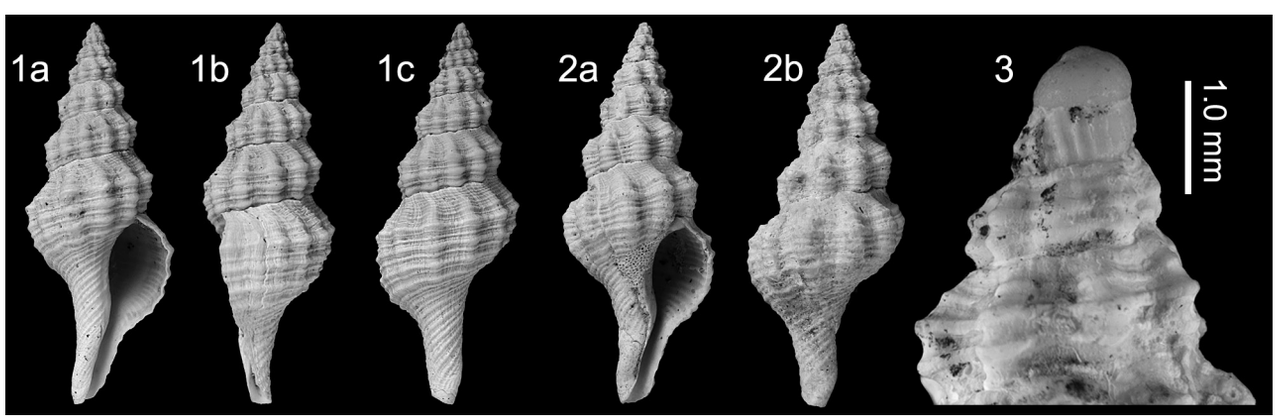

Plate 7. *Pseudofusus affinis* (Bronn, 1831); 1. NHMW 2023/0323/0097, height 36.8 mm, width 13.4 mm; 2. NHMW 2023/0323/0098, height 30.5 mm, width 11.5 mm; 3. NHMW 2023/0323/0099, juvenile, detail of protoconch. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

equal in width to their interspaces; cords slightly swollen over ribs. Later teleoconch whorls with broad, flattened to faintly concave subsutural ramp, angled to roundly angled at shoulder, convex below, separated by deeply incised, shallowly undulating suture. Axial sculpture of broad orthocline ribs, 9-12 on penultimate whorl, weakening over subsutural ramp. Spiral sculpture of close-set narrow cords over subsutural ramp; one cord short distance above shoulder stronger than the rest, three strong primary cords below with regular secondary and tertiary spirals intercalated; primaries swollen over ribs. Last whorl ~65% of total height, profile and sculpture as described above, three primary cords mid-whorl plus peribasal cord; fasciole moderately developed, rounded, regular cords of alternating strength over base and fasciole. Aperture moderately wide, pyriform. Columellar callus forming narrow, adherent rim. Columella broadly and weakly excavated, smooth, slightly twisted at transition to siphonal canal. Anal canal weakly incised, no parietal denticle. Outer lip thin, with numerous delicate lirae extending a variable distance within aperture. Siphonal canal moderately long, moderately short, moderately deflected to the left.

Discussion – We consider these specimens to be conspecific with those illustrated by Chirli (2000) as *Fusinus affinis* (Bronn, 1831). The series illustrated by that author shows some considerable intraspecific variability, but one of the specimens (2000, pl. 45, fig. 6) is identical to that illustrated here (Pl. 7, fig. 1). Our specimens also coincide with the specimen illustrated by d'Ancona (1872, pl. 14, fig. 5). We have not found any further discussion nor illustrations of the species.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2000). Upper Pliocene: western Mediterranean, Estepona Basin (this paper).

***Pseudofusus rostratus* (Olivi, 1792)**
Plate 8, figs 1-3

*1792 *Murex rostratus* Olivi, p. 153.
1793 *Murex sanctaeluciae* Salis Marschlins, p. 371, pl. 7, fig. 6.
1821 *Fusus crispus* Borson, p. 317.
1822 *Fusus strigosus* Lamarck, p. 130.
1840 *Murex cinctus* Bellardi & Michelotti, p. 12, pl. 1, fig. 15.
1847 *Fusus crispus* Borson – Bellardi & Michelotti, p. 272, pl. 9, fig. 17.
1847 *Fusus caelatus* Reeve, pl. 8, sp. 35.
1848 *Fusus fragosus* Reeve, pl. 19, sp. 71.
1847 *Murex rubicundus* Nardo, p. 59.
1872 *Fusus cinctus* Bell. & Micht. – d'Ancona, p. 126, pl. 10, figs -8.
1883 *Fusus rostratus* var, *carinata* Del Prete, p. 259.
1883 *Fusus rostratus* var, *subcarinata* Del Prete, p. 259.
1886 *Fusus carinulatus* Locard, p. 171, 562
1896 *Fusus bengasiensis* Sturany, p. 8, pl. 1, figs 1, 2.
1904 *Fusus rostratus* (Oliv.) – Sacco, p. 24, pl. 7, figs 1, 2.
1904 *Fusus rostratus* var. *cincta* Bell. Micht. – Sacco, p. 24, pl. 7, figs 3, 4.
1904 *Fusus rostratus* (Olivi) – Grabau, p. 58, pl. 7, figs 1-10.
1911 *Fusus rostratus* Olivi – Cerulli-Irelli, p. 239 [289], pl. 22 [39], fig. 2.
1911 *Fusus rostratus* var. *crispa* Bors. – Cerulli-Irelli, p. 239 [289], pl. 22 [39], fig. 3.
1918 *Fusus* (*Pseudofusus*) *dalpiazi* Coen, p. 318, fig. 1.
1959 *Fusinus rostratus* (Olivi) – Ruggieri *et al*., p. 69, pl. 19, figs 94, 95.
1959 *Fusinus rostratus crispus* Borson – Ruggieri *et al*., p. 70, pl. 15, fig. 85, pl. 16, fig. 99.
1973 *Fusinus* (*Fusinus*) *rostratus* (Olivi), 1792 f. *crispa* Borson – Caprotti & Vescovi, p. 169, pl. 2, fig. 10.
1973 *Fusinus* (*Fusinus*) *rostratus* (Olivi), 1792 – Caprotti & Vescovi, p. 169, pl. 2, fig. 11.
1974 *Fusinus* (*Fusinus*) *cinctus* (Bellardi & Michelotti, 1840) – Malatesta, p. 345, pl. 28, fig. 4.
1974 *Fusinus* (*Fusinus*) *rostratus* (Olivi, 1792) – Malatesta, p. 350, pl. 27, fig. 6.
1975 *Fusus rostratus* (Olivi) – Fekih, p. 111, pl. 33, fig. 4, pl. 34, fig. 16.
1988 *Fusinus crispus* (Borson, 1821) – Chirli, p. 21, pl. 8, fig. 12.
1988 *Fusinus rostratus* (Olivi, 1792) – Chirli, p. 21, pl. 8, fig. 15.
1992 *Fusinus* (*Fusinus*) *rostratus* (Olivi, 1792) – Cavallo & Repetto, p. 102, fig. 236.
2000 *Fusinus rostratus* (Olivi, 1792) – Chirli, p. 121, pl. 49, figs 4-12.
2008 *Fusinus rostratus* (Olivi, 1792) – Chirli & Richard, p. 50, pl. 9, fig. 10.
2010 *Fusinus rostratus* (Olivi, 1792) – Sosso & Dell' Angelo, p. 40, p. 57 unnumbered fig. bottom row centre.
2011 *Fusinus rostratus* (Olivi, 1792) – Chirli & Linse, p. 153, pl. 51, fig. 5.
2014 *Fusinus rostratus* (Olivi, 1792) – Tabanelli, p. 29, pl. 6, figs 5-9.
2018 *Fusinus rostratus* (Olivi, 1792) – Brunetti & Cresti, p. 76, fig. 279.
2022 *Fusinus rostratus* (Olivi, 1792) – Fassio *et al*., p. 633, figs 3C, D.

non 1853 *Fusus rostratus* Olivi – Hörnes, p 290, pl. 32, figs 1, 2. [fig. 1 = *Pseudofusus austriacus* (Hoernes & Auinger, 1890); fig. 2 = *Pseudofusus rostratoides* Harzhauser, Landau & Vermeij, 2024].
non 1853 *Fusus rostratus* Olivi – Hörnes, p 290, pl. 32, fig. 2.
non 1969 *Fusus* (*Fusus*) *rostratus cinctus* Bellardi – Atanacković, p. 208, pl. 11, fig. 8 [= *Euthria stuetzii* (Naumann, 1852)].
non 2000 *Fusinus crispus* (Borson, 1821) – Chirli, p. 117, pl. 46, figs 11, 12, pl. 47, figs 1-3 [?= *Apertifusus clavatus* (Brocchi, 1814)].
non 2023 *Pseudofusus rostratus* (Olivi, 1792) – Kovács & Vicián, p. 235, fig. 6F [= *Pseudofusus rostratoides* Harzhauser, Landau & Vermeij, 2024].

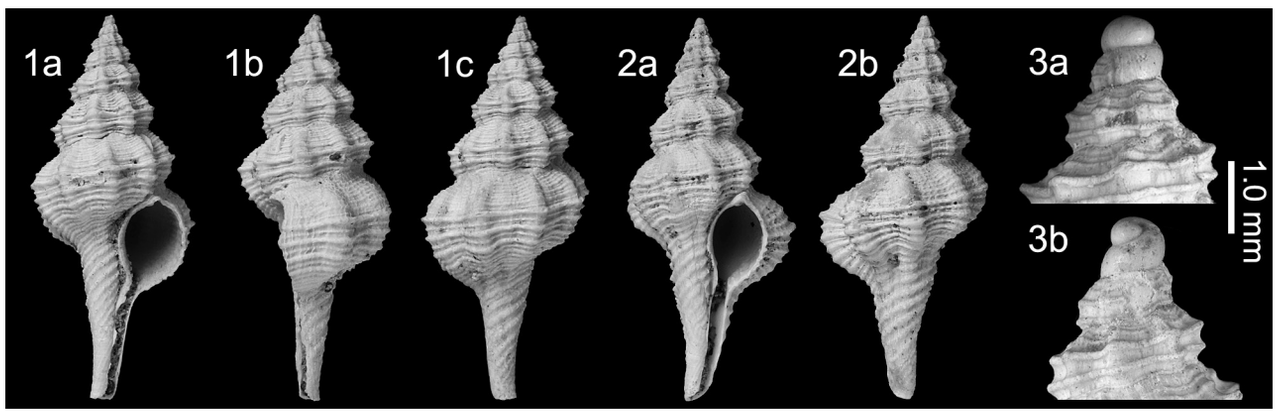

Plate 8. *Pseudofusus rostratus* (Olivi, 1792); 1. NHMW 2023/0323/0102, height 28.8 mm, width 12.4 mm; 2. NHMW 2023/0323/0103, height 29.3 mm, width 11.7 mm. Velerín conglomerates. 3. NHMW 2023/0323/0105, juvenile, detail of protoconch. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Material and dimensions – Maximum height 31.8 mm, width 12.6 mm. **CO**: NHMW 2023/0323/0102-0103 (2), NHMW 2023/0323/0104 (32). **VC**: NHMW 2023/0323/0105 (1), NHMW 2023/0323/0106 (1).

Description – Shell medium sized, moderately slender fusiform shell of up to six teleoconch whorls; apical angle 44-48°. Protoconch paucispiral, of two smooth, convex whorls with large nucleus. Last whorl with faint axial riblets close to transition to teleoconch and thickened scar delimiting protoconch. First two teleoconch whorls convex, with three primary cords at beginning of teleoconch; second cord delimiting shoulder, third cord just above suture, overrunning eight narrow, widely spaced ribs. Abapically subsutural ramp flattens to become weakly convex, angular and sharply delimited by strengthened shoulder cord, third primary cord strengthens, although remains slightly weaker than shoulder cord; small spinous tubercles developed on primary cords at axial intersections in some specimens; numerous secondary and tertiary cords develop over subsutural ramp, one secondary intercalated between primaries below shoulder. Prominent axial growth lines give surface finely imbricate appearance. Suture deeply incised, shallowly undulating. Last whorl wide, attaining ~68% of total height, with broad, weakly convex subsutural ramp, sharp shoulder, weakly convex below, rapidly constricting at base; siphonal canal and insignificant fasciole covered by very prominent primary spiral cords. Aperture ovate, moderately wide. Columellar callus forming narrow, sharply delimited rim. Columella smooth, moderately excavated, weakly twisted at transition to siphonal canal. Anal canal small, indistinct, accentuated by small parietal denticle. Outer lip thickened by terminal varix, smooth to weakly lirate within. Siphonal canal moderately long, narrow, straight.

Discussion – *Pseudofusus rostratus* (Olivi, 1792) is a highly variable species, which has led to numerous varietal descriptions in both the literature reviewing fossil and present-day molluscs. Typical *P. rostratus* has strongly carinate whorls (see Chirli, 2000, pl. 49, figs 4-8, 11, 12). Weakly carinate fossil specimens, or specimens in which the shoulder carina is subobsolete, have been given the name *F. crispus* (*e.g.*, Ruggieri *et al*., 1959; Malatesta, 1974). However, we agree with Tabanelli (2014, p. 31) in uniting these forms.

This species has been widely recorded from the Middle Miocene Paratethys. However, as shown by Harzhauser *et al*. (2024) these records are based on misidentifications. Some refer to *Pseudofusus austriacus* (Hoernes & Auinger, 1890) (*i.e*., Hörnes, 1853 *partim*) that differs in being a much larger species (about 100-112 mm in height) and has a multispiral protoconch, others to *Pseudofusus rostratoides* Harzhauser, Landau & Vermeij, 2024 (*i.e*., Hörnes, 1853 *partim*; Kovács & Vicián, 2023) which is similar in size and teleoconch characters to *P. rostratus*, but again differs in its multispiral protoconch.

It therefore seems that the genus *Pseudofusus* is an example of a genus that has lost its planktotrophic mode of development, as numerous Miocene species have multispiral protoconch whilst Pliocene to extant species (22 extant Mediterranean species recorded by Fassio *et al*., 2022) are characterised by their paucispiral protoconchs (for further discussion see Harzhauser *et al*., 2024, p. 49). We note that specimens of *Fusinus crispus* illustrated by Chirli (2000, pl. 46, figs 11, 12, pl. 47, figs 1-3) are not that species and possibly represent juvenile *Apertifusus clavatus* (Brocchi, 1814).

Distribution – Lower Pliocene: western Mediterranean, Tunisia (Fekih, 1975); central Mediterranean, Italy (Chirli, 1988, 2000; Tabanelli, 2014; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al*., 1959; Caprotti & Vescovi, 1973; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Tabanelli, 2014). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Tabanelli, 2014); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Mediterranean and Atlantic coast of Morocco (Fassio *et al*., 2022).

Genus *Takashius* Kantor, Fedosov, Snyder & Bouchet, 2022

Type species (by typification of replaced name) – *Fusolatirus kuroseanus* Okutani, 1975, present-day, Indo-West Pacific.

2018 *Okutanius* Kantor, Fedosov, M.A. Snyder & Bouchet, 2018. Junior homonym of *Okutanius* D.R. Smith, 1981.

2022 *Takashius* Kantor, Fedosov, Snyder & Bouchet, p. 117. Replacement name for *Okutanius* Kantor, Fedosov, M.A. Snyder & Bouchet, 2018, *non Okutanius* D.R. Smith, 1981.

***Takashius ligusticus* (Bellardi, 1884)**
Plate 9, figs 1, 2

*1884 *Latirus ligusticus* Bellardi, p. 46, pl. 2, fig. 25.

1981 *Latirus ligusticus* Bellardi, 1884 – Ferrero Mortara *et al*., p. 145, pl. 40, fig. 2.

2000 *Fusinus lamellosus* (Borson, 1821) – Chirli, p. 119, pl. 48, figs 1-9 [*non Parvofusus lamellosus* (Borson, 1821)].

Material and dimensions – Maximum height 17.9 mm, width 7.6 mm. **EL**: NHMW 2023/0323/0095-0096 (2).

Description – Shell small, moderately slender fusiform, of up to six teleoconch whorls; apical angle 40°. Protoconch tall dome-shaped, multispiral, of 3.5 smooth, convex whorls. Junction with teleoconch delimited by prosocline scar. Teleoconch whorls very strongly convex, separated by deeply impressed undulating suture. Sculpture of strong, elevated cords overrunning eight rounded ribs extending between sutures, roughly half width of their interspaces; cords very slightly swollen over ribs. On later whorls 2-3 weaker cords develop in subsutural area, secondary thread intercalated between last two primaries on penultimate whorl. Last whorl 59% of total height, strongly convex, with nine axial ribs continuing over base, weakening over fasciole; base strongly constricted with prominent primary and secondary spiral cords; indistinct fasciole. Aperture moderately wide pyriform. Columellar callus forming narrow rim, sharply delimited from base. Columella deeply excavated in upper half, with 2-3 well-developed columellar denticles on abapical half, strongly twisted at fasciole. Anal canal wide, accentuated by weak parietal denticle. Outer lip thickened by terminal varix with prominent lirae extending deep within aperture. Siphonal canal moderately short, moderately narrow, almost straight or deflected to the left.

Discussion – *Takashius ligusticus* (Bellardi, 1884) is extremely similar to *Parvofusus lamellosus* (Borson, 1821) with which it co-occurs in the Estepona assemblages. They have similar dome-shaped multispiral protoconchs and the teleoconch is almost identical in profile and sculpture. They differ most notably by the main character separating the two genera, that is the folds on the abapical half of the columella in the genus *Takashius*, whereas in *Parvofusus* the columella is smooth (see Harzhauser *et al*., 2024, p. 63).
As noted by Tabanelli (2014, p 35), the Italian Pliocene specimens identified as *Fusinus lamellosus* by Chirli (2000, pl. 48, figs 1-9) are not that species, but *T. ligusticus*, as he clearly describes the columellar denticles "*Bordo columellare con due dentelli poco visibile presso il canale* [columella edge bearing two weak denticles close to the (siphonal) canal]" (Chirli, 2000, p. 119).
Takashius ligusticus was said to differ from the slightly older *T. cognatus* (Bellardi, 1884) from the Tortonian Upper Miocene of Italy (see Ferrero Mortara *et al*., 1981, pl. 40, fig. 3 for illustration of syntype) in having a more acute spire, more numerous and narrower spiral cords, with only one secondary intercalated between primaries, and a longer siphonal canal (Bellardi, 1884, p. 46). We have not seen this species and cannot comment on any intraspecific variability. They are certainly closely similar.

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1884; Ferrero Mortara *et al*., 1981; Chirli, 2000; Tabanelli, 2014). Upper Pliocene: western Mediterranean, Estepona Basin (this paper).

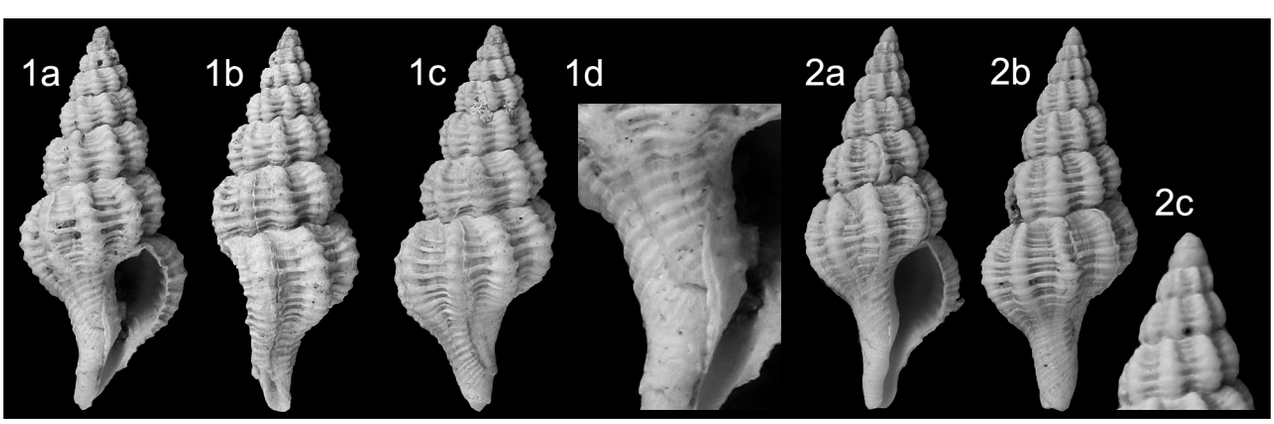

Plate 9. *Takashius ligusticus* (Bellardi, 1884); 1. NHMW 2023/0323/0095, height 17.9 mm, width 7.6 mm; 2. NHMW 2023/0323/0096, height 15.2 mm, width 6.1 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Subfamily Peristerniinae Tryon, 1880
Genus *Tarantinaea* Monterosato, 1917

Type species (by monotypy) – *Murex lignarius* Linnaeus, 1758, present-day, Mediterranean.

1917 *Tarantinaea* Monterosato, p. 19.

***Tarantinaea danconai* (Pecchioli, 1864)**
Plate 10, figs 1, 2; Plate 14, fig. 2

*1864 *Fusus D'Anconae* Pecchioli, p. 506, pl. 5, figs 1, 2.
1872 *Fasciolaria etrusca* D'Anc. – d'Ancona, p. 201, pl. 12, figs 1, 2 [*non Fusus etruscus* Pecchioli, 1862; = *Apertifusus clavatus* (Brocchi, 1814)]
1884 *Latirus D'Anconae* (Pecch.) – Bellardi, p. 33, pl. 2, fig. 5.
1904 *Fasciolaria* (*Plesiolatirus*) *D'Anconae* var. *sexcostata* Sacco, p. 30, pl. 9, fig. 5.
1959 *Lathyrus d'Anconae* (Pecchioli) – Ruggieri *et al*., p. 61, pl. 14, fig. 82.
1969 *Lathyrus D'Anconae* (Pecchioli) – Mastrorilli, p. 119, pl. 8, fig. 18.
1974 *Fasciolaria* (*Plesiolatirus*) *danconae* (Pecchioli, 1864) – Malatesta, p. 344, pl. 27, fig. 7.
1998 *Latirus danconai* (Pecchioli, 1864) – Muñiz Solís, p. 7, pl. 2, figs A-E.
?2014 *Pleuroploca* cf. *danconae* (Pecchioli, 1864) – Tabanelli, p. 11, pl. 3, fig. 8 (poorly preserved).

non 2011 *Fasciolaria danconae* (Pecchioli, 1864) – Chirli & Linse, p. 149, pl. 50, fig. 3.

Material and dimensions – Maximum height 68.0 mm, width 29.1 mm. **CO**: NHMW 2023/0323/0015-0016 (2), NHMW 2023/0323/0017 (2).

Description – Shell large, very robust, broad fusiform, of up to eight teleoconch whorls; apical angle 51-58°. Protoconch poorly preserved, but seems to be paucispiral, of about two whorls, with large nucleus (Pl. 14, fig. 2). Earliest teleoconch whorls almost flat-sided, with broad flattened subsutural ramp, whorl very slightly swollen and convex below, bearing three primary spiral cords, overrunning indistinct broad axial ribs. Abapically, subsutural ramp becomes weakly concave, poorly delimited by rounded shoulder, increasingly convex abapical half of whorl, separated by moderately impressed undulating shoulder. Axial sculpture becomes predominant; 7-8 broad rounded ribs, weakening over subsutural ramp, broadening further towards lower suture, overrun by narrow subequal spiral cords, on penultimate whorl about five slightly weaker over subsutural ramp, seven below; one secondary spiral intercalated between lower two primaries in some specimens. Two most adapical cords slightly strengthened in some specimens forming weak subsutural collar. Last whorl 64-70% of total height, with moderate width, concave subsutural ramp, roundly angled at shoulder, convex below, moderately constricted at base; sculpture as described above, with single weak secondary thread intercalated in primary interspaces over base and fasciole. Aperture moderately wide, pyriform. Columella moderately and broadly excavated, smooth, weakly twisted at fasciole. Columellar callus forming narrow, thickened rim, sharply delimited from base. Anal canal broad, weakly incised, accentuated by weak parietal denticle. Outer lip not thickened, bearing weak elongated denticles within. Siphonal canal moderately short, narrow, slightly deflected to the left.

Discussion – We interpret these specimens as being within the intraspecific range of *Tarantinaea danconai* (Pecchioli, 1864), as the Estepona specimens are similar to those from the Italian Pliocene illustrated by Bellardi (1884, pl. 2, fig. 5) and Ruggieri *et al*. (1959, pl. 14, fig. 82). We note that the type specimen illustrated by Pecchioli (1864, pl. 5, figs 1, 2) and specimens illustrated by Chirli (2000, pl. 43, figs 1-7) have stronger shoulder knobs and the shoulder cord and a primary cord on either side of it are stronger than the others, which is not seen in the Estepona specimens. Moreover, the anal canal is not as deeply incised as it is in the type. Two specimens of *T. danconai* from Pietrafitta (San Gimignano, Siena; RGM.SSS.40608, RGM.SSS.44586) in the Naturalis collection were examined (BL). They compare in size with the Es-

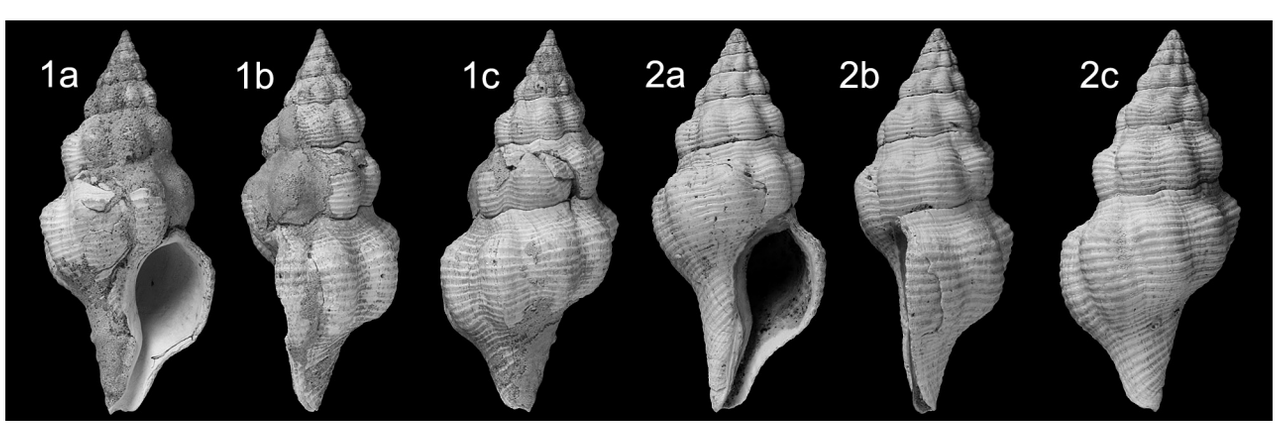

Plate 10. *Tarantinaea danconai* (Pecchioli, 1864); 1. NHMW 2023/0323/0015, 64.3 mm, width 31.0 mm; 2. NHMW 2023/0323/0016, height 53.1 mm, width 23.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

tepona specimens and like them have a far more weakly incised anal canal than that illustrated by Pecchioli and Chirli. One of the San Gimignano specimens has two cords at the periphery slightly stronger, but less marked than in Pecchioli's specimen, and the shoulder nodes are also weaker. In the second specimen the peripheral cords are hardly strengthened. Therefore, there is no clear distinction between the Estepona and Italian specimens.

We note that Muñiz Solís (1998, p. 7) corrected the name ending to *danconai*. This emendation is justified as in the species discussion is written "*Mi faccio il piacere di dedicare questa conchiglie all'egregio amico signor dottor Cesare D'Ancona*,…." (Pecchioli, 1964, p. 508), thus making a clear statement as to whom this species was dedicated.

Bellardi (1884, p. 32) erected the genus *Plesiolatirus* with *Latirus d'anconae* as one of five species included in the group [type species *Latirus nodosus* Michelotti, in Bellardi, 1884, by subsequent designation Cossmann, 1901, Lower Miocene, Italy]. Malatesta (1974, p. 344) overlooked Cossmann's type designation and selected *Fusus d'anconae* as type for *Plesiolatirus*. According to Snyder *et al*. (2012, p. 26) the holotype of *L. nodosus* is poorly preserved and the five species included in *Plesiolatirus* by Bellardi (1884) form a disparate group and are unlikely to be congeneric. Glibert (1963, p. 136) proposed placement in the present genus with the combination *Fasciolaria* (*Tarantinaea*?) *d'anconae*, at the time placed within the subfamily Fasciolariinae. Snyder *et al*. (2012, p. 26) argued for placement of *Tarantinaea* in the Peristerniinae based on the presence of an adapical sinus, which, according to those authors, was the most distinctively peristerniine feature.

Malatesta (1974, p. 345) suggested that in Italian deposits this species was associated with deeper water clays. This is not the case in Estepona, where it occurs in the shallower water Velerín conglomerates assemblage. Bongo (1914) recorded this species from the Upper Miocene Tortonian of Stazzano (Alessandria, Italy). We have included this record in our distribution although we have not seen any Miocene specimen illustrated.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Bongo, 1914). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1884; Sacco, 1904). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Muñiz Solís, 1998); central Mediterranean, Italy (Ruggieri *et al*., 1959; Mastrorilli, 1969; Malatesta, 1974).

Tarantinaea fimbriata (Brocchi, 1814)

Plate 11, figs 1-3

*1814 *Murex fimbriatus* Brocchi, p. 419, pl. 8, fig. 8.
1872 *Fasciolaria fimbriata* Bronn [*sic*] – d'Ancona, p. 79, pl. 11, fig. 8.
1904 *Pleuroploca*? *fimbriata* (Br.) – Sacco, p. 28, pl. 8, figs 18, 19.
1904 *Pleuroploca*? *fimbriata* var. *duocostata* Sacco, p. 28, pl. 8, figs 20, 21.
1904 *Pleuroploca*? *fimbriata* var. *variocarinata* Sacco, p. 28, pl. 8, figs 20, 21.
1904 *Pleuroploca*? *fimbriata* var. *parvolongiuscula* Sacco, p. 28.
1911 *Fasciolaria* (*Pleuroploca*) *fimbriata* Br. – Cerulli-Irelli, p. 240 [290], pl. 22 [39], fig. 6.
1955 *Fasciolaria* (*Pleuroploca*) *fimbriata* (Brocchi 1814) – Rossi Ronchetti, p. 232, fig. 123.
1959 *Pleuroploca fimbriata* (Brocchi) – Ruggieri *et al*., p. 63, pl. 14, fig. 81, pl. 15, fig. 88.
1973 *Fasciolaria* (*Fasciolaria*) *fimbriata* (Brocchi), 1814 – Caprotti & Vescovi, p. 168, pl. 2, fig. 14.
1974 *Fasciolaria* (*Pleuroploca*) *fimbriata* (Brocchi, 1814) – Malatesta, p. 345, pl. 28, fig. 4.
1975 *Fasciolaria* (*Pleuroploca*) *fimbriata* (Brocchi) – Fekih, p. 113, pl. 34, fig. 7.
1976 *Fasciolaria fimbriata* (Brocchi) – Caprotti, p. 11, pl. 16, fig. 4.
1978 *Murex fimbriatus* Brocchi, 1814 – Pinna & Spezia, p. 148, pl. 36, fig. 4.
1998 *Latirus fimbriatus* (Brocchi, 1814) – Muñiz Solís, p. 8, pl. 2, figs F-K.
1992 *Fasciolaria fimbriata* (Brocchi, 1814) – Cavallo & Repetto, p. 102, fig. 232.
2000 *Fasciolaria fimbriata* (Brocchi, 1814) – Chirli, p. 112, pl. 44, figs 1-5.
2014 *Pleuroploca fimbriata* (Brocchi, 1814) – Tabanelli, p. 11, pl. 2, fig. 4, pl. 3, fig. 2, pl. 5, fig. 8.

non 1852 *Fasciolaria fimbriata* – Naumann, plate captions, pl. 70, fig. 12 [=*Tarantinaea hoernesii* (Seguenza, 1875)].
non 1854 *Fasciolaria fimbriata* Brocc. – Hörnes, p. 299, pl. 33, figs 5–7 [=*Tarantinaea hoernesii* (Seguenza, 1875)].
non 1884 *Fasciolaria fimbriata* – Quenstedt, p. 616, pl. 209, fig. 70 [=*Tarantinaea hoernesii* (Seguenza, 1875)].
non 1962 *Fasciolaria* (*Pleuroploca*) *fimbriata* Brocchi var. – Strausz, p. 80, pl. 29, fig. 2 [*non Tarantinaea fimbriata* (Brocchi, 1814)].
non 1966 *Fasciolaria* (*Pleuroploca*) *fimbriata* Brocchi, 1814 var. – Strausz, p. 353, pl. 29, fig. 2 [=*Tarantinaea hoernesii* (Seguenza, 1875)].
non 1995 *Fasciolaria fimbriata* (Brocchi, 1814) – Bałuk, p. 248, pl. 36, fig. 6 [*non Tarantinaea fimbriata* (Brocchi, 1814)].
non 1998 *Fasciolaria* (*Pleuroploca*) *fimbriata* Brocchi – Schultz, p. 68, pl. 27, fig. 9 [*non Tarantinaea fimbriata* (Brocchi, 1814)].

Material and dimensions – Maximum height 47.7 mm, width 21.4 mm. **CO**: NHMW 2023/0323/0108-0110 (3), NHMW 2023/0323/0107 (19).

Description – Shell medium-sized, robust, broad fusiform, of up to six teleoconch whorls; apical angle 46-50°. Protoconch paucispiral, of two convex whorls with large nucleus. Junction with teleoconch marked by prosocline scar. Early teleoconch whorls with broad

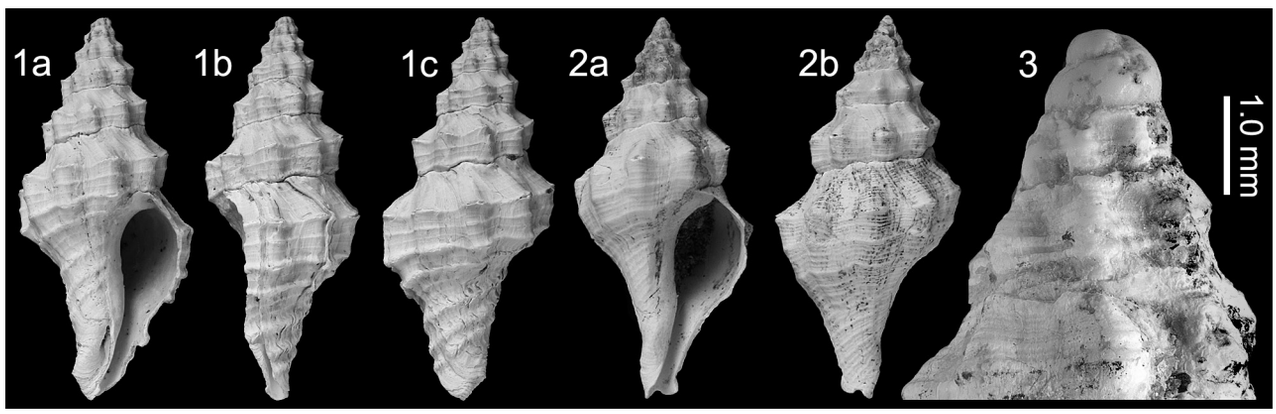

Plate 11. *Tarantinaea fimbriata* (Brocchi, 1814); 1. NHMW 2023/0323/0108, height 47.7 mm, width 21.4 mm; 2. NHMW 2023/0323/0109, height 36.7 mm, width 17.6 mm: 3. NHMW 2023/0323/0110, juvenile, detail of protoconch. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

concave subsutural ramp, weakly shouldered, bearing prominent subsutural cord, 3-4 weaker cords over ramp and three stronger primary cords below, mid-cord delimiting shoulder, overrunning eight widely spaced, rounded axial ribs extending between sutures, about half width of their interspaces. Secondary cords intercalated from third teleoconch whorl. Suture narrowly impressed, undulating. Abapically whorls become more strongly and sharply shouldered, axials weaken over subsutural ramp, spirals remain thin; weakening over subsutural ramp, three primary cords slightly spinous over axial intersections, especially at shoulder, secondary sculpture remains weak; surface covered in axial growth lines of irregular strength. Last whorl ~ 68% of total height, strongly and sharply shouldered, subcylindrical between shoulder and basal angulation; base strongly constricted; fasciole prominent, slightly twisted, separated from columellar callus by broad chink. Sculpture of three primary spiral cords placed at shoulder, mid-whorl, and base, with weak secondary and tertiary cords intercalated; ribs fade below periphery. Aperture moderately wide, pyriform. Columella moderately excavated in adapical half; two weak columellar folds on abapical half, usually not visible on apertural view. Columellar callus forming broad, thickened rim, sharply delimited in fully grown specimens. Anal canal weakly incised, accentuated by broad, low parietal fold. Outer lip not thickened, smooth within. Siphonal canal moderately short, narrow, slightly deflected to the left.

Discussion – Snyder *et al.* (2012, p. 55) placed *Murex fimbriatus* Brocchi, 1814 in the Peristerniinae genus *Tarantinaea* Monterosato, 1917 [type species *Murex lignarius* Linnaeus, 1758; by monotypy; present-day, Mediterranean Sea], a position followed by Landau *et al.* (2013), Kovács (2022), and Harzhauser *et al*. (2024).
Paratethyan specimens identified as this species represent *T. hoernesii* (Seguenza, 1875) that differs in having a multispiral protoconch, wider apical angle, in having a lower spire with the whorls less stepped, in having sharper sculpture with more strongly developed secondary cords and in having more strongly developed columellar folds (see Landau *et al*., 2013, p. 198; Harzhauser *et al*., 2014, p. 31). Ruggieri *et al*. (1959, p. 64, pl. 14, fig. 80) described *Pleuroploca fimbriata amplectens* Ruggieri, Bruno & Curti, 1959 from the Pliocene of Altavilla (Palermo). It was based on two specimens, of which only the holotype was illustrated that differs from *T. fimbriata* in its less scalate spire and much stronger secondary spiral sculpture. Indeed, it is more closely similar to the Middle Miocene Paratethyan *T. hoernesii* and differs from the Paratethyan species in having a less scalate spire, broader subsutural ramp, two primary cords mid-whorl on the last whorl delimiting the shoulder and base, as opposed to *T. hoernesii* that has three, a mid-cord between the shoulder and peribasal cords. The three species are undoubtedly closely related and *T. hoernesii* is probably ancestral to these Pliocene species.
Numerous congeners have been described from the Italian Pliocene that have not been found in Estepona. These Italian species require revision, but amongst these *Tarantinaea iriae* (Bellardi, 1884) (see Ferrero Mortara *et al*., 1981, pl. 38, fig. 5 for syntype) is smaller, slenderer and with finer sculpture; *T. coppiana* (D'Ancona, 1872) (see Brunetti & Cresti, 2018, figs 283, 283A) has similar sculpture but is squatter and more constricted at the base, and *T. subfimbriata* (Bellardi, 1884) (see Ferrero Mortara *et al*., 1981, pl. 38, fig. 10 for syntype) is smaller and squatter, the outer lip has more numerous denticles and there are four folds on the columella.

Distribution – Lower Pliocene: western Mediterranean, Tunisia (Fekih, 1975); central Mediterranean, Italy (Chirli, 2000; Tabanelli, 2014). Upper Pliocene: western Mediterranean, Estepona Basin (Muñiz Solís, 1998); central Mediterranean, Italy (Bellardi, 1884; Sacco, 1904; Ruggieri *et al*., 1959; Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992; Tabanelli, 2014). Lower Pleistocene. Central Mediterranean, Italy (Cerulli-Irelli, 1911).

***Tarantinaea micalii* nov. sp.**
Plate 12, figs 1-4

ZooBank registration – urn:lsid:zoobank.org:act:9FF13116-B23E-407B-A9FE-54659910943D

Type material – Holotype NHMW 2023/0323/0018, 88.6 mm, width 36.2 mm; paratype 1 NHMW 2023/0323/0019, height 76.3 mm, width 32.6 mm; paratype 2 NHMW 2023/0323/0020, height 68.6 mm, width 28.6 mm; paratype 3 NHMW 2023/0323/0021, height 72.2 mm, width 30.0 mm; paratype 4 NHMW 2023/0323/0022, height 75.2 mm, width 30.1 mm.

Other material – Known from type series only.

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

Type stratum – unnamed beds lower Piacenzian, Upper Pliocene.

Etymology – Named after Pasquale Micali of Fano (Italy), friend and collaborator of the first author, in recognition of his enormous contribution to both extinct and extant molluscan taxonomy. *Tarantinaea,* gender feminine.

Diagnosis – *Tarantinaea* species of large size, paucispiral protoconch, teleoconch of up to eight convex whorls, bearing 7-8 broad axial ribs that fade on last two whorls, fine spiral sculpture covering entire surface, outer lip weakly lyrate within.

Description – Shell large, very robust, broad fusiform, of up to eight teleoconch whorls; apical angle 51-53°. Protoconch poorly preserved, but seems to be paucispiral, of about two whorls, with large nucleus. Earliest teleoconch whorls with broad subsutural ramp, whorl swollen and convex below, bearing three primary spiral cords, overrunning 7-8 broad axial ribs. Abapically, subsutural ramp becomes concave, poorly delimited by rounded shoulder, axial ribs strengthen, profile abapical half of whorl increasingly convex, separated by moderately impressed undulating shoulder. At beginning penultimate whorl axials rapidly fade, leaving narrow subequal spirals covering entire surface. Last whorl ~68% of total height, with moderate width, concave subsutural ramp, roundly angled at shoulder, convex below, moderately constricted at base; sculpture as described above, with single weak secondary thread intercalated in primary interspaces below shoulder. Aperture moderately wide, pyriform. Columella moderately and broadly excavated, smooth, weakly twisted at fasciole. Columellar callus forming narrow, thickened rim, sharply delimited from base. Anal canal broad, weakly incised, accentuated by very weak parietal denticle. Outer lip not thickened, bearing weak elongated denticles or short lirae within. Siphonal canal moderately short, narrow, slightly deflected to the left.

Discussion – These specimens are highly reminiscent of *Tarantinaea crassosicula* (Ruggieri, Bruno & Curti, 1959). This taxon was originally described as a subspecies of *Lathyrus d'Anconae* (Pecchioli, 1864) and said to differ from it in having more inflated and rounded whorls, the ribs far more numerous and weaker, reduced to undulations on the last whorl. The Estepona specimens agree in all characters, except in the number of ribs. According to Ruggieri *et al*. (1959, p. 62), *T. crassosicula* has 10-13 ribs, whereas the Estepona specimens never have more than 7-8 ribs. Apart from the type series, other Estepona specimens in private collections (Henk Mulder collection) are consistent in this difference, and we therefore consider it a distinct species within the *T. danconai* species group.
Tarantinaea micalii nov. sp. occurs together with *T. danconai* (Pecchioli, 1864) in the Velerín conglomerates assemblage. They are of similar size and can easily be separated as the ribs continue well developed to the outer lip in the latter.

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

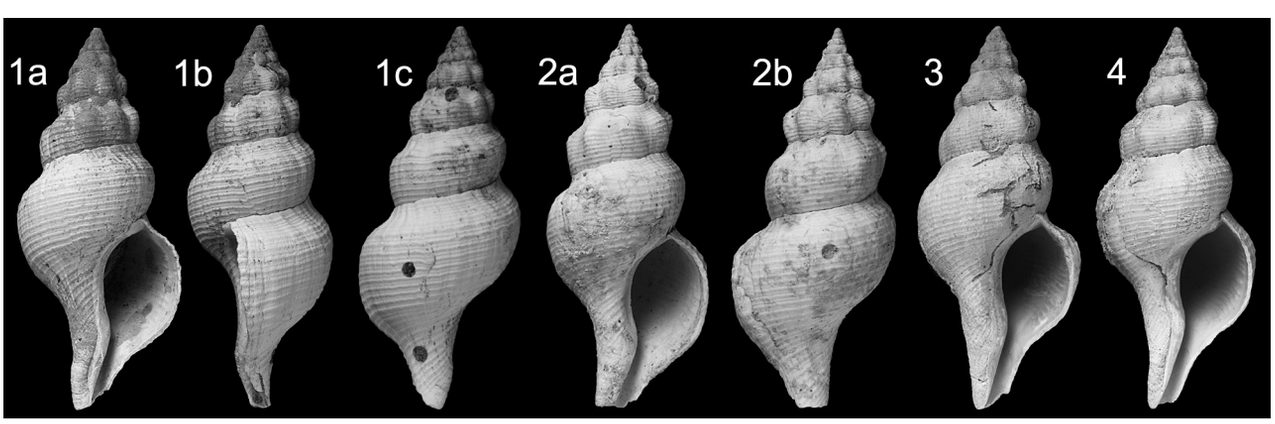

Plate 12. *Tarantinaea micalii* nov. sp.; 1. **Holotype** NHMW 2023/0323/0018, 88.6 mm, width 36.2 mm; 2. **Paratype 1** NHMW 2023/0323/0019, height 76.3 mm, width 32.6 mm; 3. **Paratype 2** NHMW 2023/0323/0020, height 68.6 mm, width 28.6 mm; 4. **Paratype 3** NHMW 2023/0323/0021, height 72.2 mm, width 30.0 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

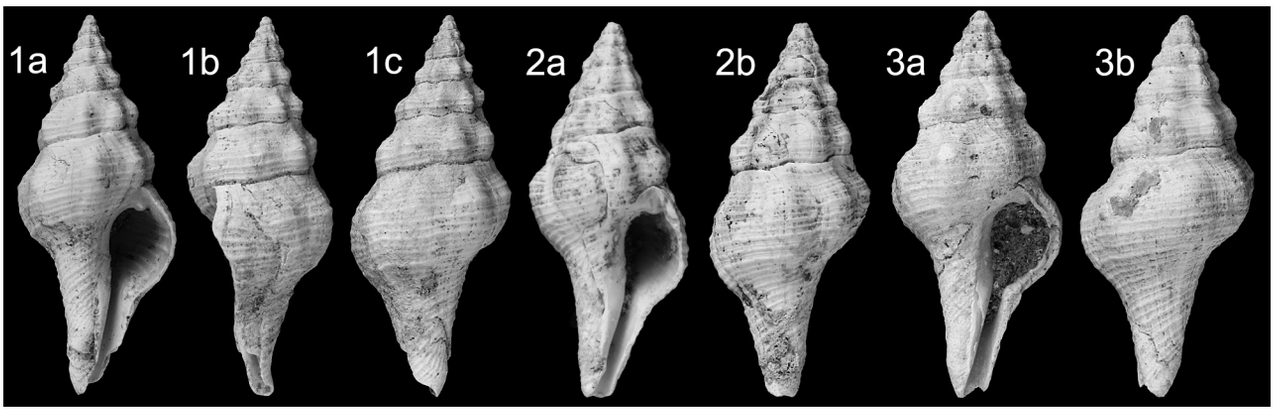

Plate 13. *Tarantinaea proxima* (Bellardi, 1884); 1. NHMW 2023/0323/0111, 34.0 mm, width 13.5 mm; 2. NHMW 2023/0323/0112, height 33.5 mm, width 13.3 mm; 3. NHMW 2023/0323/0113, height 38.4 mm, width 16.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

***Tarantinaea proxima* (Bellardi, 1884)**
Plate 13, figs 1-3

*1884 *Latirus proximus* Bellardi, p. 35, pl. 2, fig. 7.
1981 *Latirus proximus* Bellardi, 1884 – Ferrero Mortara *et al*., p. 143, pl. 39, fig. 1.

Material and dimensions – Maximum height 38.4 mm, width 16.6 mm. **CO**: NHMW 2023/0323/0111-0113 (3), NHMW 2023/0323/0114 (2).

Description – Shell medium-sized, robust, slender fusiform, of up to six teleoconch whorls; apical angle 45-53°. Protoconch poorly preserved but paucispiral, of probably just over one whorl with large nucleus. Junction with teleoconch not clearly preserved. Early teleoconch whorls with broad concave subsutural ramp, strongly shouldered, bearing weak subsutural cord, ramp smooth, and three stronger primary cords below, mid-cord delimiting shoulder, overrunning seven broad rounded axial ribs, slightly narrower than their interspaces, weakening over subsutural ramp, strongly developed below shoulder. Fourth cord appears at abapical suture from second whorl. Further weak cords developed over subsutural ramp from penultimate whorl and secondaries intercalated below shoulder. Suture shallow, narrowly impressed, undulating. Last two whorls shoulder weakens, ribs broaden. Close-set weak axial growth lines and frequent stronger growth halts prominent on last two whorls. Last whorl ~69% of total height, roundly shouldered, moderately constricted at base; fasciole poorly delimited. Sculpture of weak cords or alternating strength; shoulder and peribasal cords slightly stronger; ribs fade below periphery. Aperture small, ovate, moderately wide; outer lip not thickened, bearing seven strong, elongated lirae starting some distance behind peristome, extending deep within aperture, tooth-like thickening developed abapically at edge of siphonal canal; anal canal marked by narrow groove, accentuated by strongly developed parietal fold; siphonal canal moderately long, straight, narrow, shallowly notched at tip. Columella moderately excavated in adapical half; three weak columellar folds, abapical subobsolete. Columellar callus forming broad, thickened rim, sharply delimited.

Discussion – We can find no illustrated records for this species following its original description by Bellardi (1884) and the illustration of the syntype by Ferrero Mortara *et al*. (1981, pl. 39, fig. 1). It is quite distinctive, differing from its congeners in its relatively slender elongated profile, shallow suture, convex late teleoconch whorls, moderately strongly constricted base, three columellar folds, of which the abapical is subobsolete, and long straight siphonal canal. Indeed, these distinctive characters led Bellardi to place this species in a section of its own (4ª Serie; 1884, p. 35).

Distribution – Lower Pliocene: central Mediterranean, Italy (Bellardi, 1884). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

***Tarantinaea* sp.**
Plate 14, fig. 1

Material and dimensions – Height 29.4 mm, width 14.0 mm. **VC**: NHMW 2023/0323/0123 (1).

Discussion – A single juvenile specimen from the deeper water Velerín carretera assemblage resembles a juvenile specimen of *Tarantinaea danconai* (Pecchioli, 1864), and has the same number of rounded ribs, but differs in having a more pointed apex with a multispiral protoconch of 3.25 whorls, whereas *T. danconai* has a paucispiral protoconch of about two whorls (compare Pl. 14, figs 1c and 2). We have not seen such a protoconch illustrated from other fossil congeners and await adult specimens to better characterize the species.

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

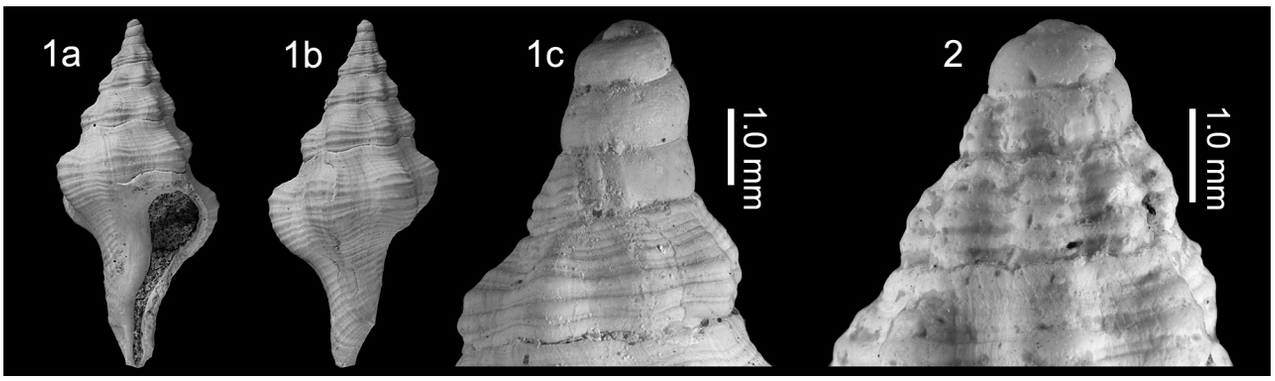

Plate 14. 1. *Tarantinaea* sp.; NHMW 2023/0323/0123, 1c, detail of protoconch, height 29.4 mm, width 14.0 mm. 2. *Tarantinaea danconai* (Pecchioli, 1864); NHMW 2023/0323/0124 (juvenile), detail of protoconch, height 35.6 mm, width 16.4 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion

Dolicholatiridae

One species is reported within this family and described as new, *Dolicholatirus alboranensis* nov. sp. This species was also illustrated by Muñiz Solís (1998; as *D. bronni*). This is the only Pliocene record of the genus that is widespread, although never common, in the European Miocene Atlantic, Paratethys and Proto-Mediterranean (Figure 1). As already mentioned in previous parts of this monograph the Pliocene Alboran Sea acted as a refuge for Miocene taxa that did not manage to survive elsewhere in the Pliocene Mediterranean (see Landau *et al*., 2003, 2004, 2007 for other examples), and still does today for Pliocene lineages (see Rubio & Gofas, 2024).

Fasciolariidae

In this family 13 species representing seven genera are recognised, of which one is new *Tarantinaea micalii* nov. sp., and one is left in open nomenclature (Figure 1). Within this group our taxonomy differs markedly from that of Muñiz Solís (1998). Within the genus *Latirus* that author illustrated specimens as *L. lawleyanus* (D'Ancona, 1872), *L.* cf. *asperulus* Bellardi, 1884, and *L.* cf. *bugellensis* Bellardi, 1884, all originally described from the Lower Pliocene of Italy, and *L. gastaldii* Bellardi, 1884 originally from the Upper Miocene of Italy. The specimens illustrated are all fairly similar in shape and sculpture and most are quite worn. They could represent gerontic abraded specimens of *Tarantinaea fimbriata* (Brocchi, 1814).

Of the 13 species only one, *Pseudofusus rostratus* (Olivi, 1792) is still living in the Mediterranean and Atlantic coasts of Morocco today. This group is relatively thermophilic, and the assemblage of species is fairly typical for the tropical Pliocene Mediterranean-West African palaeobiogeographic province.

Acknowledgements

We would like to thank Pasquale Micali for his advice on certain species included herein and Geerat J. Vermeij of the University of California, Davis, California and Roland Hadorn of the Natural History Museum Bern for reviewing the paper. Our thanks also to Carlos Marques da Silva of the University of Lisbon, Portugal, for his advice and help with graphics.

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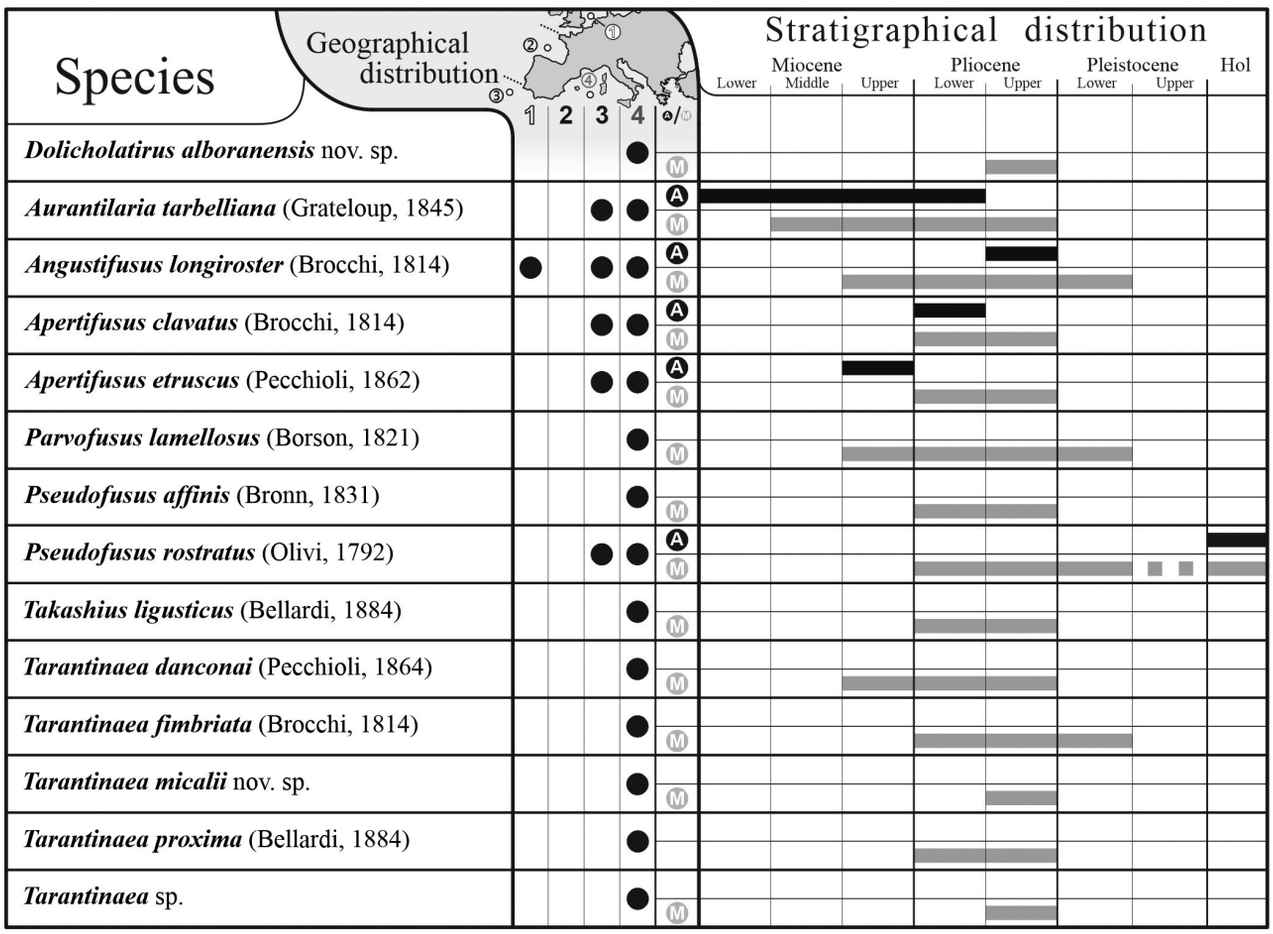

Figure 1. Geography, stratigraphy and distribution of species found in the Upper Pliocene Lower Piacenzian of the Estepona Basin, southern Spain. For present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan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

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