

# The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 21: Terebridae (Conoidea)

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In this paper we review the Terebridae of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. Ten species are recorded within four genera, of which three are described as new: *Hastula wilmulderae* nov. sp., *Terebra henkmulderi* nov. sp. and *Terebra praehistrio* nov. sp. Terebridae are an important marker of thermophilia in the Plio/Pleistocene Mediterranean. This relatively high diversity seen in the Estepona assemblages again reflects the fully tropical conditions prevailing during ecostratigraphic unit MPPMU1. Moreover, tentative phylogenetic associations are suggested for some of the Estepona augers and extant West-African species.

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

## Introduction

In this paper we continue to revise the astoundingly diverse Pliocene assemblage of Estepona in south-western Spain. The Terebridae (in vernacular known as auger shells) is not a particularly diverse group in the Pliocene Mediterranean. Having said that, it is more diverse in the western Mediterranean Pliocene of Estepona than it is in the rest of the Pliocene Mediterranean. They are an important group in Mediterranean palaeobiogeography and ecostratigraphy, as it is a thermophilic group used in ecostratigraphic models for the Pliocene Mediterranean, with high diversity associated with fully tropical sea temperatures (see Raffi & Monegatti, 1993; Monegatti & Raffi, 2001; Landau *et al.*, 2011; *inter alia*).

This work is to be used together with Harzhauser & Landau (2023) revising the Paratethyan Terebridae. We have revised the Estepona Pliocene Mediterranean and Paratethyan Middle Miocene assemblages in tandem in order to construct a congruous taxonomic framework for the Neogene of these two seas, based on the molecular phylogeny for the family given by Fedosov *et al.* (2020).

## 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).

## 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 categorise the shells as: small (SL < 25 mm), medium-sized (25–55 mm), large (>55–80 mm)

and very large (SL >80 mm). We distinguish shells according to the shell length/maximum diameter ratio (SL/MD ratio) as moderately slender (SL/MD<4.0), slender (SL/MD =4.0–5.0) and very slender (SL/MD>5.0). The height of the last whorl [= 100/(SL/LWH)] is categorised as low (<30%), moderately high (30-35%) and high (>35%). The spire profiles of the herein described Terebridae are conical, coeloconoid or cyrtoconoid. Several species are weakly gradate, and rarely telescopic whorls occur. Colour pattern is preserved in many specimens but not enhanced under UV light.

For systematics of the Terebridae we follow Fedosov *et al.* (2020).

#### **Abbreviations:**

**CO:** Velerín conglomerates; **VC:** Velerín Carretera; **EL:** El Lobillo; see Landau *et al.* (2004, p. 4, text-fig. 1). **NHMW:** Natural History Museum Vienna (Austria) **RGM:** Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

#### **Systematic palaeontology**

Superfamily Conoidea J. Fleming, 1822

Family Terebridae Mörcz, 1852

Subfamily Terebrinae Mörcz, 1852

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

*Type species* (by subsequent designation by Cossmann, 1896) – *Buccinum strigilatum* Linnaeus, 1758. Present-day, Indo-West Pacific.

- 1853 *Hastula* H. Adams & A. Adams, p. 225.
- 1873 *Impages* E.A. Smith, p. 263. Type species (subsequent designation by Cossmann, 1896): *Terebra caerulescens* Lamarck, 1822, present-day, Australia.
- 1908 *Acuminia* Dall, p. 124. Type species (by original designation): *Buccinum lanceatum* Linné, 1767, present-day, Indian Ocean.
- 1961 *Hastulina* Oyama, p. 183. Type species (by original designation): *Terebra casta* Hinds, 1844, present-day, Philippines.
- 1980 *Egentelaria* Rehder, p. 93. Type species (by original designation): *Terebra stylata* Hinds, 1844 [*Hastula cinerea* (Born, 1778)], present-day, Philippines.

#### ***Hastula costulata* (Borson, 1820)**

Plate 1, fig. 1

- \*1820 *Terebra costulata* Borson, p. 223, pl. 5, fig. 16.
- 1891 *Hastula costulata* (Bors.) – Sacco, p. 48, pl. 2, fig. 37.
- 1891 *Hastula costulata* var. *colligens* Sacco, p. 49, pl. 2, fig. 38.
- 1891 *Hastula costulata* var. *perplacatellata* Sacco, p. 49, pl. 2, fig. 39.
- 1891 *Hastula costulata* var. *conoidea* Sacco, p. 49, pl. 2, fig. 40.

- 1891 *Hastula costulata* var. *dertorugosa* Sacco, p. 49, pl. 2, fig. 41.
- 1952a *Hastula costulata* Borson 1820 [sic] – Glibert, p. 379, pl. 14, fig. 3.
- 1976b *Hastula (H.) costulata* (Borson 1820) – Pavia, p. 157, pl. 2, fig. 14.
- 1988 *Hastula costulata* (Borson) – Chirli, p. 23, pl. 11, fig. 1.
- 1974 *Hastula (Hastula) costulata* (Borson, 1820) – Malatesta, p. 394, pl. 32, fig. 5.
- 1997 *Hastula costulata* (Borson, 1820) – Chirli, p. 20, pl. 6, figs 15–17.

*Material and dimensions* – Maximum height 27.6 mm, width 6.5 mm. **CO:** NHMW 2022/0202/0021 (1), NHMW 2022/0202/0022 (1).

*Description* – Medium sized, slender shell, cyrtoconoid spire, seven teleoconch whorls preserved; apical angle initially ~24°; decreasing to ~10° on late teleoconch whorls. Protoconch and earliest teleoconch whorls not preserved. Teleoconch whorls initially weakly convex, later almost straight sided, subcylindrical last three whorls, separated by narrowly and weakly impressed suture. Sculpture of narrow, widely spaced, axial ribs extending between sutures, initially weakly opisthocline passing to weakly prosocline on last whorl, 16 on last whorl. Last whorl high, 41% of total height. Base weakly contracting. Fasciole broad, low, relatively smooth, sharply delimited adapically by low carina. Aperture narrow, elongate. Columella very weakly twisted, weakly excavated in adapical half. No columellar fold. Columellar callus thin, indistinct, not delimited from base. Anterior canal narrowly incised. Outer lip thin. Basal lip wide, convex. Siphonal canal wide, short, shallowly notched at tip. Colour pattern preserved consisting of row of dark blotches in the axial interspaces placed just below suture.

*Discussion* – Three closely similar species occur along West Africa today. *Hastula knockeri* (E.A. Smith, 1872) found from Liberia to Benin, *H. lepida* (Hinds, 1844) from Mauritania to the Cape Verde Islands, and *H. leloaeuffi* Bouchet, 1983 from Ivory Coast to Angola (for comparison between these species, see Bouchet, 1983). *Hastula costulata* (Borson, 1820) is most like *H. lepida*. Indeed, Bouchet (1983, p. 200) considered *H. lepida* a descendant of the fossil species, without comparing the two. We see no difference between the specimen from Estepona (Pl. 1, fig. 1) and that figured by Bouchet (1983, fig. 42) from Senegal. The colour pattern of dark blotches just below the suture in the intercostals is also preserved in the Estepona specimen. We refrain from synonymising the two, as the protoconch in the fossil specimen is not preserved, and its character was found important for separating West African *Hastula* species by Bouchet (1983). This *Hastula* species group might be represented in the Middle Miocene Paratethys by *Hastula hungarica* Csepreghy-Meznerics, 1954 which has similar sculpture, but that species is immediately separated by its very broad shell (H/L = 3.4 vs. 4.1) (see Harzhauser & Landau, 2023).

**Distribution** – Upper Miocene: central Proto-Mediterranean, Italy (Borson, 1820; Sacco, 1891; Pavia, 1976b). Lower Pliocene: central Mediterranean, Italy (Sacco, 1891; Chirli, 1988, 1997). Upper Pliocene: western Mediterranean, Estepona (this paper); central Mediterranean, Italy (Sacco, 1891; Malatesta, 1974).

### ***Hastula farinesi* (Fontannes, 1880)**

Plate 1, figs 2-4

- \*1880 *Terebra Farinesi* Fontannes, p. 128, pl. 7, fig. 21.
- 1891 *Hastula subcinerea* var. *scalarinula* Sacco, p. 52, pl. 2, fig. 46.
- 1891 *Hastula Farinesi* (Font.) – Sacco, p. 52, pl. 2, fig. 50.
- 1891 *Hastula Farinesi* var. *dimidiolaevis* Sacco, p. 54, pl. 2, fig. 51.
- 1891 *Hastula Farinesi* var. *subrectilinearis* Sacco, p. 55, pl. 2, fig. 52.
- 1891 *Hastula Farinesi* var. *sublateplicata* Sacco, p. 55, pl. 2, fig. 52<sup>bis</sup>.
- 1891 *Hastula Farinesi* var. *strangulatina* Sacco, p. 55, pl. 2, fig. 53.
- 1974 *Hastula* (*Hastula*) *farinesi* (Fontannes, 1880) – Malatesta, p. 395, pl. 32, fig. 4.
- 1976a *Hastula* (*H.*) *farinesi* (Fontannes) – Pavia, p. 114, pl. 9, fig. 13.
- 1976a *Hastula* (*H.*) *striata* (Basterot) – Pavia, p. 114, pl. 9, fig. 14.
- 1984 *Hastula subcinerea* var. *scalarinula* Sacco, 1891 – Ferrero Mortara *et al.*, 63, pl. 8, fig. 2.
- 1984 *Hastula farinesi* var. *dimidiolaevis* Sacco, 1891 – Ferrero Mortara *et al.*, 64, pl. 8, fig. 4.
- 1992 *Hastula farinesi* (Fontannes, 1881 [sic]) – Cavallo & Repetto, p. 148, fig. 409.
- 1997 *Hastula farinesi* (Fontannes, 1880) – Chirli, p. 21, pl. 6, figs 18-20.
- 2011 *Hastula farinesi* (Fontannes, 1880) – Landau *et al.*, p. 38, pl. 21, fig. 6.
- 2018 *Hastula farinesi* (Fontannes, 1880) – Brunetti & Cresti, p. 102, fig. 431.

**Material and dimensions** – Maximum height 47.7 mm, width 7.8 mm. **CO:** NHMW 2022/0202/0025 (3), NHMW 2022/0202/0026 (20), RGM.1404357 (2). **EL:** NHMW 2022/0202/0027 (4).

**Description** – Medium sized, slender to very slender shell, weakly cyrtoconoid spire, of up to ten weakly telescopic teleoconch whorls; apical angle initially 21-24°; decreasing to 9.4-12.7° on late teleoconch whorls. Protoconch not preserved. Teleoconch whorls weakly convex, subcylindrical, separated by weakly impressed suture. Sculpture of extremely weak axial ribs, most evident on the apical half of early spire whorls, fading by 7<sup>th</sup> whorl; some specimens almost completely smooth. Last whorl high, 37-38% of total height. Base weakly contracting. Fasciole broad, low, smooth, sharply delimited adapically by low carina. Aperture narrow, elongate. Columella very

weakly twisted, weakly excavated in apical half. No columellar fold. Columellar callus thin, indistinct, not delimited from base. Anterior canal narrowly incised. Outer lip thin. Basal lip wide, convex. Siphonal canal wide, short, shallowly notched at tip. Colour pattern preserved consisting of row of dark blotches placed just below suture, two further rows of blotches on last whorl placed just above and below level of insertion of outer lip, lighter colour band just below suture and between mid-whorl rows of blotches.

**Discussion** – Glibert (1952a, p. 377) discussed the *H. striata* (de Basterot, 1825) / *H. subcinerea* (d'Orbigny, 1852) / *H. farinesi* (Fontannes, 1880) group, and the gradual weakening of the axial sculpture over time. Although Glibert described *H. farinesi* as not having any axial ribs at all, only growth lines, most of the Estepona specimens do have some weak axial ribs developed below the suture, blurring the distinction between *H. subcinerea* and *H. farinesi*. Unfortunately, none of the Pliocene specimens at hand have their protoconch preserved. Protoconch characters were shown to be important within *Hastula* (see Bouchet, 1983). Therefore, we provisionally follow Davoli (1977, p. 148) in using the name *farinesi* for the Pliocene forms, with or without weak axial ribs. The Middle Miocene Paratethyan species *Hastula duboisiana* (d'Orbigny, 1852) also belongs within this group of *Hastula* species and is extremely similar to *H. farinesi*. They seem to differ in that *H. duboisiana* has lower whorls, and most notably in the character of the last whorl; in *H. farinesi* the base is more slowly contracting, the siphonal fasciole is flatter, the carina demarcating the apical limit of the fasciole less elevated, and the siphonal notch is even shallower (for comparison see Harzhauser & Landau, 2023, figs 4A-G).

**Distribution** – Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); western Mediterranean, Rousillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1891; Pavia, 1976; Chirli, 1997; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona (this paper); central Mediterranean, Italy (Sacco, 1891; Malatesta, 1974; Ferrero Mortara *et al.*, 1984; Cavallo & Repetto, 1992).

### ***Hastula wilmulderae* nov. sp.**

Plate 1, figs 5-7

**ZooBank registration** – urn:lsid:zoobank.org:act:54D113F9-AFA2-47D7-B6BF-D582C3D6F5E7

**Type material** – Holotype NHMW 2022/0202/0028, height 10.0 mm, width 3.0 mm; paratype 1 NHMW 2022/0202/0029, height 9.7 mm, width 2.9 mm; paratype 2 NHMW 2022/0202/0030, height 8.7 mm, width 2.6 mm; paratype 3 NHMW 2022/0202/0031, height 10.0 mm, width 2.9 mm; paratype 4 NHMW 2022/0202/0032, height 9.0 mm, width 2.9 mm; paratype 5 RGM.1404358, height 10.5 mm, width 3.2 mm; paratype 6 RGM.1404359, height 9.2 mm,

width 2.8 mm; paratype 7 RGM.1404360, height 9.1 mm, width 2.9 mm; **Velerín carretera**. Paratype 8 NHMW 2022/0202/0034, height 14.4 mm, width 3.6 mm; **Velerín conglomerates**.

*Other material* – Maximum height 14.4 mm, width 3.6 mm. VC: NHMW 2022/0202/0033 (50+).

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

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

*Etymology* – Named after Wil Mulder-van der Stoel, wife of Henk Mulder, without her support Henk would not be able to follow his passion. *Hastula* gender feminine.

*Diagnosis* – Small, relatively thin-shelled *Hastula* species with dome-shaped protoconch of 2.25 whorls, first whorl flattened, smooth, last whorl with axial riblets, teleoconch whorls with narrow poorly developed subsutural band, 9-12 axial narrow axial ribs below weakening on later whorls, almost no spiral sculpture, no columellar folds.

*Description* – Small, relatively thin shelled, moderately slender conical shell of up to eight teleoconch whorls; apical angle ~30°, later decreasing to ~17°. Protoconch dome-shaped, of 2.5 convex whorls, with medium-sized nucleus, first 1.5 whorls smooth, flattened, second whorl with axial riblets. Teleoconch boundary marked by prosocline scar. Early teleoconch whorls slightly concave below suture at narrow, poorly delimited, recessed subsutural band, convex below, with periphery just below mid-whorl, separated by narrowly impressed suture. Sculpture of narrow, opisthocyst ribs, about one-third width of their interspaces, 9-12 on third teleoconch whorl, subobsolete over subsutural band. Abapically, whorls become more evenly and weakly convex, subsutural band indistinct, ribs weaken, subobsolete on last two whorls in some specimens. Occasional extremely weak and irregular spiral threads present in some specimens. Last whorl high, 42-43% of total height, weakly convex, moderately contracted at base. Fasciole weak, flattened with few stronger growth increments, adapically delimited by weak carina. Aperture moderately narrow pyriform. Columella twisted, moderately excavated in adapical half. No columellar fold. Anal canal weakly incised. Outer lip thin. Siphonal canal moderately long, narrow, twisted, deflected to the left, shallowly notched at tip.

*Discussion* – *Hastula wilmulderae* nov. sp. is the smallest terebrid in the Estepona assemblages, and is predominantly a deeper water species, found relatively frequently in the Velerín carretera deposit. In the fossil assemblages, it is similar to *Hastula exilis* (Bell, 1871) from the Pliocene (?Pleistocene) of the North Sea Basin and NW France [note that the Upper Miocene record of Brébion (1964, p. 638) was not confirmed by Landau *et al.* (2020) and is removed from the distribution]. *Hastula exilis* was

discussed at length by Landau *et al.* (2020) [as *Terebra exilis*] and a wide range of forms from the Lower Pliocene of NW France were illustrated (2020, pl. 6, figs 5-9) including forms with the ribs fading relatively early or persisting to the last whorl, and forms with the base rounded to angular. However, the Estepona species differs in having half a protoconch whorl less, the early whorls are more strongly convex, and the ribs are more prominent, especially on the earliest teleoconch whorls. The character of the late teleoconch whorls and aperture are, nevertheless, similar and we suspect they are closely related. In the extant West African fauna *H. denizi* Rolán & Gubboli, 2000 is extremely similar in size and profile, and differs most markedly in having fewer and stronger axial ribs, especially on the early teleoconch whorls. In *H. denizi* the axials are very weak and more arcuate or sinuous (see Terryn & Ryall, 2014, figs 23-26). Moreover, in *H. wilmulderae* the protoconch is more depressed and blunter, the apical angle is narrower when shells of the same size are compared (16° vs. 20°), and the last whorl is less inflated. This inflated last whorl gives the shell a weakly coeloconoid profile, whereas the profile is regularly narrowly conical in *H. wilmulderae*. The two are undoubtedly closely related.

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

#### Genus *Oxymeris* Dall, 1903

*Type species* (by subsequent designation, Dall, 1908) – *Buccinum maculatum* Linnaeus, 1758. Middle Miocene, Central Paratethys Sea.

- |      |  |
|------|--|
| 1847 | <i>Acus</i> Gray, p. 139. Junior homonym of <i>Acus</i> Lacépède, 1803 [Pisces].   |
| 1853 | <i>Abretia</i> H. Adams & A. Adams, p. 225. Type species (by subsequent designation, Dall, 1908): <i>Terebra cerithina</i> Lamarck, 1822, present-day, Indo-Pacific. Junior homonym of <i>Abretia</i> Rafinesque, 1814.              |
| 1903 | <i>Oxymeris</i> Dall, p. 951. <i>Nom. nov. pro Acus</i> Gray 1847.   |
| 1923 | <i>Abretiella</i> Dall in Bartsch. Type species (by typification of replaced name): <i>Terebra cerithina</i> Lamarck, 1822, present-day, Indo-Pacific. <i>Nom. nov. pro Abretia</i> H. Adams & A. Adams, 1853, non Rafinesque, 1814. |
| 1947 | <i>Nototerebra</i> Cotton, p. 667. Type species (by original designation): <i>Terebra albida</i> Gray, 1834, present-day, Victoria, Australia.   |

#### *Oxymeris fuscata* (Brocchi, 1814)

Plate 1, fig. 8

- |       |   |
|-------|---|
| *1814 | <i>Buccinum fuscatum</i> Brocchi, p. 344.                           |
| 1880  | <i>Terebra fuscata</i> Brocchi – Fontannes, p. 124, pl. 7, fig. 18. |

- 1891 *Subula fuscata* (Br.) – Sacco, p. 7, pl. 1, figs 1, 1 bis.  
 1891 *Subula fuscata* var. *subasulcata* Sacco, p. 8.  
 1891 *Subula fuscata* var. *subscalarata* Sacco, p. 9, pl. 1, fig. 3.  
 1891 *Subula fuscata* var. *basicarinata* Sacco, p. 9.  
 1891 *Subula fuscata* var. *suprainflata* Sacco, p. 9, pl. 1, fig. 4.  
 1891 *Subula fuscata* var. *planoinflata* Sacco, p. 9, pl. 1, fig. 5.  
 1891 *Subula fuscata* var. *pseudocerithoidea* Sacco, p. 10, pl. 1, fig. 6.  
 1891 *Subula fuscata* var. *conicolaevia* Sacco, p. 10, pl. 1, fig. 7.  
 1891 *Subula fuscata* var. *pseudomodesta* Sacco, p. 10, pl. 1, fig. 8.  
 1891 *Subula fuscata* var. *lanceolatissima* Sacco, p. 10, pl. 1, fig. 9.  
 1891 *Subula fuscata* var. *subulatissima* Sacco, p. 10, pl. 1, fig. 10.  
 1891 *Subula fuscata* var. *plioplicaria* Sacco, p. 11, pl. 1, fig. 11.  
 1955 *Terebra (Subula) fuscata* (Brocchi 1814) – Rossi Ronchetti, p. 331, fig. 178.  
 1963 *Subula (S.) fuscata* (Brocchi) – Venzo & Pelosio, p. 132, pl. 11, fig. 38.  
 1967 *Subula (Subula) fuscata* (Brocchi) – Palla, p. 1005, pl. 75, fig. 10.  
 1974 *Subula (Subula) fuscata* (Brocchi, 1814) – Malatesta, p. 397, pl. 32, fig. 1.  
 1974 *Subula fuscata* (Brocchi) – Davoli & Russo, p. 114, figs 9, 10, 14, 15.  
 1975 *Terebra (Subula) fuscata* (Brocchi) – Fekih, p. 136, pl. 40, fig. 20.  
 1976 *Subula fuscata* (Brocchi) – Caprotti, p. 12, pl. 17, fig. 1.  
 1976 *Subula (S.) fuscata* (Brocchi) – Pavia, p. 114, pl. 9, fig. 11.  
 1992 *Subula fuscata* (Brocchi, 1814) – Cavallo & Repetto, p. 148, fig. 413.  
 1992 *Subula (Subula) fuscata* (Brocchi, 1814) – González Delgado, p. 50, pl. 6, figs 13, 14.  
 1988 *Subula fuscata* (Brocchi, 1814) – Chirli, p. 23, pl. 11, fig. 4.  
 1997 *Subula fuscata* (Brocchi, 1814) – Chirli, p. 23, pl. 6, figs 21-25.  
 2008 *Subula fuscata* (Brocchi, 1814) – Chirli & Richard, p. 72, pl. 14, fig. 7.  
 2011 *Subula fuscata* (Brocchi, 1814) – Landau et al., p. 38, pl. 21, fig. 7.  
 2022 *Subula fuscata* (Brocchi, 1814) – Brunetti, p. 18, 76, fig. 170.
- non* 1852 *Terebra fuscata* Brocc. – Höernes, p. 128, pl. 11, figs 15–18, 26 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1866 *Subula fuscata* Brocc. – Pereira da Costa, p. 78, pl. 12, figs 14-16, pl. 13, figs 1-2 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1880 *Terebra (Acus) fuscata* Brocc. var. – Hoernes & Auinger, 106, pl. 12, fig. 17 [= *Oxymeris buiturica* (Moisescu, 1955)].
- 1896 *Subula fuscata* Br – Cossmann, p. 52, pl. 4, fig. 8 [= *Oxymeris plicaria* (de Basterot, 1825)].  
*non* 1911 *Terebra (Subula) fuscata* Brocc. – Friedberg, p. 1, pl. 1, fig. 1 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1955 *Terebra (Subula) fuscata* Brocc. – Korobkov, plate captions, pl. 92, figs 7a, 7b [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1958 *Terebra (Subula) fuscata* (Brocchi) – Erünal-Erentöz, p. 125, pl. 20, figs 15, 16 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1964 *Terebra (Subula) fuscata* (Brocchi) – Răileanu & Negulescu, p. 188, pl. 15, fig. 7 [= *Oxymeris cf. plicaria* (de Basterot, 1825)].  
*non* 1966 *Terebra (Subula) fuscata* Brocchi, 1814 – Strausz, p. 394, pl. 5, fig. 11 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1967 *Subula (Oxymeris) fuscata* (Brocchi, 1914) – Tejkal et al., p. 209, pl. 12B, fig. 3 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1968 *Terebra fuscata* (Brocchi, 1814) – Zelinskaya et al., p. 231, pl. 52, figs 6-7 [= *Oxymeris modesta* (Defrance, 1829)].  
*non* 1969 *Terebra (Subula) fuscata* Brocchi – Atanacković, p. 216, pl. 14, figs 2-2a [= *Oxymeris modesta* (Defrance, 1829)].
- Material and dimensions* – Maximum height 54.2 mm, width 11.8 mm. **CO:** NHMW 2022/0202/0035 (1), NHMW 2022/0202/0036 (3).
- Description* – Large, slender shell of up to ten teleoconch whorls; apical angle ~15°. Protoconch unknown. Early spire typically conical or weakly gradate, whorl profile conical to subcylindrical, broad subsutural band with weak axial ribs delimited by weak spiral groove, below weak, faintly opisthocyst axial ribs. Axial sculpture fading abapically, typically around sixth teleoconch whorl, but variable. Later teleoconch whorls almost flat sided, usually smooth, except for delicate growth lines, spiral groove delimiting subsutural band obsolete or subobsolete on later whorls. Spiral threads or grooves may occur on last teleoconch whorls. Last whorl high, weakly convex, about 36% of total height. Base slowly contracting. Fasciole prominent, broad, adapically delimited by sharp carina and separated from base by moderately narrow groove. Aperture elongate, moderately narrow. Columella weakly twisted, angulated at transition into convex parietal area. Columellar callus forming thin, broad rim, moderately delimited from base. Anal canal indistinct, narrowly incised. Outer lip thin. Basal lip convex, wide. Siphonal canal short, wide, twisted, slightly deflected to the left, moderately notched at tip.
- Discussion* – *Oxymeris fuscata* (Brocchi, 1814) is widespread in the Mediterranean Pliocene, although in the Estepona assemblages it is uncommon and none of the specimens are well preserved, nor are they as large as those found in other Mediterranean Pliocene assemblages. It is also an extremely variable species in both profile and sculpture, as can be seen by the large number of

varieties erected by Sacco (1891). The subsutural groove disappears on the last 3-4 whorls in three out of the four Estepona specimens at hand; in one it continues faintly to the aperture.

The relationship between *Oxymeris plicaria* (de Basterot, 1825) and *O. modesta* (Defrance, 1829) was discussed by Harzhauser & Landau (2023). To summarise, Early Miocene *Oxymeris plicaria* and the latest Early to Middle Miocene *O. modesta* are considered as an anagenetic succession of two (chrono)species. *Oxymeris plicaria* has more prominent axial ribs on early teleoconch whorls, persisting down to about 8<sup>th</sup>-12<sup>th</sup> whorl, whilst *O. modesta* has a larger maximum size (but small adults may also occur), usually has weaker axial sculpture, which fades earlier around 8<sup>th</sup>-9<sup>th</sup> teleoconch whorl, has more convex whorls and is slightly more obtuse. *Oxymeris fuscata* is the Pliocene representative of this group. It differs from *O. modesta* in its slenderer shell, with more flat-sided whorls, weaker axial sculpture and narrower aperture.

**Distribution** – Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1992; Landau *et al.*, 2011; Brunetti, 2022); western Mediterranean, Rousillon Basin (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1891; Venzo & Pelosio, 1963; Pavia, 1976; Chirli, 1988, 1997), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1891; Palla, 1967; Malatesta, 1974; Davoli & Russo, 1974; Caprotti, 1976; Cavallo & Repetto, 1992).

#### Genus *Strioterebrum* Sacco, 1891

**Type species** (by original designation) – *Terebra basteroti*, Nyst, 1845. Middle Miocene, North Sea Basin.

- 1891 *Strioterebrum* Sacco, p. 33.
- ?1923 *Punctoterebra* Bartsch, p. 63. Type species (by original designation): *Terebra nitida* Hinds, 1844, present-day, Tasmania, Australia.

#### *Strioterebrum pliocenicum* (Fontannes, 1880)

Plate 1, fig. 9

- \*1880 *Terebra Basteroti* var. *pliocenica* Fontannes, p. 126, pl. 7, fig. 19.
- 1891 *Strioterebrum pliocenicum* (Font.) – Sacco, p. 38, pl. 2, fig. 15.
- 1891 *Strioterebrum pliocenicum* var. *pertorquata* Sacco, p. 39.
- 1891 *Strioterebrum pliocenicum* var. *pseudolaevis* Sacco, p. 39.
- 1891 *Strioterebrum pliocenicum* var. *plioparvecostata* Sacco, p. 38, pl. 2, fig. 16.
- 1891 *Strioterebrum pliocenicum* var. *pyramidalis* Sacco, p. 40, pl. 2, fig. 17.
- 1891 *Strioterebrum reticulare?* var. *paucisulcata* Sacco, p. 45, pl. 2, fig. 34.

- 1904 *Myurella pliocenica* var. *pertorquata* (Sacc.) – Sacco, p. 107, pl. 23, fig. 34.
- 1904 *Myurella pliocenica* var. *pseudolaevis* (Sacc.) – Sacco, p. 107, pl. 23, fig. 35.
- 1960 *Terebra (Strioterebrum) pliocenica* Fontannes, 1880 – Malatesta, p. 189, pl. 9, fig. 11.
- 1963 *Strioterebrum pliocenicum* Sacco – Caretto, p. 22, pl. 3, fig. 19.
- 1973 *Strioterebrum (Strioterebrum) pliocenicum* (Fontannes) – Caprotti & Vescovi, p. 183, pl. 3, fig. 5.
- 1976 *Strioterebrum pliocenicum* (Font.) – Caprotti, p. 12, pl. 17, fig. 5.
- 1976 *Strioterebrum (Strioterebrum) pliocenicum* (Fontannes) – Marasti & Raffi, p. 197, pl. 2, fig. 29.
- 1978 *Strioterebrum pliocenicum* (Fontannes) – Martinell & Marquina, p. 126, pl. 1, fig. 15.
- 1982 *Strioterebrum pliocenicum* (Fontannes, 1881 [sic]) – Martinell, p. 113, pl. 1, figs 25, 26.
- 1988 *Strioterebrum pliocenicum* (Fontannes) – Chirli, p. 23, pl. 11, fig. 2.
- 1992 *Strioterebrum reticulare* Pecchioli in Sacco, 1891 – Cavallo & Repetto, p. 148, fig. 412b [*non Strioterebrum reticulare* Sacco, 1891].
- 1997 *Strioterebrum pliocenicum* (Fontannes, 1880) – Chirli, p. 21, pl. 6, figs 8-10.
- 2008 *Terebra pliocenica* (Fontannes, 1880) – Chirli & Richard, p. 71, pl. 14, fig. 6.
- 2014 *Strioterebrum reticulare* Pecchioli in Sacco, 1891 – Brunetti, p. 72, figs C [*non Strioterebrum reticulare* Sacco, 1891].
- 2022 *Strioterebrum pliocenicum* (Fontannes, 1881) – Brunetti, p. 76, fig. 167.
- non 1974 *Strioterebrum (Strioterebrum) pliocenicum* (Fontannes, 1880) – Malatesta, p. 396, pl. 28, fig. 6, pl. 32, fig. 3 [= *Strioterebrum reticulare* Sacco, 1891].
- non 1992 *Strioterebrum (Strioterebrum) pliocenicum* (Fontannes, 1881 [sic]) – González Delgado, p. 50, pl. 6, figs 3-5 [= *Strioterebrum reticulare* Sacco, 1891].
- non 1994 *Strioterebrum (Strioterebrum) pliocenicum* (Fontannes) – Karakus & Taner, p. 91, pl. 3, fig. 10 [= *Strioterebrum reticulare* Sacco, 1891].
- non 2011 *Strioterebrum pliocenicum* (Fontannes, 1880) – Landau *et al.*, p. 38, pl. 21, fig. 5 [= *Strioterebrum reticulare* Sacco, 1891].
- non 2017 *Strioterebrum pliocenicum* (Fontannés [sic], 1880) – Büyükmeliç *et al.*, p. 7, p. 14, fig. 5A1-A2 (plate legend under fig. 6, p. 15; *lapsus*) [= *Strioterebrum reticulare* Sacco, 1891].

**Material and dimensions** – Maximum height 37.6 mm, width 7.6 mm. CO: NHMW 2022/0202/0002 (1), NHMW 2022/0202/0006 (1).

**Description** – Medium sized, slender weakly cyrtoconoid shell of up to 13 teleoconch whorls; apical angle ~20°, later decreasing to ~10°. Protoconch not preserved. Early teleoconch whorls conical, flat sided, with subsutural

band well developed, delimited by deep groove. Sculpture below band of prominent, rounded, more or less orthocline axial ribs, 10-12 on spire whorls, separated by interspaces broader than ribs, and narrow, flattened, subequal spiral cords separated by relatively deep, narrow grooves that cut the axial ribs. Axials broaden and become subobsolete over subsutural band on late adult whorls. Abaxially whorl profile weakly convex below subsutural band with periphery just below mid-whorl. Suture distinctly incised. Last whorl moderately high, ~32% of total height, convex below subsutural band. Base convex, moderately constricted. Fasciole moderately narrow and prominent, delimited adapically by weak carina. Aperture narrow. Columella strongly excavated in apical half. No columellar fold. Columellar callus forming broad, thin rim, poorly delimited from base. Anal canal narrow. Outer lip thin. Siphonal canal moderate length, narrow, moderately twisted, shallowly notched at tip.

**Discussion –** Relationships within the *Terebra/Strioterebrum pliocenica* (Fontannes, 1880) –*reticulare* (-is) Sacco, 1891 species complex are controversial, and until now unresolved. [We note that although authorship of *S. reticulare* is often credited to Pecchioli, 1891, this is merely a manuscript name. The name was made available by Sacco (1891, p. 40)]. Some authors have recognised two distinct, but closely related species present in the Mediterranean Pliocene (e.g., Sacco, 1891; Chirli, 1988, 1997; *inter alia*), whilst others considered the forms extremes of a single variable species (e.g., Cavallo & Repetto, 1992; Landau *et al.*, 2011; *inter alia*). Bouchet (1983) considered *T. reticulare* still to be present in the West African faunas and recognised two coexisting forms: one with fine and subequal axials and spirals forming a finely reticulated surface sculpture, and a second in which the axials are wider spaced and predominant. This position was followed by Terry & Ryall (2014).

We have not seen the type material of *T. pliocenica*, but according to the original description and illustration (Fontannes, 1880, p. 126, pl. 7, fig. 19) it has relatively widely spaced predominant axial ribs and much weaker fine spiral cords separated by deep grooves. Fontannes compared his new species to *S. basterotii* (Nyst, 1845), but already this comparison is confusing, as he states “*Bien qu'ils appartiennent vraisemblablement à la même espèce, les exemplaires de Perpignan ne sont pas absolument identiques au type miocène du Sud-Ouest* [referring to *T. Basterotii* (*sic*)]”. However, the type of *S. basterotii* is from the Middle Miocene of the North Sea Basin and not from the Miocene of SW France (see Harzhauser & Landau, 2023). Nevertheless, Fontannes considered the Pliocene specimens to differ in being larger in size, with fewer, rounder axial ribs, and the spiral cords not only being present in the axial interspaces, but also cutting the ribs, although not as deeply incised. When compared with *S. basterotii* from the North Sea Basin (Janssen, 1984, pl. 77, figs 1, 2; Wienrich, 2007, pl. 156, figs 1-3) the Estepona specimen is considerably larger (37 mm height vs. max 19 mm; *fide* Wienrich, 2007, p. 722), the apical angle is narrower, it has fewer ribs that are not as sharp, the subsutural band is

more rounded, more clearly delimited, with the ribs subobsolete over the band on later adult whorls, and the fasciole is more strongly twisted. The same differences can be seen when compared to *S. basterotii* from the Atlantic Lower Miocene of France (Lozouet *et al.*, 2001, pl. 31, fig. 11). Whether the Middle Miocene North Sea Basin and Lower Miocene French Atlantic specimens are conspecific needs reassessment: the French specimens seem to have an even wider apical angle and a narrower subsutural band.

In Sacco's description of *S. reticulare* he again compared it to *S. basterotii* [*sic*] “*Testa saepe major. Costae longitudinales saepe propinquiores, sat numerosiores. Sulcus subsuturalis profundior. Costicillae transversae valde elatiiores et evidenteriores (interdum subbifidae, interdum, perparvulae crassioribus alternae), costa» longitudinales intercidentes, deinde testai superficies subreticularis* [The shell is often larger. Ribs are often closer together, more numerous. Subsutural groove deeper. Cords are much more prominent (sometimes subbifid, sometimes alternating, with very small and thicker ones), forming subreticular surface sculpture with the ribs]” (Sacco, 1891, p. 40). Sacco did not directly compare his species to *S. pliocenicum*, but three shell characters are stressed in his description: the numerous axial ribs, the irregular character of the spiral cords, and the tendency to form a reticulated surface pattern.

We consider the specimen illustrated herein (Pl. 1, fig. 9) to represent *S. pliocenicum*. It has wide-spaced axial ribs that are rounded and regular narrow cords separated by relatively deep grooves that cut the ribs. This is contrast to *S. reticulare* (Pl. 1, figs 10-12) with considerably more crowded ribs that are sharper, irregular spirals that are not so deeply divided, and a tendency to form reticulated sculpture.

Present-day specimens from West Africa reported as *S. reticulare* are not conspecific with the fossil specimens and together they may well represent a species complex (Yves Terry personal comm. BL, 01/09/2023), although molecular data that could resolve this issue is so far lacking. We note that all the specimens illustrated by both Bouchet (1983) and Terry & Ryall (2014) have two columellar folds, absent in *S. reticulare*.

In view of this, we consider *S. pliocenicum* and *S. reticulare* separate species. *Strioterebrum reticulare* continues to be highly variable in sculpture, and it may well continue to be a species complex. Present-day specimens from West Africa are considered not to be conspecific and await review.

Members of this species complex from the Middle Miocene Paratethys were reviewed by Harzhauser & Landau (2023). *Strioterebrum volhynia* (d'Orbigny, 1852), the Middle Miocene Paratethyan species that has consistently been misidentified as *S. basterotii* in the Paratethyan literature (see Harzhauser & Landau, 2023), differs in being slenderer, the subsutural band is even more strongly developed than in *S. pliocenicum*, the columella is less excavated adapically and less twisted abapically. *Strioterebrum volhynia* is also variable in its sculpture and similarly axially predominant and reticulated forms occur. The other two Paratethyan congeners are less simi-

lar; *S. borianum* (Švagrovský, 1982) has more regular axial sculpture and no spirals, *S. exhibstriatum* (Sacco 1891) has a slightly gradate spire and very fine spiral sculpture.

**Distribution** – Upper Miocene: central Proto-Mediterranean, Italy (Brunetti, 2014). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (Brunetti, 2022); western Mediterranean, NE Spain (Martinell & Marquina, 1978; Martinell, 1982), Rousillon Basin (Fontannes, 1880); central Mediterranean, Italy (Chirli, 1988, 1997). Upper Pliocene: western Mediterranean, Estepona (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1891; Caretto, 1963; Caprotti & Vescovi, 1973; Caprotti, 1976; Marasti & Raffi, 1976; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Malatesta, 1960).

### ***Strioterebrum reticulare* Sacco, 1891**

Plate 1, figs 10–12

- ?1891 *Strioterebrum pliocenicum* var. *perplicatoconica* Sacco, p. 40, pl. 2, fig. 18.
- ?1891 *Strioterebrum pliocenicum* var. *depressicostata* Sacco, p. 40, pl. 2, fig. 19.
- \*1891 *Strioterebrum reticulare* (Pecchioli m.s.) Sacco, p. 40, pl. 2, fig. 20.
- 1891 *Strioterebrum reticulare* var. *turritoreticularis* Sacco, p. 41, pl. 2, fig. 22.
- 1891 *Strioterebrum reticulare* var. *varioreticularis* Sacco, p. 41, pl. 2, fig. 23.
- 1891 *Strioterebrum reticulare* var. *scalarioreticularis* Sacco, p. 42, pl. 2, fig. 24.
- 1891 *Strioterebrum reticulare* var. *scalariomutinensis* Sacco, p. 42, pl. 2, fig. 25.
- 1891 *Strioterebrum reticulare* var. *medioareticularis* Sacco, p. 42, pl. 2, fig. 26.
- 1891 *Strioterebrum reticulare* var. *subbitorquata* Sacco, p. 42.
- 1891 *Strioterebrum reticulare* var. *superneareticularis* Sacco, p. 42.
- 1891 *Strioterebrum reticulare* var. *percosticillata* Sacco, p. 42.
- 1891 *Strioterebrum reticulare* var. *cancellatoidea* Sacco, p. 43, pl. 2, fig. 27.
- 1891 *Strioterebrum reticulare* var. *cingulocostata* Sacco, p. 43.
- 1891 *Strioterebrum reticulare* var. *percancellata* Sacco, p. 43, pl. 2, fig. 28.
- 1891 *Strioterebrum reticulare* var. *strangulatolonga* Sacco, p. 43, pl. 2, fig. 29.
- 1891 *Strioterebrum reticulare* var. *crassetorquata* Sacco, p. 44, pl. 2, fig. 30.
- 1891 *Strioterebrum reticulare* var. *perplicata* Sacco, p. 44, pl. 2, fig. 31.
- 1891 *Strioterebrum reticulare* var. *parvulesulcata* Sacco, p. 44.
- 1891 *Strioterebrum reticulare* var. *depressiplicata* Sacco, p. 44, pl. 2, fig. 32.
- 1891 *Strioterebrum reticulare?* var. *planocosticillata* Sacco, p. 44, pl. 2, fig. 33.

- 1904 *Myurella reticularis* var. *subbitorquata* (Sacc.) – Sacco, p. 107, pl. 23, fig. 36.
- 1904 *Myurella reticularis* var. *superneareticularis* (Sacc.) – Sacco, p. 107, pl. 23, fig. 37.
- 1904 *Myurella reticularis* var. *percosticillata* (Sacc.) – Sacco, p. 107, pl. 23, fig. 38.
- 1904 *Myurella reticularis* var. *cingulocostata* (Sacc.) – Sacco, p. 107, pl. 23, fig. 39.
- 1904 *Myurella reticularis* var. *parvulesulcata* (Sacc.) – Sacco, p. 107, pl. 23, fig. 40.
- 1940 *Terebra* (*Myurella*) *reticularis* Pech. – Roman, p. 359, pl. 1, fig. 22.
- 1967 *Strioterebrum* (*Strioterebrum*) *reticulare* (Pecchioli, 1864) – Palla, p. 1004, pl. 75, fig. 12.
- 1973 *Strioterebrum* (*Strioterebrum*) *reticulare* (Pecchioli) – Caprotti & Vescovi, p. 184, pl. 3, fig. 4.
- 1974 *Strioterebrum* (*Strioterebrum*) *piocenicum* (Fontannes, 1880) – Malatesta, p. 396, pl. 28, fig. 6, pl. 32, fig. 3 [*non Strioterebrum piocenicum* (Fontannes, 1880)].
- 1975 *Terebra* (*Myurella*) *piocenica* Fontannes – Fekih, p. 136, pl. 40, fig. 19.
- 1976 *Strioterebrum reticulare* (Pecch.) – Caprotti, p. 12, pl. 17, fig. 4.
- 1976a *Strioterebrum* (*S.*) *reticulare* (Pecchioli) – Pavia, p. 114, pl. 9, figs 15, 16.
- 1977 *Strioterebrum* (*Strioterebrum*) *reticulare* (Pecchioli) – Davoli, p. 153, pl. 2 [18], fig. 6.
- 1984 *Strioterebrum reticulare* Sacco, 1891, Pecchioli in *schedis* – Ferrero Mortara et al., 60, pl. 7, fig. 11.
- 1984 *Strioterebrum reticulare?* var. *paucisulcata* Sacco, 1891 – Ferrero Mortara et al., 62, pl. 8, fig. 1.
- 1988 *Strioterebrum reticulare* (Pecchioli ms.) – Chirli, p. 23, pl. 11, fig. 3.
- 1992 *Strioterebrum* (*Strioterebrum*) *piocenicum* (Fontannes, 1881 [sic]) – González Delgado, p. 50, pl. 6, figs 3–5 [*non Strioterebrum piocenicum* (Fontannes, 1880)].
- 1992 *Strioterebrum reticulare* Pecchioli in Sacco, 1891 – Cavallo & Repetto, p. 148, fig. 412a [not b = *Strioterebrum piocenicum* (Fontannes, 1880)].
- 1994 *Strioterebrum* (*Strioterebrum*) *piocenicum* (Fontannes) – Karakus & Taner, p. 91, pl. 3, fig. 10 [*non Strioterebrum piocenicum* (Fontannes, 1880)].
- 1997 *Strioterebrum reticulare* (Pecchioli ms.) – Chirli, p. 22, pl. 6, figs 11–14.
- 2001 *Strioterebrum reticulare* Pecchioli, 1864 ms. in Sacco, 1891 – Silva, p. 557, pl. 26, figs 1–5.
- 2005 *Strioterebrum reticulare* (Pecchioli in Sacco, 1891) – Andri et al., p. 184, fig. G. 142.
- 2010 *Terebra reticulare* (Pecchioli in Sacco, 1891) – Sosso & Dell’Angelo, p. 50, 65 unnumbered fig. bottom row left.
- 2011 *Strioterebrum piocenicum* (Fontannes, 1880) – Landau et al., p. 38, pl. 21, fig. 5 [*non Strioterebrum piocenicum* (Fontannes, 1880)].
- 2017 *Strioterebrum piocenicum* (Fontannés [sic], 1880) – Büyükmeliç et al., p. 7, p. 14, fig. 5A1–A2 (plate legend under fig. 6, p. 15; *lapsus*) [*non Strioterebrum piocenicum* (Fontannes, 1880)].

- 2018 *Strioterebrum reticulare* (Pecchioli in Sacco, 1891)  
– Brunetti & Cresti, p. 102, fig. 432.
- 2022 *Strioterebrum reticulare* (Pecchioli in Sacco, 1891)  
– Brunetti, p. 76, fig. 168.
- non* 1891 *Strioterebrum reticulare* (Pecchioli m.s.) forma juvenilis Sacco, p. 41, pl. 2, fig. 21.
- non* 1983 *Terebra reticulare* (Pecchioli in Sacco, 1891) – Bouchet, p. 195, figs 6, 30-33.
- non* 1987 *Terebra reticularis* (Pecchioli in Sacco, 1891) – Bratcher & Cernohorsky, p. 168, pl. 51, fig. 201a, pl. 52, figs 201b-e.
- non* 2005 *Terebra reticularis* (Pecchioli in Sacco, 1891) – Rolán, p. 174, fig. 811.
- non* 2014 *Terebra reticularis* (Pecchioli in Sacco, 1891) – Terryn & Ryall, p. 31, pl. 7, figs 8-17.

**Material and dimensions** – Maximum height 53.5 mm, width 10.4 mm. **CO**: NHMW 2022/0202/0003-0004 (2), NHMW 2022/0202/0005 (11), RGM.1404364 (3). **EL**: NHMW 2022/0202/0037 (3).

**Description** – Medium sized, slender weakly cyrtoconoid shell of up to 14 teleoconch whorls; apical angle 20-23°, later decreasing to 10-12°. Protoconch not preserved. Early teleoconch whorls conical, flat sided, with subsutural band well developed, delimited by deep groove. Sculpture below band of sharp, prominent, crowded, more or less orthocline arcuate axial ribs, separated by narrower interspaces and narrow irregular spiral cords and threads, tending to form finely reticulated surface sculpture. Number of axials and spirals highly variable, but always crowded. Abaxially whorl profile weakly convex below subsutural band with periphery mid-whorl. Suture distinctly incised. Last whorl moderately high, 31-32% of total height, convex below subsutural band, axials well-developed on band and below. Base convex, moderately constricted. Fasciole moderately broad and prominent, delimited adapically by weak carina. Aperture narrow. Columella strongly excavated in adapical half. No columellar fold. Columellar callus forming broad, thin rim, poorly delimited from base. Anal canal narrow. Outer lip thin. Siphonal canal moderate length, narrow, moderately twisted, shallowly notched at tip.

**Discussion** – Authorship of this species is complex. Although authorship is often ascribed to Pecchioli, this is incorrect, because it refers to an unpublished manuscript name. The name first appeared as a manuscript name in Seguenza (1875, p. 278) as *Terebra reticularis* Pecchioli (M. S.) where it is a *nomen nudum*. It next appears in Coppi (1881, p. 40) who wrote the manuscript name as *T. reticulata* Pecc. and made it available by comparing specimens from Orciano toscano (Italy) to *Terebra basisteroti* [sic] Nyst, 1845. However, this is a junior homonym of *Terebra reticulata* J. de C. Sowerby 1840 who described a terebrid from the Burdigalian Early Miocene Kutch Formation of India, referred to as *Myurella reticulata* by Harzhauser *et al.* (2009, p. 363). Sacco (1891, p. 40) referred to this species as *Strioterebrum reticulare*

(Pecchioli m.s.) and included Coppi's reference in his chresomy. It is unclear whether Sacco realised Pecchioli's name, made available by Coppi, was a primary homonym, or whether his use of *reticulare* rather than *reticulata* is merely a *lapsus*. In any case, in order to preserve nomenclatural stability, we suggest 1) *Terebra reticulata* Coppi, 1881 is a primary homonym of J. de C. Sowerby, 1840; 2) for the Mediterranean Pliocene species to retain the well-known name of *S. reticulare* with Sacco, 1891 as author. We note that the junior homonym *Terebra reticulata* Simone & Verissimo, 1995 from present-day deep-water Brazil was replaced by *T. crassireticula* Simone, 1999. For further discussion see above under *Strioterebrum pliocenicum*.

**Distribution** – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1891; Davoli, 1977). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1992; Landau *et al.*, 2011; Brunetti, 2022); central Mediterranean, Italy (Sacco, 1891; Pavia, 1976a; Ferrero Mortara *et al.*, 1984; Chirli, 1988, 1997; Andri *et al.*, 2005; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975); eastern Mediterranean (Büyükmeliç *et al.*, 2017). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona (this paper); central Mediterranean, Italy (Sacco, 1891; Palla, 1967; Malatesta, 1974; Caprotti & Vescovi, 1973; Caprotti, 1976; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010); eastern Mediterranean, Turkey (Karakus & Taner, 1994), Syria (Roman, 1940).

#### Genus *Terebra* Bruguière, 1789

**Type species** – By subsequent designation, Lamarck (1799): *Buccinum subulatum* Linné, 1767. Present-day, Indo-West Pacific.

- 1789 *Terebra* Bruguière, p. xv.
- 1810 *Terebrum* de Montfort, p. 431. Type species (by typification of replaced name): *Buccinum subulatum* Linnaeus, 1758, present-day, Indo-Pacific. Unjustified emendation of *Terebra* Bruguière, 1789.
- 1817 *Subula* Schumacher, p. 233. Unnecessary replacement name for *Terebra* Bruguière, 1789.
- 1896 *Noditerebra* Cossmann, p. 47, 51. Type species (by original designation): *Terebra geniculata* Tate, 1886, Eocene, South Australia.
- 1908 *Triplostephanus* Dall, p. 124, 125. Type species (by original designation): *Terebra triseriata* Gray, 1834, present-day, Philippines.
- 1923 *Myurellina* Bartsch, p. 62, 63. Type species (by original designation): *Terebra ornata* Gray, 1834, present-day, Indo-Pacific.
- 1923 *Terebrina* Bartsch, p. 62, 63. Type species (by original designation): *Terebra cingulifera* Lamarck, 1822, present-day, Indo-Pacific. Junior homonym of *Terebrina* Rafinesque, 1815.

- 1928 *Paraterebra* Woodring, p. 135. Type species (by original designation): *Terebra texana* Dall, 1898 [*Terebra taurina* ([Lightfoot], 1786)], present-day, Gulf of Mexico.
- 1929 *Dimidacus* Iredale, p. 341. Type species (by typification of replaced name): *Terebra cingulifera* Lamarck, 1822, present-day, Indo-Pacific. *Nom. nov. pro Terebrina* Bartsch, 1923, *non* Rafinesque, 1815. *Cinguloterebra* Oyama, p. 183. Type species (by original designation): *Terebra hedleyana* Pilsbry, 1905, present-day, Japan.
- 1967 *Panaterebra* Olsson, p. 14. Type species (by original designation): *Terebra robusta* Hinds, 1844, present-day, Caribbean.

*Note* – Above we have given above a list of genera/subgenera presently considered synonyms of *Terebra* Bruguière, 1789. However, Fedosov *et al.* (2020) recognised seven separate clades within *Terebra* including shells with quite disparate shell morphology (Fedosov *et al.*, 2020, fig. 5). Some of these have columellar folds and some do not. In almost all other gastropod families/genera columellar folds are at least genus specific, and further molecular sampling may well show some of the above to be valid at genus/subgenus level.

#### *Species with columellar folds:*

##### *Terebra acuminata* Borson, 1820

Plate 2, figs 1-3

- \*1820 *Terebra Acuminata* Borson, p. 224, pl. 1, fig. 17.
- 1852 *Terebra acuminata* Borson – Höernes, p. 130, pl. 11, figs 23-24 [non fig. 22 = *Terebra neglecta* Michelotti, 1847].
- 1866 *Terebra acuminata* Borson – Pereira da Costa, p. 79, pl. 13, figs 8, 9.
- 1891 *Terebrum acuminatum* (Bors.) – Sacco, p. 18, pl. 1, fig. 29.
- 1891 *Terebrum acuminatum* var. *ascalarata* Sacco, p. 19, pl. 1, fig. 30.
- 1891 *Terebrum acuminatum* var. *subagranulata* Sacco, 19.
- 1891 *Terebrum acuminatum* var. *subagranulata* Sacco, p. 19.
- 1891 *Terebrum acuminatum* var. *granulatoparva* Sacco, p. 19, pl. 1, fig. 32.
- 1891 *Terebrum acuminatum* var. *inflatella* Sacco, p. 19, pl. 1, fig. 33.
- 1891 *Terebrum acuminatum* var. *taurocrassa* Sacco, p. 20, pl. 1, fig. 34.
- 1891 *Terebrum acuminatum* var. *simplicoscalaris* Sacco, p. 20, pl. 1, fig. 35.
- 1891 *Terebrum acuminatum* var. *suprangulata* Sacco, p. 20, pl. 1, fig. 36.
- 1891 *Terebrum acuminatum* var. *asulcoelegans* Sacco, p. 21, pl. 1, fig. 37.
- 1891 *Terebrum acuminatum* var. *magnoplicata* Sacco, p. 21, pl. 1, fig. 38.

#### Plate 1

1. *Hastula costulata* (Borson, 1820), NHMW 2022/0202/0021, height 27.6 mm, width 6.5 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
2. *Hastula farinesi* (Fontannes, 1880), NHMW 2022/0202/0023, height 46.3 mm, width 8.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
3. *Hastula farinesi* (Fontannes, 1880), NHMW 2022/0202/0024, height 33.3 mm, width 6.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
4. *Hastula farinesi* (Fontannes, 1880), NHMW 2022/0202/0025, height 29.3 mm, width 6.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
5. *Hastula wilmulderae* nov. sp. **Holotype** NHMW 2022/0202/0028, height 10.0 mm, width 3.0 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
6. *Hastula wilmulderae* nov. sp. **Paratype 1** NHMW 2022/0202/0029, height 9.7 mm, width 2.9 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
7. *Hastula wilmulderae* nov. sp. **Paratype 2** NHMW 2022/0202/0030, height 8.7 mm, width 2.6 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
8. *Oxymeris fuscata* (Brocchi, 1814), NHMW 2022/0202/0035, height 54.2 mm, width 11.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
9. *Strioterebrum pliocenicum* (Fontannes, 1880), NHMW 2022/0202/0002, height 37.6 mm, width 7.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
10. *Strioterebrum reticulare* Sacco, 1891, NHMW 2022/0202/0003, height 33.2 mm, width 6.9 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
11. *Strioterebrum reticulare* Sacco, 1891, NHMW 2022/0202/0004, height 29.1 mm, width 6.3 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
12. *Strioterebrum reticulare* Sacco, 1891, NHMW 2022/0202/0007, height 53.5 mm, width 10.4 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

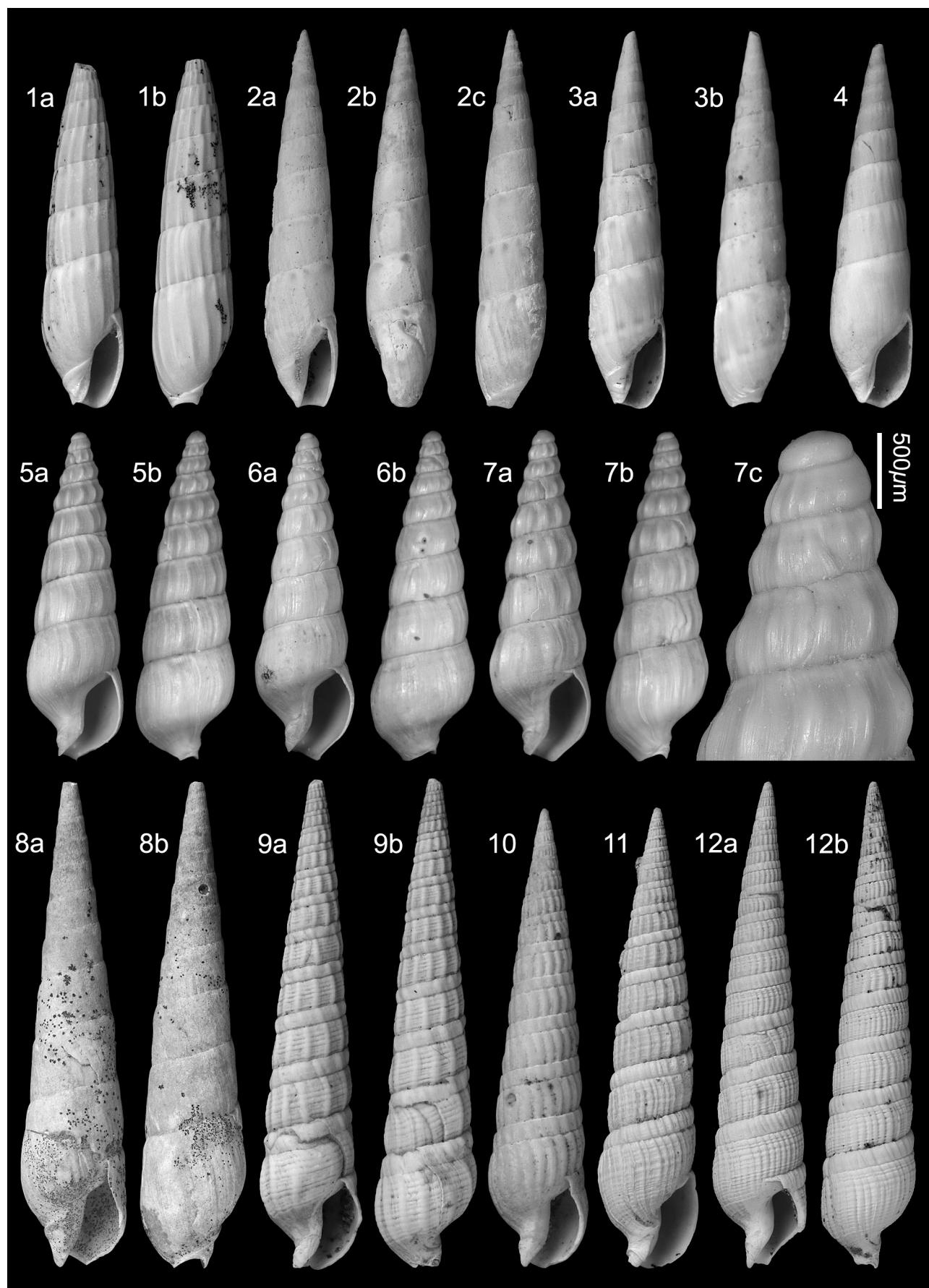


Plate 1

- 1896 *Terebra acuminata* Borson – Cossmann, p. 48, pl. 4, fig. 11.
- 1904 *Terebra acuminata* var. *subagranulata* Sacco, p. 106, pl. 23, fig. 32.
- 1911 *Terebra acuminata* Bors. – Friedberg, p. 4, pl. 1, figs 2, 3.
- 1952a *Terebra (Terebra) acuminata* Borson, 1820 – Glibert, p. 381, pl. 14, fig. 6.
- 1952b *Terebra (Terebra) acuminata* forme *magnoplicata* Sacco, 1891 – Glibert, p. 136, pl. 10, fig. 7a.
- 1952b *Terebra (Terebra) acuminata* forme *acuminata* Sacco, 1891 – Glibert, p. 137, pl. 10, fig. 7b.
- 1954 *Terebra acuminata* Bors. – Strausz, p. 36, 60, 113, pl. 2, fig. 40.
- 1954 *Terebra neglecta* Micht. – Strausz, p. 36, pl. 2, fig. 42 [non *Terebra neglecta* Michelotti, 1847].
- 1955 *Terebra (Terebra) acuminata* Bors. – Korobkov, plate captions, pl. 92, figs 1-4.
- 1960 *Terebra (Terebra) acuminata* Borson 1820 – Kojumdgieva in Kojumdgieva & Strachimirov, p. 216, pl. 51, fig. 5.
- 1960 *Terebra (Myurellina) acuminata* Borson, 1820 – Malatesta, p. 188, pl. 9, fig. 10.
- 1962 *Terebra neglecta* Nyst – Strausz, p. 30, pl. 4, figs 36-37 [non *Terebra neglecta* Michelotti, 1847].
- 1962 *Terebra acuminata* Borson – Strausz, p. 30, pl. 5, figs 4-5.
- 1966 *Terebra neglecta* Michelotti, 1847 – Strausz, p. 391, pl. 4, figs 36-37.
- 1966 *Terebra acuminata* Borson, 1820 – Strausz, p. 392, pl. 5, figs 4-5.
- 1966 *Terebra (Terebra) acuminata* Borson – Symeonidis, p. 293, pl. 65, fig. 6.
- 1973 *Terebra neglecta* (Michelotti) 1847 – Bohn-Havas, p. 1072, pl. 8, fig. 8 [non *Terebra neglecta* Michelotti, 1847].
- 1973 *Terebra* nov. sp. Bohn-Havas, p. 1129, pl. 8, fig. 12.
- 1973 *Terebra (Terebra) acuminata* Borson – Caprotti & Vescovi, p. 185, pl. 3, fig. 2.
- 1974 *Terebra (Myurellina) acuminata* Borson, 1820 – Malatesta, p. 398, pl. 32, fig. 6.
- 1975 *Terebra (Terebra) acuminata* Borson – Fekih, p. 136, pl. 40, fig. 18.
- 1976 *Terebra acuminata* Borson – Caprotti, p. 12, pl. 17, fig. 2.
- 1976b *Terebra (T.) acuminata* Borson, 1820 – Pavia, p. 157, pl. 2, figs 15, 16.
- 1977 *Terebra (Myurellina) acuminata* Borson – Davoli, p. 161, pl. 4, figs 2, 3 [non figs 12-14, = *Terebra tuberculifera* Manzoni, 1870].
- 1977 *Terebra (Myurellina) neglecta* Michelotti – Davoli, p. 165, pl. 4, fig. 4 (only) [non *Terebra neglecta* Michelotti, 1847].
- 1981 *Terebra acuminata* Borson – Krach, p. 78, pl. 22, fig. 18.
- 1982 *Terebra (Myurellina) acuminata* Borson, 1820 – Martinell, p. 114, pl. 1, figs 27, 28.
- 1982 *Terebra (Terebra) cfr. acuminata* Borson, 1820 – Švagrovský, p. 406, pl. 7, fig. 5.
- 1984 *Terebra (Myurellina) acuminata neglecta* Michelotti, 1847 – A.W. Janssen: 340, pl. 13, fig. 11, pl. 77, figs 9–10 [non *Terebra neglecta* Michelotti, 1847].
- 1988 *Terebra (Myurellina) acuminata* Borson, 1820 – Chirli, p. 23, pl. 11, fig. 5.
- 1992 *Terebra acuminata* Borson, 1820 – Cavallo & Repetto, p. 148, fig. 414.
- 1993 *Terebra (Terebra) acuminata* Borson, 1820 – Iljinina, p. 107, pl. 14, fig. 9.
- 1997 *Terebra (Myurella) acuminata* Borson, 1820 – Bahuk, p. 69, pl. 24, figs 1-5.
- 2005 *Terebra acuminata* Borson, 1820 – Andri et al., p. 183, fig. G. 141.
- 2013 *Terebra acuminata* Borson, 1820 – Landau et al., p. 297, pl. 51, figs 10-13.
- 2014 *Terebra acuminata* Borson, 1820 – Brunetti, p. 72, fig. A.
- 2017 *Terebra acuminata* Borson, 1820 – Büyükerç et al., p. 7, p. 14, fig. B1-B2 (plate legend under fig. 6, p. 15; lapsus).
- 2022 *Terebra cingulata* Foresti, 1882 – Brunetti, p. 76, fig. 166 (non Foresti, 1882).
- non 1880 *Terebra acuminata* Borson – Hoernes & Auinger, p. 110, pl. 12, fig. 13 [= *Terebra asulcoornata* Sacco, 1891].
- non 1956 *Terebra acuminata* Borson – Csepreghy-Meznerics, p. 436, pl. 12, fig. 12 [= *Terebra neglecta* (Michelotti, 1847)].
- non 1968 *Terebra (T.) acuminata acuminata* (Brocch.) – Stancu & Andreescu, p. 465, pl. 6, fig. 71 [= *Terebra tuberculifera* (Manzoni, 1870)].
- non 1984 *Terebra (Myurellina) acuminata* Borson – Ruggieri & Davoli, p. 74, pl. 14, fig. 17 [= *Terebra tuberculifera* Manzoni, 1870].
- non 2002 *Terebra (Myurella) acuminata* Borson, 1820 – Harzhauser, p. 116, pl. 10, fig. 9 [= *Terebra neglecta* Michelotti, 1847].
- non 2010 *Terebra (Myurella) acuminata* Borson, 1820 – Moths et al., p. 70, pl. 21, fig. 1.
- non 2014 *Terebra acuminata* Borson, 1820 – Popa et al., p. 18, pl. 6, fig. 1.
- non 2020 *Strioterebrum acuminatum* (Borson, 1820) – Landau et al., p. 94, pl. 83, fig. 1 [= *Terebra neglecta* (Michelotti, 1847)].

*Material and dimensions* – Maximum height 65.7 mm, width 11.1 mm. **CO:** NHMW 2022/0202/0011-0013 (3), NHMW 2022/0202/0014 (6).

*Description* – For revised description, see Harzhauser & Landau (2023). Colour pattern is partially preserved in some specimens consisting of axially elongated reddish dots over the subsutural band.

*Discussion* – The species concept for *T. acuminata* of Landau et al. (2013) was far too broad. This error is corrected (Harzhauser & Landau, 2023; *hoc opus*). We therefore provide a revised chresonymy above to replace that given by Landau et al. (2013, p. 297). *Terebra acuminata* is charac-

terised by its very high spired, slender shell and reduced sculpture, the axial fading by about the 12<sup>th</sup> Teleoconch whorl. *Terebra neglecta* Michelotti, 1847, which was erroneously synonymized with *T. acuminata* in Landau *et al.* (2013), is much smaller, has a lower spire composed of fewer whorls, prominent beads on the subsutural band and prominent axial ribs that persist onto the last whorl.

All specimens from the Estepona assemblages are incomplete. Protoconch and first teleoconch whorls are not preserved. However, early, mid and late teleoconch whorls are represented (Pl. 2, figs 1-3), and can be ascribed with confidence to *Terebra acuminata* Borson, 1820.

Brunetti (2022) figured a specimen from the Atlantic Lower Pliocene Guadalquivir Basin assemblages as *Terebra cingulata* Foresti, 1882. In our opinion this is not that species but *T. acuminata*, which is known to occur in the assemblages. *Terebra cingulata* has a more evenly swollen and rounded subsutural cord and the last whorl is considerably shorter (see Davoli, 1977, pl. 4 figs 8-10). As far as we are aware, *T. cingulata* is a Proto-Mediterranean Upper Miocene species. Pliocene records (*i.e.*, Sacco, 1891; Malatesta, 1974) require confirmation.

**Distribution** – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1891). Lower Middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b). Middle Miocene: northeastern Atlantic (Langhian): Loire Basin (France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1852), Bulgaria (Kojumdgieva & Strachimirov, 1960), Czech Republic (Švagrovský, 1982), Romania (Hoernes & Auinger, 1880; Stancu & Andreescu, 1968), Hungary (Strausz, 1954, 1962, 1966; Csepreghy-Meznerics, 1954, 1956, 1971; Bohn-Havas, 1973), Poland (Friedberg, 1928; Bałuk, 1997; Krach, 1981), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: northeastern Atlantic (Tortonian): Cacela Basin, Portugal (Pereira da Costa, 1866); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1891; Davoli, 1977; Brunetti, 2014). Lower Pliocene: northeastern Atlantic, Guadalquivir Basin, Spain (González Delgado, 1992; Landau *et al.*, 2011; Brunetti, 2022); western Mediterranean, northeastern Spain (Martinell, 1982); central Mediterranean, Italy (Sacco, 1892; Chirli, 1988; Andri *et al.*, 2005), Tunisia (Fekih, 1975); eastern Mediterranean (Büyükmeliç *et al.*, 2017). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1891; Malatesta, 1974; Caprotti & Vescovi, 1973; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992), Crete (Symeonidis, 1966). Lower Pleistocene: central Mediterranean, Italy (Malatesta, 1960).

### *Terebra postneglectum* Sacco 1891

Plate 2, figs 4-5

- \*1891 *Terebrum postneglectum* Sacco, p. 29, pl. 1, fig. 66.
- 1891 *Terebrum postneglectum* var. *subtessellatoides* Sacco, p. 30, pl. 1, fig. 67.

- 1891 *Terebrum postneglectum* var. *cingulatoides* Sacco, p. 30, pl. 1, fig. 68.
- 1891 *Terebrum postneglectum* var. *subexpertusata* Sacco, p. 30, pl. 1, fig. 69.
- 1973 *Terebra (Terebra) postneglecta* Sacco – Caprotti & Vescovi, p. 185, pl. 3, fig. 3.
- 1974 *Terebra (Myurellina) cingulata* Foresti, 1882 – Malatesta, p. 399, pl. 32, fig. 2 (*non Foresti*, 1882).
- 1976 *Terebra postneglecta* (Sacco) – Caprotti, p. 12, pl. 17, fig. 3.
- 1984 *Terebrum postneglectum* Sacco, 1891 – Ferrero Mortara *et al.*, 58, pl. 7, fig. 8.
- 1992 *Strioterebrum postneglectum* (Sacco, 1891) – Cavallo & Repetto, p. 148, fig. 411.
- 1992 *Terebra (Myurellina) postneglecta* Sacco, 1891 – González Delgado, p. 50, pl. 6, figs 11-12.
- 2005 *Terebra postneglecta* Sacco, 1891 – Andri *et al.*, p. 182, fig. G. 140.
- 2011 *Terebra acuminata* Borson, 1820 – Landau *et al.*, p. 38, pl. 21, fig. 4 (*non* Borson, 1820).
- 2014 *Strioterebrum postneglectum* Sacco, 1891 – Brunetti, p. 72, fig. B.

**Material and dimensions** – Maximum height 34.5 mm, width 7.5 mm. **CO:** NHMW 2022/0202/0008-0009 (2), NHMW 2022/0202/0010 (3).

**Description** – Medium sized, slender, weakly cyrtoco-noid shell of up to 14 teleoconch whorls; apical angle ~24°, later decreasing to ~12°. Protoconch not preserved. Teleoconch whorls subcylindrical, with well developed, slightly swollen subsutural band about one-third whorl height, sharply delimited by spiral groove finely undulated by tips of axial ribs, whorl profile below slightly concave, separated by narrowly impressed suture. Sculpture of narrow, close-set, opisthocyt axial ribs, initially equal in width to their interspaces, abapically the distance between ribs widens slightly; ribs subobsolete over subsutural band, strongly developed below. No spiral sculpture below subsutural groove. Last whorl low to moderately high, 29-32% of total height, slightly concave below subsutural band, rounded at base. Base convex, moderately to strongly constricted. Fasciole moderately weakly developed, delimited adapically by weak carina. Aperture small, subquadrate. Columella moderately excavated in adapical half. Two columellar folds present of roughly equal strength. Columellar callus forming broad, thin rim, poorly delimited from base. Anal canal narrow, weakly incised. Outer lip thin. Siphonal canal moderately long, narrow, slightly twisted, strongly bent to left, shallowly notched. Colour pattern preserved; subsutural band light, row of large reddish subquadrate blotches on spire whorls, coalescent on last whorl; blotches almost entire width of whorl below subsutural band.

**Discussion** – Although placed in the genus *Strioterebrum* Sacco, 1891 by some authors (Cavallo & Repetto, 1992; Brunetti, 2014), this species has two well developed columellar folds, absent in *Strioterebrum*. Following the taxonomic revision of the family based on molecular data by

Fedosov *et al.* (2020), the supraspecific importance of absence/presence of columellar folds is unclear. However, they do not occur in *Strioterebrum*, but do in certain clades (*sensu* Fedosov *et al.*, 2020) of *Terebra* Bruguière, 1789.

*Terebra postneglecta* Sacco 1891 is a small but very solid shelled species, characterised by its very sharply delimited subsutural band bearing subobsolete axial sculpture and close set opisthocyst ribs below the subsutural band. Some specimens from both Estepona and the Atlantic Guadalquivir Basin, S. Spain have reddish blotches mid-whorl. Although superficially similar to some forms of *Strioterebrum pliocenicum* (Fontannes, 1880), it is separated by the presence of columellar folds.

The specimen illustrated by Malatesta (1974, pl. 32, fig. 2) as *T. cingulata* is probably a gerontic specimen of *T. postneglecta* with severe damage and repair on the last whorl. The columellar folds are clearly illustrated.

**Distribution** – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1891; Brunetti, 2014). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1992; Landau *et al.*, 2011); central Mediterranean, Italy (Sacco, 1891; Andri *et al.*, 2005). Upper Pliocene: western Mediterranean, Estepona (this paper); central Mediterranean, Italy (Sacco, 1891; Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Ferrero Mortara *et al.*, 1984; Cavallo & Repetto, 1992).

#### **Species without columellar folds:**

##### ***Terebra henkmulderi* nov. sp.**

Plate 2, fig. 6

**ZooBank registration** – urn:lsid:zoobank.org:act:EBCF6B7C-CC28-450D-8460-9DBB75FC1586

**Type material** – Holotype NHMW 2022/0202/0001, height 99.1 mm, width 14.8 mm.

#### **Plate 2**

1. *Terebra acuminata* Borson, 1820, NHMW 2022/0202/0011, height 39.4 mm, width 8.0 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
2. *Terebra acuminata* Borson, 1820, NHMW 2022/0202/0012, height 63.2 mm, width 10.0 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
3. *Terebra acuminata* Borson, 1820, NHMW 2022/0202/0013, height 64.3 mm, width 12.5 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
4. *Terebra postneglecta* Sacco 1891, NHMW 2022/0202/0008, height 34.5 mm, width 7.5 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
5. *Terebra postneglecta* Sacco 1891, NHMW 2022/0202/0009, height 30.0 mm, width 7.2 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
6. *Terebra henkmulderi* nov. sp., **Holotype** NHMW 2022/0202/0001, height 99.1 mm, width 14.8 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.
7. *Terebra praehistrio* nov. sp., **Holotype** NHMW 2022/0202/0015, height 43.2 mm, width 9.1 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
8. *Terebra praehistrio* nov. sp., **Paratype 1** NHMW 2022/0202/0016, height 49.0 mm, width 9.8 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.
9. *Terebra praehistrio* nov. sp., **Paratype 2** NHMW 2022/0202/0017, height 40.5 mm, width 8.8 mm. Velerín conglomerates. Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

**Other material** – Known from holotype only.

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

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

**Etymology** – Named after Henk Mulder, of Monster (The Netherlands) in recognition of his enormous contribution in collecting many of the fossils described in this series, and his friendship. *Terebra* gender feminine.

**Diagnosis** – Large, very slender *Terebra* species, with weakly gradate spire of up to 18 cylindrical whorls, subsutural band hardly developed, not delimited, absent on later whorls, no axial or spiral sculpture, no columellar folds.

**Description** – Large, very slender conical shell, high, weakly gradate spire, 18 teleoconch whorls preserved; apical angle initially 12°; decreasing to 7° on late teleoconch whorls. Protoconch unknown. Early teleoconch whorls flat-sided, mid-whorls very weakly convex, last two flat-sided. Subsutural band very slightly swollen on early teleoconch whorls, but not delimited by groove; band not developed on later whorls. Sculpture absent, except for weakly opisthocyst growth lines. Last whorl low, 22% of total height, subcylindrical, with rounded basal angulation. Base strongly constricted. Aperture small, narrow. Fasciole narrow, rounded, with prominent growth increments, sharply delimited from base. Columella strongly twisted, no columellar folds. Marked angulation between columella and weakly convex parietal area. Columellar callus moderately delimited in columellar area, absent in parietal area, except for small callus just below insertion of outer lip. Anal canal indistinctly incised. Outer lip thin. Siphonal canal moderate length and width, strongly twisted, deflected to the left, weakly notched at tip. Colour pattern preserved consisting of broad, irregular, reddish, vertical flammules.

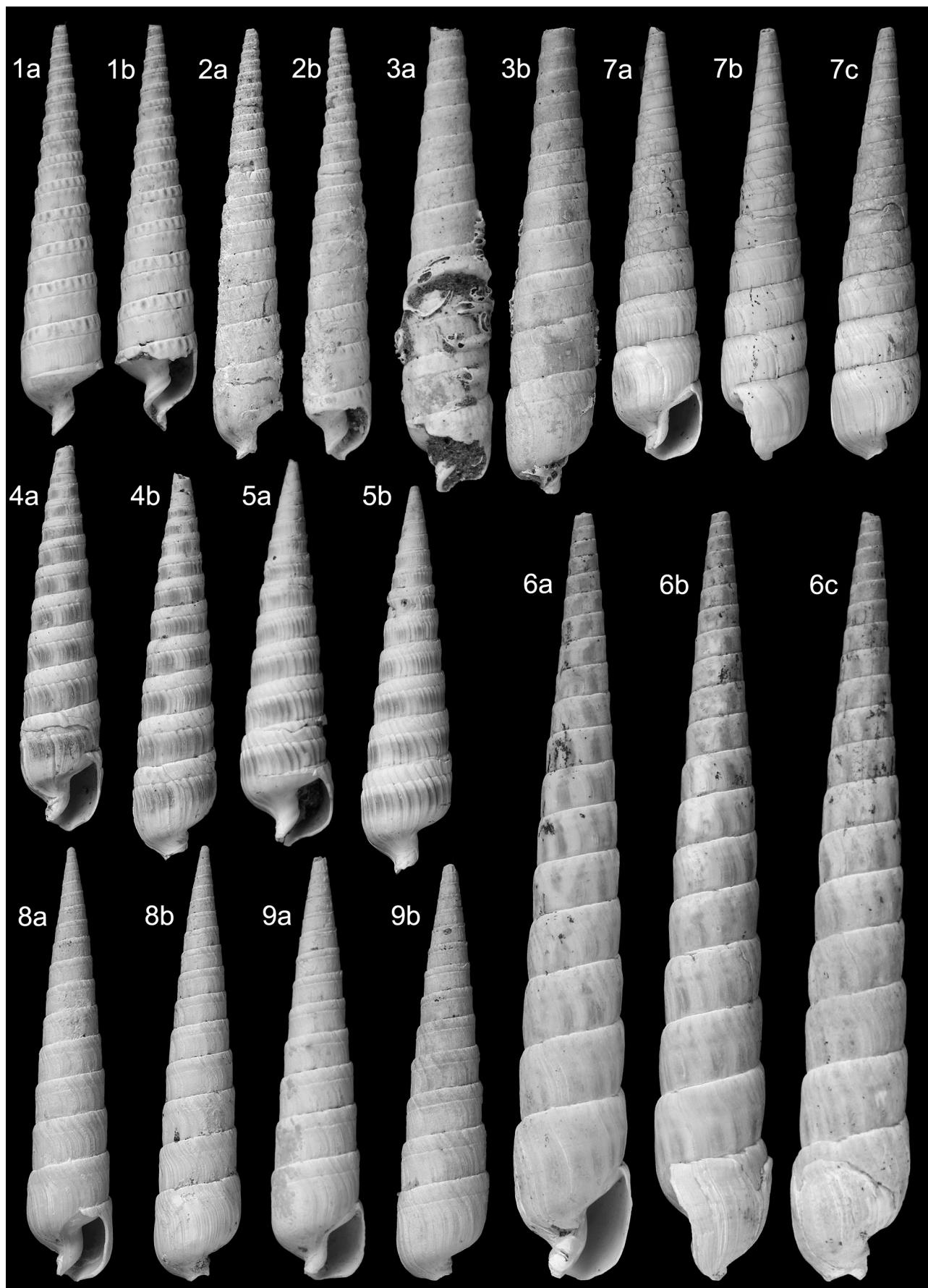


Plate 2

**Discussion** – Although represented by a single specimen, it is almost perfectly preserved and quite distinct from any known fossil or extant European-West African species. In the fossil record *Terebra henkmulderi* nov. sp. is most like *T. acuminata* Borson, 1820 in being large and slender with weak sculpture, but in that species the subsutural band is well developed, at least on early and mid-teleoconch whorls, and two folds are present on the columella. *Terebra neglecta* Michelotti, 1847 is less closely similar, smaller, more strongly sculptured than *T. acuminata*, and again with two columellar folds. In the Middle Miocene Paratethys *T. transylvanica* Hoernes & Auinger, 1880 is most similar in being large shelled, and lacking sculpture, but in that species the subsutural band although poorly delimited is swollen, and the columella bears a single strong fold abapically delimiting the siphonal canal (see Harzhauser & Landau, 2023, pl. X, figs X-XX). In the Tortonian Upper Miocene Atlantic of Portugal and Proto-Mediterranean of Italy *Terebra cacellensis* Pereira da Costa, 1867 is most similar to *T. transylvanica*, but only about half maximum adult size, with relatively narrower and taller whorls. Like *Terebra henkmulderi* nov. sp. it has no columellar folds but differs again in being much smaller and having a swollen subsutural band. *Terebra subulocacellense* (Sacco, 1891) from the Burdigalian of Italy is another species without columellar folds but differs in its convex whorls (see Sacco 1891, pl. 1, fig. 44; Ferrero Mortara *et al.* 1984, pl. 7, figs 1a–b). In the extant faunas, all the eastern Atlantic *Terebra* species illustrated by Bouchet (1983) and Terryn & Ryall (2014) differ in having a more or less well-developed subsutural band. The most similar in being very large and slender is *Terebra corrugata* Lamarck, 1822. Typically, that species has a well-developed, swollen subsutural band making the later teleoconch whorls somewhat coronate. In some specimens the subsutural band is weaker (see Terryn & Ryall, 2014, pl. 5, figs 5, 6), but never as weak as in the Estepona specimen, and *T. corrugata* is easily separated by the presence of columellar folds. In the tropical western Atlantic *Terebra taurinia* ([Lightfoot], 1786) is similar in being solid and large sized, with sculpture weakening on late teleoconch whorls, but the early teleoconch whorls in that species have tripartite sculpture.

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

#### *Terebra praehistrio* nov. sp.

Plate 2, figs 7-9

**ZooBank registration** – urn:lsid:zoobank.org:act:E937353A-9EDF-46EB-A7DC-E1B13DA4A70A

**Type material** – Holotype NHMW 2022/0202/0015, height 43.2 mm, width 9.1 mm; paratype 1 NHMW 2022/0202/0016, height 49.0 mm, width 9.8 mm; paratype 2 NHMW 2022/0202/0017, height 40.5 mm, width 8.8 mm; paratype 3 NHMW 2022/0202/0018, height 45.2 mm, width 9.5 mm; paratype 4 NHMW 2022/0202/0019, height 41.3 mm, width 8.2 mm; paratype 5 RGM.1404361, height 40.1 mm,

width 8.6 mm; paratype 6 RGM.1404362, height 43.2 mm, width 8.9 mm; paratype 7 RGM.1404363, height 33.2 mm, width 8.0 mm.

**Other material** – Maximum height 43.2 mm, width 9.1 mm. CO: 2022/0202/0020 (12).

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

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

**Etymology** – Named reflecting the close similarity and possibly ancestor to *T. histrio* Deshayes, 1857. *Terebra* gender feminine.

**Diagnosis** – Medium sized, moderately slender *Terebra* species, with weakly cyrtoconoid spire of up to 16 low cylindrical whorls, subsutural band not swollen on later whorls, weakly delimited, axials very weak, fade by 5<sup>th</sup>-6<sup>th</sup> whorl, strong opisthocyst growth lines, no spiral sculpture except groove delimiting subsutural band, no columellar folds.

**Description** – Medium sized, moderately slender, weakly cyrtoconoid shell of up to 16 teleoconch whorls; apical angle ~22°, later decreasing to ~10°. Protoconch not preserved. Teleoconch whorls relatively low, subcylindrical, separated by narrowly impressed suture. Early teleoconch whorls with subsutural band about one-third whorl width slightly swollen, delimited by moderately weak groove, weak axial ribs on early teleoconch whorls. Abapically; ribs fade by 5<sup>th</sup>-6<sup>th</sup> whorl, subsutural band flattens, groove separating band weakens, sculpture restricted to opisthocyst growth lines, strongly developed in some specimens. Last whorl low, ~28% of total height, cylindrical, rounded at base. Base convex, strongly constricted. Fasciole moderately weakly developed, narrow, delimited adapically by weak carina. Aperture small, subquadrate. Columella moderately strongly excavated in apical half. No columellar folds. Columellar callus thickened, forming broad rim, sharply delimited from base. Anal canal narrow, weakly incised. Outer lip thin. Siphonal canal moderately short, narrow, slightly twisted, strongly bent to left, shallowly notched.

**Discussion** – *Terebra praehistrio* nov. sp. is closely similar to the present-day West African *T. histrio* Deshayes, 1857, and in both species the axials fade at a similar growth stage (5<sup>th</sup> or 6<sup>th</sup> teleoconch whorl). However, when specimens of the same size are compared, *H. praehistrio* is slenderer, the groove delimiting the subsutural band is weaker, the band itself slightly swollen and rounded in *T. histrio* flat and inconspicuous on later whorls in *T. praehistrio*, the last whorl is much lower (about 28% vs 33% of total height), and the fasciole is more strongly twisted and delimited adapically by a stronger carina.

Bouchet (1983) commented that *T. histrio* was a descendant of *T. postneglecta* with a paucispiral protoconch (in-

ferring, we assume, that it had lost planktotrophy and *postneglecta* had a multispiral protoconch, although we have not seen the protoconch of this species). If our interpretation of *T. postneglecta* above is correct, a phylogenetic relationship between the two is unlikely, as one has columellar folds, the other not. *Terebra praehistrio* is a more likely candidate for ancestry than *T. postneglecta*.

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

## Discussion

In this paper ten species of Terebridae are described and reviewed from the Lower Piacenzian assemblages of Estepona (Figure 1). Three species are described as new: *Hastula wilmulderae* nov. sp., *Terebra henkmulderi* nov. sp., and *Terebra praehistrio* nov. sp.

In the central Mediterranean Pliocene assemblages of Italy, the Terebridae are not particularly speciose. Recognised species are: *Hastula costulata* (Borson, 1820), *H. farinesi* (Fontannes, 1880), *Strioterebrum pliocenicum* (Fontannes, 1880), *S. reticulare* Sacco, 1891, *Terebra acuminata* Borson, 1820, *Terebra postneglecta* Sacco 1891, and *Oxymeris fuscata* (Brocchi, 1814) (see, Sacco, 1891; Malatesta, 1974; Pavia, 1976a; Cavallo & Repetto, 1992; Chirli, 1997; Andri *et al.*, 2005; Brunetti & Cresti, 2018). Other records such as those of *Hastula subcinerea* (d'Orbigny, 1852) of Sacco (1891), *H. striata* (de Basterot, 1825) of Cavallo & Repetto (1992), and *Terebra cingulata* Foresti, 1882 of Malatesta (1974) are, in our opinion, based on misidentifications. Therefore, the Estepona assemblage is relatively better represented, including the genus *Pellifronia* Terryn & Holford, 2008, which is known from the European Atlantic frontage in the Pliocene, but until now had not been recorded in the Mediterranean. This paper also presents a very large new Mediterranean Pliocene species, *Terebra henkmulderi* nov. sp. that can only be rivalled in size by the largest specimens of *T. acuminata* (*fide* Sacco, 1891 recorded height of up to 110 mm for his Pliocene variety *subagranulata*). Middle Miocene specimens from the eastern Proto-Mediterranean Karaman assemblages of Turkey and Paratethys do not attain such large sizes (Landau *et al.*, 2013; Harzhauser & Landau, 2023). However, despite the fully tropical conditions prevailing in the Pliocene Mediterranean during MPPMU1 (*sensu* Raffi & Monegatti, 1993; Landau *et al.*, 2011), terebrid diversity was far lower than the 21 species listed by Terryn & Ryall (2014) for the tropical Eastern Atlantic today. This figure will rise even further with new extant West African species still to be described (Yves Terryn in prep.; personal comm. BL, 01/09/2023).

The Estepona terebrid assemblage is most closely related to that of West Africa today. *Hastula costulata* (Borson, 1820) is closely related to the *H. knockeri* (Smith, 1872), *H. lepida* (Hinds, 1844), and *H. leloeuffi* Bouchet, 1983

group, *Oxymeris fuscata* (Brocchi, 1814) and the living *O. senegalensis* (Lamarck, 1822), *Strioterebrum pliocenicum* (Fontannes, 1880) is still living off West Africa today (although this group is under review and extant forms although closely related may not be conspecific), *Terebra acuminata* Borson, 1820 is reminiscent of the extant West African *Terebra corrugata* Lamarck, 1822 and *Terebra guineensis* (Bouchet, 1983), and we suggest herein that *T. praehistrio* nov. sp. may be ancestral to *T. histrio* Deshayes, 1857.

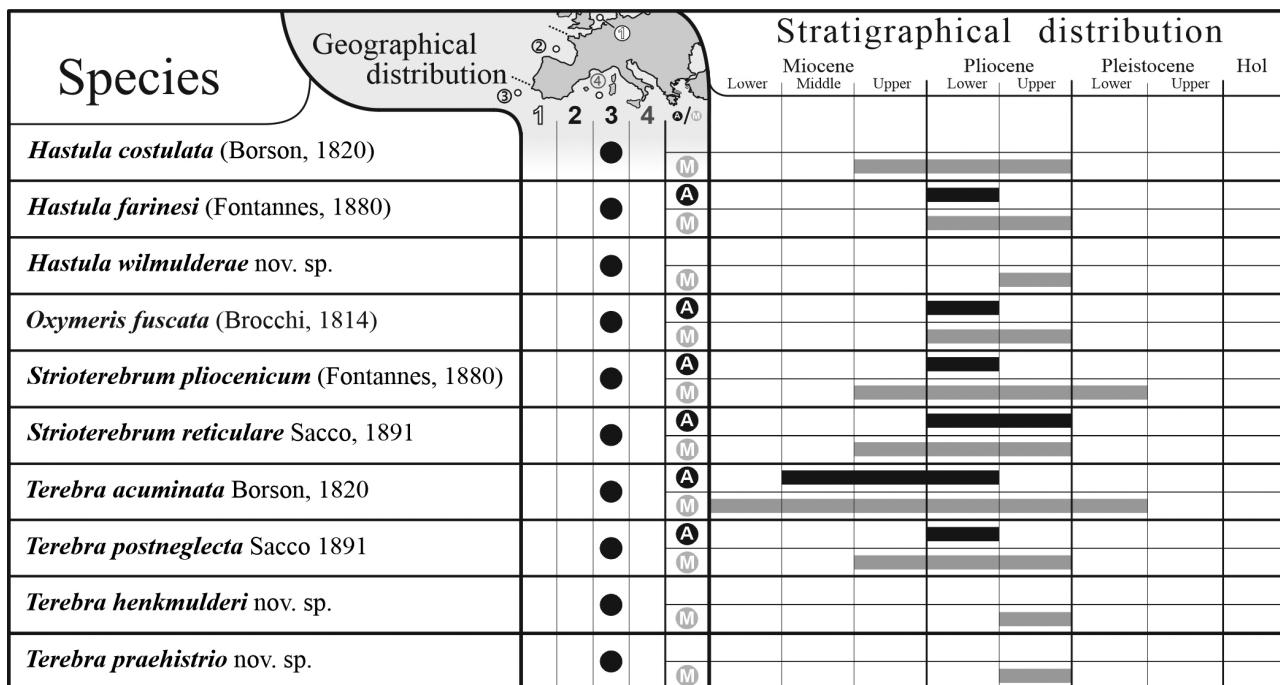
In the Estepona assemblages almost all terebrids were found in the shallower water assemblages. Only *Hastula wilmulderae* nov. sp. seems to have lived in a deeper water habitat.

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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 Pliocene-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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