The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 22: Marine Heterobranchia (excluding Pyramidelloidea)

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In this paper we review the Heterobranchia (excluding Pyramidelloidea) of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. 59 species are reviewed representing 37 genera.
Voluta exilis Eichwald, 1829 is a junior homonym of *Voluta exilis* Gmelin, 1791, therefore *Ringicula guzhovi* nov. nom. is proposed for the Paratethyan species. *Tornatina hemipleura* Fontannes,1880 is considered a junior subjective synonym of *Acteocina knockeri* (E.A. Smith, 1872).
This group includes species with mostly planktotrophic development that are widely dispersed geographically and long lived stratigraphically. This is especially true of the Architectonicidae. Hence, in contrast to other parts of this series, none of the species are endemic to the Estepona assemblages. Both shallow and deeper-water taxa are represented, and the assemblage is similar to that found in the tropical Mediterranean Pliocene of Italy (Mediterranean ecostratigraphic unit MPPMU1).

Key words: southern Spain, Upper Pliocene, Gastropoda, Heterobranchia

Introduction

In this paper we continue to revise the gastropods found in the Pliocene assemblage of Estepona in southwestern Spain. In this part we review the Heterobranchia (excluding Pyramidelloidea that were reviewed by Landau & Micali, 2021 and Pteropoda reviewed by A.W. Janssen, 2004). For further introductory discussion, see Landau *et al*. (2003).
Until now, few papers have concentrated on these groups in the Pliocene western Mediterranean. They have been discussed and figured as parts of the assemblages of the Lower Pliocene of the Barcelona region by Martinell (1982) and the adjacent Lower Pliocene Atlantic Guadalquivir Basin by González Delgado (1986) and Landau *et al*. (2011), but with relatively few species included. The Architectonicidae from northeastern Spain were listed, but not figured, by Solsona & Martinell (1996) as part of a wider discussion on the palaeobiogeography of the group in the Pliocene Mediterranean. This paper is therefore a major contribution to the knowledge of the marine Heterobranchia during the tropical Mediterranean Pliocene.

Age of the deposits

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

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL; 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 Naturalis Biodiversity Center, collection Cainozoic Mollusca, Leiden, The

Netherlands (RGM), ex. Henk Mulder collection, and the Natural History Museum Vienna (NHMW), ex. Bernard Landau collection.

For the Architectonicoidea we follow terminology of Bieler (1993, p. 9) and Harzhauser & Landau (2023, fig. 1). We note that Bieler uses the term 'spiral ribs' for what in this series we would normally call 'cords', restricting the term ribs for axial sculpture. We prefer to use 'cords' for concentric sculpture instead of 'spiral ribs'. This is reflected in the abbreviations introduced by Bieler (1993, p. 9) where the letter 'R' is replaced herein by 'C'.

Protoconch measurements:
The protoconch in architectonicids is heterostrophic and almost always multispiral. Almost planispiral protoconchs occur only in *Pseudomalaxis* author, year and *Spirolaxis* author, year (Bieler, 1993, p. 15). As the protoconch is tilted and inverted, only the diameter of the base not covered by teleoconch can be measured, as shown by Bieler (1993, p. 14, fig. 2); dp = diameter protoconch.

Protoconch (mm):
very small < 0.6 >; small < 0.9 >; medium-sized < 1.2 >; large < 1.5 >; very large > 1.5.

Teleoconch characters:
BF = basal field, IPC = infraperipheral cord.
LMC = lower midcord, LPC = lower peripheral cord,
MC = midcord(s), PUC = proxumbilical cord,
SD = widest shell diameter, SSC = subsutural cord,
UC = umbilical crenae, UD = umbilical diameter,
UMC = upper midcord, UPC = upper peripheral cord.

***Teleoconch (mm)*:**
very small < 5 >; small < 10 >; medium-sized < 20 >; large < 40 >; very large < 60 >; extremely large > 60.

Umbilical diameter (as percentage [%] of shell diameter):
very narrow < 10 >; narrow < 15 >; moderately wide < 25 >; wide < 35 >; verv wide < 45 >; extremely wide > 45.

Apertural characters:
CG = crenal groove, PG = parietal groove.

For the Mathildidae we refer to the subsutural cord, the mid-whorl cord and the abapical cord at the abapical suture as S1, S2, S3 as these cords are homologous in all species (see Harzhauser & Landau, 2023, fig. 3).

For the rest of the groups covered in this work the same size ranges are used to describe shell size as used in the architectonicids [see above *Teleoconch (mm)*], but not the umbilical diameter.

Abbreviations:
CO: Velerín conglomerates; **PA**: Rio del Padrón;
VC: Velerín carretera; **VA**: Velerín Antena;
PQ: Parque Antena; **EL**: El Lobillo; see Landau *et al*. (2003, p. 4, text-fig. 1).

NHMW Natural History Museum Vienna (Austria)
RGM Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

Systematic Palaeontology

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

Subclass Heterobranchia
"Lower" Heterobranchia
Superfamily Architectonicoidea Gray, 1850
Family Architectonicidae Gray, 1850

Note – We are not aware of any molecular phylogeny at family level. We therefore follow Bieler's (1988) cladistic analysis of the Architectonicidae Gray, 1850 and group them as presented by Bieler (1988, fig. 22).

***Solatisonax*, *Discotectonica*, *Granosolarium* clade (of Bieler, 1993, fig. 21)**

Genus *Ammotectonica* Harzhauser & Landau, 2023

Type species (by original designation) – *Ammotectonica gregorovae* Harzhauser & Landau, 2023. Middle Miocene, Czech Republic.

2023 *Ammotectonica*, p. 8.

***Ammotectonica emiliae* (Semper, 1861)**
Plate 1, figs 1-2, Plate 13, fig. 3

1832 *Solarium plicatulum* De Cristofori & Jan, p. 6 [*non* Deshayes, 1825].
*1861 *Solarium Emiliae* Semper, p. 401.
1881 *Solarium aragonae* Bagatti, p. 27, fig. 13.
1892 *Granosolarium*? *Emiliae* (Semp.) – Sacco, p. 63, pl. 2, fig. 31.
1971 *Solarium plicatulum* De Cristofori & Jan, 1832 – Pinna, p. 428, pl. 76, fig. 4.
1978 *Solarium plicatulum* De Cristofori & Jan, 1832 – Pinna & Spezia, p. 159, pl. 50, fig. 1.
1994 *Solariaxis plicatulum* (De Cr. & Jan) – Tabanelli & Segurini, p. 12, pl. 1, figs 5-6.
2002 *Discotectonica plicatula* De Cristofori & Jan, 1832 [*sic*] – Bogi *et al*., p. 33, figs 5, 6.
2002 *Discotectonica emiliae* (Semper, 1861) – Forli *et al*., p. 143, figs 24-26.
2013 *Discotectonica plicatula* (De Crist. & Jan, 1832) – Chirli, p. 9, pl. 3, figs 1-6.

Material and dimensions – Maximum diameter 11.5 mm x 7.5 mm, height 4.2 mm. **VC**: RGM.1404267-268 (2), RGM.1404269 (20), NHMW 2023/0076/0094 (9).

Description – Shell medium sized, moderately flattened,

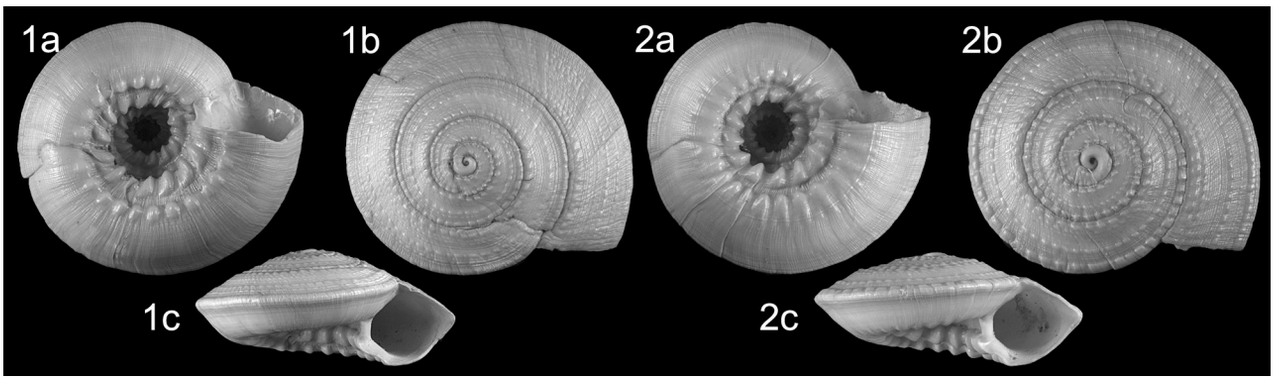

Plate 1. *Ammotectonica emiliae* (Semper, 1861); 1. RGM.1404267, diameter 8.1 mm x 7.2 mm, height 4.1 mm; 2. RGM.1404268, diameter 6.3 mm x 5.5 mm, height 3.0 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

lenticular, peripheral keel prominent, profile flattened to weakly convex above, convex below; umbilicus wide (UD approx. 27-31% of SD). Protoconch small (dp = 0.8), separated from teleoconch by prominent, sharp varix. Teleoconch: sculpture dorsum; on spire whorls SSC distinctly beaded, MC bearing 6-7 fine, irregular, weakly beaded threads, UPC beaded, roughly equal in strength to SSC, LPC strongest, beaded; a few further irregular finely beaded threads intercalated between UPC and LPC. Periphery: UPC weakly developed, LPC forms prominent, blunt keel, also serving as upper point of whorl attachment. Base: concave immediately adjacent to keel, convex below, IPC, not developed, BF bearing very numerous fine treads, with weak axial growth lines strengthening towards umbilicus, giving BF finely reticulated appearance; two coarsely tubercular, but poorly delimited spiral cords surround umbilicus, outer (PUC) strongly developed, inner (UC) wider, even stronger, bearing tubercular crenae overhanging umbilicus, tubercles pointed towards umbilicus; umbilical wall bearing strong axial growth lines, without spiral sculpture. Aperture small, subquadrate, strongly angled at peripheral keel. Columella very short, slightly thickened, straight. CG moderately weak, shallow; PG weak.

Discussion – As pointed out by Forli *et al*. (2002, p. 143) *Solarium plicatulum* De Cristofori & Jan, 1832 is a junior primary homonym of *Solarium plicatulum* Deshayes 1825 (Deshayes, 1825, pl. 24, figs 19-21; 1832, p. 220: reference courtesy of J.M. Pacaud) a species from the Eocene of the Paris Basin. The first available name is *Solarium emiliae* Semper, 1861; *Solarium aragonae* Bagatti, 1881 is a junior subjective synomym.
Ammotectonica emiliae is separated from other Estepona architectonicids by the generic characters of Harzhauser & Landau, 2023: prominent axial folds on the basal field and the blunt UC. *Solatisonax* author, year has a narrow cylindrical umbilicus, whereas the umbilicus is funnel shaped in *Ammotectonica* (for generic discussion see Harzhauser & Landau, 2023, p. 8). It is most similar to the Middle Miocene Paratethyan *Ammotectonica soproniensis* (Strausz, 1960), but differs in having less prominent peripheral cords, even coarser UC, and the distinct groove separating the UC from the base.
Forli *et al*. (2002, p. 144) noted that the species was found abundantly in Lower Pliocene deeper water deposits. In Estepona it is also found exclusively in the deeper water assemblage of Velerín carretera.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1892). Lower Pliocene: central Mediterranean, Italy (De Cristofori & Jan, 1832; Sacco, 1892; Pinna, 1971; Pinna & Spezia, 1978; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Tabanelli & Segurini, 1994).

Genus *Solatisonax* Iredale, 1931

Type species (by original designation) – *Solatisonax injussa* Iredale, 1931. Present-day, Victoria, Australia.

1931 *Solatisonax* Iredale, p. 229, 233.
1985 *Granoheliacus* Melone & Taviani, p. 175. Type species (by original designation): *Heliacus alleryi* G. Seguenza, 1876. Pliocene, Italy.
1985 *Redivivus* Melone & Taviani, p. 178. Type species (by original designation): *Solarium contextum* G. Seguenza, 1876. Pliocene, Italy.

***Solatisonax contexta* (G. Seguenza, 1876)**
Plate 2, figs 1-4, Plate 13, fig. 1

*1876 *Solarium contextum* G. Seguenza, p. 8.
1880 *Solarium contextum* G. Seguenza, p. 260.
1903 *Solarium contextum* L. Seguenza, p. 457, pl. 17, figs 3-5.
1982 *Heliacus contextus* (G. Seguenza in L. Seguenza, 1902 [*sic*] – Melone & Taviani, p. 531, 533, figs 1-6.
1985 *Heliacus* (*Redivivus*) *contextus* (L. Seguenza, 1902 [*sic*]) – Melone & Taviani, p. 178, figs 48-52.
1999 *Heliacus contextus* (Seguenza 1902 [*sic*]) – Ardovini & Cossignani, p. 72, 74, unnumbered fig. top.

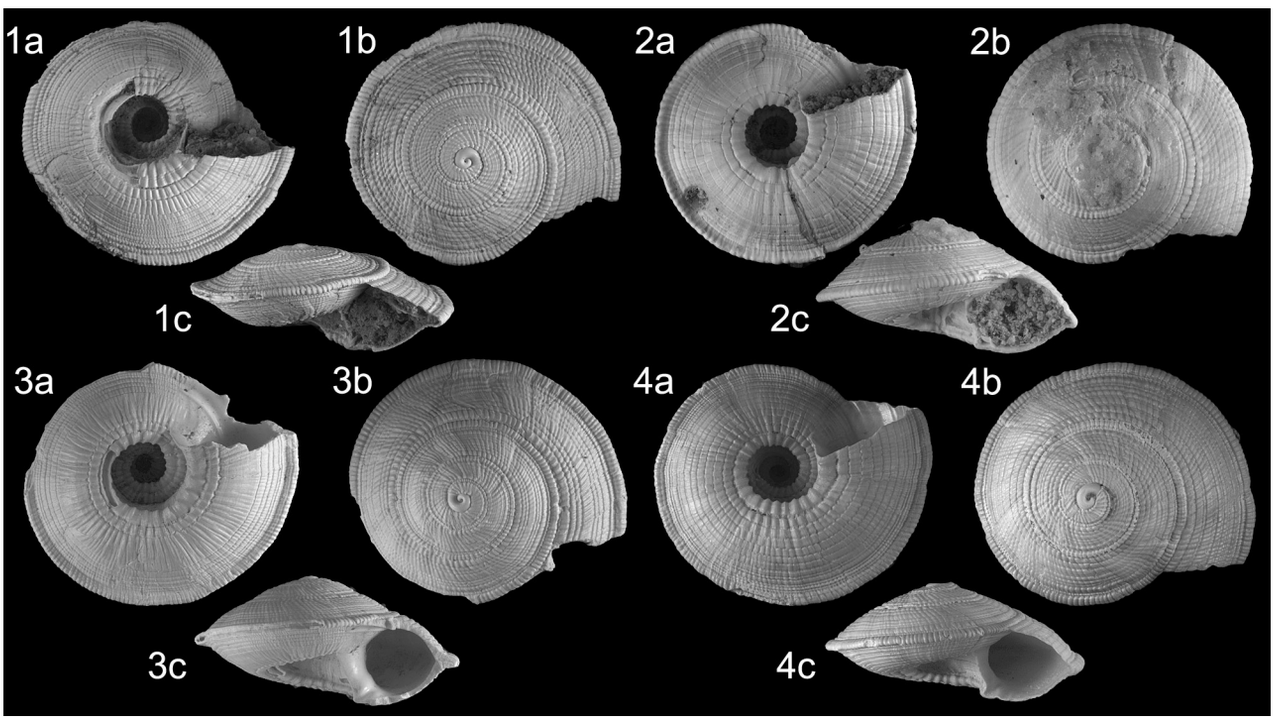

Plate 2. *Solatisonax contexta* (G. Seguenza, 1876); 1. NHMW 2023/0076/0059, diameter 11.9 mm x 10.3 mm, height 4.7 mm. Velerín sands. 2. NHMW 2023/0076/0060, diameter 12.4 mm x 11.1 mm, height 6.3 mm. Velerín conglomerates. 3. NHMW 2023/0076/0062, diameter 13.5 mm x 11.7 mm, height 6.7 mm; 3. NHMW 2023/0076/0063, diameter 11.6 mm x 10.2 mm, height 5.9 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2002 *Heliacus* (*Redivivus*) *contextus* (Seguenza, L. 1902 [*sic*]) – Bogi *et al*., p. 33, figs 12, 13.
2005 *Heliacus contextus* (Seguenza L. 1902 [*sic*]) – Repetto *et al*., p. 225, fig. 938.
2011 *Heliacus contextus* (Seguenza L. 1903 [*sic*]) – Cossignani & Ardovini, p. 32, 336, unnumbered fig.

Material and dimensions – Maximum diameter 13.5 mm x 11.7 mm, height 6.7 mm. **VC**: NHMW 2023/0076/0062-0063 (2). **CO**: NHMW 2023/0076/0060 (1), NHMW 2023/0076/0061 (1). **VS**: NHMW 2023/0076/0059 (1).

Description – Shell medium sized, moderately solid and flattened, lenticular, peripheral keel prominent, profile concave to convex above keel, convex below; umbilicus wide (UD 25-28% of SD). Protoconch large (dp = 1.24), separated from teleoconch by sharp, narrow varix. Teleoconch: sculpture dorsum; SSC moderately developed, UMC, LMC, and UPC all developed, slightly narrower than SSC, with single secondary cordlet intercalated on later whorls, all beaded by prosocline axial growth lines; LPC strong, forming elevated keel, upper point of whorl attachment at base of keel. Base: concave immediately adjacent to keel, IPC not developed, BF convex, bearing numerous finely beaded cords, widening towards the umbilicus, and irregular axial folds that strengthen towards umbilicus; PUC well developed, separated from BF by groove, UC separated from PUC by even deeper groove, bearing tubercular crenae overhanging umbilicus, tubercles pointed towards umbilicus; umbilical wall bearing fine crowded spirals and weak axial growth line. Aperture small, rounded, strongly angled at peripheral keel. Columella very short, slightly thickened, oblique. CG well developed, narrow; PG weak.

Discussion – Melone & Taviani (1982, p. 531) considered *Solarium contextum* G. Seguenza, 1876 a *nomen nudum*, and the name made available by L. Seguenza (1902 [*sic*]). Bieler & Petit (2005, p. 30) argued that even if not available from 1876, it was described by G. Seguenza in 1880. However, the description given by G. Seguenza "*Affine al precedente cogli avvolgimenti e la base più convessi e meno granosi* [Similar to the previous one with the whorls and the base more convex and less granular]" (1876, p. 8) is valid (ICZN, 1999, Art. 12.1).
Although originally described from the Plio-Pleistocene of Italy, *Solarium contextum* was later found to be living in the Mediterranean (Melone & Taviani, 1982). Specimens from Estepona have an umbilicus about half the diameter of present-day specimens of *S. contextum* (12% *vs*. 25-28%) illustrated on MolluscaBase (at: http://www.rkapeller.eu/species.html?SM_Heliacus_contextus) and sculpture is much weaker than any of the living specimens. However, the specimens on MolluscaBase seem to be different from those illustrated by Melone & Taviani (1982, 1984), with stronger sculpture and a wider umbilicus. Bogi *et al*. (2002, figs 12-13) figured a specimen as *Heliacus* (*Redivivus*) *contextus* (Seguenza, L. 1902 [*sic*]), which is closely similar to the Estepona specimens

in sculpture, but the UD is about 23% of SD, almost double the width of the Estepona specimens, and similar to the present-day ones. The umbilicus of specimens of *S. contextus* from Estepona are even wider (UD 25-28%). We therefore agree with Chirli in considering *S. pliohumilis* a separate species. As opposed to *S. contexta* that is found in all the Estepona assemblages, *S. pliohumilis* is found only in the deeper water deposits of Velerín carretera.

Bieler & Petit (2005, p. 16) considered *Redivivus* Melone & Taviani, 1985 (type species, by original designation, *Solarium contextum* G. Seguenza, 1876) a junior subjective synonym of *Solatisonax* Iredale, 1931.

Solatisonax contexta is relatively variable in profile, some specimens are relatively irregular and dorsally flattened (Pl. 2, fig. 1), whereas others have a high dorsum (Pl. 2, fig. 2). The cords on the base are somewhat variable; developed along the entire BF in most specimens, although in one the cords are only developed on the peripheral half of the BF, leaving the medial half to the PUC without cords (Pl. 2, fig. 3). Dorsal sculpture between the SSC and LPC is also variable, some cords wider than others.

For further discussion and comparison, see below under *Solatisonax pliohumilis* (Chirli, 2013).

Melone & Taviani (1985, p. 180) recorded living specimens exclusively from circalittoral environments. Bogi *et al*. (2002, p. 33) noted that in the Italian Pliocene this was a middle and deep circalittoral species. In Estepona it is found in both the shallow and deeper water assemblages but is uncommon in all deposits.

Distribution – Lower Pliocene: central Mediterranean, Italy (L. Seguenza, 1903; Bogi *et al*., 2002). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bogi *et al*., 2002). Lower Pleistocene: central Mediterranean, Italy (Melone & Taviani, 1985). Present-day: central Mediterranean, Italy (Melone & Taviani, 1982, 1985; Ardovini & Cossignani, 1999; Cossignani & Ardovini, 2011).

***Solatisonax pliohumilis* (Chirli, 2013)**
Plate 3, figs 1-2, Plate 13, fig. 2

*2013 *Heliacus pliohumile* Chirli, p. 15, pl. 5, figs 1-6.

Material and dimensions – Maximum diameter 10.8 mm x 9.4 mm, height 6.6 mm. **VC**: RGM.1404277 (1), NHMW 2023/0076/0057 (1), NHMW 2023/0076/0058 (4).

Description – Shell medium sized, moderately thin-shelled, and flattened, lenticular, peripheral keel prominent, profile convex above and below keel; umbilicus narrow (UD approx. 12-14% of SD). Protoconch large (dp = 1.42), separated from teleoconch by sharp, narrow varix. Teleoconch: sculpture dorsum; SSC weakly developed, not sharply delimited, MC-area bearing six flattened, non-beaded cords interrupted by axial growth lines; two narrow UPC of equal strength, beaded; LPC strong, forming sharp elevated keel, upper point of whorl attachment at base of keel. Base: concave immediately adjacent to keel, IPC slightly stronger, placed close to keel, BF bearing numerous finely beaded cords on outer third that weaken, broaden and become subobsolete towards the umbilicus, and axial folds that strengthen towards umbilicus. UC separated from BF by broad, shallow groove, UC bearing tubercular crenae overhanging umbilicus, tubercles pointed towards umbilicus; umbilical wall bearing axial growth lines, without spiral sculpture. Aperture small, subquadrate, strongly angled at peripheral keel. Columella very short, slightly thickened, straight. CG narrow; PG weak.

Discussion – We interpret these specimens from Estepona as being conspecific with those from the Lower Pliocene of Italy described as *Heliacus pliohumile* Chirli, 2013. However, the genus *Solatisonax* is female, so the correct ending should be *S. pliohumilis*. Chirli (2013) rightly compared his new species with *Solarium contextum* G. Seguenza, 1876, also described from the Pliocene of Italy, pointing out that it differed from that species in having a less elevated carina, weaker sculpture on the dorsum, on the venter well defined spirals restricted to the peripheral part of the whorl, and a narrower umbili-

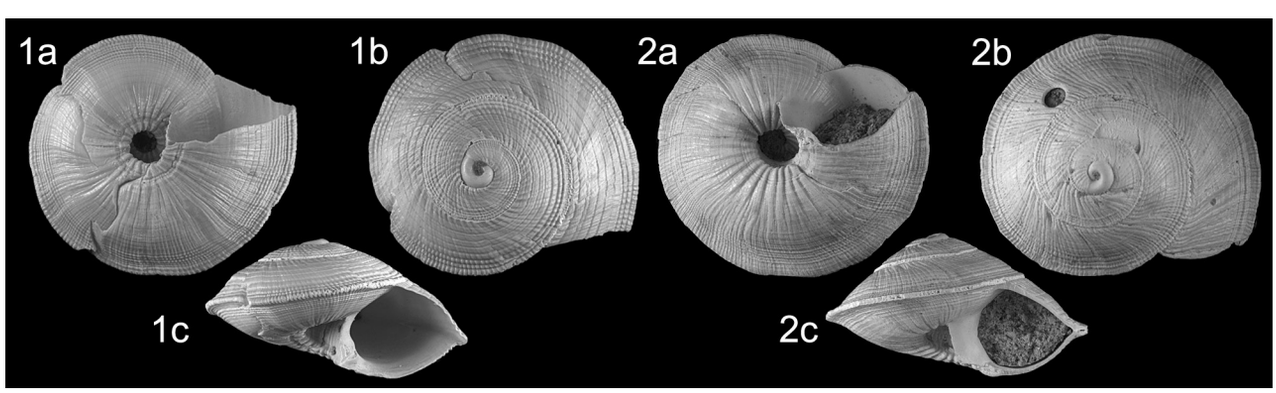

Plate 3. *Solatisonax pliohumilis* (Chirli, 2013); 1. RGM.1404277, diameter 9.7 mm x 8.4 mm, height 5.7 mm; 2. NHMW 2023/0076/0057, diameter 10.8 mm x 9.4 mm, height 6.6 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

cus. For further discussion see under *Solatisonax contexta* (G. Seguenza, 1876) (above). Considering the marked similarity between the type species of *Solatisonax* and *Heliacus pliohumile*, Chirli's species is placed in the genus *Solatisonax*.
Solatisonax rudigerbieleri Tenório, Barros, Francisco & Silva, 2011 from present-day Brazil is similar in profile, but has coarser spiral cords on the MC and BL-areas, coarser UC, and a slightly broader umbilicus.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Genus *Discotectonica* Marwick, 1931

Type species (by original designation) – *Architectonica balcombensis* Finlay, 1927. Australia, Miocene.

1931 *Discotectonica* Marwick, p. 101.
1961 *Acutitectonica* Habe, 30, and appendix p. 10. Type species (by original designation): *Solarium acutissimum* G.B. Sowerby III, 1914, present-day, Japan.
1961 *Russetia* Garrard, p. 23. . Type species (by original designation): *Russetia dilaniatus* Garrard, 1961, present-day, New South Wales, Australia.

***Discotectonica pseudoperspectiva* (Brocchi 1814)**
Plate 4, figs 1-2, Plate 13, fig. 4

*1814 *Trochus pseudo-perspectivus* Brocchi, p. 359, pl. 5, fig. 18.
1841 *Solarium pseudo-perspectivum* Brocchi – Michelotti, p. 212, pl. 2, figs 4-6.
1847 *Solarium pseudo-perspectivum* Brocchi – Michelotti, p. 167, pl. 6, fig. 3.
1892 *Solarium pseudoperspectivum* (Br.) – Sacco, p. 48, pl. 1, fig. 60.
1892 *Solarium pseudoperspectivum* var. *complanata* (Defr.) – Sacco, p. 49, pl. 1, fig. 61.
1892 *Solarium pseudoperspectivum* var. *solariocomplanata* Sacco, p. 49, pl. 1, fig. 62.
1892 *Solarium pseudoperspectivum* var. *conicocomplanata* Sacco, p. 50, pl. 1, fig. 63.
1892 *Solarium pseudoperspectivum* var. *asulcata* Sacco, p. 50, pl. 1, fig. 64.
1892 *Solarium pseudoperspectivum* var. *sastriatula* Sacco, p. 50, pl. 1, fig. 65.
1955 *Architectonica* (*Architectonica*) *pseudo-perspectiva* (Brocchi) 1814 – Rossi Ronchetti, p. 121, fig. 57.
1959 *Architectonica* (*s.s.*) *pseudoperspectiva complanata* Defrance – Ruggieri & Curti, p. 109, pl. 22, fig. 136, pl. 24, fig. 140.
1967 *Architectonica* (*Architectonica*) *pseudo-perspectiva* (Brocchi) – Pelosio, p. 116, pl. 35, fig. 12.
1974 *Architectonica* (*Architectonica*) *pseudoperspectiva* (Brocchi, 1814) – Malatesta, p. 181, pl. 13, fig. 6.
1976 *Architectonica pseudoperspectiva* (Brocchi) – Caprotti, p. 7, pl. 8, fig. 10.
1978 *Trochus pseudo-perspectivus* Brocchi, 1814 – Pinna & Spezia, p. 161, pl. 52, figs 2, 2a-b.
1985 *Discotectonica pseudoperspectiva* – Melone & Taviani, p. 156, fig. 11.
1992 *Discotectonica pseudoperspectiva* (Brocchi 1814) – Cavallo & Repetto, p. 150, fig. 416.
2002 *Discotectonica pseudoperspectiva* (Brocchi 1814) – Bogi *et al*., p. 32, figs 3, 4.
2013 *Discotectonica pseudoperspectiva* (Brocchi 1814) – Chirli, p. 10, pl. 3, figs 7-12.

non 1887 *Solarium pseudoperspectivum* Brocchi – Marshall, p. 15, pl. 5, figs 67, 68 [= *Discotectonica discus* (Philippi, 1844)].
non 1979 *Philippia pseudoperspectiva* (Brocchi, 1814) – Nordsieck & García-Talavera, p. 81, pl. 16, fig. 9 [= *Discotectonica discus* (Philippi, 1844)].

Material and dimensions – Maximum diameter 19.5 x 18.4 mm, height 9.2 mm. **PA**: NHMW 2023/0076/0023-0024 (2), NHMW 2023/0076/0025 (6)

Description – Shell medium sized, flattened, discoidal, peripheral keel sharp and very prominent, profile weakly convex above, below flattened, weakly concave adjacent to peripheral keel, weakly convex towards umbilicus; umbilicus moderately wide (UD approx. 23-28% of SD). Protoconch small (dp = 0.87), sharply delimited from teleoconch. Teleoconch: sculpture very weak; dorsum SSC not developed, MC-area bearing a few subobsolete cordlets, UPC and LPC weakly developed. Periphery: UPC weak, LPC forms prominent keel, also serving as upper point of whorl attachment. Base: concave area next to peripheral keel, IPC not developed, BF bearing a few very weak cords towards periphery, BF area smooth, except for axial growth lines and weak rugae towards the umbilicus, PUC not developed, UC weakly developed overhanging umbilicus and poorly delimited from BF by shallow groove, umbilical wall bearing strong axial growth lines, without spiral sculpture. Aperture small, subquadrate, sharply angled at peripheral keel. Columella short, narrow, oblique. Deep CG, PG moderately developed.

Discussion – *Discotectonica pseudoperspectiva* (Brocchi, 1814) differs from its Estepona congeners in having the most flattened shell with the weakest sculpture. *Ammotectonica emiliae* (Semper, 1861) is immediately separated by its smaller size and strong umbilical crenae. *Discotectonica semisquamosa* (Bronn, 1831) is more similar in having weak basal sculpture, but it is always stronger than in *D. pseudoperspectiva*. The umbilical crenae are smaller and more strongly developed, and the dorsal sculpture whilst weak, is stronger than in *D. pseudoperspectiva*.
In the Estepona assemblages, this species is found only

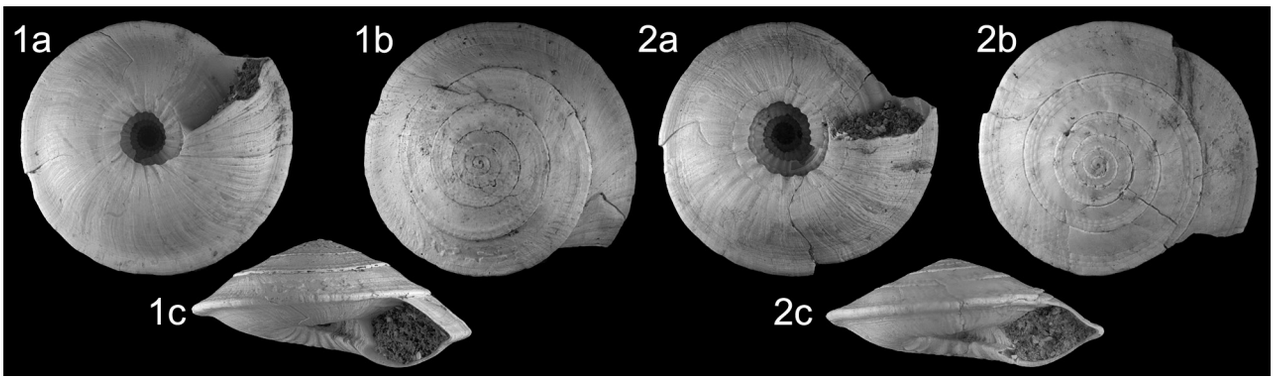

Plate 4. *Discotectonica pseudoperspectiva* (Brocchi, 1814); 1. NHMW 2023/0076/0023, diameter 19.5 x 18.4 mm, height 9.2 mm; 2. NHMW 2023/0076/0024, diameter 15.3 mm x 13.8 mm, height 6.2 mm (digital images). Rio del Padrón, Estepona, Lower Piacenzian, Upper Pliocene.

at the relatively shallow water Río del Padrón locality. Pelosio (1967, p. 116) and Bogi *et al*. (2002, p. 32) note that *D. pseudoperspectiva* was highly variable in the Italian Pliocene. However, the specimens from Estepona are all remarkably similar in their strongly flattened profile, prominent peripheral keel, and extremely weak sculpture. Some authors considered the present-day Mediterranean *D. discus* (Philippi, 1844) conspecific (Jeffreys, 1885; Marshall, 1887; Odhner, 1932; Nordsieck, 1968), whilst others have restricted *D. pseudoperspectiva* to the Pliocene and *D. discus* to the Pleistocene to present-day (Sacco, 1892; Melone & Taviani, 1984; Bogi *et al*., 2002; Chirli, 2013). Certainly, the Estepona form is quite different from *D. discus* in being more flattened, the peripheral keel is more prominent, and the dorsal sculpture much weaker.

Distribution – Lower Pliocene: central Mediterranean, Italy (Sacco, 1892; Pelosio, 1967; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992).

***Discotectonica semisquamosa* (Bronn, 1831)**
Plate 5, figs 1-2, Plate 13, fig. 5

*1831	*Solarium semisquamosum* Bronn, p. 63.
1892	*Solarium semisquamosum* Bronn – Sacco, p. 51, pl. 1, fig. 68.
1892	*Solarium semisquamosum* var. *bisulcata* Sacco, p. 51, pl. 1, fig. 69.
1892	*Solarium semisquamosum* var. *planoscalaris* Sacco, p. 51, pl. 1, fig. 70.
1892	*Solarium semisquamosum* var. *conicoligustica* Sacco, p. 51, pl. 1, fig. 71.
1892	*Solarium semisquamosum* var. *bicingulatella* Sacco, p. 51, pl. 1, fig. 72.
1892	*Solarium semisquamosum* var. *semilaeviuscula* Sacco, p. 52, pl. 1, fig. 73.
1892	*Solarium semisquamosum* var. *inflatoparva* Sacco, p. 52, pl. 1, fig. 74.
1892	*Solarium semisquamosum* var. *sulculoinflata* Sacco, p. 52, pl. 1, fig. 75.
1959	*Architectonica* (*s.s.*) *semisquamosa bisulcata* Sacco – Ruggieri & Curti, p. 110, pl. 24, fig. 142, pl. 24, fig. 143.
2002	*Discotectonica semisquamosa* (Bronn, 1831) – Bogi *et al*., p. 34, figs 10, 11.
2011	*Discotectonica semisquamosa* (Bronn, 1831) – Chirli & Linse, p. 211, pl. 84, fig. 2.
2013	*Discotectonica semisquamosa* (Bronn, 1831) – Chirli, p. 11, pl. 3, figs 13-15, pl. 4, figs 1-3.
non 1954	*Solarium semisquamosum bisulcatus* Sacco – Strausz, p. 15, pl. 6, fig. 140.
non 1966	*Solarium semisquamosum bisulcatus* Sacco – Strausz, p. 117, pl. 51, fig. 14, pl. 52, fig. 2.

Material and dimensions – Maximum diameter 23.4 mm x 12.7 mm, height 11.1. **VC**: RGM.1404270-271 (2), RGM.1404272 (20), NHMW 2023/0076/0092 (8). **CO**: RGM.1404284 (1), NHMW 2023/0076/0091 (20).

Description – Shell medium sized, flattened, discoidal, peripheral keel sharp and very prominent, profile weakly convex above, weakly concave to flattened below; umbilicus moderately wide (UD approx. 23-25% of SD). Protoconch large (dp = 1.47), sharply delimited from teleoconch. Teleoconch: sculpture dorsum; on spire whorls SSC only slightly stronger than MC-area cords, MC bearing 5-6 weak spiral cords, UPC slightly stronger developed, LPC strongest. Periphery: UPC moderately developed, LPC forms sharp prominent keel, also serving as upper point of whorl attachment. Base: concave area next to peripheral keel, a few additional weak spiral threads either side of weak to moderate strength IPC; besides weak threads, BF more or less smooth, with axial folds strengthening towards umbilicus; two spiral cords surround umbilicus, outer (PUC) weakly developed, separated from BF by shallow groove, inner (UC) wider and with strong nodular crenae, separated from PUC by deep, narrow groove, UC overhanging umbilicus, umbilical wall bearing strong ax-

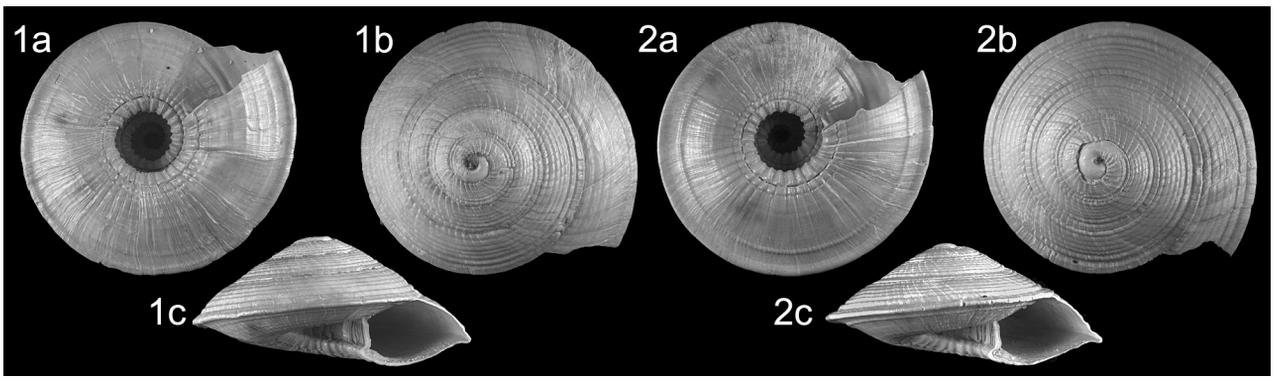

Plate 5. *Discotectonica semisquamosa* (Bronn, 1831); 1. RGM.1404270, diameter 11.6 mm x 10.6 mm, height 6.4 mm; 2. RGM.1404271, diameter 10.3 mm x 9.5 mm, height 5.2 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ial growth lines, without spiral sculpture. Aperture small, subquadrate, sharply angled at peripheral keel, Columella short, narrow, almost straight. Deep CG, PG moderately developed.

Discussion – *Discotectonica semisquamosa* (Bronn, 1831) is immediately separated from *Ammotectonica emiliae* (Semper, 1861) by its more flattened profile, sharper carina, and much smaller umbilical crenae. It is more closely similar to *D. pseudoperspectiva* (Brocchi, 1814) but differs in having the basal ornament more clearly developed; IPC, PUC and UC are all well delimited, whereas in *D. pseudoperspectiva* IPC and PUC are not developed, and the UC in some specimens is hardly delimited from the BF. Specimens from the Middle Miocene of the Paratethys, described by Strausz (1954. 1966) as *Solarium semisquamosum bisulcatus* Sacco, differs from the Estepona specimens by its much wider umbilicus and represents another species.
Bogi *et al*. (2002, p. 33) noted that in the Italian Pliocene *D. semisquamosa* was a circalittoral species, whereas in Estepona almost all specimens come from the deeper water assemblage of Velerín carretera.

Distribution – Upper Miocene: central Proto-Mediterranean (Tortonian), Italy (Sacco, 1892). Lower Pliocene: central Mediterranean, Italy (Sacco, 1892; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Genus *Granosolarium* Sacco, 1892

Type species (by original designation) – *Solarium millegranum* Lamarck, 1822. Italy, Pliocene.

1892 *Granosolarium* Sacco, p. 59.
1892 *Solariaxis* Dall, p. 323. Type species (by original designation): *Solarium elaboratum* Conrad, 1833, Eocene, Alabama, USA.
1936 *Claraxis* Iredale, p. 327. Type species (by monotypy): *Claraxis illustris* Iredale, 1936, present-day, New South Wales, Australia.

***Granosolarium millegranum* (Lamarck, 1822)**
Plate 6, figs 1-2, Plate 13, fig. 6

*1822 *Solarium millegranum* Lamarck, p. 6.
1840 *Solarium millegranum* Lam. – Bellardi & Michelotti, p. 65, pl. 6, figs 6, 7.
1841 *Solarium millegranum* Lamarck – Michelotti, p. 216, pl. 2, figs 16-18.
1892 *Solarium* (*Granosolarium*) *millegranum* Lk. – Sacco, p. 59, pl. 2, fig. 18.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *expansicarinata* Sacco, p. 60, pl. 2, fig. 19.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *complanata* Cocc. – Sacco, p. 60, pl. 2, fig. 20.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *elatoconica* Sacco, p. 61, pl. 2, fig. 21.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *latecrenulata* Sacco, p. 61, pl. 2, fig. 22.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *miocenica* Sacco, p. 61, pl. 2, fig. 23.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *conicodertonensis* Sacco, p. 61, pl. 2, fig. 24.
1892 *Solarium* (*Granosolarium*) *millegranum* var. *miojuventula* Sacco, p. 61, pl. 2, fig. 25.
1959 *Architectonica* (*s.s.*) *millegranum latecrenulata* Sacco – Ruggieri & Curti, p. 111, pl. 25, fig. 145.
1967 *Architectonica* (*Solariaxis*) *millegranum* (Lamarck) f. *latecrenulata* – Pelosio, p. 115, pl. 35, figs 14-16.
1967 *Architectonica* (*Solariaxis*) *millegranum* (Lamarck) – Pelosio, p. 115, pl. 35, fig. 15.
1974 *Architectonica* (*Granosolarium*) *millegrana* (Lamarck, 1822) – Malatesta, p. 184, pl. 13, fig. 5.
1976 *Architectonica millegranum* (Lk.) – Caprotti, p. 7, pl. 8, fig. 12.
1992 *Granosolarium millegranum* (Lamarck, 1822) – Cavallo & Repetto, p. 152, fig. 419.
2002 *Architectonica* (*Granosolarium*) *millegranum* (La-

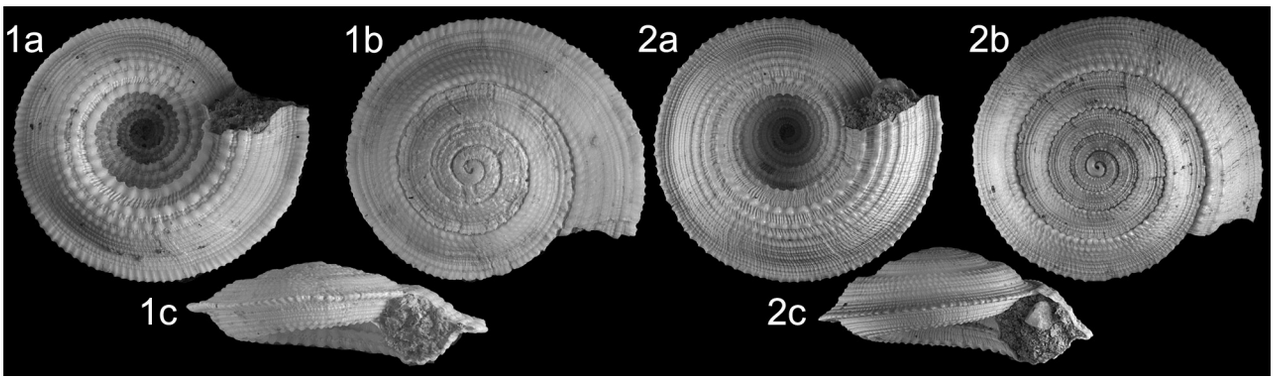

Plate 6. *Granosolarium millegranum* (Lamarck, 1822); 1. NHMW 2023/0076/0064, diameter 12.7 mm x 10.9 mm, height 4.1 mm. El Lobillo 2. NHMW 2023/0076/0066, diameter 17.5 mm x 15.7 mm, height 9.2 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

marck, 1822) – Bogi *et al*., p. 35, figs 21-22.

2013 *Granosolarium millegranum* (Lamarck, 1822) – Chirli, p. 12, pl. 4, figs 4-9.

non 1856 *Solarium millegranum* Lam. – Hörnes, p. 465, pl. 46, fig. 4 [= *Granosolarium semilaevis* (Sacco, 1892)].

non 1923 *Solarium millegranum* Lam. (?) – Friedberg, p. 414, pl. 25, fig. 6 [= *Solatisonax exmonilifera* (Sacco, 1892)].

non 1951 *Solarium millegranum* Lmk. – Montanaro Gallitelli & Tacoli, p. 177, pl. 2, fig. 5 [= *Granosolarium semilaevis* (Sacco, 1892)].

non 1955 *Architectonica* (*Solariaxis*) millegranum Lamk. – Korobkov, pl. 13, figs 19a-c [= *Solatisonax exmonilifera* (Sacco, 1892)].

non 1961 *Architectonica* (*Architectonica*) *millegranum* Lamarck – Marinescu, p. 532, pl. 5, figs 20a-f [= *Granosolarium semilaevis* (Sacco, 1892)].

non 1968 *Solarium millegranum* Lamarck, 1822 – Zelinskaya *et al.*, p. 133, pl. 34, figs 9-12 [= *Granosolarium semilaevis* (Sacco, 1892)].

Material and dimensions – Maximum diameter 17.5 mm x 15.7 mm, height 9.2 mm. **VC**: NHMW 2023/0076/0066 (1), NHMW 2023/0076/0067 (2). **EL**: NHMW 2023/0076/0064 (1), NHMW 2023/0076/0065 (1).

Description – Shell medium sized, flattened, discoidal, periphery sharply carinate, profile squatly scalate above periphery, base convex; umbilicus very wide (UD approx. 36% of SD). Protoconch large (dp = 1.39) sharply delimited from teleoconch. Teleoconch: sculpture of beaded cords on dorsum; SSC relatively strong, UMP and LMC slightly weaker than SSC, with secondary cordlets intercalated, UPC developed in some specimens, in others numerous cordlets of alternating strength towards periphery. Periphery: LPC forms strong, sharp, narrow keel, also serving as upper point of whorl attachment, bearing numerous axially elongated tubercles serrating periphery. Base: convex, BF with numerous finely beaded cords of roughly alternating strength on peripheral half, widening towards mid-base, on medial half four coarser cords bearing larger tubercles with fine threads intercalated, cords widening towards umbilicus, PUC broadest, UC sunken into umbilicus, bearing fine crenae overhanging umbilicus, umbilical wall bearing axial growth lines and very fine spiral threads. Aperture small, rounded, sharply pointed at peripheral keel. CG and PG weak.

Discussion – *Granosolarium millegranum* (Lamarck, 1822) is easily separated from all other Estepona architectonicids by its very wide umbilicus, with the umbilical crenae sunken into the umbilicus. The peripheral keel is also sharper and more protruding than any other Mediterranean Pliocene architectonicid, bearing fine, axially elongated tubercles serrating the periphery. In the Estepona specimens, apart from the major cords SSC, LPC, PUC and UC, the development of the rest of the cords is highly variable. Similar variability was noted by Pelosio (1967, p. 115), and led Sacco (1892) to erect numerous varieties.

Specimens from the Middle Miocene of the Paratethys, described as *Solarium millegranum* by Hörnes (1856) were recognised as being different by Sacco (1892, p. 61), and erected *Solarium millegranum* var. *semilaevis*. *Granosolarium millegranum* differs from *G. semilaevis* in its much larger size (max. diameter 17.5 mm versus 10.4 mm), more sharply carinate periphery, the narrower umbilicus, and the reduced sculpture of beads on the spiral cords of the dorsal and ventral sides (Harzhauser & Landau, 2023).

Bogi *et al*. (2002, p. 35) considered this an infralittoral and bathyal species. In Estepona it is extremely uncommon in both the shallower and deeper water facies.

Distribution – Upper Miocene: central Proto-Mediterranean (Tortonian), Italy (Sacco, 1892). Lower Pliocene. Central Mediterranean, Italy (Sacco, 1892; Pelosio, 1967; Bogi *et al*., 2002; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992).

***Pseudotorinia*, *Pseudomalaxis*, *Spirolaxis* clade (of Bieler, 1993, fig. 21)**

Genus *Pseudotorinia* Sacco, 1892

Type species (by original designation) – *Solarium obtusum* Bronn, 1831, Pliocene, Italy.

1892b *Pseudotorinia* Sacco, p. 66.

For generic synonymy see Landau *et al*. (2020, p. 257).

***Pseudotorinia architae* (O.G. Costa, 1841)**
Plate 7, figs 1-2, Plate 13, fig. 7

*1841 *Solarium Architae* O.G. Costa, p. 5, pl. 1, figs 1a-c.
1862 *Solarium soverbii* Hanley, p. 206.
1873 *Solarium Architae* O.G. Costa – Monterosato, p. 10, pl. 4, figs 21-23.
1887 *Torinia Architae* Costa – Marshall, p. 21, pl. 6, figs 9-11.
1974 *Heliacus* (*Torinista*) *architae* (O.G. Costa) – Turolla, p. 193, pl. 1.
1974 *Heliacus architae* (O.G. Costa) – Melone, p. 22, pl. 1, figs 4-6.
1985 *Heliacus* (*Torinista*) *architae* (O.G. Costa 1839 [*sic*]) – Melone & Taviani, p. 170, figs 34-37.
1986 *Architectonica* (*Nipteraxis*) sp. – González Delgado, p. 95, pl. 3, figs 4-6.
1987 *Heliacus architae* (O.G. Costa 1839 [*sic*]) – Rindone, p. 300, pl. 1, fig. 2.
1992 *Pseudotorinia architae* (Costa, O.G., 1841) – Cavallo & Repetto, p. 152, fig. 420.
1999 *Heliacus architae* (O.G. Costa 1867 [*sic*]) – Ardovini & Cossignani, p. 72, 73, unnumbered fig. bottom.
2001 *Pseudotorinia architae* (O.G. Costa, 1841) – Redfern, p. 139, pl. 63, fig. 575.
2002 *Pseudotorinia architae* (Costa, O.G., 1841) – Bogi *et al*., p. 36, figs 16-18.
2005 *Pseudotorinia architae* (Costa, O.G., 1841) – Repetto *et al*., p. 226, fig. 943.
2006 *Pseudotorinia architae* (Costa, O.G., 1841) – Ruestes & Soriano, p. 12, fig. C.
2011 *Pseudotorinia architae* (Costa, O.G., 1841) – Chirli & Linse, p. 213, pl. 84, fig. 5.
2011 *Pseudotorinia architae* (Costa, O.G., 1841) – Cossignani & Ardovini, p. 32, 337, unnumbered fig.
2011 *Pseudotorinia architae* (Costa, O.G., 1841) – Gofas *et al*., p. 350, unnumbered fig. middle.
2011 *Heliacus* (*Granoheliacus*) *subvariegatus* (d'Orbigny, 1852) – Landau *et al*., p. 39, pl. 22, fig. 2 (*non* d'Orbigny, 1852).
2011 *Pseudotorinia architae* (Costa, O.G., 1841) – Hernández *et al*., p. 241, figs 81 U-W.
2013 *Pseudotorinia architae* (O.G. Costa, 1841) – Cavallari *et al*., p. 7, figs 6-9.
2013 *Pseudotorinia architae* (O.G. Costa, 1841) – Redfern, p. 230, fig. 640.
2014 *Pseudotorinia architae* (O.G. Costa, 1841) – Cavallari *et al*., p. 36, figs 1-3.
2006 *Pseudotorinia architae* (Costa, O.G., 1841) – Chirli, p. 19, pl. 6, figs 3-9.

Material and dimensions – Maximum diameter 9.0 mm x 7.9 mm, height 4.1 mm. **EL**: RGM.1404273-274 (2), RGM.1404300 (2), NHMW 2023/0076/0077 (3).

Description – Shell small, flattened, discoidal, periphery rounded, profile weakly convex above, base angled; umbilicus wide (UD approx. 31-32% of SD). Protoconch medium-sized (dp = 1.04) sharply delimited from teleoconch. Teleoconch: sculpture of beaded cords on dorsum; on spire whorls SSC relatively strong, initially two MC later three, UPC strong, equal to SSC, LPC strongest. Periphery: UPC moderately developed, LPC forms periphery, not prominent, also serving as upper point of whorl attachment. Base obtusely keeled mid-base: moderate strength IPC; 4-5 further weaker beaded cords on BF between IPC and basal keel, three slightly broader spiral cords between keel and UC, UC overhanging umbilicus, umbilical wall bearing strong axial growth lines, and fine spirals. Aperture small, rounded. CG well developed; PG moderately developed.

Discussion – Bieler (1993, p. 281) highlighted the differences between present-day specimens of *Pseudotorinia architae* (O.G. Costa, 1841) from the Mediterranean and eastern Atlantic and those from the western Atlantic and suggested they may represent two distinct species. Specimens from Brazil described and discussed by Cavallari *et al*. (2013) as *P. architae*, although those authors suggested that they might represent a third species within this Atlantic species complex. Similar discussion arises in the Mediterranean fossil literature. Melone & Taviani (1985, p. 170) recorded its presence in the Mediterranean early Pleistocene but said that Italian Upper Miocene Tortonian records by (Coppi, 1881) and Pliocene records of Tiberi (1872) and Cocconi (1873) needed to be confirmed. Melone & Taviani argued that the Neogene specimens they had seen could always be separated from Quaternary to present-day specimens by a series of constant shell characters but did not specify what they were. Bogi *et al*. (2002) illustrated specimens from the Italian Pliocene as *P. architae*, noting that the fossil specimens were higher spired, had a less concave base, more rounded profile, and stronger axial sculpture. They concluded that they could not exclude the possibility that the Italian Pliocene fossil specimens they has could be *P. theresae* (Semper, 1861). Those authors went on to illustrate a specimen of *P. theresae* from the Italian Pliocene that has both the UPC and LPC strongly developed giving the periphery a bicarinate profile.
The specimens from Estepona are very similar to the Italian Pliocene specimen illustrated by Bogi *et al*. (2002, figs 16-18) and identical to those illustrated by Chirli (2013, pl. 6, figs 3-9). We agree that they are a little more elevated that present-day Mediterranean specimens illus-

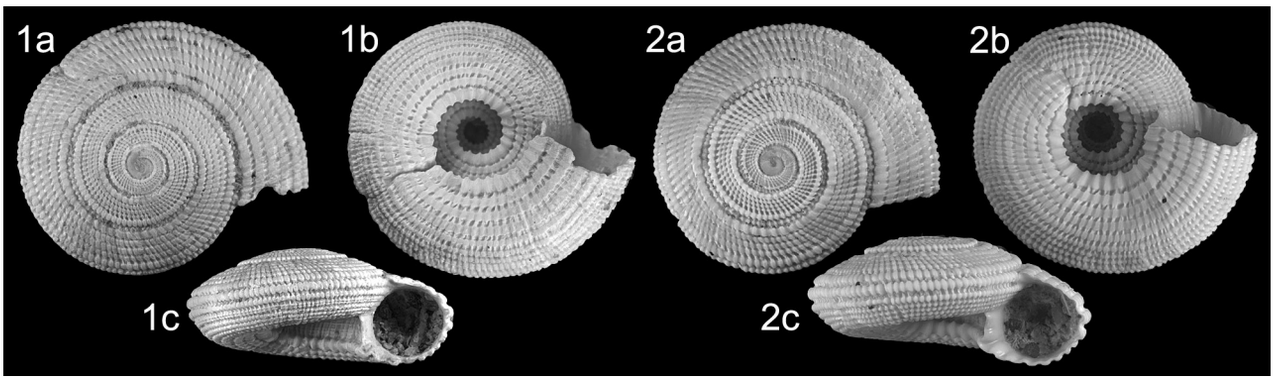

Plate 7. *Pseudotorinia architae* (O.G. Costa, 1841); 1. RGM.1404273, diameter 8.7 mm x 7.6 mm, height 4.1 mm; 2. RGM.1404274, diameter 7.5 mm x 6.5 mm, height 3.3 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

trated by Bieler (1993, fig. 225) and Melone & Taviani (1985, fig. 38). Bieler described the eastern Atlantic form as "…*umbilical side of columellar wall without spiral ribs*" (1993, p. 280). This is difficult to judge on apertural views of present-day specimens as they are so flat. However, the Estepona specimens have fine spirals within the umbilicus (Pl. 7, fig. 1c). Moreover, the third spiral on the dorsal midcord section appears earlier in the Estepona material. Like previous authors, we are unsure where boundaries between members of this species group lie and prefer to provisionally consider them a single variable species.

In their work on the distribution of Architectonicidae in the western Atlantic Pliocene, Solsona & Martinell, 1996, p. 282) listed *Architectonica planulata* (Grateloup, 1832) as occurring in NE Spain and northern Italy, and gave a stratigraphic distribution for the species starting in the Middle Miocene and extending throughout the Pliocene. That work does not provide references nor illustrations for the species. *Solarium planulatum* belongs within the *Pseudotorinia architae* species group (Bieler, 1993, p. 277). Bieler & Petit (2005, p. 57) listed the type material as being Pliocene. This is a *lapsus*, as Grateloup (1832, p. 137) records the locality as Faluns de Saint-Paul, which refers to the Chattian Oligocene locality of Saint-Paul-lès-Dax, Landes, France. The specimens from the Lower Miocene of St.-Paul-lès-Dax and Mérignac illustrated by Cossmann & Peyrot (1919, pl. 15, figs 57-58, 71-73, 77) differ from *P. architae* in having coarser sculpture, SSC is more strongly developed with coarser beading, the basal carina is sharper, also bearing stronger tubercles, and there are fewer cords between the basal carina and the UC. *Pseudotorinia subplicata* (d'Orbigny, 1852), another of the *P. architae* species group, from the French Atlantic Miocene (see Landau *et al*., 2020, pl. 1, figs 1-2), is more closely similar to *P. architae*, but has wider-spaced axial lamellae making the sculpture coarser, but not as coarse as that of *P. planulata*. This is especially evident on the base where there are fewer and stronger UC than in *P. architae*. We suspect that Solsona & Martinell's (1996) references to *P. planulata* refer to *P. architae*, but we cannot be certain. In any case, we have not seen any specimens or reliable references of *P. planulata* in the Pliocene Mediterranean.

Today, *P. architae* is primarily circalittoral, although occasionally infralittoral, and extends down to bathyal habitats in the western Mediterranean and adjacent Atlantic (Melone & Taviani, 1985; Gofas *et al*., 2011). In Estepona in has only been found in the shallower water assemblage of El Lobillo.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1986; Landau *et al*., 2011); central Mediterranean, Italy (Bogi *et al*., 2002; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Cavallo & Repetto, 1992; Bogi *et al*., 2002). Lower Pleistocene: central Mediterranean, Italy (Melone & Taviani, 1985); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Pleistocene (indet.): Canary Islands (Concepción *et al*., 2011). Present-day: western Atlantic, North Carolina to Cuba, Caribbean Sea (Redfern, 2001), Brazil (Cavallari *et al*., 2013, 2014), eastern Atlantic, Canary Islands (Hernández *et al*., 2011), Spain to Azores (Ávila *et al*., 2000), Madeira (Segers *et al*., 2009), Mediterranean Sea (Monterosato, 1873; Turolla, 1974; Melone, 1974; Melone & Taviani, 1985; Rindone, 1987; Ardovini & Cossignani, 1999; Repetto *et al*., 2005; Ruestes & Soriano, 2006; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Pseudomalaxis* P. Fischer, 1885

Type species (by monotypy) – *Bifrontia zanclaea* Philippi, 1844, Pliocene, Italy.

1885 *Pseudomalaxis* P. Fischer, p. 714.

1892 *Discosolis* Dall, p. 331. Type species (by original designation): *Omalaxis nobilis* Verrill, 1885 [= *Pseudomalaxis zanclaeus* (Philippi, 1844)], present-day, NE USA.

1930 *Mangonuia* Mestayer, p. 144. Type species (by original designation): *Mangonuia bollonsi* Mestayer, 1930 [= *Pseudomalaxis zanclaeus meridionalis* (Hedley, 1903)], present-day, New Zealand.

***Pseudomalaxis aldrovandii* (Foresti, 1868)**
Plate 8, figs 1-2, Plate 13, fig. 8

*1868	*Solarium aldrovandii* Foresti, p. 625, pl. 2, figs 17-20.
1891	*Discohelix Castellii* Mantovani, p. 6, figs 1, 2, 5.
1892	*Discohelix* (*Pseudomalaxis*) *Aldrovandi* [*sic*] var. *ligustica* – Sacco, p. 75, pl. 2, fig. 65.
1892	*Discohelix* (*Pseudomalaxis*) *Aldrovandi* [*sic*] var. *Castellii* (Mant.) – Sacco, p. 75, pl. 2, fig. 65bis.
1991	*Pseudomalaxis aldrovandii* (Foresti, 1868) – Ricordi, p. 23, figs 1, 2.
2002	*Pseudomalaxis aldrovandii* (Foresti, 1868) – Bogi *et al*., p. 35, figs 23, 24.
2008	*Pseudomalaxis aldrovandii* (Foresti, 1868) – Chirli & Richard, p. 74, pl. 25, figs 5, 6.
2010	*Solarium aldrovandii* Foresti, 1868 – Ceregato *et al*., p. 60, pl. 2, figs 17-20.
2011	*Pseudomalaxis aldrovandii* (Foresti, 1868) – Chirli & Linse, p. 213, pl. 84, fig. 4.
2013	*Pseudomalaxis aldrovandii* (Foresti, 1868) – Chirli, p. 18, pl. 5, figs 13-15, pl. 6, figs 1-2.

Material and dimensions – Maximum diameter 14.1 mm x 11.2 mm, height 4.8 mm. **VC**: RGM.1404276 (1), RGM.1404304 (5), NHMW 2023/0076/0046 (1), NHMW 2023/0076/0047 (4). **CO**: RGM.1404290 (1), NHMW 2023/0076/0048 (2). **EL**: RGM.1404299 (1), NHMW 2023/0076/0049 (2). **PQ**: NHMW 2023/0076/0050 (8).

Description – Shell medium sized, almost planispiral, spire almost completely depressed, discoidal, with two strong peripheral keels, upper more prominent, flat dorsal surface wider than base resulting in trapezoidal cross-section, umbilicus extremely wide (UD approx. 55% of SD). Protoconch medium-sized (dp = 1.08) sharply delimited from teleoconch. Teleoconch of up to 3.25 whorls of regular growth. Dorsum: flat, SSC extremely weak, MC-area initially appears smooth and glossy, very fine spiral threads becoming slightly more prominent abapically, UPC strong, narrow, finely beaded, placed close to stronger LPC. Periphery: LPC sharp, forming periphery, also serving as upper point of whorl attachment. Base sharply keeled mid-base by prominent beaded spiral cord: whorl surface between peripheral and basal keels flat and tapering inwards, IPC not developed; BF with very fine spiral threads and close-set axial growth lines, PUC and UC not developed, inner edge fused with basal keel or preceding whorl. Aperture small, subtrigonal.

Discussion – This very characteristic species can only be confused with its living Mediterranean congener *Pseudomalaxis zanclaeus* (Philippi, 1844) which is immediately separated by having a single peripheral carina, whereas in *P. aldrovandii* (Foresti, 1868) there are two cords forming the peripheral carina (UPC and LPC close together).
In the Italian Pliocene the specimens can get relatively large, up to 11 mm diameter (var. *ligustica* Sacco, 1892). In Estepona the maximum diameter is even greater (14.1 mm). There is little intraspecific variability; in some specimens the spire is a little elevated, but most specimens are planispiral.
Pseudomalaxis aldrovandii var. *torrei* Moroni & Ruggieri, 1985 from the Upper Miocene of Italy was probably based on a juvenile shell at only 1.5 teleoconch whorls. Nevertheless, it was said to differ from *P. aldrovandii* in having a greater rate of growth of the first teleoconch whorl resulting in a greater diameter (at the same whorl count), and the MC-area on the dorsum is more concave and tapering inwards, so that it is almost symmetrical to the equally concave BF on the venter. In *P. aldrovandii* the MC-area is flattened. We have not seen Miocene specimens, but the differences highlighted by Moroni & Ruggieri hold true for specimens from the Pliocene Estepona assemblages, and we therefore provisionally consider them distinct.
Therefore, *P. aldrovandii* seems to have been a Mediterranean Pliocene species preceded by *P. aldrovandii torrei* in the Upper Miocene and succeeded by *P. zanclaeus* from the Upper Pleistocene (Melone & Taviani, 1985). Today, *P. zanclaeus* is a circalittoral and bathyal species. In Estepona it is found in both the deeper water assemblage of Velerín carretera and the shallower water Velerín conglomerates and El Lobillo deposits.

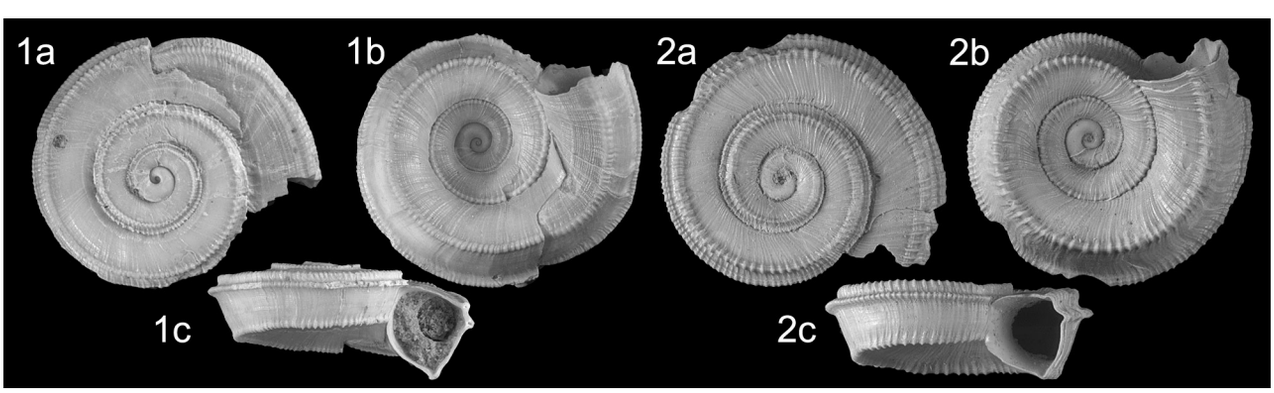

Plate 8. *Pseudomalaxis aldrovandii* (Foresti, 1868); 1. RGM.1404276, diameter 7.4 mm x 6.3 mm, height 2.5 mm; 2. NHMW 2023/0076/0046, diameter 6.8 mm x 6.0 mm, height 2.0 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Distribution – Lower Pliocene: central Mediterranean, Italy (Sacco, 1892; Bogi *et al*., 2002; Chirli, 2013), Sicily (Ricordi, 1991). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Bogi *et al*., 2002; Ceregato *et al*., 2019). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Genus *Spirolaxis* Monterosato, 1913

Type species (by monotypy) – *Pseudomalaxis centrifuga* Monterosato, 1890, present-day, Madeira, NE Atlantic.

1913 *Spirolaxis* Monterosato, p. 362, 362.
1935 *Paurodiscus* Rehder, p. 128. Type species (by monotypy): *Pseudomalaxis lamellifera* Rehder, 1935, present-day, Florida, USA.
1946 *Aguayodiscus* Jaume & Borro, p. 18. Type species (by monotypy): *Spirolaxis clenchi* Jaume & Borro, 1946, present-day, Cuba.

***Spirolaxis clenchi* Jaume & Borro, 1946**
Plate 9, fig. 1, Plate 13, fig. 9

1920 *Discohelix* (*Pseudomalaxis*) *corniculum* (Boettger) – Hornung, p. 85, pl. 2, fig. 15 [*non Spirolaxis corniculum* (Boettger, 1902)].
*1946 *Spirolaxis clenchi* Jaume & Borro, p. 18, pl. 2, figs 3-4.
1985 *Spirolaxis clenchi* Jaume & Borro, 1946 – Melone & Taviani, p. 188, figs 65-67.
1999 *Spirolaxis clenchi* (Jaume & Borro, 1946) [*sic*] – Ardovini & Cossignani, p. 72, 73, unnumbered fig. bottom right.
2002 *Spirolaxis clenchi* Jaume & Borro, 1946 – Bogi *et al*., p. 37, fig. 25.
2005 *Spirolaxis clenchi* Jaume & Borro, 1946 – Repetto *et al*., p. 226, fig. 944.
2011 *Spirolaxis clenchi* Jaume & Borro, 1916 [*sic*] – Cossignani & Ardovini, p. 32, 338, unnumbered fig.
2011 *Spirolaxis clenchi* Jaume & Borro, 1946 – Gofas *et al*., p. 351, unnumbered fig. centre.

Material and dimensions – Maximum diameter 7.4 mm x 6.5 mm. **VC**: RGM.1404188 (1), NHMW 2023/0076/0096-0098 (4). **VS**: NHMW 2023/0076/0095 (1).

Description – Shell small, open coiled, planispiral, with identical sculpture of dorsum and venter, cross-section rectangular with columellar side slightly convex; outer keels formed by two sharp strong cords, inner keels formed by two weaker cords, all bearing small, axially-elongated tubercles; umbilicus extremely wide (UD approx. 72% of SD). Protoconch small, almost planispiral, of 2.5 smooth, strongly convex whorls with small nucleus (dp = 0.75), separated from teleoconch by prominent, raised varix. Teleoconch of up to 2.25 whorls. Dorsum: SSC narrow, MC-area flattened, bearing weak, sinuous axial cordlets. Periphery: LPC strong, forming upper keel, IPC equally strong forming lower peripheral keel. Base: BF flattened, with weak axial sculpture similar to MC-area dorsum; UC weaker forming inner lower keel. Aperture small, rectangular.

Discussion – The number of *Spirolaxis* species in the present-day Atlantic is unclear. In the extant faunas, *S. exquisitus* (Dall & Simpson, 1901) is sometimes considered a synonym of *S. centrifuga* (*e.g.*, Merrill, 1970, Bieler, 1984; *fide* Melone & Taviani, 1985, p. 185). The Caribbean species *Spirolaxis clenchi* Jaume & Borro, 1946, originally described from Cuba, was considered to differ from *S. exquisita* [*sic*] in having only the nucleus disjunct, in having sculpture consisting of fine irregular axial cordlets without spirals on both sides, whereas *S. exquisita* [*sic*] has spirals on the dorsum and the venter is entirely smooth, the keels in *S. exquisita* [*sic*] are bifid and simple in *S. clenchi*, and the tubercles on the keels much finer in *S. exquisita* [*sic*] (Jaume & Borro, 1946, p. 18). Melone & Taviani (1985) considered some Mediterranean specimens conspecific with the Caribbean species and stated that they differed from *S. centrifuga* in having coarser tubercles on the keels and the outer keels non-bifid in frontal view (see Melone & Taviani, 1985, fig. 65 *vs.* fig. 62). Those authors recognised both species to be present in the extant Mediterranean and did not consider only the nucleus being disjunct nor the sculpture on the dorsum and venter, as originally described by Jaume & Borro, to be species specific features. Negri & Corselli (2016, p. 74) suggested that *Spirolaxis clenchi* could also be a synonym of *S. centrifuga*.
We have not been able to find a consistent distinguishing feature between specimens illustrated by authors as *S. centrifuga* and *C. clenchi* in the present-day Mediterranean. The specimens illustrated by Melone and Taviani (1985, *S. centrifuga* fig. 62; *S. clenchi* figs 65-67) all have completely disjunct whorls and do show the differences highlighted by Melone & Taviani, but not Jaume & Borro. The lectotype of *Pseudomalaxis macandrewi* Iredale, 1911 from Madeira (for illustration see Bieler, 1984, fig. 19), also considered a synonym of *S. centrifuga*, is disjunct throughout, has fine tubercles on the keels, the outer keel LPC is not bifid, IPC possibly weakly bifid. The specimen from Italy illustrated by Negri & Corselli (2016, *S. centrifuga*, figs 16o-q) has only the first whorl disjunct, and after about one whorl, subsequent whorls are fused, and the outer keels bear relatively fine tubercles and are not bifid in profile (*i.e*., a mixture of features between *C. centrifuga* and *C. clenchi*). Mediterranean specimens identified as *S. clenchi* by Ardovini & Cossignani (1999), Cossignani & Ardovini (2011) and Gofas *et al*. (2014) all have only the first teleoconch whorl disjunct leaving a crescent-shaped opening in the centre of the shell, coarse tubercles on the keels and the outer keels not bifid (*i.e*., features of *C. clenchi*). The specimen illustrated by Repetto *et al*. (2005, fig. 955) is completely disjunct and simple keels (*i.e*., a mixture of features between *C. centrifuga* and *C. clenchi*). The specimen from

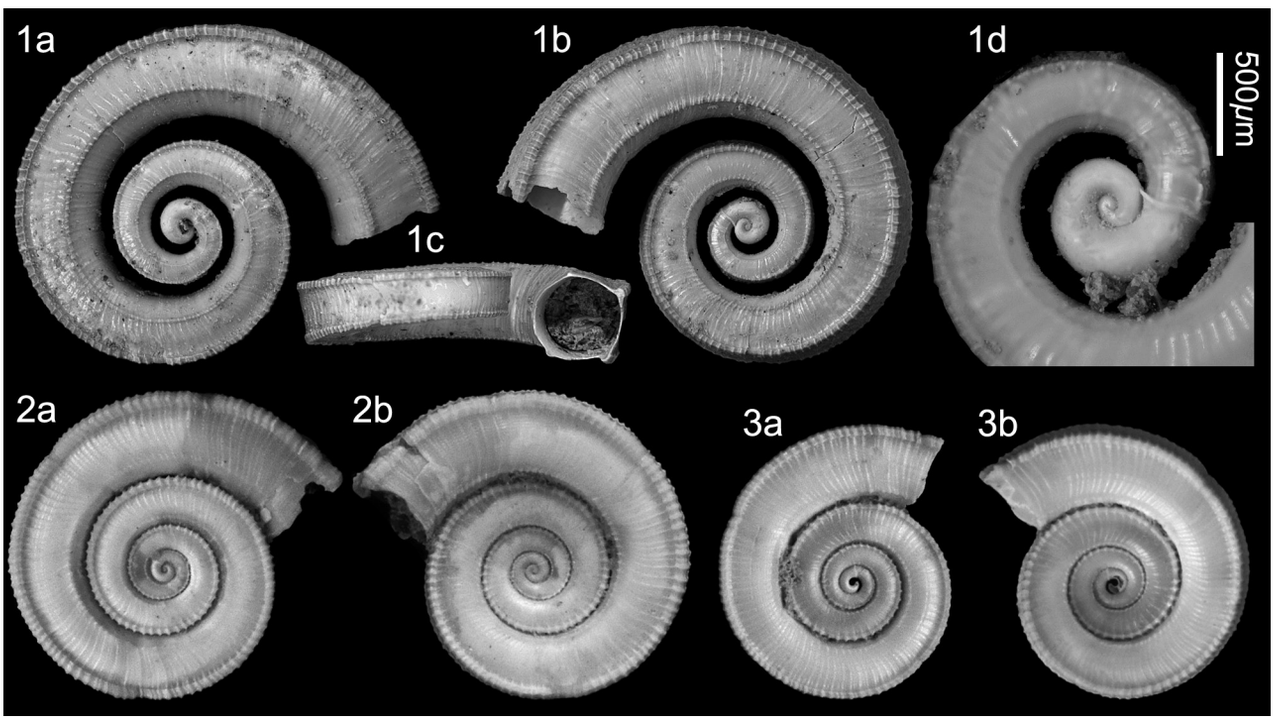

Plate 9. *Spirolaxis clenchi* Jaume & Borro, 1946; 1. RGM.1404188, diameter 5.9 mm x 4.6 mm, 1d, detail of protoconch; 2. NHMW 2023/0076/0096, diameter 7.4 mm x 6.5 mm; 3. NHMW 2023/0076/0097, diameter 6.3 mm x 5.0 (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

the Canary Islands illustrated by Rolán (2005, fig. 833) as *S. centrifugus* [*sic*] seems to agree with the description of that species, although we cannot tell from the illustration whether the keels are simple or bifid.

In the western Atlantic, the Brazilian specimen illustrated by Cavallari *et al*. (2014, figs 16-18) as *S. centrifuga* is disjunct for one teleoconch whorl, after which the whorls are fused, and has relatively coarse tubercles on the outer keels (*i.e*., features of *C. clenchi*). Conversely, the two specimens from Abaco, Caribbean, figured by Redfern (2001, pl. 63, fig. 574 and 2013, fig. 639) are completely disjunct but with clearly bifid peripheral keels (*i.e*., a mixture of features between *C. centrifuga* and *C. clenchi*). The specimen figured by Rios (2009, fig. 951) is fully disjunct, but does not illustrate the form of the peripheral keels.

Specimens from Estepona have whorls that are completely disjunct to loosely fused throughout; none have a crescent shaped hole in the centre, fine tubercles on all four keels, as described for *S. centrifuga*, the outer keels are not bifid on apertural view, as described for *S. clenchi*, and the dorsum and venter bear fine axial cordlets on both sides, without spirals, that does not agree with the descriptions of either *S centrifuga* or *S. clenchi*. Melone & Taviani (1985, fig. 67) illustrated an Italian Pliocene specimen as *C. clenchi* that shares similar characters to the Estepona specimens.

It is unclear if these Neogene to present-day Atlanto-Mediterranean specimens represent a single variable species or a species complex. In the literature, separation of *S centrifuga* and *S. clenchi* has depended on which shell characters are considered most important by various authors. The outer keels being bifid or not has been considered by most authors to separate the two species, whereas the amount of disjuncture has not. We provisionally follow this concept and consider the Estepona specimens *S. clenchi* primarily based on the non-bifid outer keels. Ideally molecular data is needed to resolve this issue.

Today in the Mediterranean *S. clenchi* is found in deep circalittoral and bathyal zones (Melone & Taviani, 1985; Gofas *et al*., 2011). In Estepona it is found only in the deeper water assemblage of Velerín carretera.

Distribution – Lower Pliocene: central Mediterranean, Italy (Hornung, 1920; Bogi *et al*., 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: western Atlantic, Caribbean, Cuba (Jaume & Borro, 1946), western Mediterranean (Cossignani & Ardovini, 2011), central Mediterranean (Taviani, 1974; Melone & Taviani, 1985; Ardovini & Cossignani, 1999; Cossignani & Ardovini, 2011), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Heliacus clade (of Bieler, 1993, fig. 21)

Genus *Heliacus* d'Orbigny in Sagra, 1842

Type species (by monotypy) – *Solarium herberti* Deshayes, 1830 [= *Heliacus cylindricus* (Gmelin, 1791)], present-day, Atlantic.

1840 *Torinia* Gray, p. 147, *nomen nudum*; 1842 [no nominal species included]. Type species (by secondary monotypy): *Trochus cylindraceus* Dillwyn, 1817 [= *Heliacus cylindricus* (Gmelin, 1791)], present-day, Atlantic. *Torinia* suppressed to insure stability (ICZN Opinion 2185, 2007).
1842 *Heliacus* d'Orbigny in Sagra, p. 68.
1930 *Heliacus* (*Awarua*) Mestayer, p. 145. Type species (by original designation): *Omalaxis amoena* Murdoch & Suter, 1906, present-day, New Zealand.
1959 *Astronacus* Woodring, p. 168. Type species (by original designation): *Heliacus planispira* Pilsbry & Lowe, 1932, present-day, Pacific Mexico.

***Heliacus fallaciosus* (Tiberi, 1872)**
Plate 10, figs 1-2, Plate 13, fig. 10

*1872 *Solarium fallaciosum* Tiberi, p. 35.
1880 *Solarium fallaciosum* Tiberi – Fontannes, p. 139, pl. 8, figs 6, 7.
1892 *Torinia obtusa* var. *basitaeniata* Sacco, p. 70, pl. 2, fig. 49.
1892 *Torinia obtusa* var. *cingulellata* Sacco, p. 70, pl. 2, fig. 50.
1892 *Torinia obtusa* var. *depressecingulata* Sacco, p. 70, pl. 2, fig. 52.
1892 *Torinia obtusa* var. *bicingulellata* Sacco, p. 70, pl. 2, fig. 53.
1892 *Torinia obtusa* var. *alternecingulata* Sacco, p. 70, pl. 2, fig. 54.
1892 *Torinia obtusa* var. *alternecosticillata* Sacco, p. 70, pl. 2, fig. 55.
1904 *Torinia obtusa* var. *subvariegata* d'Orb – Sacco, p. 111, pl. 24, fig. 38.
1914 *Solarium* (*Torinia*) *obtusum* Brn. – Cerulli-Irelli, p. 188, pl. 15, figs 17-20 [*non Heliacus obtusus* Bronn, 1831].
1955 *Torinia obtusa subvariegata* d'Orb – Moroni, p. 95, pl. 3, fig. 16.
1959 *Torinia obtusa subvariegata* d'Orb – Ruggieri & Curti, p. 111, pl. 24, fig. 144, pl. 25, fig. 146.
1972 *Architectonica* (*Pseudotorinia*) *obtusa* (Bronn, 1831) s. l. – A.W. Janssen, p. 26, pl. 5, fig. 2 [*non Heliacus obtusus* Bronn, 1831].
1974 *Architectonica* (*Pseudotorinia*) *fallaciosa* (Tiberi, 1872) – Malatesta, p. 185, pl. 13, fig. 7.
1974 *Heliacus fallaciosus* (Tiberi) – Melone, p. 24, pl. 1, figs 7-9.
1984 *Heliacus* (*Heliacus*) *fallaciosus* (Tiberi, 1872) – Melone & Taviani, p. 167, figs 29-33.
1984a *Architectonica* (*Pseudotorinia*) *obtusa* (Bronn, 1831) s. lat. – A.W. Janssen, p. 143, pl. 47, fig. 4 [*non Heliacus obtusus* Bronn, 1831].
1986 *Architectonica* (*Pseudotorinia*) *obtusa* (Bronn, 1831) – González Delgado, p. 91, pl. 3, figs 1-3 [*non Heliacus obtusus* Bronn, 1831].
1992 *Heliacus* (*Grandeliacus*) *subvariegatus* (d'Orbigny, 1852) – Cavallo & Repetto, p. 150, fig. 418.
2002 *Heliacus* (*Granoheliacus*) *subvariegatus* (d'Orbigny, 1852) – Bogi *et al*., p. 33, figs 14, 15.
2004 *Heliacus subvariegatus* (D'Orbigny, 1842) – Ardovini & Cossignani, p. 38, 232, unnumbered figs.
2005 *Heliacus subvariegatus* (D'Orbigny, 1852) – Repetto *et al*., p. 225, fig. 940.
2005 *Heliacus subvariegatus* Orbigny, 1852 – Rolán, p. 177, pl. 55, figs 823-825
2007 *Architectonica* (*Pseudotorinia*) *obtusa* (Bronn, 1831) s. lat. – Wienrich, p. 730, pl. 119, fig. 1, pl. 158, fig. 5 [*non Heliacus obtusus* Bronn, 1831].
2011 *Heliacus fallaciosus* (Tiberi, 1872) – Cossignani & Ardovini, p. 32, 336, unnumbered fig.
2011 *Heliacus fallaciosus* (Tiberi, 1872) – Gofas *et al*., p. 350, unnumbered fig. top.
2011 *Heliacus subvariegatus* (d'Orbigny, 1852) – Chirli & Linse, p. 212, pl. 84, fig. 3.
2011 *Heliacus subvariegatus* (d'Orbigny, 1852) – Hernández *et al*., p. 240, figs 81 K-M.
2013 *Heliacus subvariegatus* (d'Orbigny, 1852) – Chirli, p. 15, pl. 5, figs 7-12.
2018 *Heliacus fallaciosus* (Tiberi, 1872) – Trigo *et al*., p. 357, unnumbered figs. top.

non 2011 *Heliacus* (*Granoheliacus*) *subvariegatus* (d'Orbigny, 1852) – Landau *et al*., p. 39, pl. 22, fig. 2 [= *Pseudotorinia architae* (O.G. Costa, 1841)].

Material and dimensions – Maximum diameter 12.0 mm x 10.1 mm, height 7.9 mm. **CO**: NHMW 2023/0076/0076 (12). **EL**: RGM.1404275-276 (2), RGM.1404301 (2).

Description – Shell medium sized, relatively flattened, discoidal, periphery angular, profile moderately convex above, base weakly convex; umbilicus moderately wide (UD approx. 22% of SD). Protoconch large (dp = 1.33), separated from teleoconch by prominent, raised varix. Teleoconch: sculpture of beaded cords on dorsum; on spire whorls SSC relatively strong, two narrow MC, UPC strong, equal to SSC, LPC strongest. Periphery: angled at LPC that forms periphery, also serving as upper point of whorl attachment, tapering inwards below to slightly weaker IPC, angled at base, single secondary cord of variable strength intercalated between LPC and IPC. Base weakly convex: 5-6 further weakly beaded cords on BF broadening towards umbilicus, PUC and UC of roughly equal width, separated by narrow groove, UC overhanging umbilicus, umbilical wall bearing strong axial growth lines, without spirals. Aperture small, rounded. CG well developed, PG moderately developed.

Discussion – This species is sometimes placed in the subgenus *Grandeliacus* Iredale, 1957 (see Bieler, 1985, p. 100).
Melone & Taviani (1984) commented that the fossil form usually known as *Solarium obtusum* Bronn, 1831 or *Solarium fallaciosum* Tiberi, 1872 was indistinguishable from the present-day species identified as *Solarium subvariegatum* d'Orbigny, 1852. *Solarium subvariegatum* d'Orbigny, 1852 was based on *Solarium variegatum* (Gmelin, 1791), *sensu* Sismonda (1847, p. 49) and is a *no-*

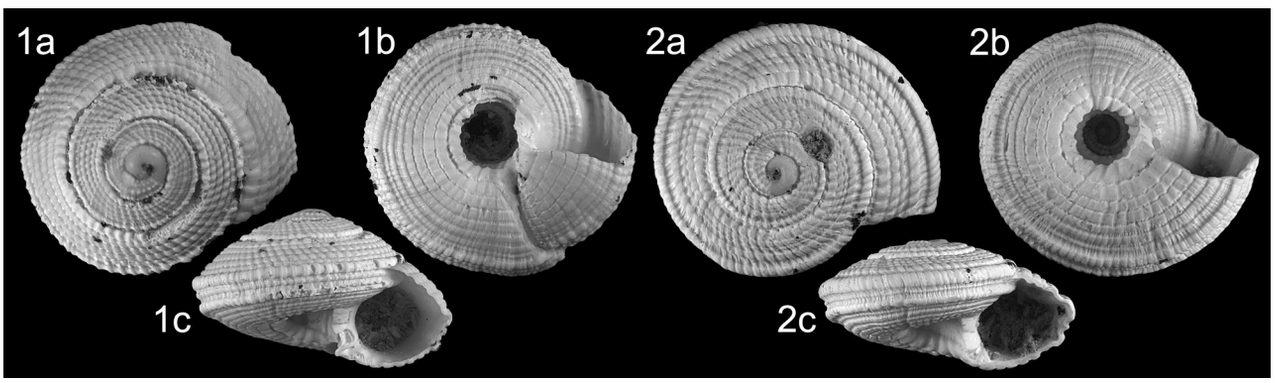

Plate 10. *Heliacus fallaciosus* (Tiberi, 1872); 1. RGM.1404275, diameter 7.7 mm x 7.0 mm, height 5.1 mm; 2. RGM.1404276, diameter 6.8 mm x 6.2 mm, height 4.1 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

men nudum. Therefore, the valid name for the present-day shells is *Heliacus fallaciosus*. Landau *et al*. (2013, p. 301) argued that although both forms were very similar on dorsal and ventral views, *Pseudotorinia obtusa* had only two prominent cords at the carina (LPC and IPC), whereas *H. fallaciosus* has a further, finer cord between the two major cords. Sacco (1892) interpreted Bronn's species as having only two cords at the periphery, clearly illustrated in the specimen he figured (Sacco, 1892, pl. 2, fig. 45, refigured by Ferrero Mortara *et al*., 1984, pl. 15, fig. 4). Sacco (1892, p. 68) went on to say that the variety *subvariegata* d'Orb. differed in having a finer cord between the two major cords at the periphery. The same arrangement of peripheral cords is seen in the specimen figured by Bieler (1985, pl. 1, fig. 1). Therefore, Landau *et al*. (2013) restricted the name *Pseudotorinia obtusa* (Bronn, 1831) to shells with only two cords at the periphery, without a finer central cord. The specimens from Estepona are typical for *H. fallaciosus* with an intermediate cord of variable strength clearly seen between LPC and IPC (Pl. 10, figs 1c, 2c). *Heliacus fallaciosus*, with intermediate peripheral cords, is already present in the Middle Miocene North Sea Basin (A.W. Janssen, 1984; Wienrich, 2007).

Melone & Taviani (1984, p. 169) noted the Pliocene specimens from Italy were constantly smaller than present-day specimens (18-20 mm diameter for present-day shells, Pliocene shell size not specified by those authors; 4.7-8.2 mm in Chirli, 2013), and that the Pleistocene specimens were similar in size to the present-day ones. Like the Italian Pliocene specimens, those from Estepona are usually small, mostly about 7-9 mm diameter (maximum 12.0 mm).

Today this species is primarily found in circalittoral habitats (Melone & Taviani, 1985; Gofas *et al*., 2011). In Estepona in has only been found in the shallower water assemblages of Velerín carretera and El Lobillo.

Distribution – Middle Miocene: North Sea Basin, Germany (A.W. Janssen, 1972; Wienrich, 2007), The Netherlands (A.W. Janssen, 1984). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1986), western Mediterranean, Roussillon Basin, France (Fontannes, 1880); central Mediterranean (Sacco, 1892, 1904; Bogi *et al*., 2002; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959; Malatesta, 1974; Cavallo & Repetto, 1992; Bogi *et al*., 2002). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914; Melone & Taviani, 1984); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic, Bay of Biscay (Trigo *et al*., 2018), Madeira (Segers *et al*., 2009), Canary Islands (Nordsieck & García-Talavera, 1979; Hernández *et al*., 2011), Senegal (Ardovini & Cossignani, 2004), Cape Verde Archipelago (Rolán, 2005), entire Mediterranean (Melone, 1974; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Nipteraxis* Cossmann, 1916

Type species (by original designation) – *Solarium plicatum* Lamarck, 1804. Eocene, France.

1916 *Nipteraxis* Cossmann, p. 162, 167.

Note – In his cladistic analysis of the Architectonicidae, Bieler (1988, p. 225) noted that *Nipteraxis* Cossmann, 1916 was very close to *Heliacus* d'Orbigny in Sagra, 1842). However, Bieler (1993, p. 292) also noted the shell similarities between some *Pseudotorinia* Sacco, 1892 species and member of the fossil genus *Nipteraxis* concerning shape, size, and position of the peripheral cords.

***Nipteraxis monilifer* (Bronn, 1831)**
Plate 11, figs 1-2, Plate 13, fig. 11

*1831 *Solarium moniliferum* Bronn, p. 63.
1976 *Architectonica monilifera* (Bronn) – Caprotti, p. 7, pl. 8, fig. 9.
2013 *Nipteraxis monilifera* (Bronn, 1831) – Landau *et al*., p. 300, pl. 52, fig. 1 (*cum syn*.).
2022 *Heliacus moniliferum* (Bronn, 1831) – Brunetti, p. 76, fig. 171.

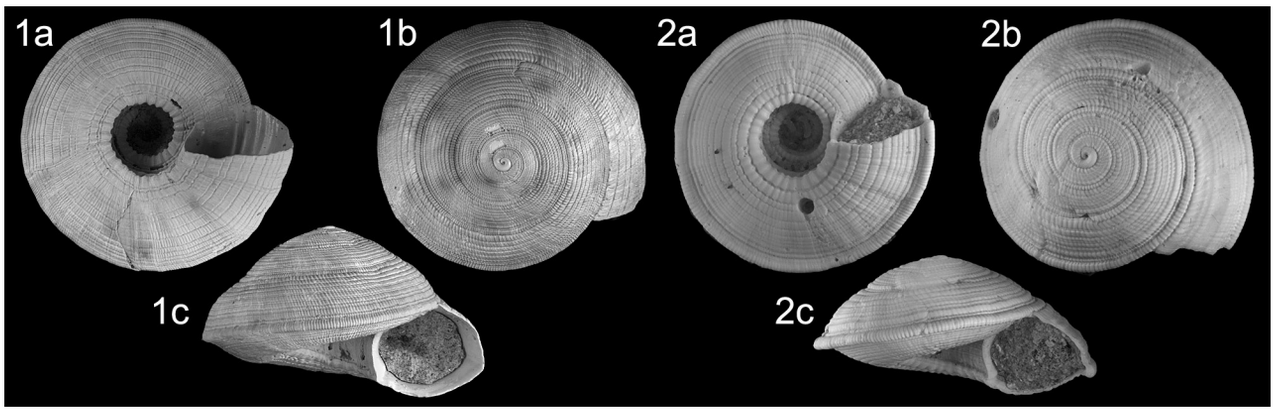

Plate 11. *Nipteraxis monilifer* (Bronn, 1831); 1. RGM.1404278, diameter 19.3 mm x 17.6 mm, height 13.0 mm Velerín carretera, Velerín. 2. NHMW 2023/0076/0054, diameter 15.2 mm x 13.8 mm, height 8.3 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

2023 *Nipteraxis monilifer* (Bronn, 1831) – Harzhauser & Landau, p. 31, figs 4H, 18A–B (*cum syn*.).

non 1856 *Solarium moniliferum* Bronn – Hörnes, p. 466, pl. 46, fig. 5 [= *Nipteraxis exmonilifera* (Sacco, 1892)].

non 1956 *Architectonica monilifera* (Bronn) – Csepreghy-Meznerics, p. 386, pl. 1, figs 29, 30 [= *Nipteraxis exmonilifera* (Sacco, 1892)].

non 1962 *Solarium moniliferum* Bronn – Strausz, p. 123, pl. 51, figs 8-10 [= *Nipteraxis exmonilifera* (Sacco, 1892)].

non 1966 *Solarium moniliferum* Bronn, 1831 – Strausz, p. 118, pl. 51, figs 8-10 [= *Nipteraxis exmonilifera* (Sacco, 1892)].

non 1969b *Solarium moniliferum* Bronn – Csepreghy-Meznerics, p. 20, pl. 2, figs 12, 17, 21, 27 [= *Nipteraxis exmonilifera* (Sacco, 1892)].

non 1973 *Architectonica* (*A*[*rchitectonica*].) *monilifera* (Bronn, 1831) – Steininger, p. 404, pl. 4, fig. 4.

non 1985 *Architectonica* (*Architectonica*) *monilifera* (Bronn, 1831) – Atanacković, p. 96, pl. 23, figs 1-3 [= *Heliacus* sp.].

Material and dimensions – Maximum diameter 19.3 mm x 17.6 mm, height 13.0 mm. **VC**: RGM.1404278 (1). **CO**: NHMW 2023/0076/0056 (3). **EL**: NHMW 2023/0076/0054 (1), NHMW 2023/0076/0055 (4).

Description – Shell medium sized, elevated discoidal, periphery angled, profile convex above, flattened, weakly convex below; umbilicus wide (UD approx. 26% of SD). Protoconch large (dp = 1.37), separated from teleoconch by prominent, raised varix. Teleoconch: sculpture of finely beaded cords on dorsum; SSC slightly strengthened, MC with five narrower beaded cords, six on last whorl, UPC slightly strengthened, equal to SSC, LPC strongest. Periphery: UPC weakly developed, LPC forms angled periphery, not prominent, also serving as upper point of whorl attachment. Base: IPC not stronger than other basal cords; eight further flattened cords on BF between IPC and PUC, widening considerably towards umbilicus, interrupted by close-set axial growth lines, PUC narrower, weakly tuberculate, separated from UC by narrow cord, UC overhanging umbilicus, umbilical wall bearing fine axial growth lines. Aperture small, rounded, weakly angled at LPC. CG narrow, shallow; PG not developed.

Discussion – The genus name *Nipteraxis* is male (based on the Latin noun *axis*), so correct ending should be *Nipteraxis monilifer*. This species has been placed in the genus *Heliacus* d'Orbigny in Sagra, 1842 by most authors during the last decades. However, the weak infraperipheral cord (*sensu* Bieler, 1985), its general profile and the absence of spiral sculpture in the umbilicus are characters corresponding to the genus *Nipteraxis* Cossmann, 1916.

Its large size, relatively elevated shell, and fine, beaded sculpture make it impossible to confuse with any other architectonicid in the assemblage. The specimen illustrated by Landau *et al.* (2013) from the Middle Miocene of the Karaman Basin (Turkey) agrees with this species in profile and sculpture but has a much narrower umbilicus. The shell suffered damage and repair about one-half whorl from the aperture. Unfortunately, the species is represented by a single specimen from these deposits, and although it is likely that the narrowed umbilicus is pathological, we cannot exclude the possibility it represents a further species within the group. The Paratethyan specimens recorded as *monilifera* are not this species but *Nipteraxis exmonilifera* (Sacco, 1892). *Nipteraxis monilifer* differs from the Paratethyan species in having finely granulose spiral sculpture on the dorsal side, the more prominent keel, the well-defined LPC on the base, the relatively equal width of the spiral cords on the base, the deeper groove delimiting the UC and slightly wider umbilicus (see Harzhauser & Landau, 2023).

Distribution – Middle Miocene: Paratethys, Austria (Harzhauser & Landau, 2023). Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): Cacela

Basin, Portugal (NHMW collection); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1892). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Gonzàlez Delgado, 1986; Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, Roussillon Basin, France (Fontannes, 1880; Chirli & Richard, 2008), central Mediterranean (Bogi *et al*., 2002). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), western Mediterranean, Morocco (Lecointre, 1952); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992; Bogi *et al*., 2002; Sosso & Dell'Angelo, 2010; Chirli, 2013).

Psilaxis clade (of Bieler, 1993, fig. 21)

Genus *Simplexollata* Harzhauser & Landau, 2023

Type species (by original designation) – *Simplexollata anticollata* Harzhauser & Landau, 2023, Middle Miocene, Paratethys.

2023 *Simplexollata* Harzhauser & Landau, p. 13.

Note – *Simplexollata* Harzhauser & Landau, 2023 includes species similar in shape to *Architectonica* Röding, 1798, *Basisulcata* Melone & Taviani, 1985 and *Psilaxis* Woodring, 1928, but base with two prominent cords at periphery (LPC and IPC), almost smooth basal field with weak axial folds. No PUC but prominent spiral groove delimiting prominent UC (see Harzhauser & Landau, 2023, fig. 3).

Simplexollata simplex (Bronn, 1831)

Plate 12, figs 1-2, Plate 13, fig. 12

*1831 *Solarium simplex* Bronn, p. 63.
1837 *Solarium carocollatum* var. *laevigata* Pusch 1837, p. 111, pl. 10, fig. 11 [*non* Lamarck, 1816].
1841 *Solarium neglectum* Michelotti, p. 213, pl. 2, figs 7-9.
1846 *Solarium carocollatum* Grateloup (*partim*, pl. 12, figs 27-28 only) [*non* fig. 29 = *Simplexollata carocollata* (Lamarck, 1822)].
1852 *Solarium subconoideum* d'Orbigny, p. 45, no. 715.
1856 *Solarium simplex* Bronn – Hörnes, p. 463, pl. 46, fig. 3.
1862 *Solarium simplex* Br. – Bronn in Reiss, p. 32.
1864 *Solarium simplex* Bronn – Mayer, p. 58.
1880 *Solarium simplex* Bronn – Fontannes, p. 137, pl. 8, fig. 4.
1892 *Solarium simplex* var. *crassulosa* Sacco, p. 46, pl. 1, fig. 50.
1892 *Solarium simplex* var. *subacrenula* Sacco, p. 46, pl. 1, fig. 51.
1892 *Solarium simplex* var. *gibbosoacrenula* Sacco, p. 46, pl. 1, fig. 52.
1892 *Solarium simplex* var. *subacingulosa* Sacco, p. 46, pl. 1, fig. 53.
1892 *Solarium simplex* var. *rugulodepressa* Sacco, p. 46, pl. 1, fig. 54.
1892 *Solarium simplex* var. *infernelineata* Sacco, p. 47, pl. 1, fig. 56.
1892 *Solarium simplex* var. *trilineata* Sacco, p. 47, pl. 1, fig. 57.
1892 *Solarium simplex* var. *antiquoscalarata* Sacco, p. 47, pl. 1, fig. 58.
1892 *Solarium simplex* var. *pyramidata* Sacco, p. 48, pl. 1, fig. 59.
1897 *Solarium simplex* var. *bicinctum* Penecke, p. 61, pl. 3, fig. 14.
1903 *Solarium simplex* Bronn – Dollfus *et al*., p. 8, pl. 32, fig. 7.
1904 *Solarium simplex* var. *neglecta* Micht. – Sacco, p. 111, pl. 24, fig. 37.
1919 *Solarium simplex* Bronn – Cossmann & Peyrot, p. 460, pl. 15, figs 33-38.
1919 *Solarium simplex* var. *subconoideum* d'Orbigny – Cossmann & Peyrot, p. 460, pl. 15, figs 42-44.
1923 *Solarium simplex* Bronn – Friedberg, p. 413, pl. 25, fig. 5.
1949 *Solarium simplex* Bronn, 1831 – Glibert, p. 123, pl. 7, fig. 6.
1951 *Solarium simplex* Bronn – Montanaro Gallitelli & Tacoli, p. 177, pl. 2, figs 6-8.
1952b *Solarium simplex* Bronn, 1831 – Glibert, p. 29, pl. 2, fig. 14.
1954 *Architectonica simplex* Bronn – Csepreghy-Meznerics, p. 18, pl. 1, figs 16-18.
1955 *Solarium simplex* Bronn – Ferreira, p. 26, pl. 6, figs 35, 36.
1955 *Architectonica* (*Architectonica*) *simplex* Bronn – Korobkov, plate captions, pl. 13, fig. 18.
1958 *Solarium simplex* Bronn – Erünal-Erentöz, p. 16, pl. 2, figs 6, 7.
1959 *Architectonica* (*s.s.*) *simplex* (Bronn) – Ruggieri & Curti, p. 109, pl. 23, fig. 138.
1959 *Architectonica* (*s.s.*) *simplex rugulodepressa* Sacco – Ruggieri & Curti, p. 110, pl. 23, fig. 139.
1960 *Architectonica* (*Architectonica*) *simplex* (Bronn 1831) – Anderson, p. 47, pl. 8, fig. 2.
1960 *Architectonica* (*Architectonica*) *simplex* (Bronn 1831) – Kojumdgieva *in* Kojumdgieva & Strachimirov, p. 91, pl. 29, fig. 14.
1960 *Solarium simplex szobiense* Strausz, p. 349, pl. 19, figs 4-5.
*19*62 *Solarium simplex* Bronn – Strausz, p. 124, pl. 51, fig. 15, pl. 52, fig. 1.
1962 *Solarium simplex szobiensis* Strausz, 124, pl. 52, figs 3-5.
1966 *Solarium simplex* Bronn, 1831 – Strausz, p. 116, pl. 51, fig. 15, pl. 52, fig. 1.
1966 *Solarium simplex sobiense* [*sic*] Strausz, 1960 – Strausz, p. 116, pl. 52, figs 3, 4, 6.
1967 *Architectonica* (*Architectonica*) *simplex* (Bronn 1831) – A.W. Janssen, p. 133, pl. 7, fig. 1.
1968 *Solarium simplex* Bronn, 1831 – Zelinskaya *et al*., p. 133, pl. 34, figs 12-14.

1969b *Solarium simplex* Bronn – Csepreghy-Meznerics, p. 20, pl. 2, figs 18, 22, 25.
1970 *Architectonica* (*Architectonica*) *simplex* (Bronn) – Caprotti, p. 142, pl. 1, fig. 11.
1972a *Architectonica* cf. *simplex* (Bronn) – Nordsieck, p. 56, pl. 13, fig. 31.
1973 *Architectonica* (*Architectonica*) *simplex* (Bronn) – Steininger, p. 404, pl. 4, fig. 4.
1974 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Malatesta, p. 182, pl. 13, fig. 3.
1975 *Solarium simplex* Bronn – Fekih, p. 57, pl. 21, fig. 1.
1975 *Solarium simplex* var. *crassulosa* Sacco – Fekih, p. 57, pl. 21, fig. 4.
1975 *Solarium simplex* var. *neglecta* Michelotti – Fekih, p. 58, pl. 21, fig. 7.
1975 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Bałuk, p. 117, pl. 13, figs 1, 2.
1976 *Architectonica simplex* (Bronn) – Caprotti, p. 7, pl. 8, fig. 11.
1978 *Solarium simplex* Bronn, 1831 – Pinna & Spezia, p. 159, pl. 49, fig. 1.
1984 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – A.W. Janssen, p. 142, pl. 47, fig. 2.
1984 *Architectonica simplex* (Bronn) – Ruggieri & Davoli, p. 51, pl. 1, fig. 7.
1984 *Solarium simplex* Bronn, 1831 – Ferrero Mortara *et al*., p. 92, pl. 14, fig. 2.
1985 *Philippia* (*Psilaxis*) *simplex* – Melone & Taviani, p. 164, fig. 24.
1985 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Atanacković, p. 97, pl. 23, figs 4-6.
1986 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – González Delgado, p. 86, pl. 2, figs 10, 12.
1988 *Architectonica simplex* (Bronn, 1831) – Chirli, p. 16, pl. 1, fig. 7.
1992 *Basisulcata simplex* (Bronn, 1831) – Cavallo & Repetto, p. 150, fig. 415.
1992 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Silva, p. 4, pl. 1, figs 1, 2.
1997 *Architectonica simplex* (Bronn, 1831) – Ruiz Muñoz *et al*., p. 166, pl. 30, figs 3-7.
2001 *Basisulcata simplex* (Bronn, 1831) – Silva, p. 563, pl. 26, figs 10-12.
2001 *Architectonica simplex subconoidea* (d'Orbigny, 1852) – Lozouet *et al*., p. 73.
2002 *Basisulcata simplex* (Bronn, 1831) – Bogi *et al*., p. 32, figs 1, 2.
2002 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Harzhauser, p. 122, pl. 11, figs 14-15.
2007 *Architectonica* (*Architectonica*) *simplex* (Bronn, 1831) – Wienrich, p. 727, pl. 117, figs 3-4, pl. 158, fig. 3.
2008 *Basisulcata simplex* (Bronn, 1831) – Chirli & Richard, p. 73, pl. 14, fig. 10.
2010 *Basisulcata simplex* (Bronn, 1831) – Sosso & Dell'-Angelo, p. 50, unnumbered fig. p. 66 top middle.
2010 *Psilaxis simplex* (Bronn, 1831) – Moths *et al*., p. 81, text-fig. 46, pl. 23, fig. 4.
2011 *Basisulcata simplex* (Bronn, 1831) – Landau *et al*., p. 39, pl. 21, fig. 11.
2011 *Basisulcata simplex* (Bronn, 1831) – Chirli & Linse, p. 211, pl. 84, figs 1a-f.
2013 *Basisulcata simplex* (Bronn, 1831) – Chirli, p. 7, pl. 2, figs 7-15.
2013 *Psilaxis simplex* (Bronn, 1831) – Landau *et al*., p. 301, pl. 52, fig. 3.
2014 *Basisulcata simplex* (Bronn, 1831) – Brunetti, p. 73, unnumbered fig. top.
2019 *Psilaxis simplex* (Bronn, 1827) [*sic*] – Cárdenas *et al*., p. 211, fig. 5b.
2022 *Basisulcata simplex* d'Orbigny, 1852 [*sic*] – Brunetti, p. 76, fig. 173.
2023 *Psilaxis simplex* (Bronn, 1831) – Sacchetti *et al*., p. 88, pl. 6, figs E_1 -E_2.
2023 *Simplexollata simplex* (Bronn, 1831) - Harzhauser & Landau, p. 17, figs 4D, 9A-D.

non 1954 *Solarium carocollatum simplex* Bronn – Strausz, p. 15.pl. 6, fig. 139 [= *Simplexollata anticollata* Harzhauser & Landau, 2023].
non 1961 *Architectonica* (*Architectonica*) *simplex* Bronn – Marinescu, p. 531, pl. 5, fig. 19 [= *Simplexollata carocollata* (Lamarck, 1822].

Material and dimensions – Maximum diameter 21.8 x 18.8 mm, height 12.3 mm. **CO**: RGM.1404280-281 (2), RGM.1404282 (10), NHMW 2023/0076/0089 (26). **EL**: RGM.1404307 (5), RGM.1404315 (1), NHMW 2023/0076/0090 (8).

Description – Shell large, solid, relatively flattened to elevated lentiform, periphery angled, profile weakly convex above, flattened, very weakly convex below; umbilicus moderately wide (UD 15-23% of SD). Protoconch very large (dp = 1.55), clearly delimited from teleoconch by change in lustre, but not sharply. Teleoconch: sculpture dorsum; SSC weakly developed and beaded on first two teleoconch whorls after which it disappears; MC smooth, except for weak, prosocline growth lines, UPC narrow, weakly beaded, LPC only slightly wider and stronger. Periphery: UPC weakly developed, LPC forms angled periphery, not prominent, also serving as upper point of whorl attachment. Base: IPC prominent, narrow, rounded, BF smooth, except for some shallow irregular spiral grooves present in some specimens and axial folds strengthening towards umbilicus, PUC not delimited, UC separated from BF by deep, narrow groove, UC overhanging umbilicus, umbilical wall bearing fine axial growth lines. Aperture small, rounded, angled at LPC. CG deep; PG weaker.

Discussion – Generic placement of this common and widespread species has been controversial as the shell characters do not fit comfortably in any of the genera used by various authors. Harzhauser & Landau (2023) erected the genus *Simplexollata for a group of species from the Late Oligocene to Early Pleistocene* from the NE Atlantic, Proto-/Mediterranean and Paratethys, which includes *Solarium simplex* Bronn, 1831.
Simplexollata simplex is widespread in the European

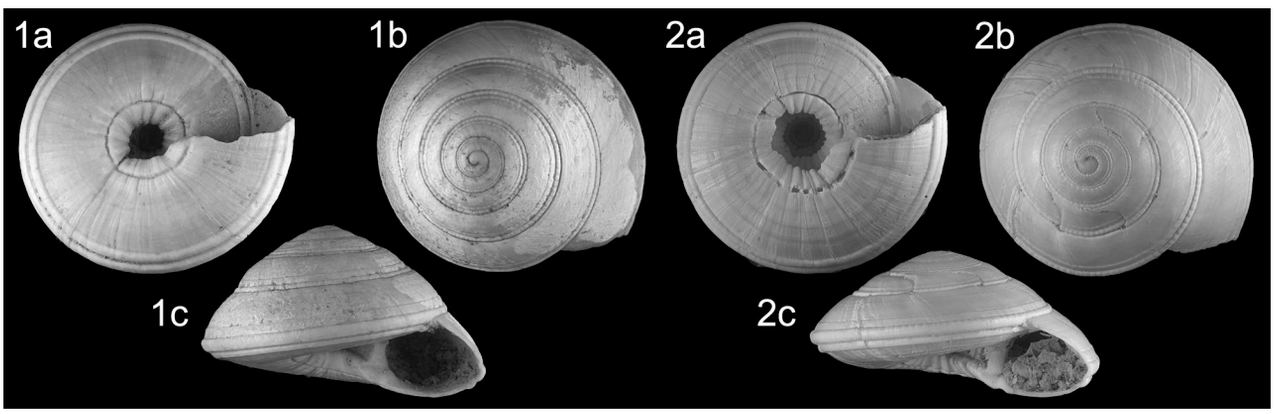

Plate 12. *Simplexollata simplex* (Bronn, 1831); 1. RGM.1404280, diameter 18.2 mm x 16.9 mm, height 12.1 mm; 2. RGM.1404281, diameter 16.6 mm x 15.1 mm, height 7.3 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Miocene and Pliocene assemblages and varies greatly in size and shape. It differs from *Psilaxis krebsii* in being larger, more solid, less evenly lentiform in profile due to a more depressed base and on the base the IPC is more prominent, and the PUC is not developed, whereas in *P. krebsii* the PUC is present. For further generic and species discussion see Harzhauser & Landau (2023).
In Estepona *S. simplex* is the most abundant architectonicid, found in the shallower water assemblages of El Lobillo and Velerín conglomerates.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot 1919; Lozouet *et al.* 2001); Proto-Mediterranean Sea (Burdigalian), Colli Torinesi, Italy (Michelotti, 1841; Sacco, 1892); Paratethys (Aquitanian and Burdigalian), Austria (Harzhauser, 2002). Middle Miocene: North Sea Basin (late Burdigalian-Langhian), Belgium (Glibert, 1952b), Germany (Anderson, 1960, 1964; A.W. Janssen, 1967; Wienrich, 2007; Moths *et al*., 2010), The Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984); Atlantic (Serravallian), Aquitaine Basin, France (Grateloup, 1846; Cossmann & Peyrot, 1919), (Langhian), Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian), Austria (Hörnes, 1856; Harzhauser & Landau, 2023), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Csepreghy-Meznerics, 1954; Strausz, 1962, 1966), Poland (Friedberg, 1923; Bałuk 1975), Romania (Harzhauser & Landau, 2023), Ukraine (Zelinskaya *et al*., 1968); north- eastern Atlantic, Azores (Ferreira, 1955); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.* 2013). Upper Miocene: northeastern Atlantic (Tortonian), Cacela Basin, Portugal (Dollfus *et al*., 1903), Seville, southwestern Spain (Cárdenas *et al.,* 2019); Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (Sacco, 1892; Ruggieri & Davoli, 1984). Lower Pliocene: Atlantic, Santa Maria Island, Azores (Bronn in Reiss, 1862; Sacchetti *et al*., 2023), Guadalquivir Basin, Spain (González Delgado, 1986; Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022), Roussillon Basin, France (Fontannes, 1880; Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1892b; Chirli, 1988; Bogi *et al*., 2002; Sosso & Dell'Angelo, 2010), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 1992, 2001), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (NHMW collection), Morocco (Lecointre, 1952); central Mediterranean, Italy (Sacco, 1892; Ruggieri & Curti, 1959; Malatesta 1974; Caprotti, 1970, 1976; Cavallo & Repetto, 1992; Bogi *et al*., 2002; Sosso & Dell'Angelo, 2010; Chirli, 2013). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Plate 13. Architectonicidae protoconchs: 1. *Solatisonax contexta* (G. Seguenza, 1876), NHMW 2023/0076/0059, Velerín carretera. 2. *Solatisonax pliohumilis* (Chirli, 2013), NHMW 2023/0076/0057, Velerín carretera. 3. *Ammotectonica emiliae* (Semper, 1861), RGM.1404267, Velerín carretera. 4. *Discotectonica pseudoperspectiva* (Brocchi 1814), NHMW 2023/0076/0023, Rio del Padrón. 5. *Discotectonica semisquamosa* (Bronn, 1831), RGM.1404271, Velerín carretera. 6. *Granosolarium millegranum* (Lamarck, 1822), NHMW 2023/0076/0066, Velerín carretera. 7. *Pseudotorinia architae* (O.G. Costa, 1841), RGM.1404273, El Lobillo. 8. *Pseudomalaxis aldrovandii* (Foresti, 1868), RGM.1404276, Velerín carretera. 9. *Spirolaxis clenchi* Jaume & Borro, 1946, RGM.1404188, Velerín carretera. 10. *Heliacus fallaciosus* (Tiberi, 1872), RGM.1404275, El Lobillo. 11. *Nipteraxis monilifer* (Bronn, 1831), RGM.1404278, Velerín carretera. 12. *Simplexollata simplex* (Bronn, 1831), RGM.1404315, El Lobillo. All: Estepona, Lower Piacenzian, Upper Pliocene.

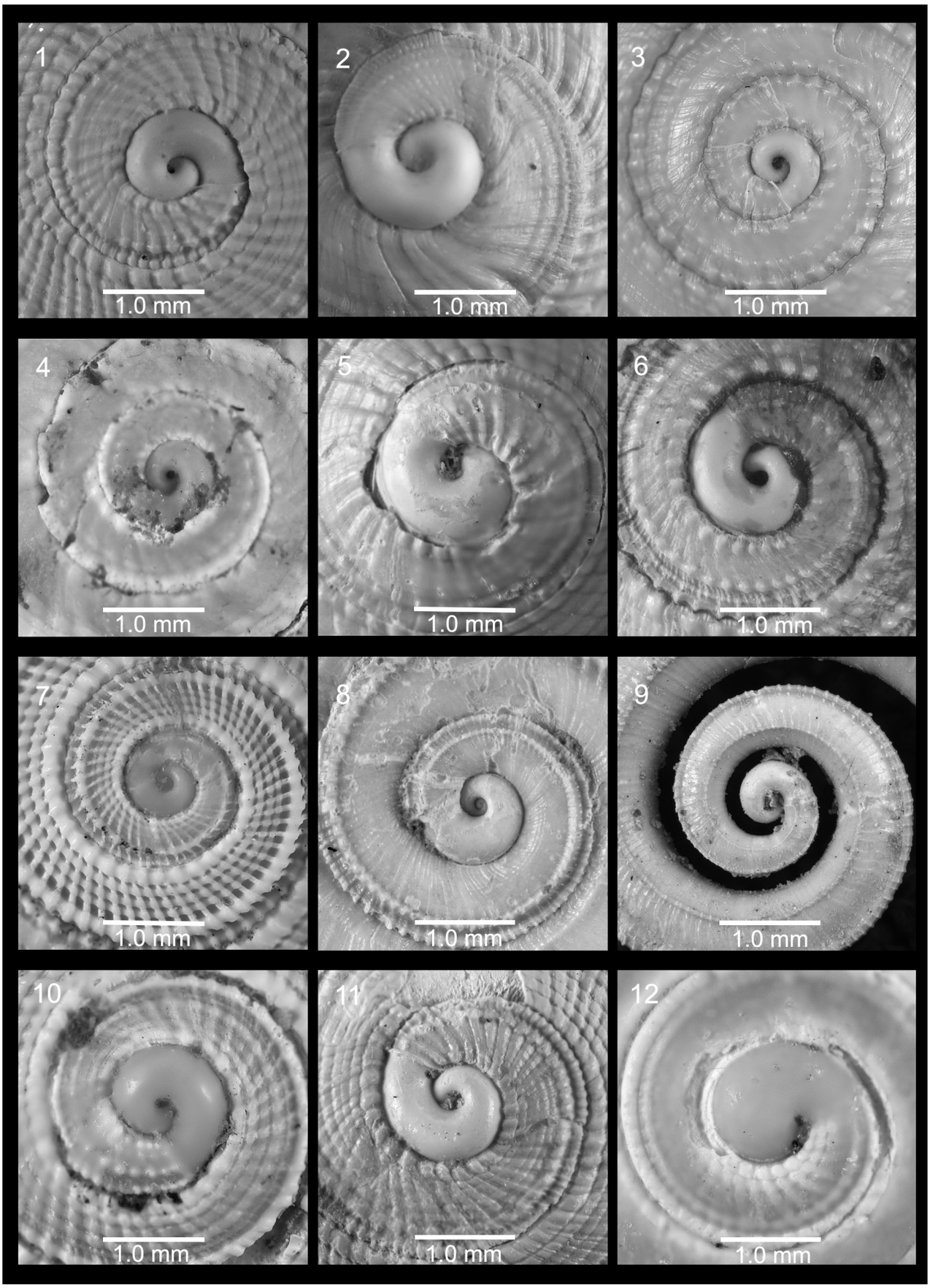
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Plate 13.

Superfamily Mathildoidea Dall, 1889
Family Mathildidae Dall, 1889
Genus *Mathilda* Semper, 1865

Type species (by subsequent designation, de Boury 1883) – *Turbo quadricarinatus,* Brocchi, 1814, Pliocene, Italy.

1865 *Mathilda* Semper, p. 330.
1869 *Mathildia* Bosquet, p. 261. Unjustified emendation of *Mathilda* Semper, 1865.
1895 *Fimbriatella* Sacco, p. 36. Type species (by original designation): *Cerithium fimbriatum* Michelotti, 1847, Miocene, Italy.
1929b *Eucharilda* Iredale, p. 187. Type species (by original designation): *Mathilda elegantula* Angas, 1871, present-day, New South Wales, Australia.
1971 *Granulicharilda* Kuroda & Habe *in* Kuroda *et al*., 416 [Japanese text], 260 [English text]. Type species (by original designation): *Granulicharilda sagamiensis* Kuroda & Habe *in* Kuroda *et al*., 1971, present-day, Japan.

***Mathilda brocchii* Semper, 1865**
Plate 14, figs 1-2

*1865 *Mathilda Brocchii* Semper, p. 338.
1895 *Fimbriatella Brocchii* var. *ornatior* Sacco, p. 37, pl. 3, fig. 39.
1895 *Fimbriatella Brocchii* var. *cingulellata* Sacco, p. 37, pl. 3, fig. 40.
1904 *Fimbriatella brocchii* var. *ornatior* Sacco, p. 126, pl. 25, fig. 46.
1904 *Fimbriatella brocchii* var. *cingulellata* Sacco, p. 126, pl. 25, fig. 47.
2018 *Mathilda quadricarinata* (Brocchi, 1814) – Brunetti & Cresti, p. 104, fig. 441 [*non Mathilda quadricarinata* Brocchi, 1814].
2021 *Mathilda brocchii* Semper, 1865 – Tabanelli *et al*., p. 5, figs 2a-b, 4a-f.

Material and dimensions – Maximum height 18.4 mm, width 7.5 mm. **VC**: RGM.1404197-198 (2), RGM.1404199 (11), NHMW 2023/0076/0044 (16).

Description – Shell of medium size and thickness, turritelliform; apical angle about 27-29°. Protoconch multispiral, of about three smooth whorls, heterostrophic, nucleus just exposed, tilted at angle of about 120°. Teleoconch of up to eight angled whorls separated by deeply impressed, canaliculate suture. Sculpture of three primary spiral cords at teleoconch/protoconch junction; S1 weakest; S2 strongest forming periphery; S3 intermediate strength placed short distance above suture. After one-quarter whorl secondary spiral intercalated between S1 and S2, almost equal in strength to S1. Axial sculpture of about 40 close-set narrow axial lamellae that overrun cords, but do not become swollen or beaded at intersections. Last whorl with double peribasal cord, base depressed, concave, bearing 3-4 weaker cords. Aperture circular, outer lip simple, crenulated by edge of cords, slightly everted abapically. Columella narrow, slightly thickened, erect. No parietal callus.

Discussion – In their excellent review of the genus *Mathilda* Semper, 1865 in the Italian Pliocene, Tabanelli *et al*. (2021) compared this species to its closest Mediterranean Pliocene congener *M. filogranata* (Sacco, 1895). They concluded that *M. brocchii* Semper, 1865 differed in having the first protoconch whorl partly obscured by the first teleoconch whorl, and less tilted (120° *vs*. 128°), a more angular first teleoconch whorl, the peripheral cord forming the carina is coarser, the axial lamellae are more numerous (last whorl ~40 *vs*. ~30), and fewer and weaker cords on the base. *Mathilda brocchii* is unusual amongst European Neogene congeners in not having tubercles developed at the sculptural intersections.
In the Estepona assemblages this species is most common in the deeper water deposits of Velerín carretera.

Distribution – Lower Pliocene: central Mediterranean, Italy (Sacco, 1895, 1904; Brunetti & Cresti, 2018; Tabanelli *et al*., 2021). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1895, 1904; Tabanelli *et al*., 2021).

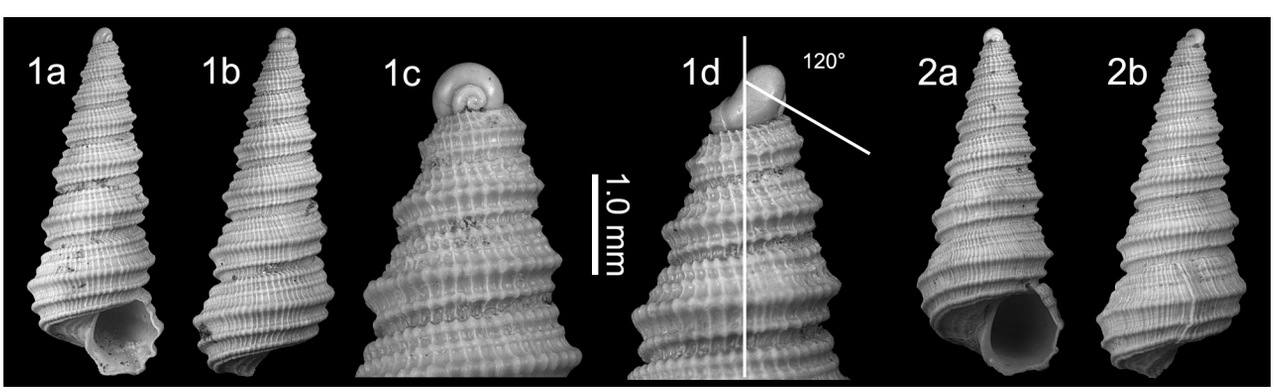

Plate 14. *Mathilda brocchii* Semper, 1865; 1. RGM.1404197, height 11.9 mm, width 4.6 mm, 1c, d, detail of protoconch; 2. RGM.1404198, height 12.1 mm, width 5.2 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

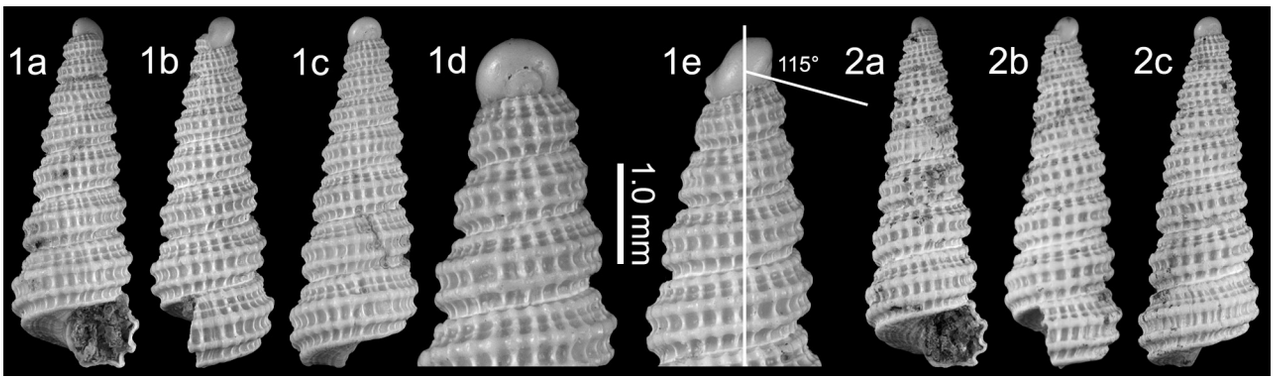

Plate 15. *Mathilda granosa* (Borson, 1821); 1. NHMW 2023/0076/0035, height 6.5 mm, width 2.3 mm, 1d, e, detail of protoconch; 2. NHMW 2023/0076/0036, height 7.9 mm, width 2.7 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

***Mathilda granosa* (Borson, 1821)**
Plate 15, figs 1-2

*1820	*Turritella granosa* Borson, p. 344, pl. 6, fig. 19.
1865	*Mathilda gemmulata* Semper, p. 340, pl. 13, fig. 4.
1895	*Mathilda granosa* (Bors.) – Sacco, p. 35, pl. 3, fig. 32.
1895	*Mathilda granosa* var. *gemmulata* Semp. – Sacco, p. 36, pl. 3, fig. 33.
1904	*Mathilda granosa* (Bors.) – Sacco, p. 126, pl. 25, fig. 41.
1904	*Mathilda granosa* var. *gemmulata* Semp. – Sacco, p. 126, pl. 25, fig. 42.
1976b	*Mathilda* (*Mathilda*) *granosa* (Borson, 1821) – Pavia, p. 152, pl. 1, fig. 2.
1981	*Mathilda* (*Mathilda*) *granosa* (Borson, 1821) – Cuerda Barceló, p. 172, fig. 1d.
2010	*Mathilda granosa* (Borson, 1821) – Sosso & Dell'Angelo, p. 51, unnumbered fig. p. 66 centre middle.
2011	*Mathilda granosa* (Borson, 1821) – Landau *et al*., p. 39, pl. 22, fig. 3.
2013	*Mathilda granosa* (Borson, 1821) – Landau *et al*., p. 303, pl. 52, fig. 4.
2021	*Mathilda granosa* (Borson, 1821) – Tabanelli *et al*., p. 8, figs 9a-f.

Material and dimensions – Maximum height 7.9 mm, width 2.7 mm. **CO**: RGM.1404314 (1), NHMW 2023/0076/0035-0036 (2), NHMW 2023/0076/0037 (2). **VC**: NHMW 2023/0076/0038 (2). **VS**: NHMW 2023/0076/0041 (7).

Description – Shell small, relatively solid, slender turritelliform; apical angle 21-23°. Protoconch multispiral, of about three smooth whorls, heterostrophic, nucleus mostly exposed, tilted at angle of about 115°. Teleoconch of up to eight convex whorls separated by deeply impressed suture. Sculpture of three primary spiral cords on first teleoconch whorl: S1 slightly weaker than spirals S2 and S3, with single secondary thread intercalated between S1 and S2. Abapically S2 and S3 prominent, elevated, equal in strength, whorl profile between spirals concave. Axial sculpture of about 24 narrow axial lamellae that overrun cords, forming small, rounded tubercles at sculptural intersections. Last whorl with single peribasal cord, base depressed, concave, bearing 4-5 weaker cords. Aperture circular, outer lip simple, crenulated by edge of cords. Columella narrow, slightly thickened, erect. No parietal callus.

Discussion – Specimens from Estepona differ from the holotype illustrated by Pavia (1976b, pl. 1, fig. 2) in having S1 less developed and S2 and S3 stronger. Indeed, these spirals are more strongly developed than in any other specimen seen, and the tubercles on the spirals are coalescent. At 14.5 mm height it is also the largest specimen we have seen, and these differences may be exaggerated by ontogeny. If one compares the specimen illustrated by Tabanelli (2021, figs 9a-b *vs*. Pl. 16, figs 1d, e; *hoc opus*), these differences are not as pronounced. The protoconch characters between the Estepona and Italian specimens are identical. We therefore consider the Estepona specimens conspecific but highlight that spirals 2 and 3 are weaker and beading at the sculptural intersections finer. We note that the specimen from the Lower Pliocene Atlantic Guadalquivir Basin of Spain (Landau *et al*., 2011, pl. 22, fig. 3) and those at hand from the Upper Pliocene Atlantic Mondego Basin assemblage of Portugal are similar in sculpture to the Estepona ones. It is possible that this is a Pliocene Atlantic and western Mediterranean form of the species. *Mathilda granosa* (Borson, 1821) is unusual amongst the European Neogene congeners in having a single peribasal cord. Most species have a double cord.
Tabanelli *et al*. (2021, p. 9) considered *Mathilda gemmulata* Semper, 1865 a junior subjective synonym of *M. granosa*. It is most similar to *M. retusa* Brugnone, 1873, which differs in having a more tilted protoconch (120° *vs*. 115°), a broader apical angle, fewer axial and stronger spirals that form larger tubercles at the sculptural intersections, and fewer cords over the base. For further discussion see Landau *et al*. (2013, p. 303).

Distribution – Lower Miocene: central Proto-Mediterranean (Burdigalian), Italy (Sacco, 1895, 1904). Middle Miocene: eastern Proto-Mediterranean (Serravallian),

Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: central Proto-Mediterranean (Tortonian), Italy (Sacco, 1895). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011); central Mediterranean, Italy (Sacco, 1895; Pavia, 1976b; Tabanelli *et al*., 2021). Upper Pliocene: Atlantic, Mondego Basin, Portugal (NHMW coll.); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1895, 1904; Sosso & Dell'Angelo, 2010; Tabanelli *et al*., 2021). Upper Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1981).

***Mathilda quadricarinata* (Brocchi, 1814)**
Plate 16, figs 1-2

*1814 *Turbo quadricarinatus* Brocchi, p. 375, pl. 7, fig. 6.
1866 *Eglisia macandreae* H. Adams, p. 753.
1895 *Mathilda quadricarinata* (Br.) – Sacco, p. 34, pl. 3, fig. 26.
1895 *Mathilda quadricarinata* var. *squamosa* (Bors.) – Sacco, p. 35, pl. 3, fig. 27.
1895 *Mathilda quadricarinata* var. *perconica* Sacco, p. 35, pl. 3, fig. 28.
1895 *Mathilda quadricarinata* var. *perelegans* Sacco, p. 35, pl. 3, fig. 29.
1895 *Mathilda quadricarinata* var. *taurocolligens* Sacco, p. 35, pl. 3, fig. 30.
1904 *Mathilda quadricarinata* (Br.) – Sacco, p. 125, pl. 25, fig. 35.
1904 *Mathilda quadricarinata* var. *squamosa* (Bors.) – Sacco, p. 126, pl. 25, fig. 36.
1904 *Mathilda quadricarinata* var. *perconica* Sacco, p. 126, pl. 25, fig. 37.
1904 *Mathilda quadricarinata* var. *taurocolligens* Sacc. – Sacco, p. 126, pl. 25, fig. 38.
1904 *Mathilda quadricarinata* var. *perelegans* Sacco, p. 126, pl. 25, fig. 39.
1955 *Mathilda* (*Mathilda*) *quadricarinata* (Brocchi) 1814 – Rossi Ronchetti, p. 119, fig. 56.
1976 *Mathilda quadricarinata* (Brocchi) – Caprotti, p. 7, pl. 8, fig. 5.
1978 *Turbo quadricarinatus* Brocchi, 1814 – Pinna & Spezia, p. 164, pl. 59, fig. 1.
1979 *Mathilda quadricarinata* (Brocchi 1815 [*sic*]) – Nordsieck & García-Talavera, p. 82, pl. 16, fig. 13.
1984 *Mathilda quadricarinata* var. *perelegans* Sacco– Ruggieri & Davoli, p. 51, pl. 1, fig. 17.
1991 *Mathilda quadricarinata* (Brocchi, 1814) – Poppe & Goto, p. 186, pl. 36, fig. 30.
1992 *Mathilda quadricarinata* (Brocchi, 1814) – Cavallo & Repetto, p. 152, fig. 421.
1999 *Mathilda quadricarinata* (Brocchi, 1814) – Ardovini & Cossignani, p. 75, unnumbered fig. bottom left.
2004 *Mathilda quadricarinata* (Brocchi, 1814) – Ardovini & Cossignani, p. 39, 234, unnumbered fig.
2005 *Mathilda quadricarinata* (Brocchi, 1814) – Repetto *et al*., p. 226, fig. 948.
2005 *Mathilda quadricarinata* (Brocchi, 1814) – Rolán, p. 178, pl. 55, fig. 834.
2008 *Mathilda quadricarenata* [*sic*] (Brocchi, 1814) – Chirli & Richard, p. 75, pl. 25, fig. 2.
2010 *Mathilda quadricarinata* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 51, 66, unnumbered figure, middle row right.
2011 *Mathilda quadricarinata* (Brocchi, 1814) – Cossignani & Ardovini, p. 32, 340, unnumbered fig.
2011 *Mathilda quadricarinata* (Brocchi, 1814) – Gofas *et al*., p. 352, unnumbered fig. top.
2011 *Mathilda quadricarinata* (Brocchi, 1814) – Chirli & Linse, p. 214, pl. 85, fig. 1.
2011 *Mathilda quadricarinata* (Brocchi, 1814) – Hernández *et al*., p. 243, figs 82 P-S.
2011 *Mathilda granosa* (Borson, 1821) – Landau *et al.*, p. 39, pl. 22, fig. 3 [*non Mathilda granosa* (Borson, 1821)].
2013 *Mathilda quadricarinata* (Brocchi, 1814) – Chirli, p. 20, pl. 7, figs 1-6.
2014 *Mathilda quadricarinata* (Brocchi, 1814) – Giannuzzi-Savelli *et al.*, p. 38, fig. 32.
2021 *Mathilda quadricarinata* (Brocchi, 1814) – Boschele *et al*., p. 18, pl. 14, fig. 25.
2021 *Mathilda quadricarinata* (Brocchi, 1814) – Tabanelli *et al*., p. 3, figs 1a-c, 2a-c.
2023 *Mathilda quadricarinata* (Brocchi, 1814) – Sacchetti *et al*., p. 90, pl. 6, fig. F.

non 2018 *Mathilda quadricarinata* (Brocchi, 1814) – Brunetti & Cresti, p. 104, fig. 441 [= *Mathilda brocchii* Semper, 1865].

Material and dimensions – Maximum height 22.0 mm, width 7.3 mm. **CO**: NHMW 2023/0076/0042 (1), NHMW 2023/0076/0043 (1). **EL**: RGM.1404200 (1).

Description – Shell large, solid, turritelliform; apical angle about 26°. Protoconch multispiral, of about two smooth whorls, heterostrophic, nucleus just exposed, tilted at angle of about 128°. Teleoconch of up to ten convex whorls separated by deeply impressed, narrowly canaliculate suture. Sculpture of three primary spiral cords at teleoconch/protoconch junction; S1 weakest; S2 strongest forming periphery; S3 intermediate strength placed short distance above suture. After one-quarter whorl secondary spiral intercalated between S1 and S2, almost equal in strength to S1.
Abapically single secondary thread intercalated in most interspaces on later whorls. Axial sculpture of very numerous, close-set narrow axial lamellae that overrun cords, forming very small tubercles at intersections. Last whorl with double peribasal cord, base depressed, concave, bearing 5-6 weaker cords. Aperture circular, outer lip simple. Columella narrow, slightly thickened, erect. No parietal callus.

Discussion – *Mathilda quadricarinata* (Brocchi, 1814) is the largest of the Pliocene *Mathilda* species. It differs from *M. brocchii* Semper, 1865 in having a taller shell composed of a greater number of whorls, one protoconch

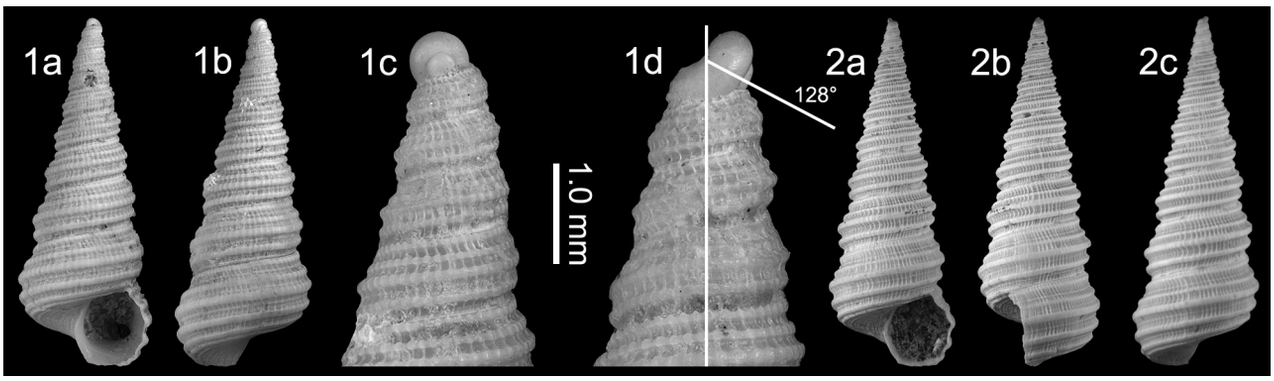

Plate 16. *Mathilda quadricarinata* (Brocchi, 1814); 1. RGM.1404200, height 12.4 mm, width 4.7 mm, 1c, d, detail of protoconch. El Lobillo. 2. NHMW 2023/0076/0042, height 20.5 mm, width 7.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

whorl less, spiral 3 is less developed and does not form a carina angulating the whorls, and the axial lamellae are weaker and more crowded.

In the Mediterranean today *M. quadricarinata* occurs from infra- to circalittoral habitats (Sabelli & Spada, 1978; Stjepčevic & Parenzan, 1982; Gofas *et al*., 2011). In Estepona it is only found in the shallower water assemblages of Velerín conglomerates and El Lobillo, whereas *M. brocchii* is abundant in the deeper water assemblage of Velerín carretera. We have included the Lower Miocene records from Italy (Sacco 1895, 1904), although these will require confirmation.

Distribution – Lower Miocene: central Proto-Mediterranean, Italy (Sacco, 1895, 1904). Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1895, 1904; Ruggieri & Davoli, 1984). Lower Pliocene: Atlantic, Santa Maria Island, Azores (Sacchetti *et al*., 2023), Guadalquivir Basin S. Spain (Landau *et al.,* 2011); central Mediterranean, Italy (Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Chirli, 2013;). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1895, 1904; Caprotti, 1976; Tabanelli *et al*., 2021). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Portugal, western Mediterranean (Repetto *et al*., 2005), West African coast to Angola, Madeira (Segers *et al*., 2009), Canaries (Nordsieck & García-Talavera, 1979), Senegal (Ardovini & Cossignani, 2004), and Cabo Verde (Poppe & Goto, 1991; Rolán, 2005; Hernández *et al*., 2011; Giannuzzi-Savelli *et al.,* 2014), into western Mediterranean (Gofas *et al*., 2011), central Mediterranean (Ardovini & Cossignani, 1999; Cossignani & Ardovini, 2011).

Genus *Fimbriatella* Sacco, 1895

Type species (by original designation) – *Cerithium fimbriatum* Michelotti, 1847, Miocene, Italy.

1895 *Fimbriatella* Sacco, p. 36.

Note – Synonymised with *Mathilda* Semper, 1865 by Bieler (1995, p. 600), Harzhauser & Landau (2023) argued on the validity of the genus based on early whorl sculpture.

***Fimbriatella fimbriata* (Michelotti, 1847)**
Plate 17, fig. 1

*1847	*Cerithium fimbriatum* Michelotti, p. 193, pl. 16, fig. 23.
1895	*Mathilda* (*Fimbriatella*) *fimbriata* (Micht.) – Sacco, p. 37, pl. 3, figs 35, 36.
1904	*Mathilda* (*Fimbriatella*) *fimbriata* (Micht.) – Sacco, p. 126, pl. 25, figs 43, 44.
1951	*Fimbriatella fimbriata* (Michelotti) – Montanaro Gallitelli & Tacoli, p. 175, pl. 2, fig. 1.
1951	*Fimbriatella fimbriata* var. *elegans* Montanaro Gallitelli & Tacoli, p. 175, pl. 2, fig. 2.
1960	*Mathilda* (*Fimbriatella*) *fimbriata* (Micht.) – Sieber, p. 266, pl. 1, figs 21, 22.
1969a	*Mathilda* (*Fimbriatella*) *fimbriata* Micht. – Csepreghy-Meznerics, p. 20, pl. 2, figs 14-15.
1969b	*Mathilda* (*Fimbriatella*) *fimbriata* Micht. – Csepreghy-Meznerics, p. 69, pl. 1, fig. 7.
2021	*Mathilda fimbriata* (Michelotti, 1847) – Tabanelli *et al*., p. 7, figs 7a-f, 8a-d.
2023	*Fimbriatella fimbriata* (Michelotti, 1847) – Harzhauser & Landau, p. 54, figs 28A-F.

Material and dimensions – Maximum height 12.5 mm, width 5.9 mm. **VC**: NHMW 2023/0076/0039 (1), NHMW 2023/0076/0040 (1).

Description – Shell of medium size and thickness, broad turritelliform; apical angle about 41°. Protoconch multispiral, of about 2.5 smooth whorls, heterostrophic, nucleus exposed, tilted at angle of about 110°. Teleoconch of seven angled whorls separated by impressed suture. Sculpture of first teleoconch whorl of three primary spiral cords: S1 moderately developed, placed abutting upper suture; S2 placed mid-whorl weakest; S3 strongest,

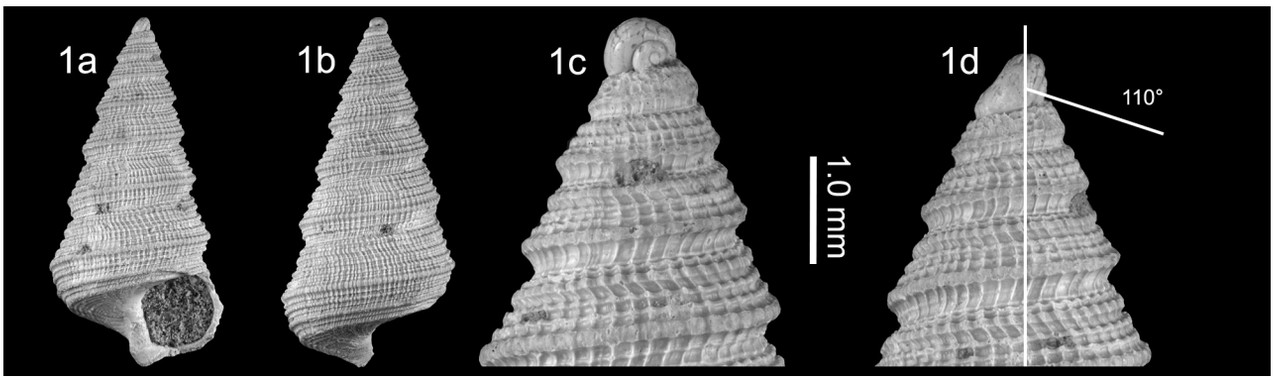

Plate 17. *Fimbriatella fimbriata* (Michelotti, 1847); 1. NHMW 2023/0076/0039, height 12.5 mm, width 5.9 mm, 1c, d, detail of protoconch (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

placed close above abapical suture. Later whorls with carinate S3, coinciding with periphery. Secondary spiral cord appears between S2 and S3 on second teleoconch whorl, forming a pair of same strength with S2. Abapically additional secondary and tertiary spiral cords appears between primaries. Axial sculpture of numerous close-set, narrow, arcuate axial lamellae that overrun cords, forming finely reticulated sculpture with small tubercles developed at intersections. Last whorl with double peribasal cord with single secondary intercalated, base depressed, flattened, bearing about ten weak cords. Aperture circular, outer lip not preserved. Columella not complete, thickened.

Discussion – *Fimbriatella fimbriata* (Michelotti, 1847) is a rather poorly known species. Sacco (1895, pl. 35, fig. 36) and Montanaro Gallitelli & Tacoli (1951, pl. 2, fig. 2) illustrated two specimens from the Tortonian of S. Agata and Montegibbio (Italy) close to the type locality. These show a comparatively stout specimen with delicate and rather uniform sculpture, a simple subsutural cord and with week keel (Montegibbio) and a relatively slenderer specimen with strongly differentiated spiral sculpture, bifid subsutural cord and prominent keel (S. Agata). The Paratethyan specimens in the NHMW collection are characterized by a bifid subsutural cord, a feature, which is also depicted in the detailed illustration of the holotype by Michelotti (1847), and is also present in the Estepona specimen, although a single thread in intercalated. In addition, Tabanelli *et al.* (2021) illustrated Pliocene specimens, which are stout, have a strongly differentiated spiral sculpture and a prominent subsutural cord adjoined by a much weaker spiral thread. The nucleus of the protoconch is covered in these Pliocene species but fully exposed in Paratethyan specimens. For the Italian Miocene specimens this information is not available. Based on these somewhat contradicting data we prefer to treat all these specimens as single variable species until a revision of the Mediterranean occurrences is available. The specimens from Estepona represent a morphology with comparatively delicate and uniform sculpture and weak keel.
Fimbriatella fimbriata (Michelotti, 1847) is extremely uncommon in the Estepona assemblages and found only in the deeper water Velerín carretera deposits. Tabanelli *et al*. (2021, p. 8) also associate it with bathyal Lower Pliocene Italian assemblages. Material at hand consists of a single adult specimen and one juvenile. Compared to the specimens from Italy illustrated by Tabanelli *et al*., (2021, figs 7a-f, 8a-d), spirals 1 and 3 are less elevated and the axial lamellae are stronger forming a finely reticulated surface sculpture in which the spiral element is only slightly dominant, whereas in the Italian specimens the spirals are strongly dominant. Nevertheless, the wide apical angle, protoconch characters and the ontogenic order of development of the spirals (seen in fig 7e of Tabanelli *et al*., 2021) agree.

Distribution – Middle Miocene: Central Paratethys, Austria (Sieber, 1960; Harzhauser & Landau, 2023), Hungary (Csepreghy-Meznerics, 1969a, 1969b), Czech Republic (Montanaro Gallitelli & Tacoli, 1951; Harzhauser & Landau, 2023), Romania (Semper, 1865; Harzhauser & Landau, 2023). Upper Miocene: central Proto-Mediterranean (Tortonian), Italy (Sacco, 1895). Lower Pliocene: central Mediterranean, Italy (Tabanelli *et al*., 2021). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper).

Order/Subterclass Acteonimorpha
Superfamily Acteonoidea d'Orbigny, 1843
Family Acteonidae d'Orbigny, 1843
Subfamily Acteoninae d'Orbigny, 1843
Genus *Acteon* de Montfort, 1810

Type species (by original designation) – *Voluta tornatilis* Linnaeus, 1758, present-day, European.

1810 *Acteon* de Montfort, p. 315.

For generic synonymy see Ceulemans *et al*. (2018, p. 112).

Note – We note that although we have allocated species to genera within the Acteonidae d'Orbigny, 1843, present-day species are assigned to a particular genus based on their radula rather than on shell morphology.

***Acteon incisus* Dall, 1881**
Plate 18, figs 1-3

*1881 *Acteon incisus* Dall, p. 95.
1889 *Acteon incisus* Dall – Dall, p. 84, pl. 17, figs 1, 1b.

Material and dimensions – Maximum height 8.3 mm, width 4.6 mm **VC**: RGM.1404316 (1), RGM.1404317 (6), NHMW 2023/0076/0068-0069 (2), NHMW 2023/0076/0070 (40). **CO**: NHMW 2023/0076/0071 (4).

Description – Shell small, ovate, with medium height, scalate spire. Protoconch heterotrophic, strongly intorted so that spire completely submerged in first teleoconch whorl. Teleoconch of up to four weakly convex whorls, roundly shouldered just below apical suture, with periphery at abapical suture, separated by deeply impressed, narrowly canaliculated suture. Sculpture of finely pitted spiral grooves, five on penultimate whorl, slightly more widely spaced mid-whorl, with fainter pitted grooves irregularly intercalated in some specimens. Pits horizontally ovate. Last whorl 76-77% of total height, regularly ovate, grooves slightly deeper over base. Aperture 57-60% of total height, pyriform. Outer lip convex in profile, slightly expanded and strongly rounded abapically. Columella short, slightly thickened, bearing fold at upper end. Columellar and parietal callus not developed. Narrow umbilical chink.

Discussion – For many years these specimens were identified by us as the extant eastern Atlantic (from Portugal to Cape Verde) and Mediterranean species *Liocarenus globulinus* (Forbes, 1844). The genus *Acteon* was considered inappropriate, as most European species have spirals made up of much larger pits.
Salvador & Cunha (2016) erected the genus *Rapturella*, with Forbes' species as the type. They characterised the genus as including species of small size, thick shelled, with a stepped spire, trapezoid aperture, thickened peristome, a weak fold on the columella, and a weak tooth-like thickening on the palatal region. The spirals are formed by very small pits. The species from Estepona is closely similar in profile and sculpture but is relatively thin shelled and lacks the small tooth-like thickening within the outer lip.
Further species of *Rapturella* were described; *R. ryani* Salvador & Cunha, 2016 from the Florida Keys differs from *R. globulina* in having a slightly rounder shell, a narrow slit-like umbilicus, and a larger number of spiral grooves (16 *vs*. 20) on the last whorl. The punctae on the pair of subsutural spiral grooves are elongated oval in *R. ryani* and rounded-quadrangular in *R. globulina*. The Estepona specimens are larger than either of the extant species discussed above (height 2.8-3.5 mm = *R. globulina*; 3.4 mm = *R. ryani*; 5.2-8.3 mm = Estepona specimens), have a more elongated shell (w/h 0.60-0.65 = *R. globulina*; 0.68 = *R. ryani*; 0.55-0.59 = Estepona specimens), they have a narrow, but clear umbilical chink, as seen in *R. ryani*, they have at least 16-20 grooved on the last whorl, with secondary grooves intercalated in at least some of the interspaces in all specimens, especially in the mid-whorl region. The punctae on the of subsutural spiral grooves are small, ovate, and close-set. A third extant species; *R. atlas* Cunha & Simone, 2018 from Brazil is even smaller (height 2.5 mm), thicker shelled, with fewer spiral grooves. Therefore, the Estepona specimens cannot be placed in the genus *Rapturella*.
As mentioned above, European *Acteon* species such as *A. monterosatoi* Dautzenberg, 1889 have rows of larger pits. However, *A. incisus* Dall, 1881, a deep-water species described from the western Atlantic Yucatan Strait is almost identical to the Estepona species with numerous rows of extremely fine pits (see syntype https://collections.nmnh.si.edu/search/iz/search.php?action=10&height=315&width=640&irn=10249105). *Acteon incisus* has also been recorded from the mid-Atlantic Azorean Archipelago (Dautzenberg & Fischer, 1896; Mikkelsen, 1995; Malaquias, 2001). *Japonacteon pusillus* (Forbes, 1844) is also superficially similar but again differs in having the pits forming the grooves much larger and deeper, forming a more evident chain-like pattern.

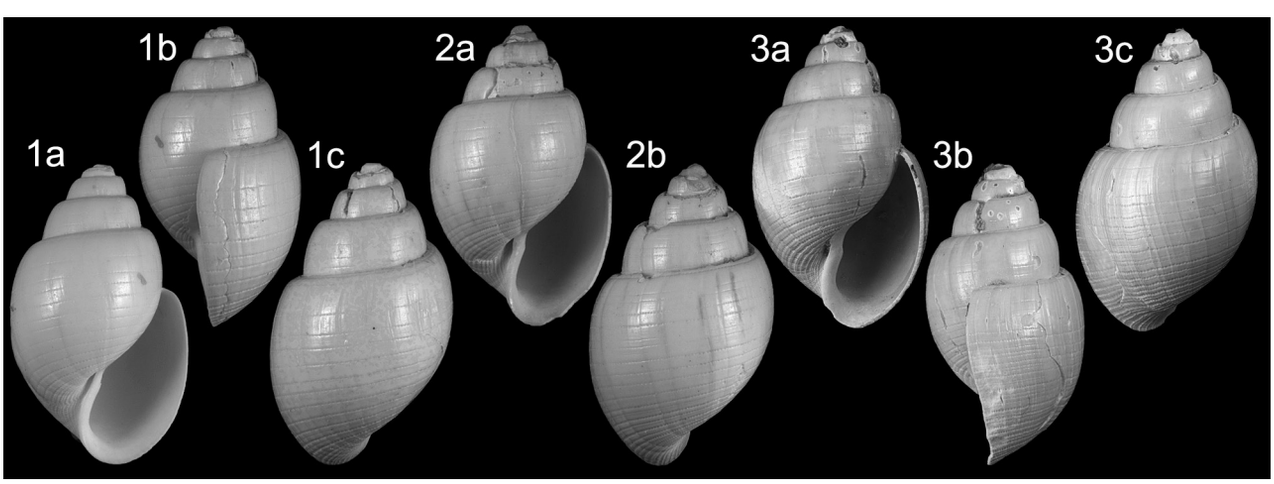

Plate 18. *Acteon incisus* Dall, 1881; 1. NHMW 2023/0076/0068, height 7.5 mm, width 4.1 mm; 2. NHMW 2023/0076/0069, height 7.1 mm, width 4.2 mm; 3. RGM.1404316, height 8.3 mm, width 4.6 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

In Estepona it is predominantly found in the deeper water assemblage of Velerín carretera, with occasional specimens found in the shallower water conglomerates.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: western Atlantic, Yucatán (Dall, 1881), Azores (Dautzenberg & Fischer, 1896; Mikkelsen, 1995; Malaquias, 2001).

***Acteon levidensis* (S.V. Wood, 1848)**
Plate 19, figs 1-3

1842	*Acteon levidensis* Wood, p. 537 (*nomen nudum*).
*1848	*Actaeon levidensis* Wood, p. 171, pl. 19, fig. 4.
2020	'*Acteon*' *levidensis* (Wood, 1848) – Landau *et al*., p. 262, pl. 6, figs 1-2 (*cum syn*.).

Material and dimensions – Maximum height 4.2 mm, width 1.8 mm. **VC**: RGM.1404306 (2), NHMW 2023/0076/0001 (1), NHMW 2023/0076/0002 (2). **CO**: NHMW 2023/0076/0003 (1), NHMW 2023/0076/0004 (2). **EL**: RGM.1404241 (1).

Description – Shell very small, solid, elongate-ovate, with elevated spire. Protoconch of 1.25 smooth whorls, with elevated nucleus. Junction with teleoconch delimited by scar and change in lustre. Teleoconch of up to five weakly convex whorls separated by narrow, deeply impressed, linear suture. Spire whorls with regular cords separated by punctate grooves covering entire surface. Punctuations close-set, but completely separated by fine axial lamellae present only in grooves. Last whorl 66-73% of total height, regularly elongate-ovate, entirely covered in punctate grooves about half the width of their interspaces. Aperture elongate pyriform, 47-50% of total height; outer lip simple, very weakly convex, strongly and narrowly rounded and slightly flared abapically. Columella thickened, with a single stout fold. Columellar and parietal callus not developed. Colour pattern preserved in a few specimens suggesting orange-red axial flammules.

Discussion – *Acteon levidensis* (S.V. Wood, 1848) seems to be widely distributed in the European Late Miocene and Pliocene, but never abundant. In Estepona it is found in both the shallow and deeper water assemblages. Despite the very small size of the specimens at hand, they all represent adult specimens judging by the thickened shell and outer lip. There is some variability in the whorl profile; in most specimens the whorls are regularly convex, but in some the whorls are slightly shouldered (Pl. 19, fig. 2). Sculpture is regularly constant, although in one specimen the cords mid-whorl become weakly bifid on the last whorl towards the outer lip (Pl. 19, fig. 2b). For full discussion see Landau *et al*. (2020, p. 263).

Distribution – Upper Miocene: Atlantic (Tortonian), northwestern France (Landau *et al*., 2020). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848, 1872; Harmer, 1923), Kattendijk Formation, Belgium (Glibert, 1960; Marquet, 1997, 1998); central Mediterranean, Italy (Sacco, 1897; Pavia, 1976a; Chirli, 2013). Upper Pliocene: North Sea Basin, Luchtbal sands, Belgium (Marquet, 1997, 1998); Atlantic, Mondego Basin, central-west Portugal (NHMW coll.); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Cavallo & Repetto, 1992; Ferrero *et al*., 1998; Sosso & Dell'Angelo, 2010). Upper Pliocene-Pleistocene: Atlantic, northwestern France (Brébion, 1964). Lower Pleistocene: eastern Mediterranean, Greece (Chirli & Linse, 2011).

***Acteon semistriatus* (Férussac, 1822)**
Plate 20, figs 1-3

*1822	*Tornatella semi-striata* Férussac, p. 108.
2013	'*Acteon*' *semistriatus* (Férussac, 1822) – Landau *et al*., p. 323, pl. 52, fig. 13 (*cum syn*.).
2018	'*Acteon*' *semistriatus* (Férussac, 1822) – Ceulemans *et al*., p. 112, pl. 7, fig. 1 (*cum syn*.).
2018	*Acteon semistriatus* (Ferussac [*sic*], 1822) – Brunetti & Cresti, p. 116, fig. 512.
2020	'*Acteon*' *semistriatus* (Férussac, 1822) – Landau *et al*., p. 264, pl. 9, figs 1-3 (*cum syn*.).
2022	*Acteon semistriatus* (Ferussac [*sic*], 1822) – Brunetti, p. 78, fig. 183.

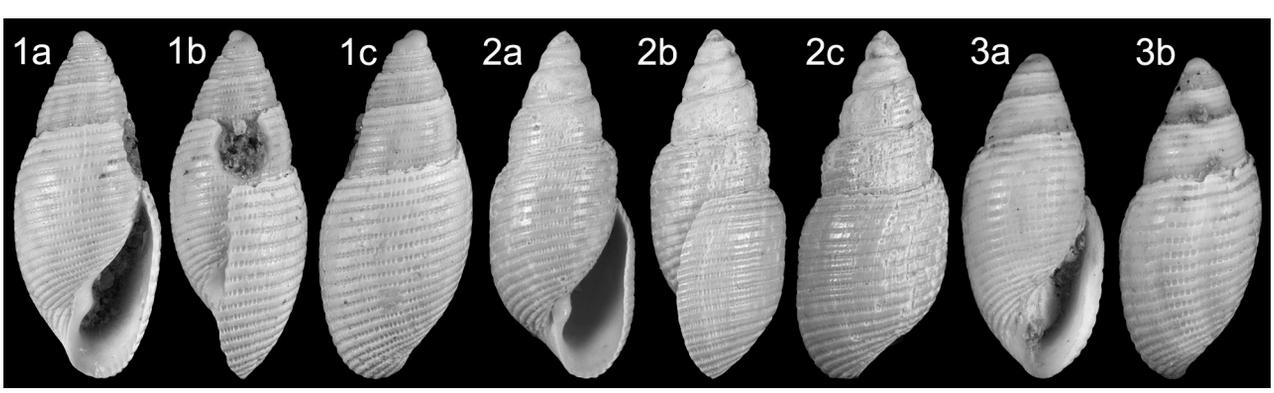

Plate 19. *Acteon levidensis* (S.V. Wood, 1848); 1. RGM.1404241. El Lobillo. 2. NHMW 2023/0076/0001, height 4.1 mm, width 1.7 mm. Velerín carretera. 3. NHMW 2023/0076/0003, height 3.4 mm, width 1.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Material and dimensions – Maximum height 16.7 mm, width 8.0 mm. **CO**: RGM.1404236-238 (3), RGM.1404239 (8), NHMW 2023/0076/0100 (13). **EL**: RGM.1404240 (33), NHMW 2023/0076/0099 (26).

Description – Shell medium sized, solid, elongate-ovate, with elevated spire. Protoconch small, depressed, 1.25 smooth whorls. Junction with teleoconch delimited by scar and change in lustre. Teleoconch of up to six weakly convex whorls separated by narrow, deeply impressed, somewhat irregular suture. Spire whorls with 3-4 punctate grooves on adapical half of whorl, grooves weakening abapically. Punctuations hardly separated, so that in some specimens grooves regularly linear. Last whorl 70-74% of total height, regularly elongate-ovate, bearing punctate grooves on upper quarter weakening abapically, and from mid-whorl to base, strengthening abapically.
Aperture elongate pyriform, 48-55% of total height; outer lip simple, very weakly convex, strongly rounded and slightly flared abapically. Columella thickened, with a single fold. Columellar callus not developed, parietal callus thin and narrow. Colour pattern preserved in many specimens consisting of two broad horizontal bands of lighter colour placed above and below mid-whorl.

Discussion –Landau *et al*. (2013, p. 323; 2020, p. 264) and Ceulemans *et al*. (2018, p. 112) discussed the intraspecific variability and the variation between Miocene and Pliocene populations, and considered *Acteon semistriatus* (Férussac, 1822) to be a very variable, widespread, and long-lived species. The Estepona specimens are larger than the average for Miocene specimens, and typical in size for the Mediterranean Pliocene populations. They show considerable variation in the height of the spire and inflation of the last whorl, but less variability in sculpture, as none of the specimens at hand have the entire last whorl spirally grooved as is often seen in Miocene populations. We continue to consider all these forms to represent a single species with a trend towards a reduction in sculpture over time.
As in Landau *et al*. (2020), pending confirmation, we exclude from the chresonymy and distribution the specimen illustrated by Chirli & Linse (2011, pl. 85, fig. 2), as it is much more inflated than usual for the species. The record from Rhodes Island was based on a single specimen, which is also much smaller than usual for the species (height 5.1 mm), even smaller than the NW France populations (Ceulemans *et al*., 2018; Landau *et al*., 2020). In Estepona, this species is found only in the shallower water deposits of Velerín conglomerates and El Lobillo.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian): Aquitaine Basin, France (Benoist, 1889; Peyrot, 1932); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1897); Paratethys (Aquitanian and Burdigalian): Austria (Steininger, 1973; Harzhauser, 2002). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Denmark (Sorgenfrei, 1958), Germany (Anderson, 1964; Moths, 1989; Wienrich, 2007), The Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984). Middle Miocene: Atlantic (Langhian and Serravallian): Aquitaine Basin, France (Grateloup, 1846; Benoist, 1889; Peyrot, 1933), (Langhian): Loire Basin, France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Kecskemétiné-Körmendy, 1962; Strausz, 1966), Poland (Friedberg, 1928); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: North Sea Basin (Tortonian): Denmark (Rasmussen, 1968; Schnetler, 2005); Atlantic (Tortonian and Messinian): NW France (Millet, 1854, 1865; Brébion, 1964; Landau *et al*., 2020), Algarve Basin, Portugal (Dollfus *et al*., 1903); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1897). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, northeastern Spain, (Martinell, 1982), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1897; Chirli, 2013; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992).

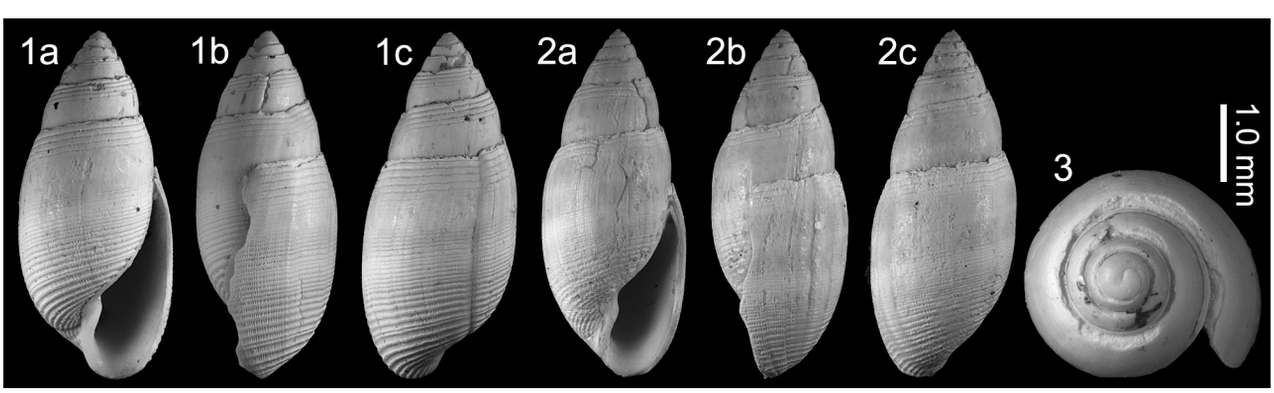

Plate 20. *Acteon semistriatus* (Férussac, 1822); 1. RGM.1404236, height 12.5 mm, width 5.7 mm; 2. RGM.1404237, height 12.5 mm, width 5.3 mm; 3. RGM.1404238, juvenile, detail of protoconch (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

***Acteon tornatilis* (Linnaeus, 1758)**
Plate 21, figs 1-5

*1758 *Bulla tornatilis* Linnaeus, p. 1187.
1778 *Turbo ovalis* da Costa, p. 101.
1791 *Voluta bifasciata* Gmelin, p. 3436.
1816 *Tornatella fasciata* Lamarck, p. 11, p. 452, fig. 3.
1829 *Voluta luteofasciata* Megerle von Mühlfeld, p. 205, pl. 7, fig. 2.
1832 *Tornatella carnea* Bivona e Bernardi, p. 17, pl. 2, fig. 9.
1843 *Tornatella pellucida* MacGillivray, p. 158.
1848 *Actaeon tornatilis* Linn. – S.V. Wood, p. 170, pl. 19, fig. 5.
1867 *Acteon tornatilis* var. *bullaeformis* Jeffreys, p. 435.
1878 *Tornatella tornatilis* L. – Nyst, pl. 7, fig. 19.
1882 *Tornatella tornatilis* L. – Nyst, p. 127.
1897 *Actaeon tornatilis* (L.) – Sacco, p. 31, pl. 3, figs 3-6.
1903 *Actaeon tornatilis* (Linne) – Dollfus *et al*., p. 16, pl. 34, figs 16-17.
1910 *Actaeon tornatilis* L. – Cerulli-Irelli, p. 31 [223], pl. 3 [34], figs 51-56.
1917 *Acteon tornatilis* var. *ancilla* Monterosato, p. 25.
1923 *Actaeon tornatilis* (Linné) – Harmer, p. 782, pl. 62, figs 13, 14.
1923 *Acteon candidulus* Monterosato, p. 12, pl. 1, fig. 17.
1932 *Acteon Augustoi* Nobre, p. 413, pl. 14, figs 20, 22.
1950 *Actaeon tornatilis* Linné – Nicklès, p. 134, fig. 275.
1959 *Acteon* (*Acteon*) *tornatilis* (Linnaeus) – Zilch, p. 6, fig. 2.
1960 *Actaeon tornatilis* Linné, 1766 [*sic*] – Glibert, p. 21, pl. 4, fig. 23.
1965 *Acteon tornatilis* (Linnaeus, 1758) – Van Regteren Altena *et al*., p. 44, pl. 19, fig. 180.
1972b *Actaeon tornatilis* (Linné, 1767 [*sic*]) – Nordsieck, p. 7, pl. 1, fig. 1.
1975 *Actaeon tornatilis* (Linné) – Fekih, p. 139, pl. 45, fig. 13.
1979 *Acteon tornatilis* (Linnaeus, 1767 [*sic*]) – Nordsieck & García-Talavera, p. 168, pl. 43, fig. 1.
1982 *Acteon tornatilis* (Linne, 1766 [*sic*]) – Martinell, p. 227, pl. 1, figs 14, 15.
1983 *Actaeon tornatilis* (Linné) – Macrì, p. 116, pl. 3, fig. 21.
1988 *Acteon tornatilis* (Linné, 1758) – Chirli, p. 24, pl. 11, fig. 18.
1988 *Acteon tornatilis* (L. 1758) – T.E. Thompson, p. 26, fig. 4.
1992 *Acteon tornatilis* (L. 1758) – Cavallo & Repetto, p. 164, fig. 470.
1996 *Acteon tornatilis* (Linné 1758) – Smriglio & Mariottini, p. 189, figs 13a-15b.
1996 *Pseudoacteon luteofasciatus* (Mühlfeld, 1829) – Smriglio & Mariottini, p. 189, fig. 16.
1997 *Acteon tornatilis* (Linné, 1578 [*sic*]) – Marquet, p. 111, pl. 10, fig. 9, pl. 11, fig. 1.
1998 *Acteon tornatilis* (Linnaeus, 1578 [*sic*]) – Marquet, p. 208, fig. 179.
2001 *Acteon tornatilis* (Linnaeus, 1766 [*sic*]) – Silva, p. 575, pl. 27, figs 3-4.
2001 *Acteon tornatilis* (Linnaeus, 1758) – Cachia *et al*., p. 119, pl. 19, fig. 11.
2004 *Acteon tornatilis* (Linnaeus, 1758) – Ardovini & Cossignani, p. 42, 241, unnumbered fig.
2011 *Acteon tornatilis* (Linnaeus, 1758) – Cossignani & Ardovini, p. 36, 368, unnumbered fig.
2011 *Acteon tornatilis* (Linnaeus, 1758) – Gofas *et al*., p. 352, unnumbered fig.
2011 *Acteon tornatilis* (Linnaeus, 1758) – Landau *et al*., p. 39, pl. 21, fig. 9.
2011 *Acteon tornatilis* (Linnaeus, 1758) – Hernández *et al*., p. 270, figs 92 A-D.
2013 *Acteon tornatilis* (Linné, 1758) – Chirli, p. 23, pl. 7, figs 13-17.
2018 *Acteon tornatilis* (Linné, 1758) – Trigo *et al*., p. 367, unnumbered fig.
2022 *Acteon tornatilis* (Linnaeus, 1758) – Brunetti, p. 80, fig. 185.

non 1856 *Actaeon tornatilis* Linn. – Hörnes, p. 508, pl. 46, fig. 24.
non 1958 *Actaeon tornatilis* (Linne) – Sorgenfrei, p. 303, pl. 66, fig. 220.
non 1972a *Actaeon tornatilis* (Linne, 1766 [*sic*]) – Nordsieck, p. 120, pl. 31, fig. 204.
non 1982 *Actaeon tornatilis* (Linne [*sic*], 1966 [*sic*]) – Martinell, p. 227, pl. 1, figs 14, 15 [= *Acteon semistriatus* (Férrusac, 1822)].
non 2011 *Acteon tornatilis* (Linnaeus, 1766 [*sic*]) – Katona *et al*., p. 9, pl. 2, fig. 4.

Material and dimensions – Maximum height 16.0 mm, width 9.2 mm. **VC**: NHMW 2023/0076/0010 (1). **CO**: RGM.1404296 (2), RGM.1404310 (1), NHMW 2023/0076/0005-0008 (2), NHMW 2023/0076/0009 (6). **EL**: NHMW 2023/0076/0011 (4).

Description – Shell medium sized, relatively solid, ovate, with low spire. Protoconch small, depressed, 1.25 smooth whorls. Junction with teleoconch delimited by scar and change in lustre. Teleoconch of up to five convex whorls separated by narrow, deeply impressed linear suture. Spire whorls with about eight narrow, flattened cords separated by finely punctate grooves. Last whorl 82-85% of total height, bearing fine cords separated by finely punctate grooves along entire surface; cords narrowing and grooves widening over base. Sculpture weaker or subobsolete mid-whorl in some specimens. Aperture 66-68% of total height, elongate pyriform; outer lip simple, weakly convex, strongly rounded and slightly flared abapically. Columella thickened, slightly erect abapically, with a single strong fold. Columellar callus not developed, parietal callus thin and narrow. Colour pattern preserved in some specimens consists of two lighter horizontal bands of variable width, the upper placed at the level of the insertion of the outer lip, the lower above the base.

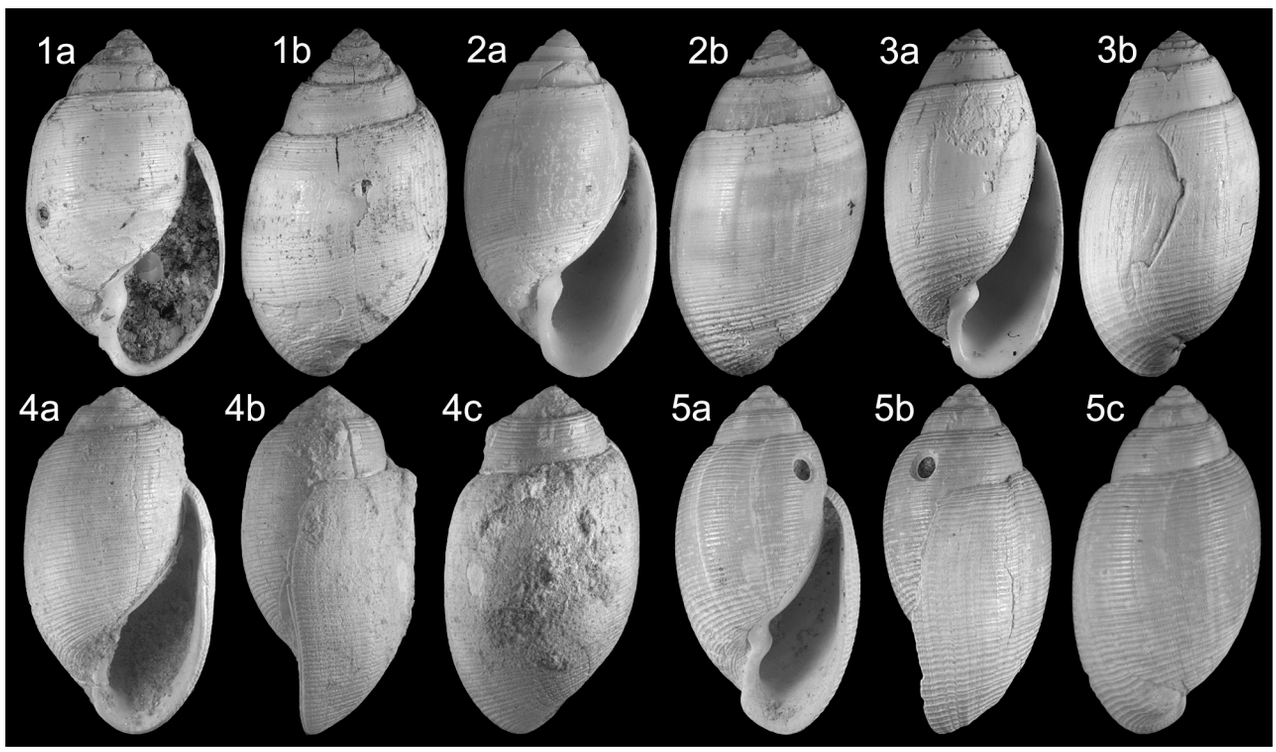

Plate 21. *Acteon tornatilis* (Linnaeus, 1758); 1. NHMW 2023/0076/0005, height 16.0 mm, width 9.2 mm; 2. NHMW 2023/0076/0006, height 11.3 mm, width 6.4 mm; 3. RGM.1404310, height 12.8 mm, width 6.5 mm; 4. NHMW 2023/0076/0007, height 21.5 mm, width 12.2 mm; 5. NHMW 2023/0076/0008, height 15.1 mm, width 8.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – *Acteon tornatilis* (Linnaeus, 1758) is characterised by its cylindrical, rather solid shell, with colour pattern often preserved (Pl. 21, figs 1b, 2b). The surface is entirely covered by fine, flattened spiral cords, slightly stronger over the base. However, as noted by Smriglio & Mariottini (1996, p. 189), Shells of dead specimens are often used by hermit crabs leading to a smooth surface due to abrasion of the fine spiral sculpture. As also noted by Cerulli-Irelli (1910, p. 31 [223]), for the specimens from the Lower Pleistocene of Italy, the height of the spire and globosity of the last whorl are somewhat variable. Similar variability is seen in the series of specimens from Estepona illustrated (Pl. 21, figs 1-5).

Brunetti (2022, p. 78, fig. 182) recently illustrated a specimen from the Lower Pliocene Guadalquivir Basin of southern Spain as *A. maculatus* (Borson, 1825). That species was originally described from the Pliocene of Cortandone, Italy and said to have three spiral rows of blotches (Borson, 1825, p. 315). Sacco (1897, p. 34, pl. 3, figs 26, 26 bis), considered it a variety of *A. semistriatus* (Férussac, 1822), and recorded it from several localities from Upper Miocene to Upper Pliocene. We can find no further references to this species between those of Sacco (1897) and Brunetti (2022). We note that in a couple of the specimens from Estepona the darker bands, on either side of the two lighter bands, are discontinuous, producing three rows of squarish blotches. A similar specimen from the Lower Pliocene of Italy is illustrated Chirli under *A. tornatilis* (2013, pl. 7, figs 15, 16). That same author also illustrated two specimens of *A. semistriatus* (2013, pl. 7, figs 9, 10, 12) in which the darker colour bands either side of the lighter bands are similarly interrupted, resulting in rows of square blotches. Therefore, we suspect that the name *A. maculatus* was erected and applied for specimens of both *A. semistriatus* and *A. tornatilis* in which the darker bands are interrupted but hesitate to formally synonymise Borson's species as we have not seen present-day specimens with the darker lines interrupted. However, the patchy loss of pigment might occur through taphonomic processes.

Acteon inflatus (Borson, 1821) was erected based on an Italian Pliocene specimen from Piemonte (exact locality unknown) (holotype refigured by Pavia, 1976b, p. 157, pl. 2, fig. 13). This is another poorly known species, and except for the illustration of the holotype the only other record we can find is that of Sacco (1897, p. 31, pl. 3, figs 8-10; and variety *fusuloides* Sacco, p. 32, pl. 3, fig. 11). This is unusual, as Sacco records it from numerous localities in the Italian Pliocene. Based on the holotype, *A. inflatus* is more inflated than the broadest specimens of *A. tornatilis*, with a lower spire, and the spiral sculpture is more strongly developed; more rounded cords separated by deeper grooves. We note that records of *A. inflatus* for the North Sea Basin Lower Miocene, Edegem Member of the Breda Formation of Belgium illustrated by Glibert (1952b, pl. 10, fig. 11) was later (Glibert, 1962, p. 29) described as a new species, *Actaeon* [*sic*] *sorgenfreii* Gli-

bert, 1962. It was said to differ from the Italian Pliocene species in having a less convex last whorl and having a taller spire composed of more scalate whorls. *Acteon sorgenfreii* is similar in profile and spire characters to the North Sea Basin *A. noae* J. de C. Sowerby, 1823 (see below), but that species differs in having finer spiral sculpture composed of closer spaced, flattened cords that are often bifid. *Acteon sorgenfreii* differs from *A. inflatus* in having the adapical three cords stronger and broader than the rest. *Acteon pinguis* d'Orbigny, 1852) from the Atlantic French Lower Miocene differs in having a sculpture of relatively wide, flattened, usually bifid cords, separated by narrower interspaces, of which the adapical 2-3 are narrower and stronger than the rest. Harzhauser (2002, p. 125) considered Middle Miocene Paratethyan records of *A. inflatus* to represent *Acteon pinguis* d'Orbigny, 1852.
Acteon noae J. de C. Sowerby, 1823 from the Pliocene North Sea Basin differs in being broader, with a lower spire, having more inflated whorls separated by a deeper suture, coarser spiral cords and in some specimens a smooth area mid last whorl.
Specimens from the Middle Miocene of the Paratethys, identified as *Acteon tornatilis* by Hörnes (1856) and Katona *et al*. (2011) differ from the specimens from Estepona in their slenderer last whorl and represent another species.
Today *A. tornatilis* is primarily a shallow water species, buried in sublittoral sand to 200 m (Gofas *et al*., 2011; Trigo *et al*., 2018). In Estepona it is also found predominantly in the shallow water assemblages; one specimen is from the deeper water Velerín carretera assemblage.

Distribution – Upper Miocene: Atlantic, Algarve Basin, Portugal (Dollfus *et al*., 1903). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848; Harmer, 1923), Kattendijk Formation, Belgium (Glibert, 1960; Marquet, 1997, 1998); Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, northeastern Spain, (Martinell, 1982); central Mediterranean, Italy (Sacco, 1897; Chirli, 2013), Tunisia (Fekih, 1975). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1923), The Netherlands (Van Regteren Altena *et al*., 1965); Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Macrì, 1983). Upper Pleistocene: North Sea Basin, Scotland (Harmer, 1923); Atlantic, Ireland (Harmer, 1923). Present-day: Atlantic, Iceland, Faroe Islands, Shetland, Norway, around British Isles (T.E. Thompson, 1988), Bay of Biscay (Trigo *et al*., 2018), Morocco (Ardovini & Cossignani, 2004), to Democratic Republic of the Congo (Nicklès, 1950), Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*. 2009), Canary Islands (Hernández *et al*., 2011), entire Mediterranean (Smriglio & Mariottini, 1996; Cachia *et al*., 2001; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Callostracon* Repetto & Bianco, 2012

Type species (by original designation) – *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996, present-day, Mediterranean.

1972b *Callostracon* Nordsieck, p. 10. Incorrect subsequent spelling of *Colostracon* Hamlin, 1884.
2012 *Callostracon* Repetto & Bianco, p. 40.

Note – For validity of generic name see Repetto & Bianco (2012).

***Callostracon tyrrhenicum* (Smriglio & Mariottini, 1996)**
Plate 22, figs 1-4

1986 *Acteon* sp. – Cecalupo & Giusti, p. 295, fig. 6.
1989 *Acteon* sp. – Cecalupo & Giusti, pl. 2, fig. 1.
*1996 *Callostracon tyrrhenicum* Smriglio & Mariottini, p. 184, figs 1a-6.
1999 *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996 – Ardovini & Cossignani, p. 80, 81, unnumbered fig. top left.
2001 *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996 – Cachia *et al*., p. 121, pl. 20, fig. 1.
2005 *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996 – Repetto *et al*., p. 254, fig. 1113.
2011 *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996 – Cossignani & Ardovini, p. 37, 368, unnumbered fig.
2012 *Callostracon tyrrhenicum* Smriglio & Mariottini, 1996 – Repetto & Bianco, p. 40, fig. 4.
2016 *Callostracon tyrrhenicum* (Smriglio & Mariottini, 1996) – Negri & Corselli, p. 81, figs 18m-o.

Material and dimensions – Maximum height 7.3 mm, width 4.6 mm. **VC**: NHMW 2023/0076/0014-0015 (2), NHMW 2023/0076/0016 (7). **CO**: NHMW 2023/0076/0017 (2). **EL**: RGM.1404311 (1), NHMW 2023/0076/0012 (1), NHMW 2023/0076/0013 (2).

Description – Shell small, ovate-conical, with low spire. Protoconch heterostrophic, about 1.5 whorls visible. Teleoconch of up to four weakly convex whorls with periphery at abapical suture, separated by deeply impressed linear suture. Sculpture of narrow, flattened cords separated by regularly punctate grooves covering entire surface. Last whorl 70-74% of total height, regularly ovate. Aperture about 52% of total height, subrhomboidal, narrow adapically, widening abapically; outer lip simple, rounded. Columella narrow, almost straight, with very weak fold midcolumella. Columellar and parietal callus not developed.

Discussion – *Callostracon tyrrhenicum* (Smriglio & Mariottini, 1996) is a very characteristic species that cannot be confused with any other Estepona opisthobranch. Today it lives on coral banks and muddy bottoms at 400-600 m depth. It is therefore odd that this species is found in both the shallow and deeper water assemblages

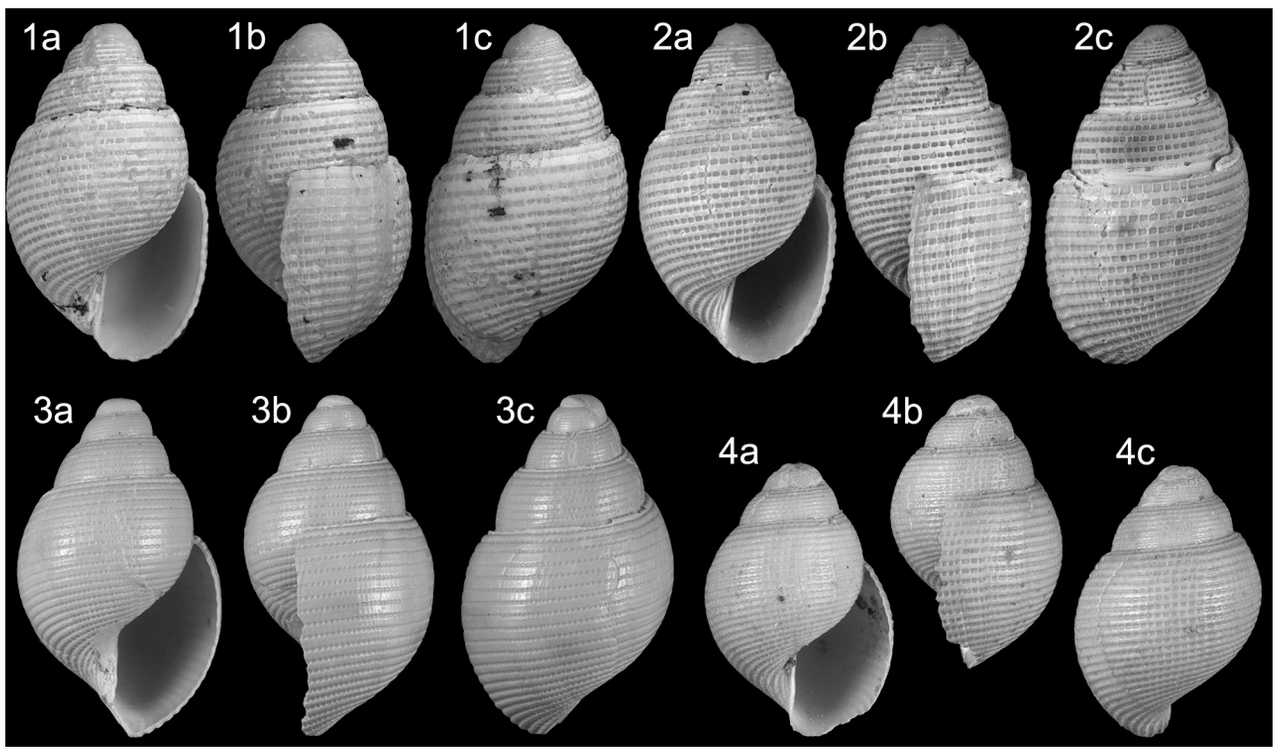

Plate 22. *Callostracon tyrrhenicum* (Smriglio & Mariottini, 1996); 1. RGM.1404311, height 5.5 mm, width 3.4 mm; 2. NHMW 2023/0076/0012, height 5.7 mm, width 3.2 mm. El Lobillo. 3. NHMW 2023/0076/0014, height 5.7 mm, width 3.4 mm; 4. NHMW 2023/0076/0015, height 4.7 mm, width 3.3 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

in Estepona. The shallower water form is thicker shelled, as with most other acteonids, and the sculpture seems a little coarser. As far as we are aware, this is the first fossil record for the species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: western and central Mediterranean (Cecalupo & Giusti, 1986; Smriglio & Mariottini, 1996; Ardovini & Cossignani, 1999; Cachia *et al*., 2001; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Negri & Corselli, 2016).

Genus *Crenilabium* Cossmann, 1889

Type species (by original designation) – *Actaeon aciculatus* Cossmann, 1889, Eocene, France.

1889 *Crenilabium* Cossmann, p. 302.
1890 *Lissactaeon* Monterosato, p. 188. Type species (by original designation): *Acteon exilis* Jeffreys, 1870, present-day, NE Atlantic.

***Crenilabium exile* (Jeffreys, 1870)**
Plate 23, figs 1-3

*1870 *Acteon exilis* Jeffreys, p. 85.
1870 *Actaeon? Etheridgii* Bell, p. 216.
1882 *Actaeon nitidus* Verrill, p. 540, pl. 58, fig. 21.
1889 *Actaeon exilis* Jeffreys – Dautzenberg, p. 20, pl. 1, fig. 1.
1895 *Acteon Browni* Jordan, p. 267, pl. 16, fig. 7.
1897 *Actaeon exilis* Jeffreys – Locard, p. 79, pl. 3, figs 1-3.
1927 *Acteon liostracoides* Dall, p. 20.
1927 *Acteon proprius* Dall, p. 20.
1972b *Crenilabium exilis* ([Forbes] Jeffreys, 1870) – Nordsieck, p. 8, pl. 1, fig. 5.
1973 *Lissactaeon exilis* (Jeffreys) – Di Geronimo & Panetta, p. 89, pl. 1, fig. 13.
1975 *Crenilabium exilis* (Jeffreys) – Bouchet, p. 319, pl. 2, fig. a.
1996 *Crenilabium exilis* (Jeffreys, 1870, ex Forbes ms.) – Smriglio & Mariottini, p. 187, figs 8a-9a.
1999 *Crenilabium exile* (Forbes in Jeffreys, 1870) – Ardovini & Cossignani, p. 80, 81, unnumbered fig. top right.
2001 *Crenilabium exilis* (Jeffreys, 1870, ex Forbes ms.) – Cachia *et al*., p. 120, pl. 19, fig. 13.
2005 *Crenilabium exilis* (Jeffreys, 1870, ex Forbes ms.) – Repetto *et al*., p. 254, fig 1114.
2011 *Crenilabium exilis* (Jeffreys, 1870) – Cossignani & Ardovini, p. 36, 368, unnumbered fig.
2011 *Crenilabium exilis* (Jeffreys, 1870) – Hernández *et al*., p. 270, figs 92 I-J.
2016 *Crenilabium exile* (Jeffreys, 1870) – Negri & Corselli, p. 79, figs 18g-i.

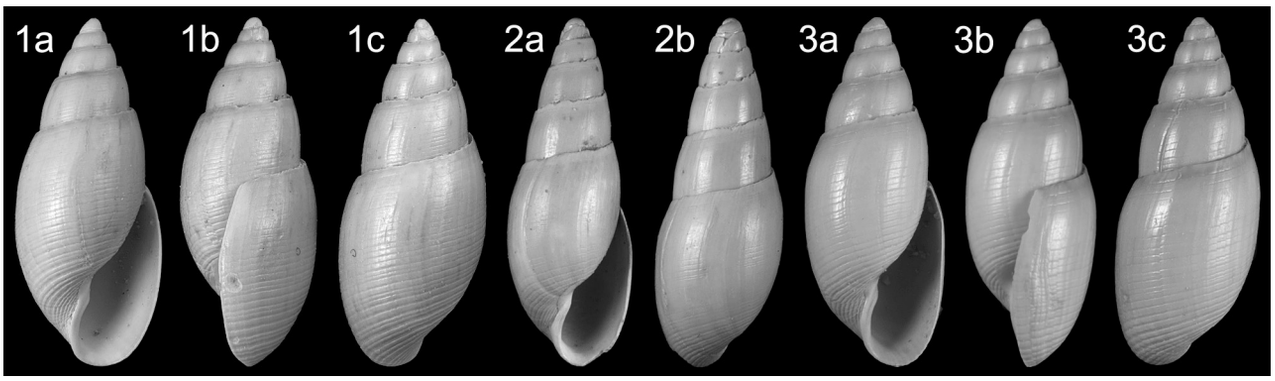

Plate 23. *Crenilabium exile* (Jeffreys, 1870); 1. RGM.1404312, height 5.5 mm, width 3.0 mm; 2. NHMW 2023/0076/0018, height 9.3 mm, width 3.4 mm; 3. NHMW 2023/0076/0019, height 7.5 mm, width 3.0 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2018 *Crenilabium exile* (Jeffreys, 1870) – Trigo *et al*., p. 368, unnumbered fig.

Material and dimensions – Maximum height 10.6 mm, width 3.9 mm. **VC**: RGM.1404312 (1), RGM.1404313 (10), NHMW 2023/0076/0018-0019 (2), NHMW 2023/0076/0020 (50+). **CO**: NHMW 2023/0076/0118 (6). **VS**: NHMW 2023/0076/0117 (11).

Description – Shell small, elongate ovate, with relatively tall, slightly scalate spire. Protoconch heterotrophic, strongly intorted so that spire completely submerged in first teleoconch whorl. Teleoconch of 4.5 weakly convex whorls with periphery at abapical suture, separated by deeply impressed, narrowly canaliculated suture with sharp, erect outer edge. Sculpture of irregular fine spiral grooves, 1-2 slightly stronger just below suture, weak to subobsolete below, strengthening again from mid-whorl towards abapical suture; weak opisthocline arcuate growth lines. Last whorl 62-71% of total height, regularly elongate-ovate, grooves deeper and wider over base. Aperture 41-49% of total height, elongate pyriform. Outer lip convex in profile, slightly expanded and strongly rounded abapically. Columella short, slightly thickened, bearing stout fold at upper end. Columellar and parietal callus not developed.

Discussion – *Crenilabium exile* (Jeffreys, 1870) is characterised by its slender bullet-shaped profile with a tall spire and fine spiral sculpture. Although the spire is high in most specimens, in some it is exceptionally so (Pl. 23, fig. 2) .

Crenilabium pedemontanum Sacco, 1897 (holotype figured by Ferrero Mortara *et al*., 1984, pl. 52, fig. 4) was described from the Lower Miocene Upper Burdigalian Colli Torinesi of Italy. Sacco (1897, p. 37) did not compare his specimen to *C. exile* [named *C. Etheridgei* (Bell.) var. *exilis* in Sacco, 1897] and commented on the poor state of preservation making detailed description and identification uncertain. We are therefore uncertain of the validity of this taxon.

Crenilabium terebelloides (Philippi, 1843) from the Lower-Middle Miocene North Sea Basin is very similar in teleoconch characters, and shows the same variability in its slenderness as seen in the Estepona specimens (see A.W. Janssen, 1984, pl. 19, figs 9, 10) but is separated by having a less intorted protoconch so that part of the protoconch spire is visible (see A.W. Janssen, 1984, pl. 19, figs 11a, b), whereas in *C. exile* the protoconch spire is entirely submerged in the first teleoconch whorl.

A very similar species recently described from depths between 53-200m off Brazil, *Crenilabium birmani* Simone, 2006, was said to differ from *C. exile* "*…in having proportionally longer aperture, spire with deeper suture and last whorl proportionally longer*" (Simone, 2006, p. 71). If we measure the three shell parameters highlighted by that author: aperture, spire, last whorl/total height (*C. exile* from Estepona *vs*. *C. birmani*: aperture 41-49% *vs*. 46-50%; last whorl 62-71% *vs*. 66-71%; spire 29-39% *vs*. 29-34%; measurements for *C. birmani* taken from Simone, 2006, figs 1, 5, 6), all morphometrics overlap. Both species have a similarly deep aperture and similar sculpture. It is possible that they represent a single species. However, in view of the disparate geographic ranges we hesitate to formally synonymise the two taxa.

Today *C. exile* is a bathyal species (Di Geronimo & Panetta, 1973; Negri & Corselli, 2016). In Estepona it is found only in the deeper water assemblages of Velerín carretera.

Distribution – Upper Pliocene: North Sea Basin, Red Crag, England (Bell, 1870); western Mediterranean, Estepona Basin (this paper). Present-day: northern western Atlantic, USA (Dall, 1927; Bouchet, 1975), northern eastern Atlantic, Faroe Channel (Jordan, 1895), Bay of Biscay (Trigo *et al*., 2018), Azores (Dautzenberg, 1889), Madeira (Segers *et al*., 2009), Canary Islands (Hernández *et al*., 2011), entire Mediterranean (Di Geronimo & Panetta, 1973; Smriglio & Mariottini, 1996; Ardovini & Cossignani, 1999; Cachia *et al*., 2001; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Negri & Corselli, 2016).

Genus *Rictaxis* Dall, 1871

Type species (by original designation) – *Tornatella punctocoelata* Carpenter, 1863, present-day, California, USA.

1871 *Rictaxis* Dall, p. 136.

For generic synonymy see Ceulemans *et al*. (2018, p. 112).

***Rictaxis tornatus* (Millet, 1854)**
Plate 24, figs 1-2

*1854 *Auricula Tornata* Millet, p. 154.
2018 *Rictaxis tornatus* (Millet, 1854) – Ceulemans *et al*., p. 112, pl. 7, fig. 2 (*cum syn*).
2020 *Rictaxis tornatus* (Millet, 1854) – Landau *et al*., p. 266, pl. 11, figs 1-3 (*cum syn*.).

Material and dimensions – Maximum height 13.3 mm, width 6.8 mm. **CO**: NHMW 2023/0076/0079 (1), NHMW 2023/0076/0080 (3). **EL**: NHMW 2023/0076/0081 (1), NHMW 2023/0076/0082 (3)

Description – Shell medium sized, relatively fragile, elongate-ovate, with elevated spire. Surface of protoconch and earliest teleoconch whorls abraded. Teleoconch of four weakly convex whorls separated by narrowly impressed suture. Penultimate whorl with 9-11 punctate grooves covering entire whorl. Punctuations well separated, ovate to subquadrate. Last whorl 80-83% of total height, slightly shouldered abapically, elongate-ovate below, bearing regularly spaced punctate grooves over entire surface.
Aperture elongate pyriform, 62-66% of total height; outer lip simple, convex in lateral profile, narrowly flared abapically. Columella thickened, bearing stout fold at upper end, twisted abapically. Columellar callus thickened, narrowly expanded filling umbilical chink, parietal callus not developed.

Discussion – This species was fully discussed by Ceulemans *et al*. (2018, p. 117). In Estepona it is uncommon and found only in the shallower water deposits of Velerín conglomerates and El Lobillo.

Distribution – Lower Miocene: Atlantic, Aquitaine Basin (Peyrot, 1932). Middle Miocene: (Langhian): Aquitaine Basin (Peyrot, 1932), Loire Basin, France (Glibert, 1952a). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964; Landau *et al*., 2020), Cacela Basin (Dollfus *et al*., 1903). Lower Pliocene: Atlantic, NW France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011); central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Ferrero *et al*., 1998; Sosso & Dell'Angelo, 2010).

Cohort Ringipleura Kano, Brenzinger, Nützel, Wilson & Schrödl, 2016
Superfamily Ringiculoidea Philippi, 1853
Family Ringiculidae Philippi, 1853
Genus *Ringicula* Deshayes *in* Lamarck, 1838

Type species (by subsequent designation) – *Marginella auriculata* Ménard de la Groye, 1811, present-day, Europe.

1838 *Ringicula* Deshayes *in* Lamarck, p. 342.

For generic synonymy see Ceulemans *et al*. (2018, p. 113).

***Ringicula auriculata* (Ménard de la Groye, 1811)**
Plate 25, figs 1-2

*1811 *Marginella auriculata* Ménard de la Groye, p. 332.
1830 *Voluta oryza* O.G. Costa, p. 72 (*non* Wood, 1818).
1832 *Marginella candida* Bivona e Bernardi, p. 19, pl. 3, fig. 4.
1878 *Ringicula auriculata* Ménard – Morlet, p. 130, pl. 5, fig. 14.
1881 *Ringicula auriculata* var. *incrassata* Seguenza, p. 32, pl. 1, fig. 9.

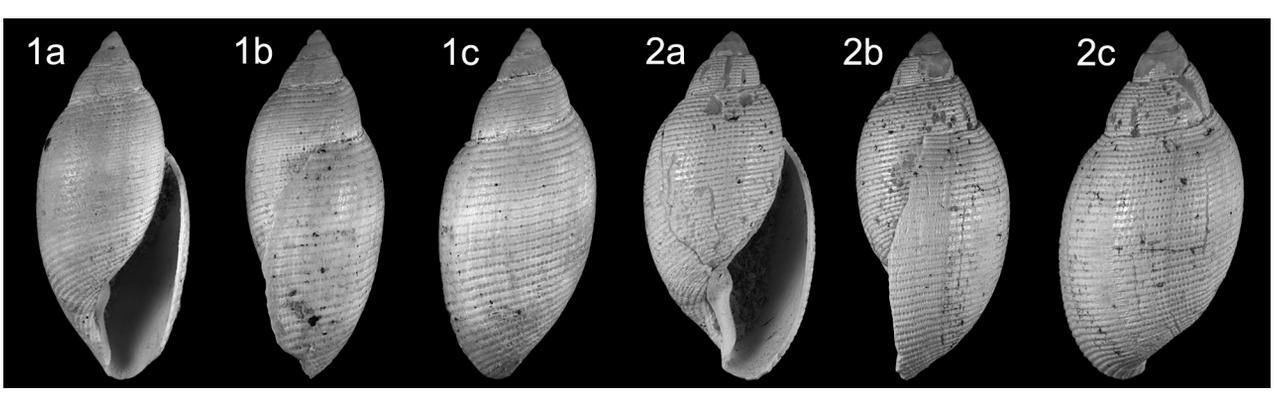

Plate 24. *Rictaxis tornatus* (Millet, 1854); 1. NHMW 2023/0076/0079, height 12.7 mm, width 5.7 mm. Velerín conglomerates, Velerín; 2. NHMW 2023/0076/0081, height 13.3 mm, width 6.8 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

1881 *Ringicula auriculata* var. *crispata* Seguenza, p. 32, pl. 2, fig. 1.
1910 *Ringicula* (*Ringiculella*) *auriculata* Mén. – Cerulli-Irelli, p. 42 [234], pl. 4 [35], figs 27-29.
1954 *Ringicula* (*Ringiculella*) *auriculata* Menard – Berger, p. 115, pl. 7, figs 1-2.
1982 *Ringicula* (*Ringiculina*) *auriculata* (Ménard de la Groye, 1811) – Ciccone & Savona, p. 20, pl. 1, fig. 4.
1982 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby 1824 [*sic*]) – Martinell, p. 229, figs 18, 19 [*non Ringicula ventricosa* (J. de C. Sowerby, 1823)].
1988 *Ringicula auriculata* (Ménard de la Groye, 1811) – Chirli, p. 24, pl. 11, fig. 20.
1975 *Ringicula* (*Ringiculella*) *ventricosa* (Sowerby) – Fekih, p. 142, fig. 6 [*non Ringicula ventricosa* (J. de C. Sowerby, 1823)].
1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *paulucciae* Morlet – Fekih, p. 143, fig. 2.
1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *gaudryana* Morlet – Fekih, p. 143, fig. 3.
1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *placentina* Seguenza – Fekih, p. 143, fig. 4.
1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *incrassata* Seguenza – Fekih, p. 143, fig. 5.
1979 *Ringicula auriculata* (Ménard 1811) – Nordsieck & García-Talavera, p. 169, pl. 43, fig. 5.
2004 *Ringicula auriculata* (Menard de la Groye, 1811) – Ardovini & Cossignani, p. 241, unnumbered figs.
2005 *Ringicula auriculata* (Menard de la Groye, 1811) – Repetto *et al*., p. 259, fig. 1142.
2005 *Ringicula auriculata* (Menard de la Groye, 1811) – Rolán, p. 202, pl. 62, figs 930-931.
2008 *Ringicula auriculata* (Menard, 1811) – Chirli & Richard (*partim*), p. 80, pl. 16, fig. 5 right hand side only.
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Cossignani & Ardovini, p. 37, 373, unnumbered figs.
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Gofas *et al*., p. 401, unnumbered fig. top.
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Landau *et al*., p. 42, pl. 23, fig. 8.
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Chirli & Linse, p. 215, pl. 85, fig. 4.
2011 *Ringicula ventricosa* (Sowerby 1825 [*sic*]) – Chirli & Linse, p. 216, pl. 85, fig. 5 [*non Ringicula ventricosa* (J. de C. Sowerby, 1823)].
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Hernández *et al*., p. 275, fig. 93 F-G.
2017 *Ringicula auriculata* (Ménard, 1811) – Büyükmeríç *et al*., p. 7, 9, figs 4 J1, J2, K.
2018 *Ringicula auriculata* (Ménard de la Groye, 1811) – Trigo *et al*., p. 370, unnumbered fig. bottom.
2018 *Ringicula* sp. – Brunetti & Cresti, p. 118, fig. 523.

non 1984 *Ringicula* (*Ringiculina*) *auriculata* (Ménard) – Ruggieri & Davoli, p. 75, pl. 6, fig. 3 [= *Ringicula buccinea* (Brocchi, 1814)].
non 1992 *Ringicula auriculata* (Ménard de la Groye, 1811) – Cavallo & Repetto, p. 166, fig. 478 [= *Ringicula buccinea* (Brocchi, 1814)].
non 2013 *Ringicula auriculata* (Ménard de la Groye, 1811) – Chirli, p. 26, pl. 8, figs 1-8 [= *Ringicula buccinea* (Brocchi, 1814)].

Material and dimensions – Maximum height 4.8 mm, width 3.2 mm. **CO**: RGM.1404288 (10), NHMW 2023/0076/0154 (10). **EL**: RGM.1404205-206 (2), RGM.1404207 (37), NHMW 2023/0076/0155 (20).

Description – Shell very small, globose, with mid-height conical spire. Protoconch paucispiral, of about 1.5 whorls with slightly elevated nucleus (dp = 300 μm, hp = 230 μm). Junction with teleoconch marked by beginning of spiral sculpture. Teleoconch of 3.5 convex whorls separated by impressed, linear suture. Spire whorls bearing 5-6 equal flattened cords separated by narrow, shallow grooves. Last whorl 76% of total height, strongly globose, weakly constricted at base, bearing about 12 subequal flattened cords. Aperture 53-54% of total height, elon-

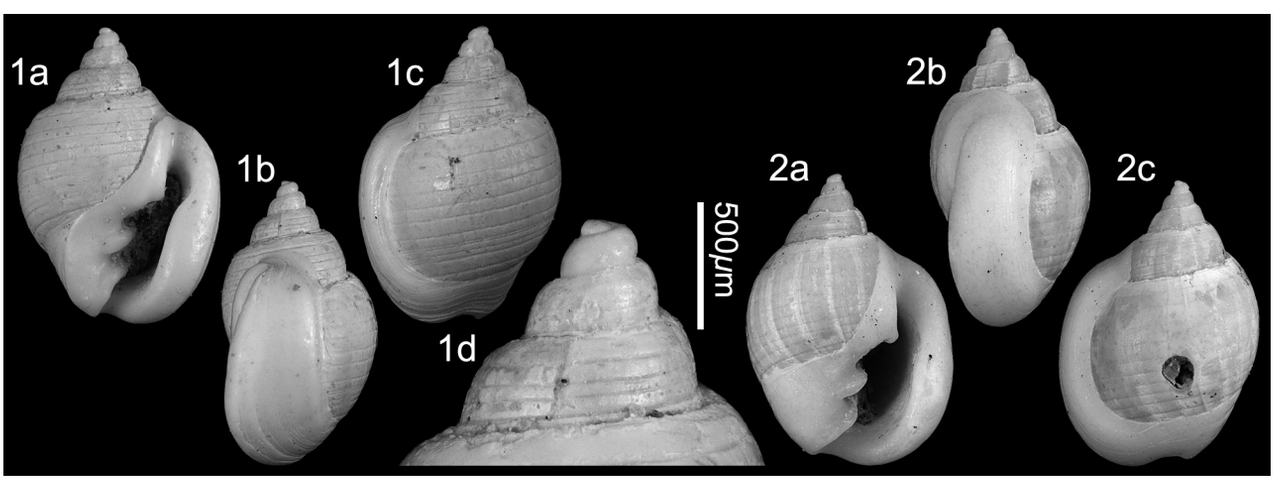

Plate 25. *Ringicula auriculata* (Ménard de la Groye, 1811); 1. RGM.1404205, height 3.8 mm, width 2.6 mm, 1d, detail of protoconch; 2. RGM.1404206, height 4.0 mm, width 2.8 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

gate, narrowed by apertural armature; outer lip strongly thickened by extremely broad labial varix; anal sinus well developed, U-shaped, forming depressed notch on adapical end of outer lip, below which is broad palatal swelling; siphonal canal open, moderately narrow, shallowly notched at tip. Columella with two strong abapical folds abapically and strong triangular parietal denticle. Columellar and parietal callus thickened, sharply delimited, expanded over base abapically, forming broad callus rim in parietal area.

Discussion – The distinctive characters of this species are its relatively small size compared to its Estepona congeners, the presence of three inner lip denticles (two columellar, one parietal), the shape of the outer lip that is relatively straight and angled abapically, the last whorl is about two-thirds total height, the presence of a palatal tubercle or swelling within the outer lip, and the sculpture of regular flattened cords separated by narrow grooves that covers the entire surface. The only species it can be confused with in the Estepona assemblages is *Ringicula ventricosa* (J. de C. Sowerby, 1823) that also has spiral sculpture over the entire surface, but *R. ventricosa* is larger shelled, the last whorl is more strongly inflated, and the spirals are slightly more widely spaced in the upper third, becoming slightly more crowded towards the base, whereas in *R. auriculata* (Ménard de la Groye, 1811) the spirals are regularly spaced along the entire width of the whorl.
Today *R. auriculata* is found in muddy bottoms starting from 10-200 m depth (Gofas *et al.,* 2011; Trigo *et al*., 2018). In Estepona it is found only in the shallower water assemblages of Velerín conglomerates and El Lobillo.

Distribution – Lower Pliocene: Atlantic, Mondego Basin, Portugal (NHMW coll.), Guadalquivir Basin, S. Spain (Landau *et al*., 2011); western Mediterranean, northeastern Spain, (Martinell, 1982), central Mediterranean, Italy (Brunetti & Cresti, 2018), Tunisia (Fekih, 1975), eastern Mediterranean, Turkey (Büyükmeríç *et al*., 2017). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Chirli, 1988). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic, Bay of Biscay (Trigo *et al*., 2018), Madeira (Nordsieck & García-Talavera, 1979), Canary Islands (Hernández *et al*., 2011), Guinea Bissau (Ardovini & Cossignani, 2004), to Cape Verde Archipelago (Rolán, 2005), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

***Ringicula buccinea* (Brocchi, 1814)**
Plate 26, figs 1-4

*1814 *Voluta buccinea* Brocchi, p. 319, pl. 4, fig. 9.
1814 *Voluta pisum* Brocchi, p. 642, pl. 15, fig. 10 (juvenile).
1830 *Auricula marginata* Deshayes, p. 95.
1848 *Ringicula buccinea J. Sow*.[*sic*] – S.V. Wood, p. 22, pl. 4, fig. 2.
1864 *Ringicula elegans* Pecchioli, p. 508, pl. 5, figs 32-34.
1868 *Ringicula intermedia* Foresti, p. 588, pl. 2, figs 7-9.
1878 *Ringicula buccinea* Brocc. – Nyst (*partim*), pl. 7, fig. 20c, d [not a, b = *Ringicula ventricosa* (J. Sowerby, 1824)].
1878 *Ringicula buccinea* Brocchi – Morlet, p. 132, pl. 8, fig. 6.
1878 *Ringicula elegans* Pecchioli – Morlet, p. 281, pl. 7, fig. 8.
1878 *Ringicula intermedia* Foresti – Morlet, p. 284, pl. 8, fig. 3.
1878 *Ringicula quadriplicata* Morlet (*partim*, Pliocene forms), p. 286, pl. 7, fig. 1.
1878 *Ringicula marginata* Deshayes – Morlet, p. 286, pl. 8, fig. 7.
1881 *Ringicula buccinea* Brocchi, 1814 – G. Seguenza, p. 20, pl. 1, fig. 3.
1882 *Ringicula buccinea* (Brocchi) – Nyst (*partim*), p. 131.
1891 *Ringicula obliqua* Monterosato, p. 125 (*nomen nudum*).
1892 *Ringicula* (*Ringiculella*) *auriculata* var. *buccinea* (Br.) – Sacco, p. 20, pl. 1, fig. 7.
1893 *Ringicula ovalis* Bell, p. 631 (*nomen nudum*).
1898 *Ringicula ovalis* Bell *in* Etheridge & Bell, p. 158, pl. 3, fig. 11.
1910 *Ringicula* (*Ringiculella*) *auriculata* var. *buccinea* Br. – Cerulli-Irelli, p. 235, pl. 35, figs 30-32.
1923 *Ringicula buccinea* (Brocchi) – Harmer, p. 811, pl. 63, fig. 23.
1923 *Ringicula Searlesi* Harmer, p. 812, pl. 63, fig. 22.
1923 *Ringicula ovalis* Bell, 1898 – Harmer, 815, pl. 63, fig. 25.
1946 *Ringicula* (*Ringiculella*) *ovata* Bell, 1898 – Beets, p. 113, pl. 6, figs 38-48.
1955 *Ringicula* (*Ringiculina*) *auriculata* var. *buccinea* Brocchi – Rossi Ronchetti, p. 333, fig. 179.
1959 *Ringicula buccinea* Brocchi – Zbyszewski, p. 102, pl. 11, figs 49, 53.
1964 *Ringicula* (*Ringiculina*) *ovata* Etheridge & Bell, 1898 – Van Regteren Altena *et al*., p. 2, pl. 19, fig. 182.
1964 *Ringicula* (*Ringiculina*) *buccinea* Brocchi, 1814 – Brébion (*partim*), p. 649, pl. 15, figs 32-33 only.
?1968 *Ringicula buccinea* (Brocchi, 1814) – Rasmussen, p. 232, pl. 25, figs 3-5.
1973 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi) 1814 – Caprotti & Vescovi, p. 186, pl. 3, fig. 21.
1974 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – Malatesta, p. 445, pl. 32, fig. 21.
1975 *Ringicula buccinea* (Brocchi) – Fekih, p. 142, pl. 52, fig. 7.
1976 *Ringicula buccinea* (Brocchi) – Caprotti, p. 13, pl. 17, fig. 21.
1978 *Voluta buccinea* Brocchi, 1814 – Pinna & Spezia, p. 167, pl. 62, fig. 2.

1982 *Ringicula buccinea* (Brocchi) – Ciccone & Savona, pl. 1, fig. 2.
1982 *Ringicula* (*Ringiculina*) *buccinea buccinea* (Brocchi, 1814) – Martinell, p. 227, pl. 1, figs 16-17.
1984 *Ringicula* (*Ringiculina*) *auriculata* (Ménard) – Ruggieri & Davoli, p. 75, pl. 6, fig. 3 [*non Ringicula auriculata* (Ménard de la Groye, 1811)].
1985 *Ringicula* (*Ringiculina*) *buccinea buccinea* (Brocchi, 1814) – Martinell & Domènech, p. 60, pl. 1, fig. 7.
1988 *Ringicula buccinea* (Brocchi, 1814) – Chirli, p. 24, pl. 11, fig. 21.
1989 *Ringicula* (*Ringiculina*) *buccinea buccinea* (Brocchi) – Lauriat-Rage *et al*., p. 150, pl. 8, fig. 22.
1992 *Ringicula auriculata* (Ménard de la Groye, 1811) – Cavallo & Repetto, p. 166, fig. 478 [*non R. auriculata* (Ménard de la Groye, 1811)].
1992 *Ringicula obliqua* Monterosato (*nomen nudum*) Gaglini, p. 166, 151, fig. 150 (*nomen nudum*).
1997 *Ringicula buccinea* (Brocchi, 1814) – Marquet, p. 113, pl. 11, fig. 3.
1997 *Ringicula buccinea* (Brocchi) – Ruiz Muñoz *et al*., p. 188, pl. 41, fig. 9.
1998 *Ringicula buccinea* (Brocchi, 1814) – Marquet, p. 215, fig. 187.
2001 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – Silva, p. 581, p. 27, figs 15-16.
2008 *Ringicula auriculata* (Ménard de la Groye, 1811) – Chirli & Richard (*partim*), p. 80, pl. 16, fig. 3 (only).
2010 *Ringicula buccinea* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 54, p. 68 unnumbered fig botton row left.
2011 *Ringicula buccinea* (Brocchi, 1814) – Landau *et al*., p. 42, pl. 23, fig. 9.
2013 *Ringicula auriculata* (Ménard de la Groye, 1811) – Chirli, p. 26, pl. 8, figs 1-8 [*non R. auriculata* (Ménard de la Groye, 1811)].
2014 *Ringicula* cf. *buccinea* (Brocchi, 1814) – Brunetti, p. 75, unnumbered fig. top.
2018 *Ringicula buccinea* (Brocchi, 1814) – Ceulemans *et al*., p. 118, fig. 3 (*cum syn*.).
2018 *Ringicula buccinea* (Brocchi, 1814) – Brunetti & Cresti, p. 118, fig. 521.
2022 *Ringicula* sp. – Brunetti, p. 80, fig. 186.

non 1853 *Ringicula buccinea* Desh. – Eichwald, p. 258 (*non* Brocchi, 1814) [= *Ringicula exilis* (Eichwald, 1829)].
non 1854 *Ringicula Buccinea* Desh. [*sic*] – Millet, p. 155 [= *Ringicula munieri* Morlet, 1880].
non 1866 *Ringicula buccinea* Desh. in Hörn. – Pereira da Costa (*partim*), p. 58, pl. 12, figs 1a, b (= *Ringicula cacellensis* Morlet, 1878) [not 2a, b = *Ringicula ventricosa* (J. Sowerby, 1824)].
non 1932 *Ringicula* (*Ringiculella*) *buccinea* Brocchi – Peyrot, p. 308, pl. 11, figs 9, 14, 15.
non 1952b *Ringicula* (*Ringiculina*) *buccinea* Brocchi, 1814 – Glibert, p. 141, pl. 10, fig. 13.
non 1954 *Ringicula* (*Ringiculella*) *auriculata buccinea* (Brocchi) – Berger, p. 126, pl. 10, fig. 53, pl. 11, figs 54-60, pl. 12, figs 61-63 [= *Ringicula exilis* (Eichwald, 1829)].
non 1954 *Ringicula* (*Ringiculella*) *auriculata buccinea* Brocchi, 1814 – Strausz, p. 38, pl. 5, fig. 117 [= *Ringicula exilis* (Eichwald, 1829)].
non 1956 *Ringicula* (*Ringiculella*) *auriculata buccinea* Br. – Csepreghy-Meznerics, p. 436, pl. 12, figs 13-14 [= *Ringicula exilis* (Eichwald, 1829)].
non 1958 *Ringicula buccinea* (Brocchi) – Sorgenfrei, p. 334, pl. 73, fig. 249.
non 1958 *Ringicula* (*Ringiculella*) *buccinea* (Brocchi) – Erünal-Erentöz, p. 127, pl. 21, fig. 1 [= *Ringicula exilis* (Eichwald, 1829)].
non 1962 *Ringicula* (*Ringiculina*) *auriculata buccinea* Brocchi – Strausz, p. 101, pl. 41, figs 3-6, pl. 72, figs 11-14 [= *Ringicula exilis* (Eichwald, 1829)].
non 1964 *Ringicula* (*Ringiculina*) *buccinea* Brocchi, 1814 – Brébion, p. 649, pl. 15, figs 30-33 [= *Ringicula munieri* Morlet, 1880].
non 1964 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – Anderson, p. 332, pl. 51, fig. 299.
non 1966 *Ringicula* (*Ringiculina*) *auriculata buccinea* Brocchi, 1814 – Strausz, p. 469, pl. 41, figs 3-6, pl. 72, figs 11-14 [= *Ringicula exilis* (Eichwald, 1829)].
non 1972a *Ringicula buccinea* (Brocchi, 1814) – Nordsieck, p. 122, pl. 31, fig. 210.
non 1984 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – A.W. Janssen, p. 369, pl. 13, figs 14-15.
non 2007 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – Wienrich, p. 772, pl. 133, fig. 5, pl. 170, figs 1-4.
non 2008 *Ringicula auriculata* var. *buccinea* (Brocchi, 1814) – Chirli & Richard, p. 80, pl. 16, fig. 5 [3 figures left = *R. auriculata* (Ménard de la Groye, 1811); 3 figures right = *R. ventricosa* (J. Sowerby, 1824)].
non 2010 *Ringicula* (*Ringiculina*) *buccinea* (Brocchi, 1814) – Moths *et al*., p. 89, pl. 25, fig. 3, pl. 46, fig. 8.

Material and dimensions – Maximum height 9.6 mm, width 6.4 mm. **VC**: RGM.1404209-210 (2), RGM.1404211 (45), NHMW 2023/0076/0101 (50+). **CO**: RGM.1404212-213 (2), RGM.1404214 (50+), NHMW 2023/0076/0102 (50+). **EL**: RGM.1404215 (50+), NHMW 2023/0076/0103 (50+).

Description – Shell small, very globose, with short conical spire. Protoconch paucispiral, of about 1.5 whorls with slightly elevated nucleus (dp = 465 μm, hp = 305 μm). Junction with teleoconch marked by beginning of spiral sculpture. Teleoconch of four convex whorls separated by narrowly impressed, linear suture. Spiral sculpture very weak, visible only under magnification. Last whorl 82% of total height, strongly globose, not constricted at base, smooth in most specimens, a few very weak spirals visible in some. Aperture 59% of total height, narrow in upper third, widening abapically; outer lip thickened by moderately wide labial varix; anal sinus narrow, deep, U-shaped, not distorting adapical end of outer lip; siphonal canal very short, open, broad, shallowly notched at tip. Columella with two elevated robust folds abapically, pa-

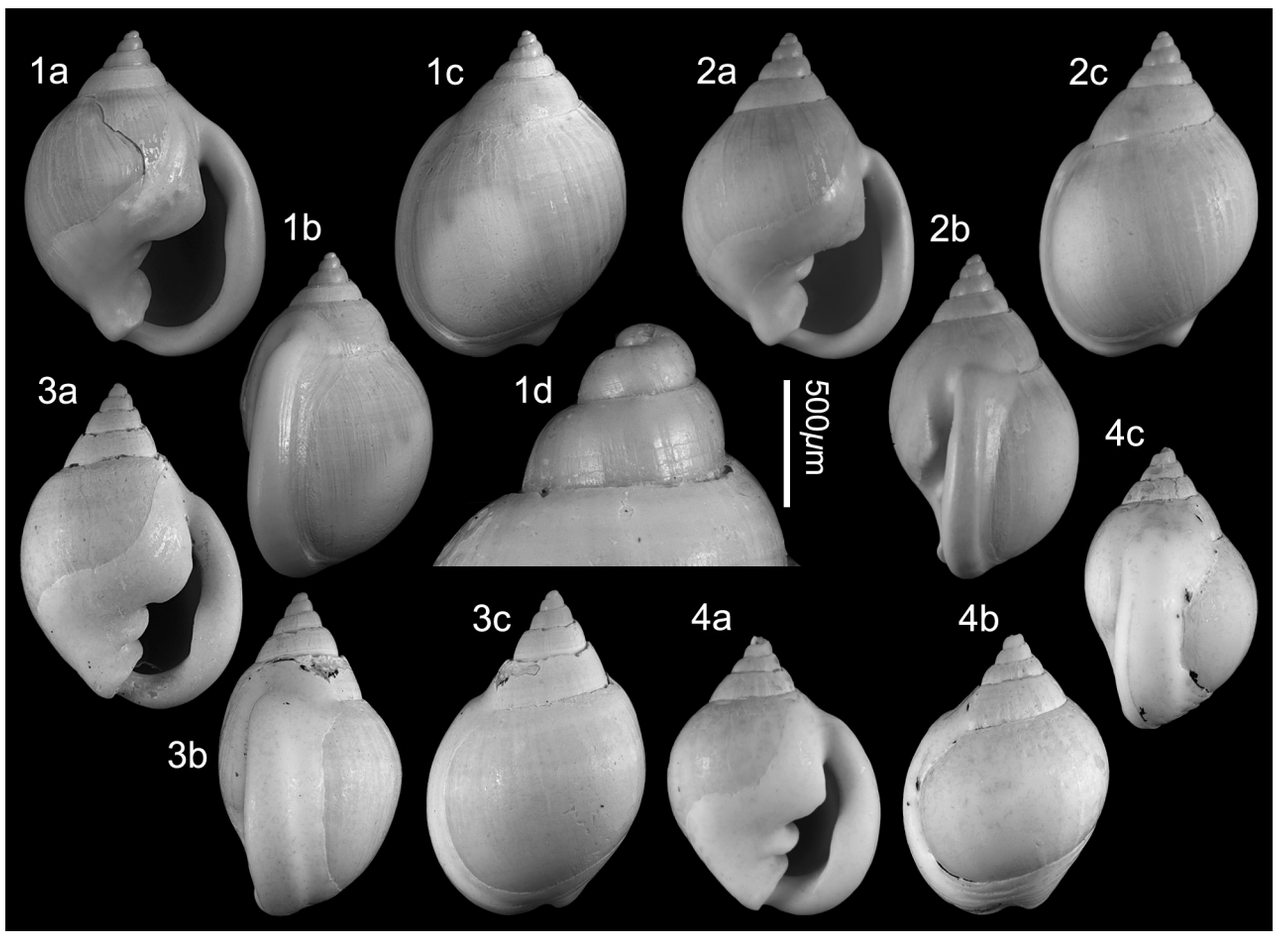

Plate 26. *Ringicula buccinea* (Brocchi, 1814); 1. RGM.1404209, height 8.9 mm, width 6.6 mm, 1d, detail of protoconch; 2. RGM. 1404210, height 8.5 mm, width 6.0 mm. Velerín carretera. 3. RGM.1404212, height 8.6 mm, width 5.9 mm; 4. RGM.1404213, height 5.9 mm, width 4.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

rietal denticle fused with robust V-shaped parietal callus overhanging and narrowing aperture adapically. Columellar and parietal callus thickened, sharply delimited, widely expanded and thickened over medial half of venter.

Discussion – *Ringicula buccinea* (Brocchi, 1814) in its typical form is characterised by its relatively large, solid to very solid shell for the genus, short spire, strongly globose last whorl, spiral sculpture usually absent or at most very weak, outer lip strongly thickened narrowing aperture, and two strong, elevated columellar folds plus one parietal tooth placed on the apex of a variably developed thickened parietal pad. A fourth fold may be present in some specimens. However, it is strongly variable in size, height of spire, globosity, the strength of the apertural armature, and some specimens may bear some very irregular weak spiral grooves.

In the Estepona assemblages, specimens from the deeper water deposits of Velerín carretera (Pl. 26, figs 1-2) are, on average, larger, thinner shelled, with less strongly thickened apertural armature, than those of the shallower water assemblages (Pl. 26, figs 3-4). A similar trend is seen in *R. ventricosa* (J. Sowerby, 1824) (see below) and many other gastropod species, in which the deeper water form is thinner shelled. We therefore interpret these to be ecophenotypic differences.

Middle Miocene specimens from the Paratethys, described as *Ringicula buccinea* in the literature, represent *Ringicula exilis* (Eichwald, 1829). Note that Guzhov (2022) pointed out that *Voluta exilis* Eichwald, 1829 is preoccupied by *Voluta exilis* Gmelin, 1791 and supposed that the Miocene species was a synonym of *Ringicula ventricosa* (J. Sowerby, 1824), which it is not. The Paratethyan species requires, therefore, a new name for which we propose *Ringicula guzhovi* nov. nom. in honour of Aleksandr Guzhov of the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, in recognition of his contribution to the Ringiculidae.

For full discussion see Ceulemans *et al*. (2018, p. 119). Although Gaglini (1992, p. 166, 151, fig. 150) described and illustrated *Ringicula obliqua* (and *R. contracta*; see below) these *nomina nuda* of Monterosato were not made available by Gaglini since they were explicitly stated as *nomina nuda* in his 1992 paper.

Distribution – Miocene records such as that of Rassmussen (1968) need to be reviewed.

Lower Pliocene: North Sea Basin, Coralline Crag, Eng-

land (S.V. Wood, 1848; Harmer, 1923), Belgium (Marquet, 1997, 1998); Atlantic, northwestern France (Brébion, 1964; Lauriat-Rage *et al*., 1989; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, northeastern Spain, (Martinell, 1982; Martinell & Domènech, 1985); central Mediterranean, Italy (Sacco, 1892b; Caprotti, 1974; Chirli, 2013; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: North Sea Basin, Red Crag, England (S.V. Wood, 1848; Harmer, 1923); Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1892b; Malatesta, 1974; Caprotti & Vescovi, 1973; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Brunetti, 2014). Pliocene (indeterminate): North Sea Basin, The Netherlands (Beets, 1946; Van Regteren Altena *et al*., 1964). Upper Pliocene-Pleistocene: Atlantic, northwestern France (Brébion, 1964). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1923); central Mediterranean, Italy (Cerulli-Irelli, 1910).

***Ringicula pirulina* Locard, 1897**
Plate 27, figs 1-3

*1897	*Ringicula pirulina* Locard, p. 87, pl. 14, figs 1-6.
2000	*Ringicula pirulina* Locard, 1897 – Mariottini *et al*., p. 77, figs 14-16.

Material and dimensions – Maximum height 6.2 mm, width 4.1 mm. **VC**: RGM.1404319 (1), NHMW 2023/0706/0111-0113 (12).

Description – Shell medium-sized for genus, globose, with moderately tall and narrow coeloconoid conical spire. Protoconch paucispiral, of about 1.5 whorls with slightly elevated nucleus (dp = 350 μm, hp = 275 μm). Junction with teleoconch marked by change in lustre. Teleoconch of 3.5 convex whorls separated by deeply impressed, linear suture. Spire whorls smooth, except for single spiral groove appearing just above suture on penultimate whorl, and axial growth lines. Last whorl 73% of total height, strongly globose, not constricted at base, bearing 5-9 grooves over adapical half of whorl. Aperture 52% of total height, pyriform; outer lip thickened by moderately broad labial varix; anal sinus V-shaped, slightly distorting adapical end of outer lip; siphonal canal very short, open, broad, shallowly notched at tip. Columella with two elevated folds abapically, lower much thicker than the upper, and small parietal denticle placed on moderately well delimited parietal pad. Columellar and parietal callus thickened, sharply delimited, expanded and thickened over base abapically, forming moderate width callus rim in parietal area.

Discussion – This species is characterised by having a moderately high spire with a coeloconoid profile, a globose last whorl, one or two spiral grooves just above the suture on later spire whorls, and 5-9 spiral grooves on the last whorl placed below the level of the insertion of the outer lip. Apertural armature is only moderately thickened, the two columellar folds are parallel to each other, the lower much thicker than the upper, and a small parietal denticle is placed on a moderately well-developed parietal pad.
Mariottini *et al*. (2000) revised the *Ringicula leptocheila* complex in the Mediterranean. The Estepona specimens are most like *R. pirulina* Locard, 1897, originally described from waters off West Morocco, in the character of the spire and in having spiral sculpture restricted to the lower half of the last whorl. They vary slightly from the description given by Mariottini *et al*. (2000) in having a small parietal tooth and in not having the two columellar folds of equal size, but both of these features are rather variable in the Estepona material. We have only been able to find one photograph of extant *R. pirulina*, which, as far as we are aware, is known only from the type material (Mariottini *et al*., 2000, p. 79), so are un-

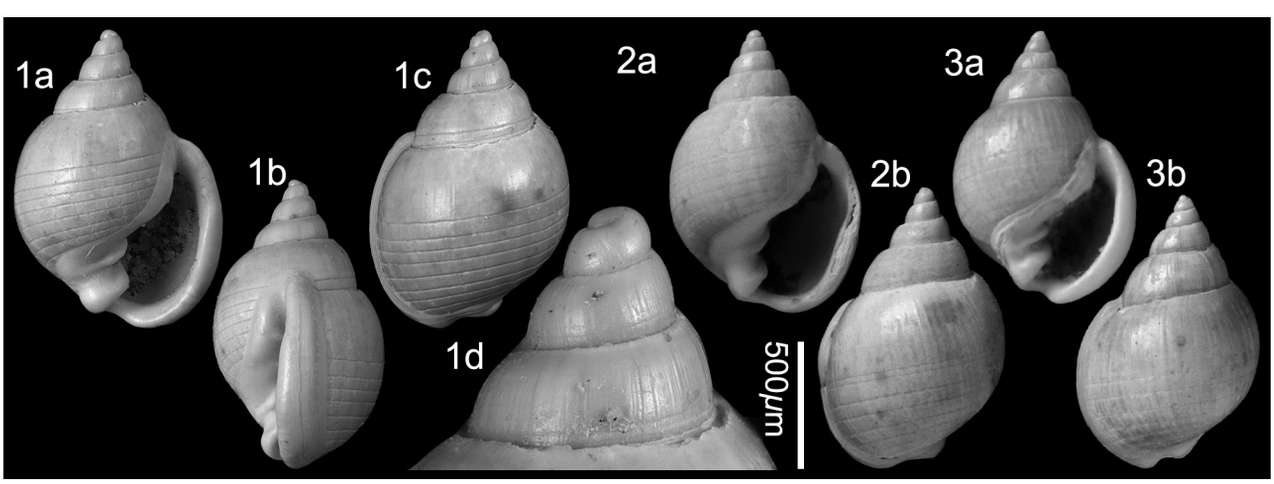

Plate 27. *Ringicula pirulina* Locard, 1897; 1. RGM.1404319, height 4.4 mm, width 3.1 mm, 1d, detail of protoconch; 2. NHMW 2023/0706/0111, height 5.6 mm, width 3.5 mm; 3. NHMW 2023/0706/0112, height 5.9 mm, width 3.8 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

sure of its modern intraspecific variability. In view of the very striking and unique character amongst European Neogene *Ringicula* species of having spiral grooves restricted to the lower half of the last whorl, we consider these fossil specimens conspecific. For comparison with other members of the *R. leptocheila* complex, see Mariottini *et al*. (2000, p. 71, table 1).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: Atlantic, West Morocco (Locard, 1897; Mariottini *et al*., 2000).

***Ringicula ventricosa* (J. de C. Sowerby, 1824)**
Plate 28, figs 1-2

*1824 *Auricula ventricosa* J. de C. Sowerby, p. 99, pl. 465, figs 1, 2.
1848 *Ringicula ventricosa* J. Sow. – S.V. Wood, p. 22, pl. 4, fig. 1.
1866 *Ringicula buccinea* Desh. in Hörn. – Pereira da Costa (*partim*), p. 58, pl. 12, figs 2a, b [*non Ringicula buccinea* (Brocchi, 1814)] (not 1a, b = *Ringicula cacellensis* Morlet, 1878).
1878 *Ringicula Brocchii* Seguenza ms. Morlet (*partim*), p. 277, pl. 8, fig. 2.
1878 *Ringicula Gaudryana* Morlet, p. 283, pl. 7, fig. 12.
1878 *Ringicula buccinea* Brocc. – Nyst (*partim*), pl. 7, fig. 20a, b [not c, d = *Ringicula buccinea* (Brocchi, 1814)].
1880 *Ringicula Gaudryana* Morlet – Fontannes, p. 130, pl. 7, fig. 23.
1881 *Ringicula placentina* Seguenza, p. 32, pl. 2, fig. 2.
1881 *Ringicula Brocchii* Seguenza, 1875 – G. Seguenza, p. 34.
1881 *Ringicula Guadryana* L. Morlet, 1878 – G. Seguenza, p. 33, pl. 2, fig. 8.
1882 *Ringicula buccinea* (Brocchi) – Nyst (*partim*), p. 131.
1891 *Ringicula contracta* Monterosato, p. 125 (*nomen nudum*).
?1904 *Ringiculella auriculata* var. *ventricosa* (Sow.) – Sacco, p. 110, pl. 24, figs 25, 26.
1910 *Ringicula* (*Ringiculella*) *ventricosa* Sow. – Cerulli-Irelli, p. 44 [236], pl. 4 [35], figs 33, 34.
1910 *Ringicula* (*Ringiculella*) *ventricosa* var. *Paulucciae* Morlet – Cerulli-Irelli, p. 45 [237], pl. 4 [35], figs 35, 36 [*non Ringicula paulucciae* Morlet, 1878 = *Ringicula minor* (Grateloup, 1838)].
1910 *Ringicula* (*Ringiculella*) *ventricosa* var. *globulina* Cerulli-Irelli, p. 45 [237], pl. 4 [35], fig. 37.
1910 *Ringicula* (*Ringiculella*) *ventricosa* var. *Gaudryana* Morl. – Cerulli-Irelli, p. 45 [237], pl. 4 [35], figs 35, 36 [*non Ringicula paulucciae* Morlet, 1878 = *Ringicula minor* (Grateloup, 1838)].
1910 *Ringicula* (*Ringiculella*) *ventricosa* var. *placentina* Seg. – Cerulli-Irelli, p. 45 [237], pl. 4 [35], figs 39.
1923 *Ringicula ventricosa* (J. Sowerby) – Harmer, p. 813, pl. 63, fig. 24.
1952b *Ringicula* (*Ringiculina*) *ventricosa* Sowerby, 1824 – Glibert, p. 142, pl. 10, fig. 14.
1958 *Ringicula ventricosa* (Sowerby) – Sorgenfrei, p. 333, pl. 72, fig. 248.
1960 *Ringicula* (*Ringicula*) *ventricosa* (Sowerby, 1825 [*sic*]) – Malatesta, p. 195, pl. 9, fig. 15.
1960 *Ringicula ventricosa* (Sowerby) – Pelosio, p. 152, pl. 2, fig. 12.
1963 *Ringicula* (*Ringiculina*) *ventricosa* (Sow.) – Venzo & Pelosio, p. 134, pl. 41, fig. 39.
1964 *Ringicula* (*Ringiculina*) *striata* Philippi, 1843 – Brébion (*partim*), p. 647 (*non* Philippi, 1843).
1964 *Ringicula* (*Ringiculina*) *auriculata ventricosa* (J. de C. Sow.) – Van Regteren Altena *et al*., p. 3, pl. 19, fig. 183.
1972a *Ringicula ventricosa* (Sowerby, 1824) – Nordsieck, p. 122, pl. 31, fig. 211.
1973 *Ringicula* (*Ringiculella*) *ventricosa* (Sowerby) – Caprotti & Vescovi, p. 186, pl. 3, fig. 16.
1974 *Ringicula* (*Ringiculina*) *auriculata* (Ménard, 1811) – Malatesta, p. 444, pl. 32, fig. 20 [*non R. auriculata* (Ménard de la Groye, 1811)].
1975 *Ringicula* (*Ringiculella*) *ventricosa* (Sowerby) – Fekih, p. 142, pl. 52, fig. 6.
1976 *Ringicula ventricosa* – Caprotti, p. 13, pl. 17, fig. 6.
1982 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby, 1824) – Martinell, p. 229, pl. 1, figs 18-19.
1984 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby, 1824) – A.W. Janssen, p. 370, pl. 13, figs 16-17.
1992 *Ringicula contracta* Monterosato (*nomen nudum*) Gaglini, p. 167, 151, fig. 151 (*nomen nudum*).
1992 *Ringicula ventricosa* (Sowerby, 1825 [*sic*]) – Cavallo & Repetto, p. 166, fig. 479.
2001 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby, 1824) – Silva, p. 582, p. 27, figs 13-14.
2007 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby, 1824) – Wienrich, p. 773, pl. 133, fig. 6, pl. 170, figs 5-6.
2008 *Ringicula auriculata* var. *buccinea* (Brocchi, 1814) – Chirli & Richard (*partim*), p. 80, pl. 16, fig. 5 [3 figures right only; 3 figures left = *R. auriculata* (Ménard de la Groye, 1811)] [*non Ringicula buccinea* (Brocchi, 1814)].
2010 *Ringicula* (*Ringiculina*) *ventricosa* (J. de C. Sowerby, 1824) – Moths *et al*., p. 90, pl. 25, fig. 5.
2010 *Ringicula ventricosa* (Sowerby, 1825 [*sic*]) – Sosso & Dell'Angelo, p. 54, p. 68 unnumbered fig. botton row middle.
2011 *Ringicula auriculata* (Ménard de la Groye, 1811) – Landau *et al*., p. 42, pl. 23, fig. 9 [*non Ringicula auriculata* (Ménard de la Groye, 1811)].
2013 *Ringicula ventricosa* (Sowerby, 1823 [*sic*]) – Chirli, p. 31, pl. 8, figs 9-16.
2014 *Ringicula* sp. – Brunetti, p. 75, unnumbered fig. bottom.
2018 *Ringicula ventricosa* (J. Sowerby, 1824) – Ceulemans *et al*., p. 119, pl. 7, figs 4-6.
2018 *Ringicula* cf. *gaudryana* Morlet, 1878 – Brunetti & Cresti, p. 118, fig. 522.

non 1975 *Ringicula* (*Ringiculella*) *ventricosa* (Sowerby) – Fekih, p. 142, fig. 6 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *paulucciae* Morlet – Fekih, p. 143, fig. 2 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *gaudryana* Morlet – Fekih, p. 143, fig. 3 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *placentina* Seguenza – Fekih, p. 143, fig. 4 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 1975 *Ringicula* (*Ringiculella*) *ventricosa* var. *incrassata* Seguenza – Fekih, p. 143, fig. 5 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 1982 *Ringicula* (*Ringiculina*) *ventricosa* (Sowerby 1824 [*sic*]) – Martinell, p. 229, figs 18, 19 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 2011 *Ringicula ventricosa* (Sowerby 1825 [*sic*]) – Chirli & Linse, p. 216, pl. 85, fig. 5 [= *Ringicula auriculata* (Ménard de la Groye, 1811)].

non 2022 *Ringicula ventricosa* (Sowerby 1824 [*sic*]) s.l. – Guzhov, p. 1135, pl. 8, figs 9-10, pl. 9, figs 1-5 [= *Ringicula exilis* (Eichwald, 1829)].

Material and dimensions – Maximum height 7.2 mm, width 4.9 mm. **VC**: RGM.1404201 (1), RGM.1404202 (1), NHMW 2023/0076/0104 (11). **CO**: RGM.1404287 (6), NHMW 2023/0076/0105 (31). **EL**: RGM.1404203 (1), RGM.1404204 (12), NHMW 2023/0076/0106 (50+).

Description – Shell small, globose, with mid-height conical spire. Protoconch paucispiral, of about 1.5 whorls with slightly elevated nucleus (dp = 335 μm, hp = 275 μm). Junction with teleoconch marked by beginning of spiral sculpture. Teleoconch of 3.5 convex whorls separated by impressed, linear suture. First teleoconch whorl bearing about 10 equal flattened cords separated by narrow, shallow grooves; second whorl 7 cords. Last whorl 74-77% of total height, strongly globose, not constricted at base, bearing about 16-18 flattened cords narrowing slightly abapically. Aperture 54-56% of total height, pyriform; outer lip thickened by moderately narrow labial varix; anal sinus weakly developed, U-shaped, not distorting adapical end of outer lip; siphonal canal very short, open, broad, shallowly notched at tip. Columella with two elevated narrow folds abapically and weak parietal denticle. Columellar and parietal callus thickened, sharply delimited, expanded and thickened over base abapically, forming narrow callus rim in parietal area.

Discussion – We follow Glibert (1952a, b) in considering *Ringicula ventricosa* (J. de C. Sowerby, 1824) distinct from *R. striata* Philippi, 1843. *Ringicula ventricosa* in the Atlantic and Mediterranean has an Upper Miocene to Pleistocene distribution, although it seems to have occurred as early as the Late Burdigalian in the North Sea Basin, whereas *R. striata* occurs in the Atlantic and Mediterranean between the Lower Miocene Aquitanian and Middle Miocene Serravallian. *Ringicula ventricosa* differs in being larger shelled, the spire is shorter, less pointed, the last whorl more inflated, the two anterior columellar folds are thinner and further separated from each other than in *R. striata*, and the parietal pad is far less strongly developed; in *R. striata* the parietal tooth develops at the apex of a thickened subtriangular parietal pad. Chirli (2013) considered *R. striata* a synonym of *R. ventricosa*, and indeed there is some overlap in the distinguishing features discussed above, however, we provisionally consider them distinct.

The variety illustrated as *paulucciae* Morlet, 1878 by Cerulli-Irelli (1910, pl. 4 [35], figs 35, 36) is a higher spired form, resulting in a more elongated profile, and is not conspecific with *Ringicula paulucciae* Morlet, 1878 [= *Ringicula minor* (Grateloup, 1838)] from the Atlantic Lower Miocene Aquitanian of France. Conversely, *R.* (*Ringiculella*) *ventricosa* var. *globulina* Cerulli-Irelli, 1910 is a form with a low spire and a strongly inflated last whorl. The specimen illustrated as *Ringicula* (*Ringiculella*) *ventricosa* var. *Gaudryana* Morlet, 1878 again

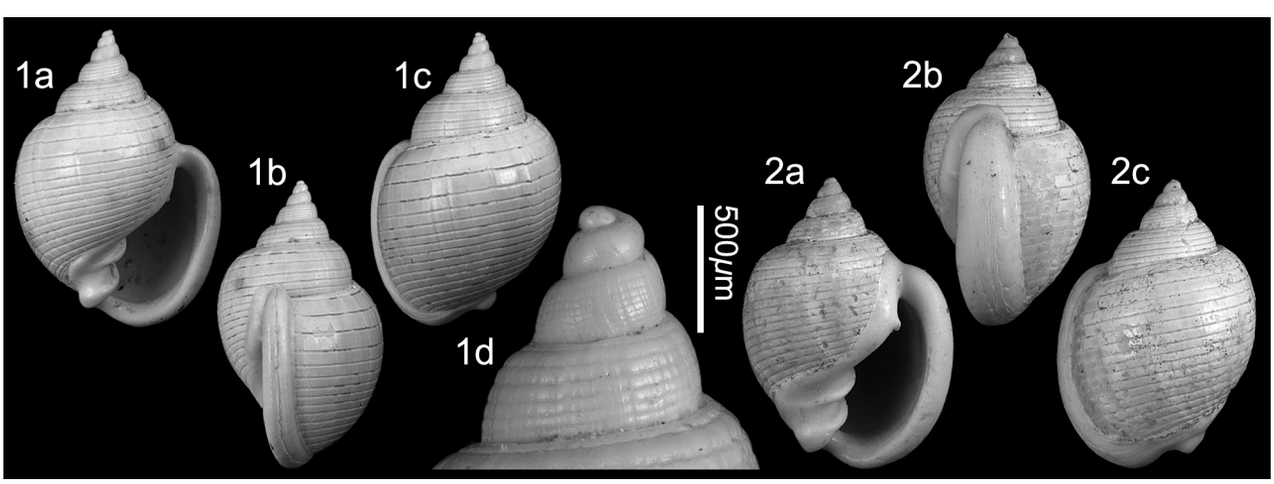

Plate 28. *Ringicula ventricosa* (J. de C. Sowerby, 1824); 1. RGM.1404201, height 7.2 mm, width 4.9 mm, 1d, detail of protoconch; Velerín carretera, Velerín. 2. RGM.1404203, height 6.1 mm, width 4.5 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

represents a form with a relatively inflated last whorl and a strongly developed outer lip varix and columellar armature. According to the original discussion "*Cette espêce se distingue de ses congénères, non seulement par sa forme globuleuse en general, mais surtout par sa dent supérieure, qui est preque nulle, et par la forme de son labre, qui est oblique et non arqué* [This species is distinguished from its congeners not only by its generally globular shape, but above all by the superior denticle that is almost non-existent, and by the oblique instead of arched shape of the lip]" (Morlet, 1878, p. 283). Morlet (1878, p. 283) based his species on material from numerous localities ranging from the Atlantic Burdigalian Lower Miocene of France to the Mediterranean Upper Pliocene of Italy. Therefore, we are unsure if *Ringicula gaundryana* is a valid species. Specimens illustrated by Cerulli-Irelli as *R.* (*R.*) *placentina* G. Seguenza, 1881 is another globose, short-spired form.

Ringicula ventricosa and *R. auriculata* (Menard de la Groye, 1811) both have the surface completely covered in flattened cords, but *R. auriculata* differs in being smaller, almost half the size, in having far stronger apertural armature that narrows the aperture, the outer lip varix is much broader and thicker, the anal canal distorts the adapical portion of the outer lip, the siphonal canal is much narrower, the columellar folds are much stronger and the parietal callus more expanded.

Ringicula ventricosa occurs in both the shallow and deeper water deposits in Estepona, although specimens from the deeper water deposits tend to be slightly thinner shelled with less developed apertural armature (Pl. 28, fig. 1 *vs*. fig. 2).

Distribution – Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848; Harmer, 1923); western Mediterranean, France (Fontannes, 1880); central Mediterranean (Chirli, 2013; Brunetti & Cresti, 2018). Upper Pliocene: North Sea Basin, Red Crag, England (S.V. Wood, 1848; Harmer, 1923); Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Pliocene (indeterminate): North Sea Basin, The Netherlands (Van Regteren Altena *et al*., 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

Order Umbraculida
Superfamily Umbraculoidea Dall, 1889 (1827)
Family Umbraculidae Dall, 1889 (1827)
Order Umbraculida
Superfamily Umbraculoidea Dall, 1889 (1827)
Family Umbraculidae Dall, 1889 (1827)
Genus *Spiricella* Rang, 1828

Type species (by monotypy) – *Spiricella unguiculus* Rang, 1828, Miocene, France.

1828 *Spiricella* Rang, p. 226.

Spiricella unguiculus Rang, 1828
Plate 29, figs 1-2

*1828 *Spiricella unguiculus* Rang, 227, pl. 1 figs 1-5.
2015 *Spiricella unguiculus* Rang, 1828 – Landau *et al*., p. 56, figs 1-3 (*cum syn*.).

Material and dimensions – Maximum length 5.6 mm, width 2.1 mm. **CO**: NHMW 2023/0076/0145 (1). **VS**: RGM.1363086 (*ex* André Jansen collection, nr EsVeSA75) (1).

Description and discussion – see Landau *et al*. (2015).

Distribution – Lower Oligocene: Aquitaine Basin, France (Valdés & Lozouet, 2000). Lower Miocene: Aquitaine Basin, France (Rang, 1828). Middle Miocene: North Sea Basin, Germany (Moths *et al*., 2010), The Netherlands (Hoeksema & A.W. Janssen, 1984). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001; Landau *et al*., 2015); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2015). Present-day: Atlantic, southern Portuguese coast (Hoeksema & A.W. Janssen, 1984), western and central Mediterranean (Romani, 2014).

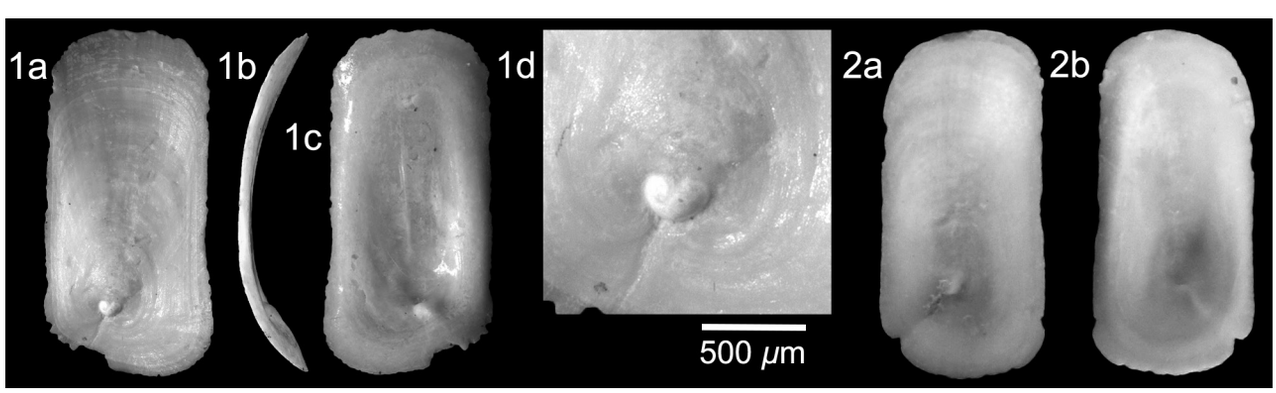

Plate 29. *Spiricella unguiculus* Rang, 1828; 1. RGM.1363086, length 5.0 mm, width 2.0 mm, 1d, detail of protoconch. Velerín sands. 2. NHMW 2023/0076/0145, length 5.6 mm, width 2.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Genus *Umbraculum* Schumacher, 1817

Type species (by monotypy) – *Umbraculum chinense* Schumacher, 1817, present-day, Indo-Pacific.

1817 *Umbraculum* Schumacher, p. 55, 177.
1819 *Gastroplax* de Blainville, p. 182. Type species (by monotypy): *Patella ombracula* de Blainville, 1819, present-day.
1819 *Umbrella* Lamarck, p. 339. Type species (by subsequent designation, Children, 1823): *Umbrella indica* Lamarck, 1819, present-day, Indian Ocean.
1852 *Operculatum* Mörch, p. 137. Type species (by subsequent designation, Valdés, 2001): *Umbrella indica* Lamarck, 1819, present-day, Indian Ocean.

***Umbraculum umbraculum* ([Lightfoot], 1786)**
Plate 30, figs 1-2

*1786 *Umbraculum umbraculum* [Lightfoot], p. 178.
1791 *Patella sinica* Gmelin, p. 3705.
1819 *Patella ombracula* de Blainville, p. 182.
1819 *Umbrella mediterranea* Lamarck, p. 343.
1819 *Umbrella indica* Lamarck, p. 343.
1830 *Patella umbellata* Delle Chiaje, p. 187.
1835 *Parmophorus patelloideus* Cantraine, p. 395.
1843 *Umbrella Lamarckiana* Récluz, p. 109.
1856 *Umbrella ovalis* Carpenter, p. 161.
1863 *Umbrella Cumingi* Deshayes, p. 52, pl. 8, figs 4, 5.
1875 *Operculatum bermudense* Mörch, p. 179.
1881 *Umbrella plicatula* von Martens, p. 104, figs 1-3.
1897 *Umbrella mediterranea* Lk. – Sacco, p. 55, pl. 4, figs 46-48.
1910 *Umbrella mediterranea* Lk. – Cerulli-Irelli, p. 47 [239], pl. 4 [35], fig. 46.
1923 *Umbraculum botanicum* Hedley, p. 315.
1959 *Umbraculum* (*Umbraculum*) *sinicum* (Gmelin) – Zilch, p. 59, fig. 190.
1979 *Umbraculum mediterraneum* (Lamarck, 1812 [*sic*]) – Nordsieck & García-Talavera, p. 180, pl. 44, fig. 56.
1981 *Umbraculum pulchrum* Lin, p. 286 [Chinese text], 289-290 [English text], figs 1-3.
1989 *Umbraculum mediterraneum* (Lamarck, 1819) – Barash & Danin, p. 254, fig. 7.
1990 *Umbraculum mediterraneum* (Lamarck, 1819) – Smiriglio *et al*., p. 330, figs 1-5.
2000 *Umbraculum umbraculum* (Lightfoot, 1786) – Valdés & Lozouet, p. 459, fig. 14.
2005 *Umbraculum umbraculum* (Roeding, 1798) – Repetto *et al*., p. 272, fig. 1224.
2005 *Umbraculum mediterraneum* (Lamarck, 1819) – Rolán, p. 229, pl. 70, fig. 1041.
2006 *Umbraculum umbraculum* (Lightfoot, 1786) – Wägele *et al*., p. 69, figs 1A-H, 2A-H, 3A-G, 4A-I.
2009 *Umbraculum umbraculum* (Lightfoot, 1786) – Martins *et al*., p. 67, fig. 296.
2011 *Umbraculum umbraculum* (Röding, 1798) – Chirli & Linse, p. 229, pl. 90, fig. 4.
2011 *Umbraculum umbraculum* (Röding, 1798) – Cossignani & Ardovini, p. 39, 385, unnumbered fig.
2011 *Umbraculum umbraculum* (Lightfoot, 1786) – Gofas *et al*., p. 439, unnumbered fig.
2013 *Umbraculum umbraculum* (Röding, 1798) – Chirli, p. 71, pl. 15, figs 5-8.

Material and dimensions – Maximum diameter 21.8 mm, width 18.0 mm. **VC**: NHMW 2023/0076/0107-0108 (2). **VS**: NHMW 2023/0076/0109 (1). **EL**: NHMW 2023/0076/0110 (1).

Description – Shell medium sized, fragile, flattened patelliform; apex subcentral, slightly left and posterior. Protoconch coiled sinstrally.

Discussion – Based on anatomical, histological and molecular data, Wägele *et al*. (2006) showed that *Umbraculum mediterraneum* (Lamarck, 1822) and *U. umbraculum* ([Lightfoot] 1786) were the same species, and thus the former a junior subjective synonym of the latter. They also considered the Antipodean records to be conspecific and concluded that there was only one species of *Umbraculum*, with a wide distribution in tropical and temperate waters in infralittoral and circalittoral habitats between 4-70 m depth (Gofas *et al*., 2011). In Estepona it is very uncommon and found in the shallower water assemblages.

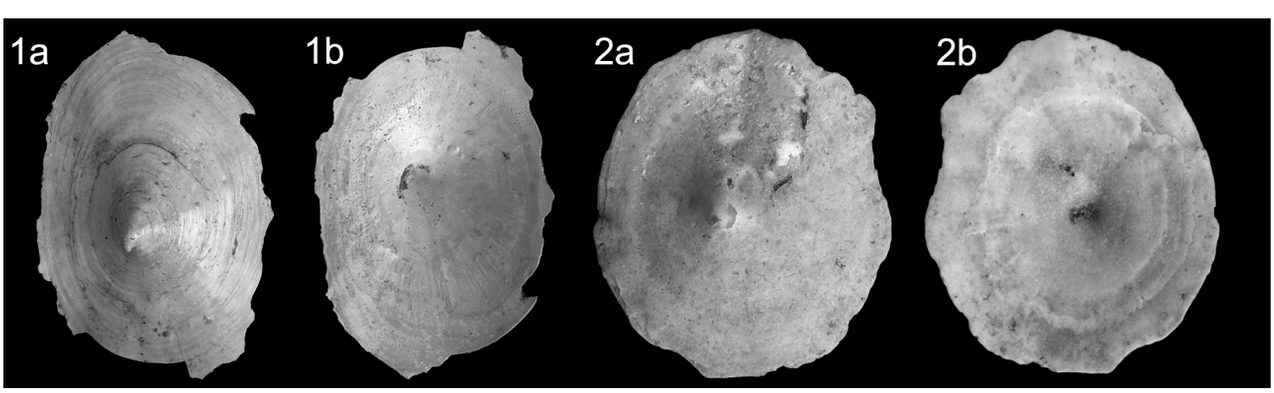

Plate 30. *Umbraculum umbraculum* ([Lightfoot], 1786); 1. NHMW 2023/0076/0107, maximum diameter 21.0 mm, width 15.0 mm, (digital image). Velerín carretera, Velerín. 2. NHMW 2023/0076/0110, maximum diameter 21.8 mm, width 18.0 mm, (digital image). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Distribution – Lower Pliocene: central Mediterranean, Italy (Valdés & Lozouet, 2000; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present day: circumglobal distributed in eastern and western Atlantic, Caribbean, Azores (Martins *et al*., 2009), Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*., 2009), Cape Verde Archipelago (Rolán, 2005), entire Mediterranean (Barash & Danin, 1989; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011), Indo-West pacific, eastern Pacific in tropical and temperate waters (Wägele *et al*., 2006).

Order Cephalaspidea P. Fischer, 1883
Superfamily Bulloidea Gray, 1827
Family Bullidae Gray, 1827
Genus *Bulla* Linnaeus, 1758

Type species (ruled by ICZN Opinion 196, 1954) – *Bulla ampulla* Linnaeus, 1758, present-day, Indo-West Pacific.

1758 *Bulla* Linnaeus, p. 725.
1810 *Bullus* de Montfort, p. 331. Type species (by monotypy): *Bulla ampulla* Linnaeus, 1758, present-day, Indo-West Pacific.
1815 *Bullaria* Rafinesque, p. 142. Substitute name for *Bulla* Linnaeus, 1758.
1825 *Bullea* de Blainville, p. 478. Type species (by monotypy): *Bulla ampulla* Linnaeus, 1758, present-day, Indo-West Pacific.
1840 *Vesica* Sainson, p. 272. Type species (by subsequent designation, Malaquias & Reid, 2008): *Bulla ampulla* Linnaeus, 1758, present-day, Indo-West Pacific.
1929a *Quibulla* Iredale, p. 349. Type species (by original designation): *Bulla botanica* Hedley, 1918, present-day, New South Wales, Australia.

***Bulla subampulla* d'Orbigny, 1852**
Plate 31, figs 1-2

1847 *Bulla ampulla* Sismonda, p. 56 (*non* Linnaeus, 1758).
*1852 *Bulla subampulla* d'Orbigny, p. 178.
1897 *Bulla subampulla* d'Orb. – Sacco, p. 47, pl. 3, figs 135-139.
1958 *Bullaria subampulla* d'Orbigny – Erünal-Erentöz, p. 128, pl. 21, figs 2-5.
1992 *Bulla subampulla* d'Orbigny, 1852 – Cavallo & Repetto, p. 168, fig. 485.
1974 *Bulla subampulla* d'Orbigny, 1852 – Malatesta, p. 449, pl. 32, fig. 16.
1976a *Bulla* (*B.*) *subampulla* d'Orbigny – Pavia, p. 115, pl. 12, fig. 3.
1992 *Bulla subampulla* d'Orbigny, 1852 – Cavallo & Repetto, p. 168, fig. 485.
2013 *Bulla subampulla* d'Orbigny, 1852 – Chirli, p. 60, pl. 13, figs 1-5.

non 2017 *Bullaria subampulla* d'Orbigny, 1852 [*sic*] – Büyükmeríç *et al*., p. 7, 9, fig. 5N [p. 7, 9 listed as *Bulla ampulla* Linnaeus, 1758, in fig. 5N legend *B. subampulla*] [?= *Roxania utriculus* (Brocchi, 1814)].

Material and dimensions – Maximum height 39.6 mm, width 25.0 mm. **CO**: RGM.1404253-254 (2), RGM.1404255 (3), NHMW 2023/0076/0133 (11). **EL**: RGM.1404297 (6), NHMW 2023/0076/0134 (4).

Description – Shell large, relatively solid, ovate, only last whorl visible. Last whorl ovate, surface smooth, without sculpture, slightly wider below mid-whorl, apex narrowly and deeply umbilicate; umbilicus round edged. Aperture elongate, narrow adapical half, widening abapically; outer lip simple, extending slightly above apex, broadly convex below, rounded at base. Columella short, thickened; columellar and parietal callus not developed.

Discussion – Following the revision of the extant *Bulla* Linnaeus, 1758 species based on animal morphology and molecular data by Malaquias & Reid (2008), the genus

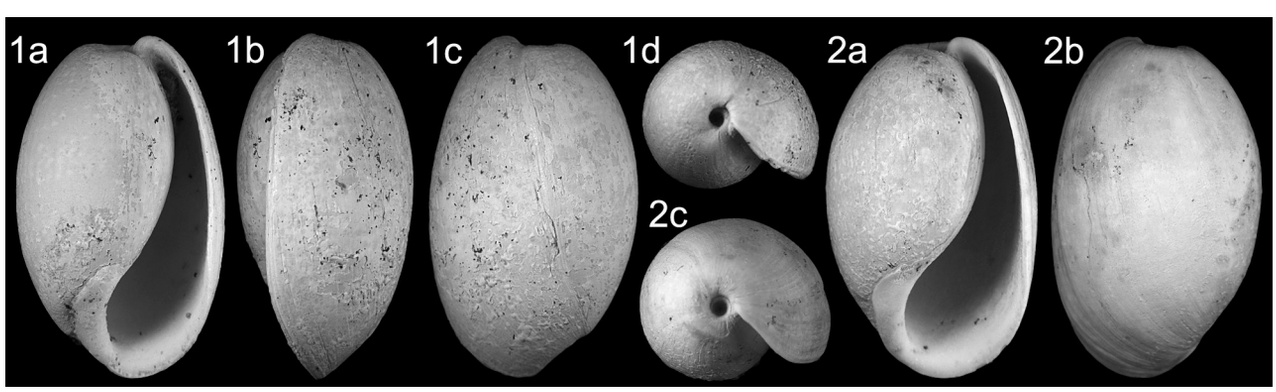

Plate 31. *Bulla subampulla* d'Orbigny, 1852; 1. RGM.1404253, height 24.4 mm, width 15.3 mm; 2. RGM.1404254, height 21.1 mm, width 13.6 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

is not speciose in the eastern Atlantic. Only two species were recognised; *B. striata* Bruguière, 1792 distributed from southern Portugal to Angola and throughout the Mediterranean, and *B. mabillei* Locard, 1897 restricted to the oceanic islands of the archipelagos of Madeira, Selvagens, Canaries, Cape Verde, and São Tomé and Princípe. Shells of *B. mabillei* are easily separated from those of *B. striata* by their more rounded profile.

Bulla subampulla d'Orbigny, 1852 from the Pliocene Mediterranean is somewhat intermediate in profile between the two extant species but larger specimens of *B. subampulla* can depict a rounder profile closer to the typical *B. mabillei* (see Figure 1); *B. subampulla* is certainly (see Figure 1); more regularly ovate that *B. striata*, which is usually slightly pyriform due to the abapical half of the last whorl being modestly inflated but is not as roundly ovate as *B. mabillei*. Moreover, Malaquias & Reid described the shell of *B. striata* as having "*9-16 anterior spiral grooves; 2-8 posterior spiral grooves (absent in West Africa, except for Cape Verde Islands)*" (2008, p. 465). Spiral grooves are absent in all specimens from Estepona.

We therefore consider *B. subampulla* a valid species which seems to have been restricted to the Pliocene Mediterranean. It is unlikely, however, to be ancestral to *B. striata*, as its western Atlantic sister species *B. occidentalis* A. Adams, 1850 has been present in the Caribbean since at least the Late Pliocene (Gurabo Formation, Dominican Republic; BL unpublished data), and possibly earlier (beds of Cercado age, Dominican Republic, BL unpublished data). *Bulla occidentalis* can reach larger dimensions than *B. striata*, has a more variable shell, and usually lacks posterior spiral spirals. However, the two cannot be reliably separated based on shell characters alone.

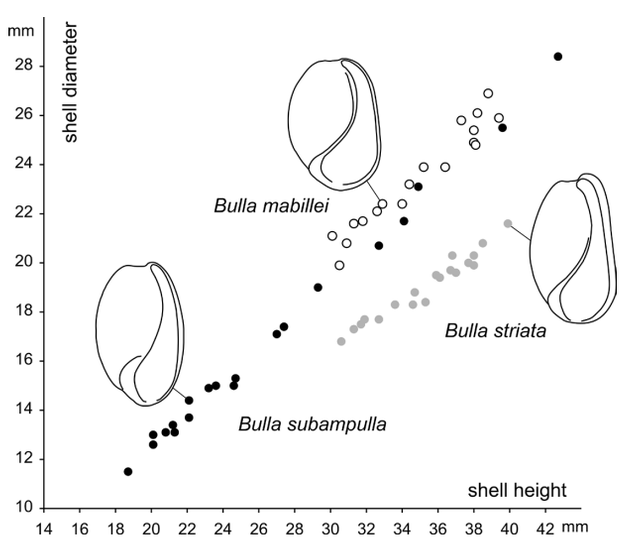

Figure 1. Plot of shell height/diameter for *B. striata* Bruguière, 1792 (20 specimens; present-day specimens from Fabrica and Cabanas, Algarve, southern Portugal; RGM coll), *B. mabillei* Locard, 1897 (20 specimens; present-day specimens from Gran Canaria, Canary Islands; RGM coll.), and *Bulla subampulla* d'Orbigny, 1852 (20 specimens; Velerín conglomerates and El Lobillo, Estepona, Spain: RGM and NHMW coll.).

Distribution – Lower Pliocene: central Mediterranean, Italy (Pavia, 1976a; Chirli, 2013), eastern Mediterranean, Turkey (Erünal-Erentöz, 1958). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Malatesta, 1974; Cavallo & Repetto, 1992).

Family Retusidae Thiele, 1925
Genus *Pyrunculus* Pilsbry, 1895

Type species (by typification of replacement name) – *Bulla pyriformis* A. Adams, 1850, present-day, China Sea.

1854 *Sao* H. Adams & A. Adams, p. 21. Type species (by monotypy): *Bulla pyriformis* A. Adams, 1850, present-day, Chine Sea. Junior homonym of *Sao* Billberg, 1820 [Crustacea]

1895 *Pyrunculus* Pilsbry, p. 229. *Nom. nov. pro Sao* H. & A. Adams, 1854, *non* Billberg, 1820 [Crustacea], *nec* Barrande, 1846 [Trilobita], *nec* Kölliker, 1853 [Cnidaria].

***Pyrunculus ovatus* (Jeffreys, 1871)**
Plate 32, figs 1-2

*1871 *Cylichna ovata* Jeffreys *in* Carpenter & Jeffreys, p. 156.

1877 *Cylichna obesiuscula* Brugnone, p. 39, pl. 1, fig. 7.

1886 *Cylichna ovata* Jeffreys – Watson, p. 664, pl. 49, fig. 9.

1904 *Cylichna obscura* Sykes, p. 37, pl. 3, fig. 9.

1975 *Pyrunculus ovatus* (Jeffreys) – Bouchet, p. 16, pl. 2, fig. d.

1975 *Cylichna* (*Cylichnina*) *conuloides* [*sic*] (Wood) – Fekih, p. 145, pl. 42, fig. 8 (fig. 11 on plate, *lapsus*) [non *Pyrunculus conuloidea* (S.V. Wood, 1851)].

1994 *Pyrunculus* sp. – Bonfitto *et al*., p. 148, 156, fig. 25.

1999 *Pyrunculus ovatus* (Jeffreys, 1870 [*sic*]) – Ardovini & Cossignani, p. 82, unnumbered fig. bottom right.

2001 *Pyrunculus ovatus* (Jeffreys in W.B Carpenter & Jeffreys, 1871) – Tringali & Oliverio, p. 155, figs 1-14, 33, 35a-b, 45.

2005 *Pyrunculus ovatus* (Jeffreys, 1871) – Repetto *et al*., p. 258, fig. 1140.

2011 *Pyrunculus ovatus* (Jeffreys, 1870 [*sic*]) – **Cossignani & Ardovini**, p. 37, 372, unnumbered fig.

2011 *Pyrunculus ovatus* (Jeffreys, 1871) – Chirli & Linse, p. 224, pl. 88, fig. 5.

Material and dimensions – Maximum height 5.2 mm, width 2.5 mm. **VC**: RGM.1404177-178 (2), RGM.1404179 (50+), NHMW 2023/0076/0148 (50+). **CO**: RGM.1404291 (5), NHMW 2023/0076/0149 (8). **PA**: NHMW 2023/0076/0150 (13).

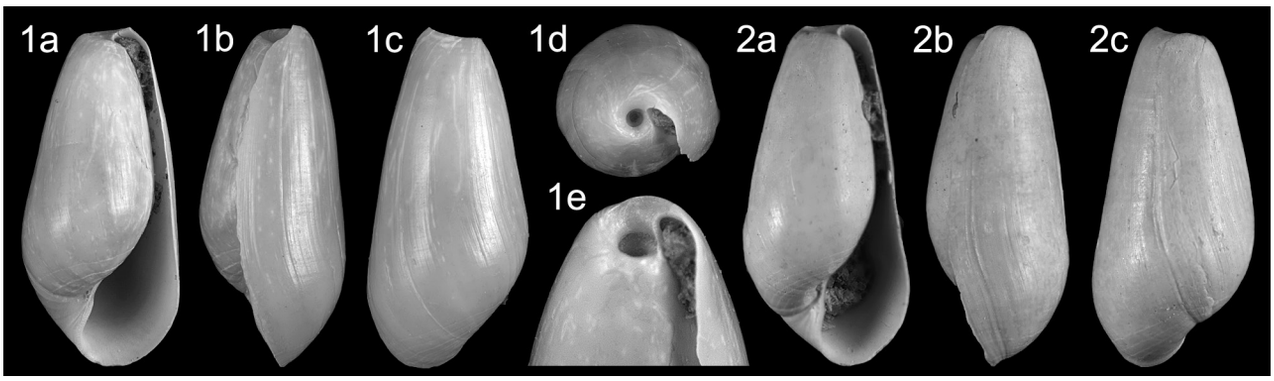

Plate 32. *Pyrunculus ovatus* (Jeffreys, 1871); 1. RGM.1404177, height 4.7 mm, width 2.2 mm; 2. RGM.1404178, height 5.2 mm, width 2.5 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell small, fragile, pyriform, only last whorl visible. Last whorl elongate, widening abapically with periphery placed about one-third whorl height, apex umbilicate, delimited by apical crest, deeply and narrowly umbilicate, sculpture of a few fine narrow grooves at extremities, surface glossy. Aperture as long as the shell, narrow posterior and mid-section, widening anteriorly. Outer lip extending slightly above apex, straight below, rounded abapically. Columella narrow, weakly thickened, bearing single weak fold.

Discussion – *Pyrunculus ovatus* (Jeffreys, 1871) is the most abundant opisthobranch in the deeper water assemblages of Estepona. In the Velerín carretera assemblage it is relatively constant in shape and sculpture, and does not display the variability illustrated by Tringali & Oliverio (2001, figs 1-14). The present-day Mediterranean and West African *P. hoernesi* (Weinkauff, 1866) differs in having axial folds bordering the apex, making the top somewhat coronate.
The Pliocene North Sea Basin *Bulla conuloidea* S.V. Wood, 1851 is closely similar in its slender pyriform profile. In more recent literature it is usually placed in the genus/subgenus *Cylichnina* (Glibert, 1960; Van Regteren Altena *et al*., 1965; Marquet, 1997, 1998), but it is probably better placed in *Pyrunculus*. We have compared specimens from the Pliocene Coralline Crag of England and the Kattendijk Formation of Belgium, and the North Sea Basin specimens differ constantly in having the apex more rounded with a narrower apical umbilicus.

Distribution – Lower Pliocene: central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Lower Pleistocene: central Mediterranean, Italy (Brugnone, 1877); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day, western Atlantic Massachusetts to Brazil (Bouchet, 1975), eastern Atlantic frontage from Norway (Bouchet, 1975), Azores (Watson, 1886), Madeira (Segers *et al*., 2009), into Mediterranean (Ardovini & Cossignani, 1999; Tringali & Oliverio, 2001, although they question if the species is still living in the Mediterranean; Repetto *et al*., 2005; Cossignani & Ardovini, 2011).

Genus *Retusa* Brown, 1827

Type species (by subsequent designation, Iredale, 1915) – *Bulla obtusa* Montagu, 1803, present-day, British Isles.

1827 *Retusa* Brown, pl. 38.

For generic synonymy see Ceulemans *et al*. (2018, p. 118).

***Retusa decussata* Sacco, 1897**
Plate 33, figs 1-3

1826 *Bulla decussata* Bonelli, No. 2868 (*nomen nudum*).
*1897 *Retusa decussata* (Bon.) Sacco, p. 41, pl. 3, figs 83-89.
1975 *Retusa decussata* (Bonelli) – Fekih, p. 141, pl. 40, fig. 10.
1984 *Retusa decusata* Sacco, Bonelli m.s. – Ferrero Mortara *et al*., p. 285, pl. 52, fig. 3.
1992 *Retusa decussata* Sacco, 1897, Bonelli m.s. – Cavallo & Repetto, p. 166, fig. 473.
2010 *Retusa decussata* Sacco, 1897 – Sosso & Dell'Angelo, p. 53, 68 unnumbered fig. middle row left.
2013 *Retusa decussata* Sacco, 1897 – Chirli, p. 47, pl. 11, figs 1-6.
2011 *Retusa decussata* Sacco, 1897 – Chirli & Linse, p. 219, pl. 87, fig. 1.
2019 *Retusa decussata* (Sacco, 1896) [*sic*] – Cárdenas *et al*., p. 215, fig. 8V.

Material and dimensions – Maximum height 5.8 mm, width 2.4 mm. **CO**: RGM.1404293 (7), NHMW 2023/0076/0151 (10). **EL**: RGM.1404180-182 (3), RGM.1404257 (19), NHMW 2023/0076/0152 (21). **PA**: NHMW 2023/0076/0153 (11).

Description – Shell small, relatively solid, subcylindrical, only last whorl visible. Last whorl elongate, widening slightly abapically, abapical half slightly swollen, with periphery placed about one-third whorl height, apex truncated, delimited by coronate apical crest, deeply and widely umbilicate, sculpture of irregular spiral

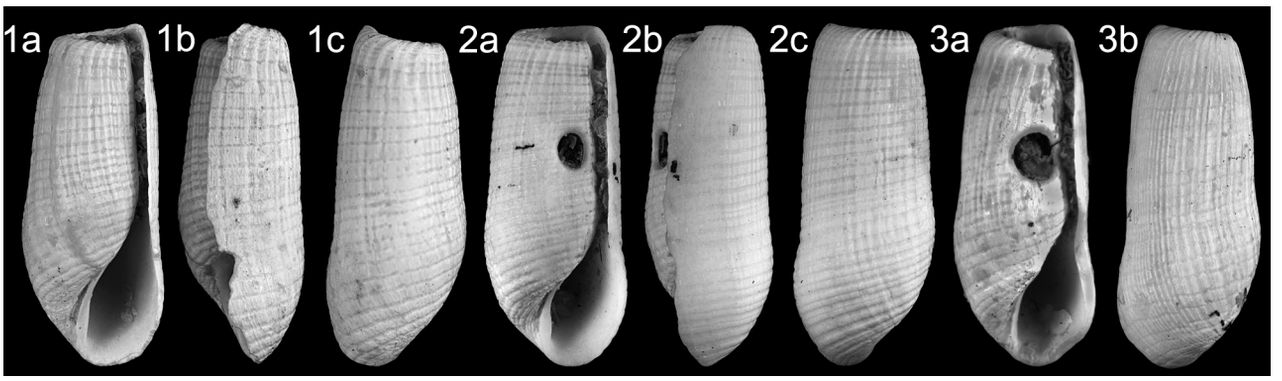

Plate 33. *Retusa decussata* Sacco, 1897; 1. RGM.1404180, height 4.3 mm, width 1.8 mm; 2. RGM.1404181, height 5.5 mm, width 2.3 mm; 3. RGM.1404182, height 4.7 mm, width 1.9 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

grooves and rugose arcuate ribs give surface reticulated appearance. Aperture as long as the shell, very narrow posterior and mid-section, widening anteriorly. Outer lip extending slightly above apex, straight below, rounded abapically. Columella narrow, weakly thickened, without fold, bordering narrow umbilical chink.

Discussion – *Retusa decussata* Sacco, 1897 differs from all its European Mediterranean congeners in having reticulated surface sculpture. Thus, it is similar to *Pyrunculus fourierii* (Audouin, 1826) which has been recorded from the Mediterranean (Tringali & Oliverio, 2001), but that species has a poorly defined apical band separated from the rest of the last whorl by a slight depression, and there is a fold on the columella, which is a character of the genus *Pyrunculus* Pilsbry, 1895 and not seen in *Retusa* Brown, 1827. Moreover, *P. fourierii* is a Lessepsian immigrant to the Mediterranean.
In Estepona *R. decussata* is found in the shallow water deposits of El Lobillo and Velerín conglomerates.

Distribution – Upper Miocene: Atlantic, Seville, southern Spain (Cárdenas *et al*., 2019). Lower Pliocene: central Mediterranean, Italy (Sacco, 1897; Chirli, 2013), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), central Mediterranean, Italy (Sacco, 1897; Ferrero Mortara *et al*., 1984; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Retusa truncatula **(Bruguière, 1792)**
Plate 34, figs 1-2

*1792 *Bulla truncatula* Bruguière, p. 377.
1950 *Retusa truncatula* Bruguière – Nicklès, p. 138, fig. 283.
1979 *Retusa truncatula* (Bruguière, 1792) – Nordsieck & García-Talavera, p. 176, pl. 44, fig. 38.
1988 *Retusa* (*R.*) *truncatula* (Brug.) – Brambilla *et al*., p. 42, pl. 10, fig. 2.
2005 *Retusa truncatula* (Bruguière, 1792) – Repetto *et al*., p. 257, fig. 1132.
2006 *Retusa truncatula* (Bruguière, 1792) – Marquet & Landau, p. 40, fig. 7/2a-c.
2011 *Retusa truncatula* (Bruguière, 1792) – Cossignani & Ardovini, p. 37, 371, unnumbered fig.
2011 *Retusa truncatula* (Bruguière, 1792) – Gofas *et al*., p. 405, unnumbered fig. Top.
2011 *Retusa truncatula* (Bruguière, 1792) – Hernández *et al*., p. 273, fig. 92 S.
2013 *Retusa truncatula* (Bruguière, 1792) – Landau *et al*., p. 337, pl. 77, fig. 11 (*cum syn*.).
2018 *Retusa truncatula* (Bruguière, 1792) – Ceulemans *et al*., p. 118, pl. 7, fig. 8 (*cum syn*.).
2020 *Retusa truncatula* (Bruguière, 1792) – Landau *et al*., p. 268, pl. 14, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 4.0 mm, width 1.8 mm. **CO**: RGM.1404289 (2), NHMW 2023/0076/0160 (6). **EL**: RGM.1404261-262 (2), RGM.1404263 (3), NHMW 2023/0076/0161 (25).

Description – Shell very small, relatively solid, subcylindrical, with squarely truncated apex, only last whorl visible. Last whorl elongate, adapical half regularly cylindrical, slightly pinched just below mid-whorl, abapical half weakly swollen, with periphery placed about one-quarter whorl height, apex squarely truncated and flattened, bearing mid-width apical umbilicus with spire whorls visible within, sculpture of low, irregular, arcuate axial rugae, the rugae not developed over flattened portion of apex, and abapically disappear at periphery. Aperture as long as the shell, very narrow posterior and mid-section, widening anterior third. Outer lip extending slightly above apex, straight below, pinched at one-third height, rounded abapically. Columella short, narrow, weakly thickened, fold weak or absent. No parietal callus.

Discussion – Specimens at hand from the Estepona assemblage are typical for the species, with a strongly and squarely truncated apex. The strength of the axial rugae is variable.

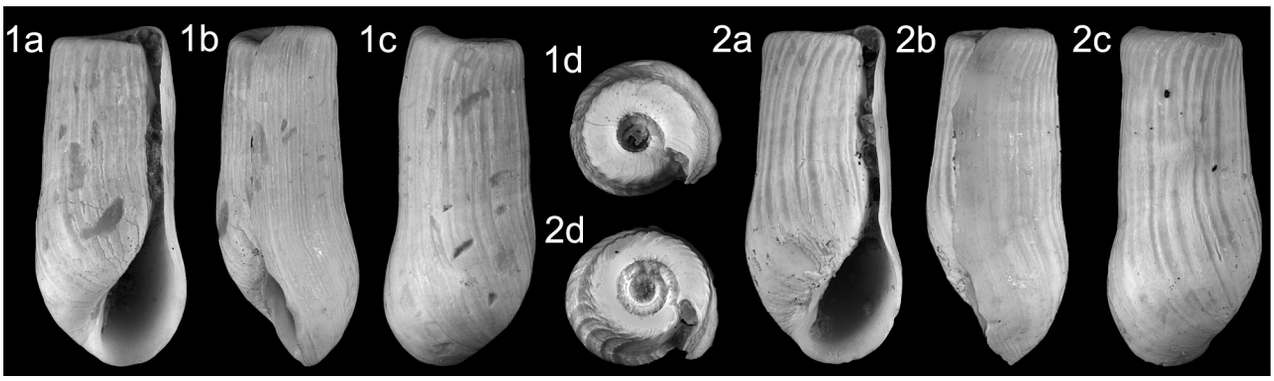

Plate 34. *Retusa truncatula* (Bruguière, 1792); 1. RGM.1404261, height 3.5 mm, width 1.5 mm; 2. RGM.1404262, height 3.9 mm, width 1.8 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Retusa minutissima (Monterosato, 1878) is very small, most specimens are about 2.0 mm in height, and have prominent U-shaped axial growth ridges on the spire whorls (see Oliverio & Tringali, 2001, figs 40-44); and *R. obtusa* (Montagu, 1803) has a shorter last whorl and the aperture attaches at three-quarters shell height (see Oliverio & Tringali, 2001, figs 46-47), lower than in *R. mamillata* (Philippi, 1836) (see Oliverio & Tringali, 2001, figs 48-49) and *R. minutissima*, and the outer lip does not rise above the apex.

Today this species lives in sandy and muddy habitats up to 50 m depth (Gofas *et al*., 2011). In Estepona *R. truncatula* is also found in the shallower water assemblages of Velerín conglomerates and El Lobillo.

Distribution – Lower Miocene: Paratethys (Burdigalian): Austria, (Harzhauser, 2002). Middle Miocene: Atlantic (Langhian): Aquitaine Basin, France (Peyrot, 1932), (Langhian): Loire Basin, France (Peyrot, 1938; Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856; Berger, 1953), Poland (Friedberg, 1928; Bałuk, 1970), Hungary (Strausz, 1954, 1966), Bosnia (Atanackovič, 1985), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian) NW France (Brébion, 1964; Landau *et al*., 2020), (Tortonian), Algarve Basin, Portugal (NHMW collection); Proto-Mediterranean Sea (Tortonian and Messinian) Po Basin, Italy (Sacco, 1897; Venzo & Pelosio, 1963; d'Amico *et al*., 2012). Lower Pliocene: North Sea Basin, England (S.V. Wood, 1848; Harmer, 1923), Belgium (Marquet & Landau, 2006); Atlantic, northeastern France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, northeastern Spain (Martinell, 1982; Martinell & Domènech, 1985); central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1897; Patrini, 1930; Aimassi & Ferrero Mortara, 1983; Cavallo & Repetto, 1992; Chirli, 2013). Lower Pleistocene: Atlantic, St. Erth, England (Harmer, 1923); central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Upper Pleistocene: Atlantic, England, Ireland (Harmer, 1923); central Mediterranean, Italy (Brambilla *et al*., 1988). Present-day: Atlantic, British Isles, Norway, Baltic Sea (T.E. Thompson, 1988) to Mauritania, Senegal, South Africa (Nicklès, 1950), Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*., 2009), Azores, Canary Islands (Nordsieck & García-Talavera, 1979; Hernández *et al*., 2011) and entire Mediterranean (T.E. Thompson, 1988; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Retusa umbilicata **(Montagu, 1803)**

Plate 35, figs 1-2

*1803	*Bulla umbilicata* Montagu, p. 222, pl. 7, fig. 4.
1827	*Volvaria subcylindrica* Brown, pl. 38, figs 19, 20.
1846	*Cylichna strigella* Lovén, p. 144.
2001	*Retusa strigella* (Lovén, 1846) – Oliverio & Tringali, p. 131, fig. 30.
2001	*Cylichnina umbilicata* (Montagu, 1803) – Cachia *et al*., p. 125, pl. 20, fig. 8.
2005	*Cylichnina umbilicata* (Montagu, 1803) – Repetto *et al*., p. 258, fig. 1139.
2011	*Cylichnina umbilicata* (Montagu, 1803) – Cossignani & Ardovini, p. 37, 372, unnumbered fig.
2011	*Cylichnina umbilicata* (Montagu, 1803) – Gofas *et al*., p. 406, unnumbered fig. top.
2013	*Retusa umbilicata* (Montagu, 1803) – Landau *et al*., p. 336, pl. 53, fig. 13, pl. 78, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 3.6 mm, width 1.5 mm. **CO**: RGM.1404292 (2). **EL**: RGM.1404258-259 (2), RGM.1404260 (23), NHMW 2023/0076/0162 (11).

Description – Shell very small, relatively solid, subcylindrical, with roundly truncated apex, only last whorl visible. Last whorl elongate, subcylindrical, widening slightly abapical, with periphery placed about one-third whorl height, apex roundly truncated, bearing deep, narrow apical umbilicus, surface bearing arcuate axial growth lines, and very weak spiral grooves in some spe-

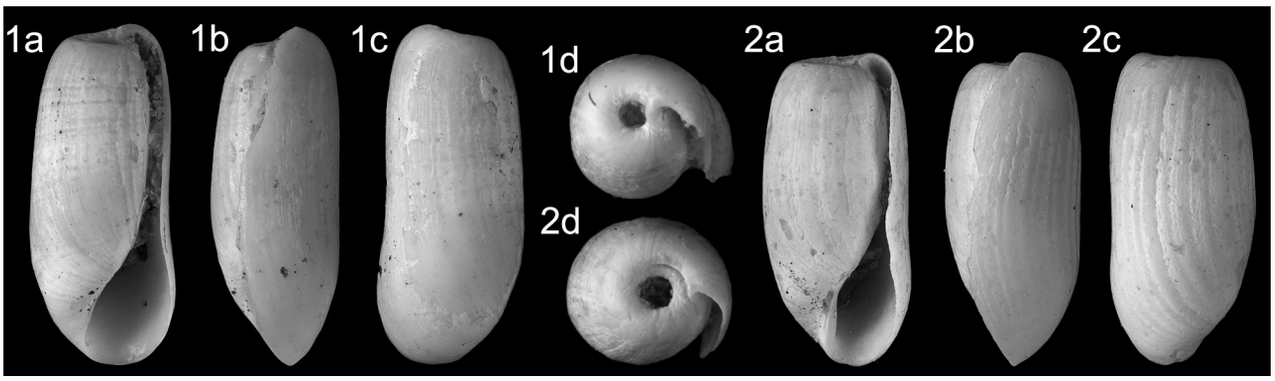

Plate 35. *Retusa umbilicata* (Montagu, 1803); 1. RGM.1404258, height 3.4 mm, width 1.4 mm; 2. RGM.1404259, height 3.1 mm, width 1.4 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

cimens. Aperture as long as the shell, very narrow posterior and mid-section, widening anterior third. Outer lip extending just above apex, straight below, slightly pinched at one-third height, rounded abapically. Columella short, narrow, weakly thickened, fold absent. No parietal callus.

Discussion – The Estepona specimens show some variability is shape, some more elongated than others and slightly pinched mid-whorl with faint spiral sculpture (Pl. 35, fig. 1), other relatively squatter bearing only axial growth lines (Pl. 35, fig. 2).
Despite *Retusa umbilicata* (Montagu, 1803) being the oldest name available for *Retusa* species with an apical umbilicus, Crocetta *et al*. (2015, p. 64) argued that the identity of the species was unclear. Montagu did not mention spiral sculpture in his original description, but subsequent authors have (Jeffreys, 1867, p. 413; Bucquoy *et al*., 1886, p. 526). Crocetta *et al*. considered *Cylichna strigella* Lovén, 1846 a junior subjective synonym with spiral sculpture (see also Oliverio & Tringali, 2001). Both striated and smooth forms occur in the Estepona assemblages. However, they excluded *Cylichna nitidula* Lovén, 1846 which had been included in the synonymy by other authors (*e.g*., Chirli, 2013). The specimen of *R. nitidula* illustrated by Crocetta *et al*. (2015, fig. 3I) clearly shows a shell with a more attenuated apex, more like *R. parvula* (Jeffreys, 1883), but larger shelled, slenderer, and less rounded posteriorly, with the adapical edge of the aperture extending further upwards. We would agree with this position, as all the Estepona specimens have a rather truncated apex and not rounded like the specimen of *R. nitidula* illustrated by Crocetta *et al*. Specimens from the Lower Pleistocene of Rhodes Island illustrated by Chirli & Linse (2011, pl. 88, fig. 3a-d) do not have an apex as pointed as that associated with *R. nitidula*.
Retusa umbilicata is found only in the shallower water assemblage of El Lobillo. Today it is widespread along the European Atlantic Frontage and Mediterranean on the continental platform to 200 m depth (Cachia *et al*., 2001; Gofas *et al*., 2011).

Distribution – Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953), ?Bulgaria (Kojumdgieva & Strachimirov, 1960), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: central Mediterranean (Messinian), Po Basin, Italy (Venzo & Pelosio, 1963). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1923), Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, Tunisia (Fekih, 1975); central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1897; Patrini, 1930; Aimassi & Ferrero-Mortara, 1983; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Present-day: eastern Atlantic, Norway, British Isles, Baltic Sea (T.E. Thompson, 1988) to Madeira, West Africa and the Cape of Good Hope (T.E. Thompson, 1988), into entire Mediterranean (Cachia *et al*., 2001; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Family Rhizoridae Dell, 1952
Genus *Volvulella* Newton, 1891

Type species (by typification of replaced name) – *Bulla acuminata* Bruguière, 1792, present-day, Mediterranean.

1891 *Volvulella* Newton, p. 268. *Nom. nov. pro Volvula* A. Adams, 1850, *non* Gistel, 1848 [Diptera].

For generic synonymy see Ceulemans *et al*. (2018, p. 119).

***Volvulella acuminata* (Bruguière, 1792)**
Plate 36, figs 1-3

*1792 *Bulla acuminata* Bruguière, p. 376.
1950 *Volvula acuminata* Bruguière – Nicklès, p. 138, fig. 284.
2005 *Volvulella acuminata* (Bruguière, 1792) – Repetto *et al*., p. 259, fig. 1141.

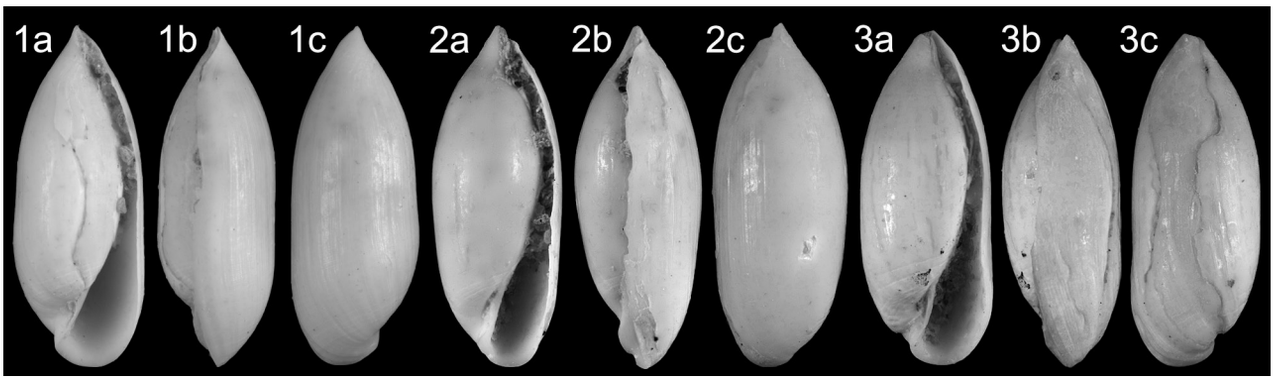

Plate 36. *Volvulella acuminata* (Bruguière, 1792); 1. RGM.1404190, height 5.1 mm, width 2.0 mm; 2. RGM.1404191, height 4.9 mm, width 1.9 mm; 3. RGM.1404192, height 4.7 mm, width 1.8 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2011 *Volvulella acuminata* (Bruguière, 1792) – Cossignani & Ardovini, p. 37, 372, unnumbered fig.
2011 *Volvulella acuminata* (Bruguière, 1792) – Gofas *et al*., p. 406, unnumbered fig. Bottom.
2013 *Volvulella acuminata* (Bruguière, 1792) – Landau *et al*., p. 339, pl. 78, fig. 2 (*cum syn*.).
2018 *Volvulella acuminata* (Bruguière, 1792) – Ceulemans *et al*., p. 119, pl. 7, fig. 10.
2020 *Volvulella acuminata* (Bruguière, 1792) – Landau *et al*., p. 270, pl. 16, fig. 1 (*cum syn*.).
2022 *Volvulella acuminata* (Bruguière, 1792) – Brunetti, p. 80, fig. 193.

Material and dimensions – Maximum height 5.1 mm, width 2.0 mm. **VC**: RGM.1404193 (8), NHMW 2019/0167/0146 (50+). **CO**: RGM.1404190-192 (3), RGM.1404294 (5), NHMW 2019/0167/0147 (17). **EL**: RGM.1404194 (3).

Description – Shell small, subcylindrical, delicate, only last whorl visible. Last whorl elongate, pointed at apex, cylindrical mid-whorl with almost parallel sides, convex at base, sculpture reduced to a few faint grooves at each extremity, slightly more evident over base. Aperture entire length of shell, apical end aperture bends over apex and parietal wall forms a short spine that completely covers apex. Very narrow abapically and mid-aperture, expanded abapically; outer lip inserted at apical spine, straight mid-aperture, rounded abapically. Columella short, thin, without fold; no umbilicus.

Discussion – As discussed by Landau *et al*. (2013, p. 340), *Volvulella acuminata* (Bruguière, 1792) is either a species complex or an unusually long-lived and widely distributed species. It is relatively uncommon in all the Estepona assemblages. The apical rostration is variable in length and the last whorl varies slightly in slenderness. Similar variability is seen in both other fossil and recent populations.
This distinctive little species is widespread in the Mediterranean, northeastern Atlantic and North Sea Basin assemblages from the Middle Miocene, and today occurs in the Atlantic from Norway southwards to Angola and throughout the Mediterranean. Interestingly, *V. acuminata* is not present in the Early to Middle Miocene Aquitaine Basin of France. It is replaced by *Volvulella acuta* (Grateloup, 1828), which is more cylindrical, less convex, with a straighter aperture and a longer rostration.
Today *V. acuminata* is found circalittoral muddy sands (Gofas *et al*., 2011). In Estepona it occurs in both the shallow and deeper water assemblages, but is uncommon in all.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1897). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984), Denmark (Ravn, 1907; Sorgenfrei, 1958), Germany (Anderson, 1964; Wienrich, 2007; Moths *et al*., 2010). Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953), Hungary (Strausz, 1962, 1966); Proto-Mediterranean Sea (Serravallian) Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Landau *et al*., 2020), (Tortonian): Algarve Basin, Portugal (NHMW collection). Lower Pliocene: North Sea Basin, England (S.V. Wood, 1848; Harmer, 1925), Belgium (Nyst, 1845; Glibert, 1960; Marquet, 1997); northeastern Atlantic, NW France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Chirli, 2013). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean (Chirli & Linse, 2011). Present-day: Atlantic, Norway, British Isles (T.E. Thompson, 1988) to Angola (Nicklès, 1950), into entire Mediterranean (T.E. Thompson, 1988; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

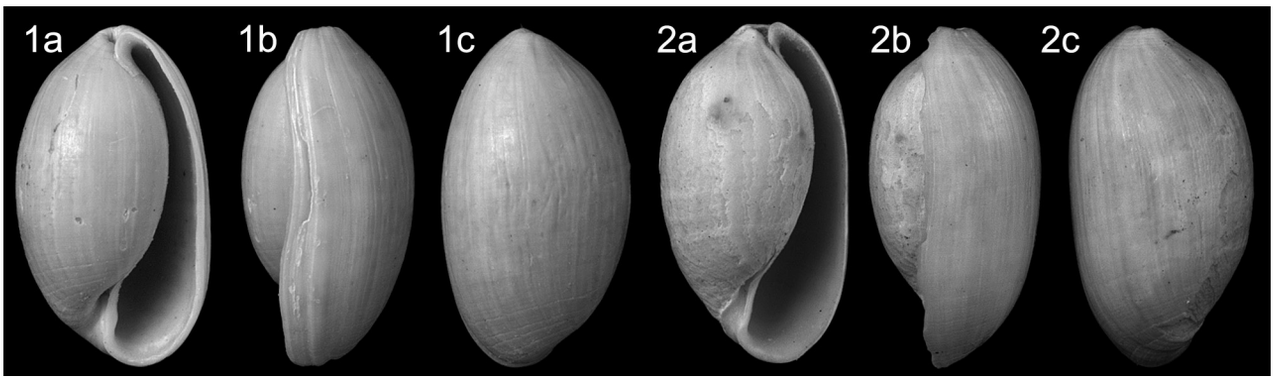

Plate 37. *Volvulella volvulaeformis* (G. Seguenza, 1880); 1. NHMW 2019/0167/0041, height 3.7 mm, width 2.1 mm; 2. NHMW 2019/0167/0042, height 3.9 mm, width 2.2 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

***Volvulella volvulaeformis* (G. Seguenza, 1880)**
Plate 37, figs 1-2

*1880	*Cylichna volvulaeformis* G. Seguenza, p. 252, pl. 16, fig. 11.
2018	*Volvulella* sp. – Brunetti & Cresti, p. 116, fig. 520.
2020	*Volvulella volvulaeformis* (Seguenza, 1880) – Landau & Mulder, p. 48, figs 37, 38.

Material and dimensions – Maximum height 3.9 mm, width 2.2 mm**. VC:** NHMW 2019/0167/0041 (1), NHMW 2019/0167/0042 (1), NHMW 2019/ 0167/0043-0044 (2), NHMW 2019/0167/0045 (7), RGM.1404189 (1). **CO:** NHMW 2019/0167/0046 (7), RGM.1404309 (2).

Description – see Landau & Mulder (2020, p. 32).

Discussion – Differs from *Volvulella acuminata* (Bruguière, 1792) in being more solid, much broader, and not having a spike of callus that usually covers the apex, but a sharp concentric ridge that develops from the apex of the outer lip and fuses with the apex, forming a small deep apical pit. For full discussion see Landau & Mulder (2020, p. 48).

Distribution – Lower Pliocene: central Mediterranean, South Italy (G. Seguenza, 1880), Western Liguria (Sosso and Dell'Angelo, BL personal communication). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Mulder, 2020); central Mediterranean, Italy (Brunetti & Cresti, 2018).

Family Tornatinidae P. Fischer, 1883b [= Acteocinidae Dall *in* Eastman, 1913]
Genus *Acteocina* Gray, 1847

Type species (by original designation) – *Acteon wetherelli* I. Lea, 1833, Miocene, eastern United States.

1847	*Acteocina* Gray, p. 160.

For generic synonymy see Ceulemans *et al*. (2018, p. 117).

***Acteocina knockeri* (E.A. Smith, 1872)**
Plate 38, figs 1-3

*1872a	*Tornatina knockeri* E.A. Smith, p. 738, pl. 75, fig. 30.
1880	*Tornatina hemipleura* Fontannes, p. 237, pl. 12, fig. 14.
1910	*Tornatina spirata* Br. – Cerulli-Irelli, p. 32 [224], pl. 3 [34], figs 58-62 [*non Acteocina spirata* (Brocchi, 1814)].
1950	*Acteocina Knockeri* E.A. Smith, 1872 – Nicklès, p. 139, fig. 285.
1975	*Tornatina spirata* (Brocchi) – Fekih (*partim*), p. 140, pl. 40, fig. 16.
1983	*Retusa truncatula* (Bruguière, 1792) – Menesini & Ughi, p. 238, pl. 2, fig. 14 [*non Retusa truncatula* (Bruguière, 1792)].
1983	*Acteocina* (*A*.) *spirata* (Brocchi) – Aimassi & Ferrero Mortara, p. 187, pl. 2, fig. 2.
1991	*Utriculastra knockeri* (E.A. Smith, 1872) – Hoenselaar & Gulden, p. 56, figs 1, 2.
2004	*Acteocina knockeri* (Smith, 1871 [*sic*]) – Ardovini & Cossignani, p. 43, 245, unnumbered fig. top right.
2005	*Acteocina knockeri* (Smith E.A., 1872) – Repetto *et al*., p. 266, fig. 1186.
2005	*Acteocina knockeri* (E.A. Smith, 1871 [*sic*]) – Rolán, p. 210, pl. 63, fig. 962.
2007	*Acteocina knockeri* (Smith E.A. 1872) – Ragaini & Bernieri, p. 153, fig. 3i.
2011	*Acteocina knockeri* (E.A. Smith, 1872) – Landau *et al*., p. 43, pl. 23, fig. 14.
2011	*Acteocina spirata* (Brocchi, 1814) – Chirli & Linse, p. 218, pl. 86, fig. 4 [*non Acteocina spirata* (Brocchi, 1814)].
2013	*Acteocina spirata* (Brocchi, 1814) – Chirli, p. 40, pl. 10, figs 1-6 [*non Acteocina spirata* (Brocchi, 1814)].
2022	*Acteocina knockeri* (E.A. Smith, 1871 [*sic*]) – Brunetti, p. 80, fig. 187.

Material and dimensions – Maximum height 4.7 mm, width 2.1 mm. **CO**: RGM.1404286 (2). **EL**: RGM.1404167-1404169 (3).

Plate 38. *Acteocina knockeri* (E.A. Smith, 1872); 1. RGM.1404167, height 4.7 mm, width 2.1 mm; 2. RGM.1404168, height 3.4 mm, width 1.6 mm; 3. RGM.1404169, height 3.6 mm, width 1.8 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell very small, solid, cylindrical, with almost parallel to slightly convex sides. Protoconch about 1.5 whorls, flattened and tilted. Teleoconch of about three whorls separated by narrowly canaliculated suture. Spire whorls greatly depressed, sharply angled at shoulder placed just above suture. Last whorl 87-90% of total height, with narrow, deeply concave subsutural platform, sharply angled at elevated shoulder carina placed almost at level of suture, cylindrical below, widening slightly abapically, rounded at base. Surface smooth except shallowly arcuate growth lines and short, close-set axial plicae just below shoulder carinae. Last whorl 87-90% of total height, narrow in upper two-thirds, widening in adapical third; outer lip simple, shallowly arcuate in profile, straight in upper two-thirds, rounded at base. Columella short, thickened, narrowly expanded over base, with broad low fold adapically. Parietal callus weakly thickened, narrowly expanded.

Discussion – Ragaini & Bernieri (2007, p. 153) argued that two species were present in the Italian Plio/Pleistocene: *Acteocina spirata* (Brocchi, 1814) and *A. knockeri* (E.A. Smith, 1872), the latter differing in having short opisthocline riblets/plicae most evident below the carinate shoulder adapically, becoming sub/obsolete below, so that the rest of the surface of the last whorl is smooth or bears only growth lines. They considered these riblets absent in *A. spirata*. Cerulli-Irelli (1910, p. 32 [224]) noted that in the Lower Pleistocene Italian specimens from Monte Mario riblets were present in most specimens. Ragaini & Bernieri suggested that the riblets may have been absent from some specimens due to wear, but did not discount the possibility of the two species being represented in those deposits.
In the Estepona assemblages *A. spirata* predominates, but a few specimens attributable to *A. knockeri* co-occur in the shallow water assemblages. Apart from the differences highlighted by Ragaini & Bernieri, the whorl profile is slightly different. In *A. knockeri* the shoulder area is narrower and the last whorl tends to widen slightly abapically, so that the maximum diameter is at the base, whereas *A. spirata* has a more regularly cylindrical profile, with the maximum diameter in most specimens placed on the adapical half of the last whorl. Moreover, the canaliculated suture is narrower in *A. knockeri*.
In his description of *Tornatina hemipleura* Fontannes,1880 from the Pliocene of the Roussillon Basin of France, that author clearly described the small oblique axial folds on the adapical portion of the whorls that are also visible in the figure. We therefore consider Fontannes species a junior subjective synonym of *A. knockeri*.
Fekih (1975, p. 140) described both smooth specimens and those with riblets below the suture, suggesting both species are present in the Tunisian assemblages.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Chirli, 2013), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Aimassi & Ferrero Mortara, 1983; Ragaini & Bernieri, 2007). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic, West Africa, Benin (E.A. Smith, 1872a), Cape Verde Archipelago (Rolán, 2005) to Angola (Nicklès, 1950), western Mediterranean, Tunisia (Hoenselaar & Gulden, 1991; Repetto *et al*., 2005).

***Acteocina spirata* (Brocchi, 1814)**
Plate 39, figs 1-3

*1814	*Voluta spirata* Brocchi, p. 644, pl. 15, fig. 12.
1847	*Bullina Agassizi* Sismonda, p. 56.
1897	*Tornatina spirata* (Br.) – Sacco, p. 38, pl. 3, figs 58, 59.
1897	*Tornatina spirata* var. *Compressior* Sacco, p. 38, pl. 3, figs 60-62.
1897	*Tornatina spirata* var. *Agassizi* (Sismd.) – Sacco, p. 38, pl. 3, figs 63-64.
1955	*Acteocina spirata* (Brocchi, 1814) – Rossi Rochetti, p. 334, fig. 180.
1975	*Tornatina spirata* (Brocchi) – Fekih (*partim*), p. 140, pl. 40, fig. 16.

1978 *Voluta spirata* Brocchi, 1814 – Pinna & Spezia, p. 170, pl. 54, fig. 3.
1982 *Acteocina* aff. *Spirata* (Brocchi, 1814) – Martinell, p. 230, pl. 1, figs 20, 21.
1992 *Acteocina spirata* (Brocchi, 1814) – Cavallo & Repetto, p. 170, fig. 490.

non 1910 *Tornatina spirata* Br. – Cerulli-Irelli, p. 32 [224], pl. 3 [34], figs 58-62 [= *Acteocina knockeri* (E.A. Smith, 1872)].
non 2011 *Acteocina spirata* (Brocchi, 1814) – Chirli & Linse, p. 218, pl. 86, fig. 4 [= *Acteocina knockeri* (E.A. Smith, 1872)].
?*non* 2019 *Acteocina spirata* (Brocchi, 1814) – Cárdenas *et al*., p. 215, fig. 8r.

Material and dimensions – Maximum height 5.4 mm, width 2.6 mm. **CO**: RGM.1404285 (12), NHMW 2023/0076/0136 (18). **EL**: RGM.1404170-172 (3), RGM.1404173 (28), NHMW 2023/0076/0135 (27).

Description – Shell very small, solid, cylindrical, with almost parallel to slightly convex sides. Protoconch about 1.5 whorls, flattened and tilted. Teleoconch of about three whorls separated by canaliculated suture. Spire whorls greatly depressed, sharply angled at shoulder placed just above suture. Last whorl 87-90% of total height, with moderately wide, deeply concave subsutural platform, sharply angled at elevated shoulder carina placed almost at level of suture, cylindrical below, rounded at base. Surface smooth except shallowly arcuate growth lines. Last whorl 87-90% of total height, narrow in upper two-thirds, widening in adapical third; outer lip simple, shallowly arcuate in profile, straight in upper two-thirds, rounded at base. Columella short, thickened, narrowly expanded over base, with broad low fold adapically. Parietal callus weakly thickened, narrowly expanded.

Discussion – For discussion see under *Acteocina knockeri* (E.A. Smith, 1872). The specimen from the Tortonian Upper Miocene of Seville, southern Spain illustrated by Cárdenas *et al*. (2019, fig. 8r) has a very different spire profile and is probably not this species.

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Martinell, 1982); central Mediterranean, Italy (Sacco, 1897), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992).

Superfamily Cylichnoidea H. Adams & A. Adams, 1854
Family Cylichnidae H. Adams & A. Adams, 1854
Genus *Cylichna* Lovén, 1846

Type species (by subsequent designation, Hermannsen, 1852) – *Bulla cylindracea* Pennant, 1777, present-day, British Isles.

1846 *Cylichna* Lovén, p. 142.

For generic synonymy see Ceulemans *et al*. (2018, p. 120).

***Cylichna brocchii* (Michelotti, 1847)**
Plate 40, figs 1-2

1814 *Bulla ovulata*? Lamarck – Brocchi, p. 277, pl. 1, fig. 8.
*1847 *Bulla Brocchii* Michelotti, p. 151.
1897 *Bullinella* (*Cylichnina*) *brocchii* (Micht.) – Sacco, p. 51, pl. 4, figs 19-23.
1992 *Atys brocchii* (Michelotti, 1847) – Cavallo & Repetto, p. 168, fig. 481.
2011 *Atys brocchii* (Michelotti, 1847) – Chirli & Linse, p. 225, pl. 89, fig. 3.
2013 *Atys brocchii* (Michelotti, 1847) – Chirli, p. 61, pl. 13, figs 15-19.

non 1856 *Bulla Brocchii* Mich. – Hörnes, p. 622, pl. 50, fig. 6 [= *Cylichna subcylindrica* (d'Orbigny, 1852)].
non 1953 *Retusa* (*Cylichnina*) *brocchii* (Michelotti) – Berger, p. 100 [= *Cylichna subcylindrica* (d'Orbigny, 1852)].

Material and dimensions – Maximum height 13.4 mm, width 5.7 mm. **VC**: RGM.1404219 (20), NHMW 2023/

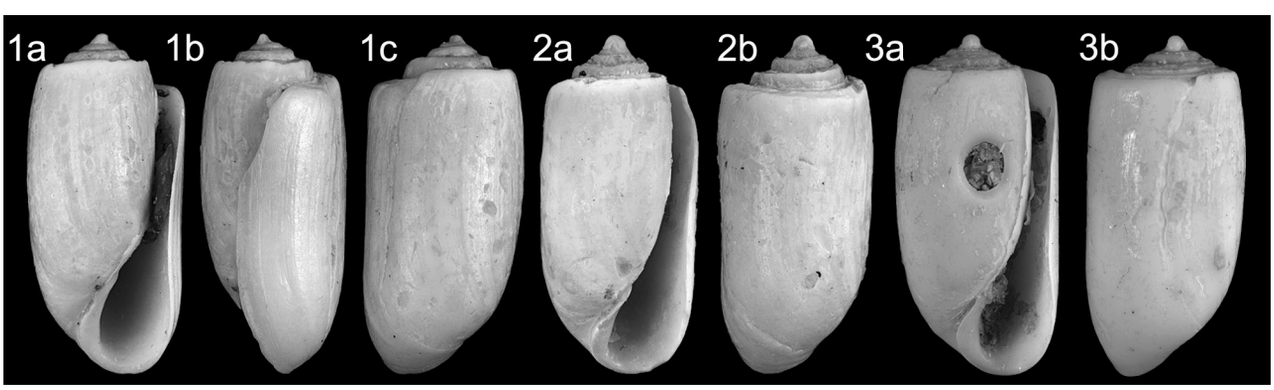

Plate 39. *Acteocina spirata* (Brocchi, 1814); 1. RGM.1404170, height 3.8 mm, width 1.7 mm; 2. RGM.1404171, height 3.7 mm, width 1.7 mm; 3. RGM.1404172, height 3.6 mm, width 1.7 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

0076/0126 (31). **CO**: RGM.1404216-217 (2), RGM.1404218 (20), NHMW 2023/0076/0128 (25). **EL**: RGM.1404220 (22), NHMW 2023/0076/0127 (8).

Description – Shell medium sized, solid, subcylindrical, widening abapically, only last whorl visible. Last whorl elongate, evenly convex, with periphery just above one-third whorl height, rounded at base; apex narrowed, deeply and narrowly umbilicate, delimited by rounded edge. Surface smooth except for some extremely weak grooves over base not seen in all specimens, and fine axial growth lines. Aperture as long as the shell, very narrow posterior and mid-section, widening anteriorly. Outer lip extending a short distance above apex, weakly convex below, rounded abapically. Columella short, moderately thickened, bearing low, robust fold abapically.

Discussion – This species has usually been placed in the genus *Atys* de Montfort, 1810, but species in that genus are thinner shelled, more barrel-shaped to bulbous-rounded, and do not have a thickened columella. Following the molecular phylogeny of Oskars *et al*. (2019), today *Atys* is an Indo-West Pacific genus. Based on the thick shell, cylindrical profile and columellar characters we place it in *Cylichna* Lovén, 1846.
Cylichna brocchii (Michelotti, 1847) is somewhat variable in profile, some specimens slenderer adapically than others (Pl. 40, fig. 2), and in many specimens the spiral grooves over the base are obsolete. It is easily separated from its congeners in the Estepona assemblages *C. cylindracea* (Pennant, 1777), which is smaller, far more regularly cylindrical and slender and the apical umbilicus is bordered by a sharp crest, and *C. pliocrassa* (Sacco, 1897) that is similar in size, but more regularly cylindrical and broader, the apex is more truncated, the apical umbilicus slightly wider, and the spiral sculpture is stronger.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1897). Lower Pliocene: central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

***Cylichna cylindracea* (Pennant, 1777)**
Plate 41, figs 1-3

*1777	*Bulla cylindracea* Pennant, p. 100, pl. 75, figs 5, 6.
1814	*Bulla convoluta* Brocchi, p. 277, pl. 1, fig. 7.
1848	*Bulla cylindracea* Penn. – S.V. Wood, p. 175, pl. 21, fig. 1.
1878	*Cylichna cylindracea* Pennant – Nyst, pl. 7, fig. 21.
1880	*Cylichna convoluta* Brocchi – Fontannes, p. 236, pl. 12, fig. 13.
1882	*Cylichna cylindracea* Pennant – Nyst, p. 132.
1897	*Bullinella cylindracea* (Penn.) – Sacco, p. 49, pl. 4, figs 8-10.
1910	*Bullinella cylindracea* Pennt. – Cerulli-Irelli, p. 229, pl. 35, figs 11-13.
1923	*Cylichna cylindracea* (Pennant) – Harmer, p. 803, pl. 63, fig. 12.
1955	*Cylichna* (*Cylichna*) *convoluta* (Brocchi, 1814) – Rossi Ronchetti, p. 335, fig. 181.
1960	*Cylichna cylindracea* (Pennant, 1777) – Malatesta, p. 196, pl. 9, fig. 17.
1964	*Cylichna cylindracea* (Pennant, 1777) – Van Regteren Altena *et al*., p. 7, pl. 21, fig. 208.
1964	*Cylichna* cf. *cylindracea* Pennant, 1777 – Brébion, p. 654, pl. 15, figs 37, 38.
1975	*Cylichna* (*Cylichnina*) *cylindracea* (Pennant) – Fekih, p. 141, pl. 42, fig. 13.
1978	*Bulla convoluta* Brocchi, 1814 – Pinna & Spezia, p. 133, pl. 50, fig. 2.
1982	*Cylichna cylindracea* (Pennant, 1777) – Martinell, p. 230, pl. 1, figs 22, 23.
1988	*Cylichna cylindracea* (Pennant, 1777) – T.E. Thompson, p. 46, fig. 14.
1992	*Cylichna cylindracea* (Pennant, 1777) – Cavallo & Repetto, p. 170, fig. 489.
1997	*Cylichna cylindracea* (Brocchi) [sic] – Ruiz Muñoz *et al*., p. 188, pl. 41, figs 10, 11.
1997	*Cylichna* (*C*.) *cylindracea* (Pennant, 1777) – Marquet, p. 116, pl. 11, fig. 8.
1998	*Cylichna* (*C*.) *cylindracea* (Pennant, 1777) – Marquet, p. 220, fig. 193.
2005	*Cylichna cylindracea* (Pennant, 1777) – Repetto *et al*., p. 266, fig. 1183.

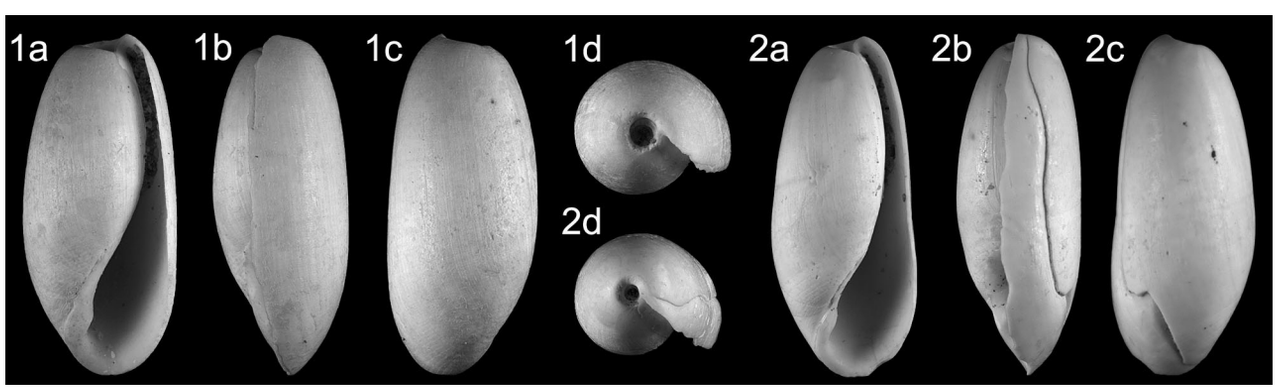

Plate 40. *Cylichna brocchii* (Michelotti, 1847); 1. RGM.1404216, height 12.0 mm, width 5.4 mm; 2. RGM.1404217, height 12.8 mm, width 5.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2005 *Cylichna cylindracea* (Pennant, 1777) – Rolán, p. 209, pl. 63, fig. 961.
2008 *Cylichna cylindracea* (Pennant, 1777) – Chirli & Richard, p. 81, pl. 16, fig. 7.
2010 *Cylichna cylindracea* (Pennant, 1777) – Sosso & Dell'Angelo, p. 54, p. 69 unnumbered fig. top right.
2011 *Cylichna cylindracea* (Pennant, 1777) – Landau *et al*., p. 43, pl. 23, fig. 13.
2011 *Cylichna cylindracea* (Pennant, 1777) – Cossignani & Ardovini, p. 38, 379, unnumbered fig.
2011 *Cylichna cylindracea* (Pennant, 1777) – Gofas *et al*., p. 407, unnumbered fig.
2011 *Cylichna cylindracea* (Pennant, 1777) – Chirli & Linse, p. 217, pl. 86, fig. 3.
2011 *Cylichna cylindracea* (Pennant, 1777) – Hernández *et al*., p. 282, fig. 94 P.
2013 *Cylichna cylindracea* (Pennant, 1777) – Chirli, p. 36, pl. 9, figs 15-20.
2018 *Cylichna cylindracea* (Pennant, 1777) – Ceulemans *et al*., p. 124, pl. 7, fig. 11 (*cum syn*.).
2018 *Cylichna cylindracea* (Pennant, 1777) – Trigo *et al*., p. 384, unnumbered figs.
2022 *Cylichna cylindracea* (Pennant, 1777) – Brunetti, p. 80, fig. 188.

non 1828 *Bulla convoluta* Brocc. – Grateloup, p. 90 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1845 *Bulla convoluta* Brocc. – Grateloup, pl. 3, figs 37, 38 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1907 *Cylichna cylindracea* (Pennant, 1777) – Ravn, p. 367, pl. 8, fig. 15 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1925 *Bullinella cylindracea* Penn. – Kautsky, p. 299 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1952b *Cylichna* (*Cylichna*) *cylindracea* (Pennant, 1777) – Glibert, p. 145, pl. 10, fig. 15 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1956 *Cylichna* (*Cylichna*) *cylindracea* (Pennant, 1777) – Rasmussen, p. 104, pl. 10, fig. 4 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1958 *Cylichna* cf. *cylindracea* (Pennant) – Sorgenfrei, p. 342, pl. 74, fig. 251[= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1963 *Cylichna* (*Cylichna*) *cylindracea* (Penn.) – Steininger, p. 57, pl. 12, fig. 17 [= *Cylichna subcylindrica* (d'Orbigny, 1852)].
non 1964 *Cylichna cylindracea* (Pennant 1777) – Anderson, p. 333, pl. 51, fig. 300 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1964 *Cylichna convoluta* Brocchi, 1814 – Brébion, p. 656, pl. 15, fig. 39 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].
non 1970 *Cylichna convoluta* (Brocchi) – Bałuk, p. 119, pl. 14, fig. 3 [= *Cylichna subcylindrica* (d'Orbigny, 1852)].
non 1972a *Cylichna cylindracea* (Pennant, 1777) – Nordsieck, p. 123, pl. 31, fig. 212 [= *C. pseudoconvoluta* (d'Orbigny, 1852)].

Material and dimensions – Maximum height 11.3 mm, width 4.4 mm. **VC**: RGM.1404226 (50+), NHMW 2023/0076/0120 (50+). **CO**: RGM.1404221-223 (3), RGM.1404224 (20), NHMW 2023/0076/0121 (50+). **EL**: RGM.1404225 (36), **VS**: NHMW 2023/0076/0119 (10).

Description – Shell medium sized, solid, slender cylindrical, only last whorl visible. Last whorl elongate, with almost parallel, straight to very weakly convex sides, weakly rounded at base; apex truncated, widely and shallowly umbilicate, delimited by low, sharp ridge. Surface glossy with extremely fine, close-set spirals visible on tangential light in some specimens (Pl. 41, fig. 2b). Aperture as long as the shell, very narrow posterior and mid-section, widening anteriorly. Outer lip not extending above apex, straight to very weakly convex below, rounded and somewhat truncated abapically. Columella short, narrowly thickened, bearing weak fold abapically.

Discussion – Several closely similar *Cylichna* Lovén, 1846 species occur in the European Neogene that have been confused or misidentified by previous authors. We therefore update the chresonymy for *C. cylindracea* (Pennant, 1777) given by Ceulemans *et al*. (2018), concentrating on fossil records.
In the North Sea Basin, Paratethys and Proto-Mediterranean Early and Middle Miocene, specimens belonging to the *C. cylindracea* species group represent a distinct species: *Cylichna subcylindrica* (d'Orbigny, 1852). It differs from *C. cylindracea* and *C. pseudoconvoluta* in having the outer lip hardly rising above the apex, and the last whorl bearing very fine but distinct, wide-set spiral grooves.
In the Atlantic French Miocene this species group is represented by *C. pseudoconvoluta* (d'Orbigny, 1852). They differ from *C. cylindracea* most notably in being smaller (for size details see Landau *et al*., 2020, p. 272). Peyrot (1933, p. 183) and Glibert (1952a, p. 397) stressed the absence of fine spiral sculpture in *C. pseudoconvoluta* as opposed to its presence in *C. cylindracea*. The spirals in *C. cylindracea* are extremely fine and often only visible only on tangential light in the best preserved specimens. Although most specimens of *C. pseudoconvoluta* are smooth, some show the faintest impression of spirals, more widely spaced than those of *C. cylindracea* (Landau *et al*., 2020, pl. 18, fig. 3). The shells of *C. pseudoconvoluta* is more regularly cylindrical than those of *C. cylindracea*, and the apex more sharply truncated and carinate, whereas in *C. cylindracea* the apex is somewhat rounded, narrowing before the apical truncation. In both species, the apex of the outer lip is raised a short distance above the apex of the last whorl. *Cylichna pseudoconvoluta* seems to have been a more northern Atlantic Miocene species, as specimens at hand from the Upper Miocene Tortonian of Cacela Velha, southern Portugal (NHMW coll.) represent *C. cylindracea*.
In the Estepona assemblages *C. cylindracea* is variable in adult size and the last whorl can be completely cylindrical (Pl. 41, fig. 2) to slightly inflated (Pl. 41, fig. 1). The outer lip profile is convex and somewhat opisthocline

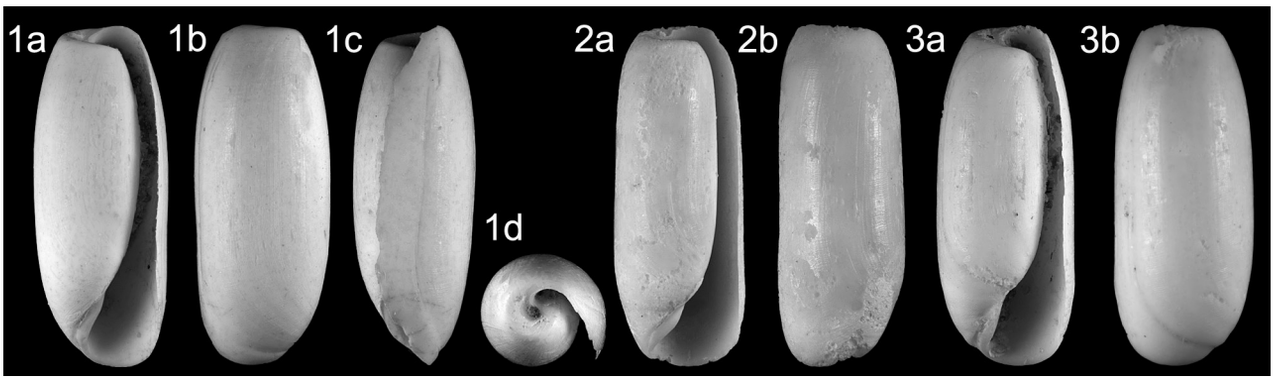

Plate 41. *Cylichna cylindracea* (Pennant, 1777); 1. RGM.1404221, height 10.1 mm, width 4.5 mm; 2. RGM.1404222, height 9.7 mm, width 3.6 mm; 2. RGM.1404223, height 9.1 mm, width 3.6 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

in many specimens. As with other opisthobranchs discussed in this paper, the deeper water specimens are thinner shelled than those of the shallower water deposits. Today it lives in infralittoral and circalittoral muddy sands between 20-60 m depth (Gofas *et al*., 2011).

Cylichna cylindracea (Pennant, 1777) is separated from its Estepona congeners by its slenderer, more evenly cylindrical shell. The apical umbilicus is also shallower than in *C. brocchii* (Michelotti, 1847) and *C. pliocrassa* (Sacco, 1897), and bordered by a low but sharp crest, whereas in the other two species the umbilical edge is rounded.

Distribution – Upper Miocene: Atlantic, southern Portugal (NHMW coll.). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848; Harmer, 1923), Kattendijk Formation, Belgium (Marquet, 1997, 1998); Atlantic, northwestern France (Brébion, 1964; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, northeastern Spain, (Martinell, 1982), France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1897; Chirli, 2013), Tunisia (Fekih, 1975). Upper Pliocene: North Sea Basin, Red Crag, England (S.V. Wood, 1848; Harmer, 1923), Oorderen Sands Formation, Belgium (Marquet, 1997b, 1998b); western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Pliocene (indeterminate): North Sea Basin, The Netherlands (Van Regteren Altena *et al*., 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Pleistocene: Atlantic, England, Ireland (Harmer, 1923); central Mediterranean, Italy (Malatesta, 1960). Present-day: Iceland, northeastern Atlantic frontage, Bay of Biscay (Trigo *et al*., 2018), Azores and Canaries (Nordsieck & García-Talavera, 1979; T.E. Thompson, 1988; Hernández *et al*., 2011) to Cape Verde Archipelago (Rolán, 2005), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

***Cylichna pliocrassa* (Sacco, 1897)**
Plate 42, figs 1-2

*1897	*Cylichnina pliocrassa* Sacco, p. 53, pl. 4, figs 33-36.
1953	*Retusa* (*Cylichnina*) *pliocrassa* (Sacco) – Berger, p. 101, pl. 19, fig. 92.
1984	*Cylichnina pliocrassa* Sacco, 1897 – Ferrero Mortara *et al*., p. 288, pl. 53, figs 5, 6.
1992	*Atys pliocrassa* Sacco, 1897 [*sic*] – Cavallo & Repetto, p. 168, fig. 482.
2005	*Atys pliocrassa* (Sacco, 1897) – Brunetti & Vecchi, p. 21, fig. 81.
2008	*Atys pliocrassa* (Sacco, 1897) – Chirli & Richard, p. 83, pl. 16, fig. 11.
2013	*Atys* cf. *pliocrassa* (Sacco, 1897) – Chirli, p. 63, pl. 14, figs 1-2.

Material and dimensions – Maximum height 16.8 mm, width 7.2 mm. **VC**: RGM.1404183-184 (2), RGM.1404185 (15), NHMW 2023/0076/0124 (50+). **CO**: RGM.1404264 (50+), NHMW 2023/0076/0123 (50+). **EL**: RGM.1404186 (22), NHMW 2023/0076/0122 (13). **PA**: NHMW 2023/0076/0125 (8).

Description – Shell medium sized, solid, relatively broad subcylindrical, only last whorl visible. Last whorl elongate, profile weakly angular at two-thirds whorl height, straight below, rounded at base; apex truncated, deeply and widely umbilicate, delimited by rounded edge. Sculpture of spiral grooves covers entire surface: very fine within apical umbilicus, wider spaced below apex, very fine and close-set mid-whorl, slightly wider spaced over base. Aperture as long as the shell, very narrow posterior and mid-section, widening anteriorly. Outer lip extending a short distance above apex, weakly convex below, rounded abapically. Columella short, moderately thickened, bearing weak fold abapically.

Discussion – Like *Bulla brocchii* Michelotti, 1847 (see above), this species has usually been placed in the genus *Atys* de Montfort, 1810. For the same reasons outlined un-

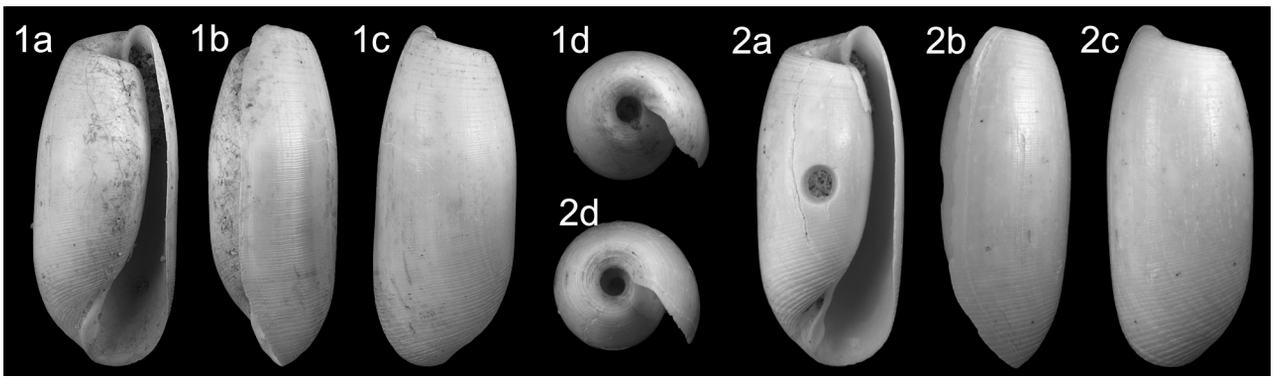

Plate 42. *Cylichna pliocrassa* (Sacco, 1897); 1. RGM.1404183, height 14.0 mm, width 5.9 mm; 2. RGM.1404184, height 12.4 mm, width 5.4 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

der that species, we place *Cylichnina pliocrassa* Sacco, 1897 in *Cylichna* Lovén, 1846. It is quite similar in its large size and profile to the extant Pacific species *C. consobrinoides* Kuroda & Habe, 1952. Indeed, it is one of the largest opisthobranchs in the assemblage reaching almost 17 mm in height, similar to the maximum height of 20 mm for Italian Pliocene specimens recorded by Brunetti & Vecchi (2005, p. 21).

A single specimen from Grund (Austria) was identified as *Retusa* (*Cylichnina*) *pliocrassa*, and drawn by Berger (1953, 101, pl. 19, fig. 92). The relatively large size of the specimen and the illustration do seem to agree with this identification. Unfortunately, Berger's material was not found in the NHMW collections, and this record requires confirmation.

For comparison with congeners see under *C. brocchii*.

Distribution – Middle Miocene: Paratethys, Austria (Berger, 1953). Lower Pliocene: central Mediterranean, Italy (Sacco, 1897; Ferrero Mortara *et al*., 1984; Cavallo & Repetto, 1992; Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin (this paper), France (Chirli & Richard, 2008); central Mediterranean, Italy (Bogi & Cauli, 1998; Brunetti & Vecchi, 2005).

Family Diaphanidae Odhner, 1914 (1857)
Genus *Diaphana* Brown, 1827

Type species (by subsequent designation, Hermannsen, 1847) – *Diaphana candida* Brown, 1827 (= *Diaphana minuta* Brown, 1827), present-day, British Isles.

1827 *Diaphana* Brown, pl. 38.
1846 *Amphisphyra* Lovén, p. 142. Type species (by subsequent designation, Hermannsen, 1847): *Diaphana pellucida* Brown, 1827, present-day, British Isles.
1854 *Physema* H. Adams & A. Adams, p. 21. Type species (by monotypy): *Bulla hiemalis* Couthouy, 1839, present-day, Massachusetts, USA.
1895 *Austrodiaphana* Pilsbry, p. 287. Type species (by monotypy): *Diaphana brazieri* Angas, 1877, present-day, New South Wales, Australia.
1996 *Prodiaphana* Chaban, p. 140. Type species (by original designation): *Diaphana makarovi* Gorbunov, 1946, present-day, Arctic.

***Diaphana minuta* Brown, 1827**
Plate 43, fig. 1

*1827 *Diaphana minuta* Brown, pl. 38 figs 7, 8.
1827 *Diaphana candida* Brown, pl. 38 figs 13, 14.
1834 *Bulla hyalina* Turton, p. 353.
1839 *Bulla nana* S.V. Wood, p. 461, pl. 5, fig. 1.
1840 *Bulla debilis* Gould, p. 196.
1841 *Bulla debilis* Gould – Gould, p. 164, fig. 95.
1848 *Bulla nana* S. Wood – Wood, p. 178, pl. 21, fig. 13.
1865 *Amphisphyra expansa* Jeffreys, p. 330.
1867 *Utriculus expansus* Jeffreys, p. 426.
1878 *Diaphana hyalina* Turt. – G.O. Sars, p. 289, pl. 18, fig. 1.
1878 *Diaphana expansa* Jeffr. – G.O. Sars, p. 289, pl. 18, fig. 2, pl. 11, fig. 10.
1893 *Diaphana debilis* Pilsbry, p. 281, pl. 59, fig. 27.
1893 *Diaphana minuta* Brown – Pilsbry, p. 283, pl. 26, figs 70, 71.
1893 *Diaphana expansa* Jeffreys – Pilsbry, p. 284, pl. 26, fig. 69.
1923 *Diaphana hyalina* (Turton) – Harmer, p. 810, pl. 63, fig. 21.
1959 *Diaphana* (*Diaphana*) *minuta* (T. Brown) – Zilch, p. 35, fig. 111.
1965 *Diaphana minuta* Brown, 1827 – Van Regteren Altena *et al.*, p. 47, pl. 21, fig. 204.
1984 *Diaphana minuta* Brown, 1827 – A.W. Janssen, p. 377, pl. 19, fig. 7.
1988 *Diaphana minuta* Brown, 1827 – T.E. Thompson (*partim*), p. 28, fig. 5a-d.
1997 *Diaphana minuta* Brown, 1827 – Marquet, p. 112, pl. 12, fig. 1.
1998 *Diaphana minuta* Brown, 1827 – Marquet, p. 211, fig. 182.
1998 *Diaphana minuta* Brown, 1827 – Schiøtte, p. 96, figs 13, 18F-H.
1999 *Diaphana minuta* Brown, 1827 – Ardovini & Cos-

signani, p. 82, unnumbered fig. top.
2005 *Diaphana minuta* Brown, 1827 – Repetto *et al*., p. 255, fig. 1120.
2011 *Diaphana minuta* Brown, 1827 – Cossignani & Ardovini, p. 37, 369, unnumbered fig.
2011 *Diaphana minuta* Brown, 1827 – Gofas *et al*., p. 403, unnumbered fig. top.
2011 *Diaphana minuta* Brown, 1827 – Hernández *et al*., p. 272, figs 92 P-Q.
2014 *Diaphana minuta* Brown, 1827 – Ohnheiser & Malaquias, p. 509, figs 7A-F.
2018 *Diaphana minuta* Brown, 1827 – Trigo *et al*., p. 372, unnumbered fig.

Material and dimensions – Maximum height 2.6 mm, width 2.1 mm. **V**C: NHMW 2023/0076/0021 (1), NHMW 2023/0076/0022 (1).

Description (based on Estepona material, only first 1.5 teleoconch whorls preserved) – Shell very small, extremely fragile, pentagonal. Protoconch low mammillate, heterostrophic, just over one whorl visible. Spire flattened, spire whorl convex, separated by narrowly impressed, linear suture. Last whorl roundly angled at shoulder placed at level of suture, convex below, periphery mid-height, surface smooth, except for fine axial growth lines. Aperture entire height of shell, adapical half narrow, abapical half wide; outer lip simple, extending slightly above aperture adapically, flared abapically. Columella slightly twisted. No columellar or parietal callus developed. Small umbilical chink.

Discussion – This species in the extant faunas was thoroughly reviewed by Schiøtte (1998) and Ohnheiser & Malaquias (2014). It is found from the intertidal down to 350 m (T.E. Thompson, 1988; Ohnheiser & Malaquias, 2014) in a wide range of habitats (Schiøtte, 1998). In Estepona it is found exclusively in the deeper water assemblage of Velerín carretera. However, this is probably due to taphonomic bias due to its extreme fragility. Even in the fine Velerín carretera sandy clays it is almost impossible to collect. These sediments need to be broken down by successive dry/soak cycles that almost invariably break the shell. In the rare event of one surviving this process, they break at the finest touch with entomological tweezers or a fine brush. Therefore, the species is likely to be more common than indicated by the material at hand. Similarly, fossil records are scarce probably for the same reasons.
Today the species lives in fine sands and shell grit on the outer continental shelf to bathyal habitats (Gofas *et al*., 2011). In Estepona it is found only in the deeper water assemblages.

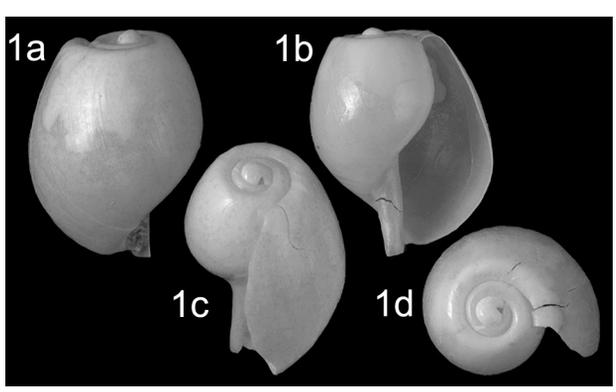

Plate 43. *Diaphana minuta* Brown, 1827; 1. NHMW 2023/0076/0021, height 2.6 mm, width 2.1 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Distribution – Middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (A.W. Janssen, 1984). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848). Upper Pliocene: Atlantic, North Sea Basin, Oorderen Sands, Belgium (Marquet, 1997, 1998), The Netherlands (Van Regteren Altena *et al*., 1965); western Mediterranean, Estepona Basin (this paper). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1923). Pleistocene (indet.): Atlantic, Ireland, Scotland (Harmer, 1923). Present-day: Circumpolar from New England, the Canadian Archipelago, over Greenland, Iceland, the Barents Sea, White Sea, Kara Sea, Laptev Sea to the east Siberian Seas, down to Japan, British Columbia, European Atlantic Frantage from Norway, British Isles, Bay of Biscay (Trigo *et al*., 2018), southwards to Canary Islands (T.E. Thompson, 1988; Schiøtte , 1998; Høisæter *et al*., 2001; Sneli *et al*., 2005; Hernández *et al*., 2011; Ohnheiser & Malaquias, 2014), into western Mediterranean (Repetto *et al*., 2005; Gofas *et al*., 2011), central Mediterranean (Ardovini & Cossignani, 1999; Cossignani & Ardovini, 2011).

Superfamily Haminoeidea Pilsbry, 1895
Family Haminoeidae Pilsbry, 1895
Genus *Haminoea* Turton & Kingston, 1830

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

1830 *Haminoea* Turton & Kingston, p. F8.

For generic synonymy see Ceulemans *et al*. (2018, p. 121).

***Haminoea* '*hydatis*' (Linnaeus, 1758)**
Plate 44, figs 1-2

*1758 *Bulla hydatis* Linnaeus, p. 726.
1975 *Haminea* (*Haminea*) *hydatis* (Linné) – Fekih, p. 145, pl. 42, fig. 15.
1979 *Haminaea* [*sic*] *hydatys* [*sic*] (Linnaeus, 1758) – Nordsieck & García-Talavera, p. 176, pl. 44, fig. 35.
2005 *Haminoea hydatis* (Linné, 1758) – Repetto *et al*., p. 261, fig. 1156.
2011 *Haminoea hydatis* (Linnaeus, 1758) – Cossignani & Ardovini, p. 37, 375, unnumbered fig.

2011 *Haminoea hydatis* (Linnaeus, 1758) – Gofas *et al*., p. 418, unnumbered fig. top.
2011 *Haminoea hydatis* (Linne, 1758) – Chirli & Linse, p. 225, pl. 89, fig. 2.
2018 *Haminoea hydatis* (Linnaeus, 1758) – Ceulemans *et al*., p. 125, pl. 7, fig. 12 (*cum syn*.).
2018 *Haminoea hydatis* (Linneo, 1758) – Trigo *et al*., p. 374, unnumbered fig.
2022 *Haminoea hydathis* [*sic*] (Linnaeus, 1758) – Brunetti, p. 80, fig. 190.

Material and dimensions – Maximum height 10.5 mm, width 8.1 mm. **CO**: RGM.1404265 (1), NHMW 2023/0076/0026 (1), NHMW 2023/0076/0027 (11). **EL**: RGM.1404266 (16), NHMW 2023/0076/0028 (5).

Description – Shell medium sized, relatively fragile, ovate, strongly inflated, only last whorl visible. Last whorl strongly globose, apex roundly truncated, shallowly and narrowly umbilicate, surface smooth. Aperture entire length of shell, narrow adapical half, widening rapidly abapically. Outer lip extending short distance above apex adapically, convex below, rounded abapically. Columella short, thickened, moderately excavated. Parietal callus not present.

Discussion – According to Malaquias & Cervera (2006) among the seven native European species of *Haminoea* Turton & Kingston, 1830, only two are distinguishable from their shells; *H. orbignyana* (Férussac, 1822) which has a pyriform shell with a broad aperture, and *H. **navicula*** (da Costa, 1778) which has the shell surface covered by fine but visible spiral striae. All remaining five species have smooth shells with a more or less rounded shape. Therefore, our assignment of the Estepona fossils to *H. hydatis* is merely tentative.
In shells with an abraded surface, *H. navicula* and *H. hydatis* (Linnaeus, 1758) cannot be reliably separated, although *H. navicula* is said to be larger, more truncated, with a wider aperture and a more excavated columella. Cerulli-Irelli (1910, p. 229) considered *H. navicula* to be the fully adult form of *H. hydatis*, but the specimen illustrated (1910, pl. 35, fig. 10) is large with a deeply excavated columella and represents *H. navicula*.
Today *H. hydatis* lives in sandy and muddy bottoms in sheltered environments from the intertidal zone to a few metres depth (Trigo *et al*., 2018). In Estepona it is also found exclusively in the shallower water deposits.

Distribution – Lower Pliocene: Atlantic, northwestern France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011; Brunetti, 2022), central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Pleistocene: English Channel, England (Harmer, 1923); central Mediterranean, Italy (Ruggieri & Greco, 1965). Present-day: Atlantic southern coast of British Isles, Atlantic coast of France (T.E. Thompson, 1988), Bay of Biscay (Trigo *et al*., 2018), Madeira, Canaries (Nordsieck & García-Talavera, 1979), Ascension Islands and St. Helena of coast of West Africa (Poppe & Goto, 1991), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Haminoea navicula **(da Costa, 1778)**
Plate 45, fig. 1

*1778 *Bulla navicula* da Costa, p. 28, pl. 1, fig. 10.
1975 *Haminea* (*Haminea*) *navicula* Da Costa [*sic*] – Fekih, p. 145, pl. 42, fig. 14.
2005 *Haminoea navicula* (Da Costa, 1778) – Repetto *et al*., p. 261, fig. 1157.
2011 *Haminoea navicula* (da Costa, 1778) – Cossignani & Ardovini, p. 37, 375, unnumbered fig.
2011 *Haminoea navicula* (da Costa, 1778) – Gofas *et al*., p. 418, unnumbered fig. bottom.
2018 *Haminoea navicula* (da Costa, 1778) – Trigo *et al*., p. 376, unnumbered fig.
2020 *Haminoea navicula* (Da Costa, 1778) – Landau *et al*., p. 273, pl. 22, figs 1, 2 (*cum syn*.).

Material and dimensions – Height 11.3 mm, width 8.7 mm. **EL**: NHMW 2023/0076/0029 (1).

Description – Shell medium sized, relatively fragile, ovate,

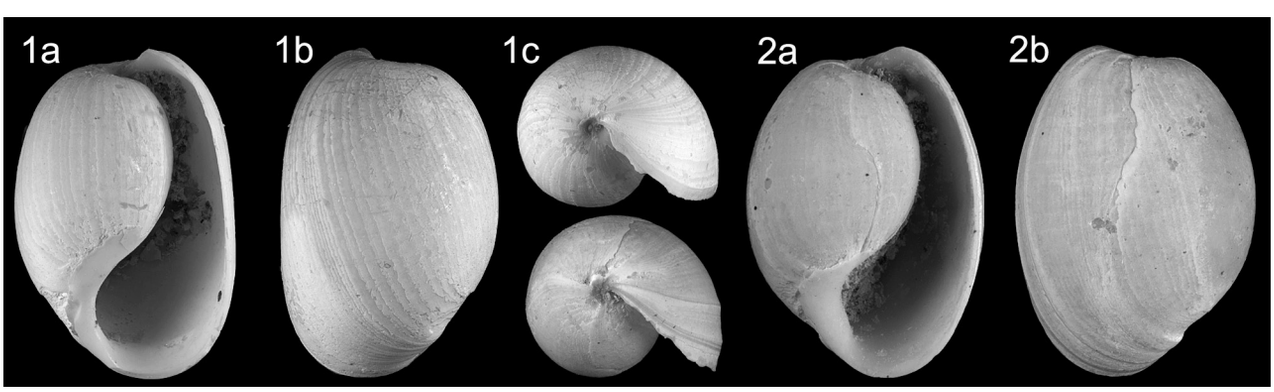

Plate 44. *Haminoea* '*hydatis*' (Linnaeus, 1758); 1. RGM.1404265, height 8.6 mm, width 5.8 mm; 2. NHMW 2023/0076/0026, height 6.4 mm, width 4.6 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Plate 45. *Haminoea navicula* (da Costa, 1778); 1. NHMW 2023/0076/0029, height 11.3 mm, width 8.7 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

strongly inflated, only last whorl visible. Last whorl strongly globose, apex truncated, shallowly and narrowly umbilicate, surface smooth, except for axial growth lines (fine spiral sculpture typical for the species abraded). Aperture entire length of shell, relatively narrow adapical half, widening rapidly abapically. Outer lip extending short distance above apex adapically, convex below, rounded abapically. Columella short, thickened, strongly excavated. Parietal callus reduced to thin callus wash on medial side aperture.

Discussion – A single specimen from El Lobillo is attributed to *Haminoea navicula* (da Costa, 1778), being larger than *H. hydatis* (Linnaeus, 1758), with a more truncated apex and a more deeply excavated columella. The fine spiral sculpture typical for the species is abraded. For further discussion see above under *H. hydatis*.
Today *H. navicula* is found in similar habitats to *H. hydatis*, sheltered environments in sandy and muddy bottoms from the intertidal zone to a few metres depth (Trigo *et al*., 2018). In Estepona it is also found exclusively in the shallower water deposits.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1952a). Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964; Landau *et al*., 2020). Lower Pliocene: central Mediterranean, Italy (Chirli, 2013), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Present-day: eastern Atlantic from British Isles to Gibraltar, and Black Sea (Talavera *et al*., 1987), Canaries, Ascension Island and St. Helena (T.E. Thompson, 1988), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Weinkauffia* Weinkauff, 1873

Type species (by monotypy) – *Scaphander gibbulus* Jeffreys, 1856 [= *Weinkauffia turgidula* (Forbes, 1844)], present-day, Italy.

1873 *Weinkauffia* Weinkauff, p. 27.
1936 *Limulatys* Iredale, p. 328, Type species (by original designation): *Limulatys reliquus* Iredale, 1936, present-day, New South Wales, Australia.
1936 *Tepidatys* Iredale, p. 329. Type species (by monotypy): *Tepidatys tremens* Iredale, 1936, present-day, New South Wales, Australia.

***Weinkauffia turgidula* (Forbes, 1844)**
Plate 46, figs 1-2

1840 *Bulla diaphana* Aradas & Maggiore, p. 359 (*non* Montagu, 1803).
*1844 *Bulla turgidula* Forbes, p. 188.
1856 *Scaphander gibbulus* Jeffreys, p. 188, pl. 2, figs 20, 21.
1872b *Atys canariensis* E.A. Smith, p. 346.
1893 *Weinkauffia diaphana* (Aradas et Maggiore) – Vayssière, p. 92, pl. 4, figs 1-8.
1950 *Weinkauffia diaphana* Aradas – Nicklès, p. 137, fig. 280.
1959 *Weinkauffia diaphana* (Aradas) – Zilch, p. 41, fig. 133.
1976a *Weinkauffia semistriata* (Réquiem) – Pavia, p. 115, pl. 12, fig. 7.
1983 *Weinkauffia turgidula* (Forbes, 1844) – Aimone & Ferrero Mortara, p. 298, pl. 1, fig. 13.
1992 *Weinkauffia turgidula* (Forbes, 1844) – Cavallo & Repetto, p. 168, fig. 483.
2001 *Weinkauffia turgidula* (Forbes, 1844) – Cachia *et al*., p. 133, pl. 21, fig. 4.
2004 *Weinkauffia turgidula* (Forbes, 1844) – Ardovini & Cossignani, p. 243, unnumbered fig.
2005 *Weinkauffia turgidula* (Forbes, 1844) – Repetto *et al*., p. 262, fig. 1163.
2011 *Weinkauffia turgidula* (Forbes, 1844) – Cossignani & Ardovini, p. 37, 376, unnumbered fig.
2011 *Weinkauffia turgidula* (Forbes, 1844) – Gofas *et al*., p. 421, unnumbered fig. top.
2011 *Weinkauffia turgidula* (Forbes, 1844) – Hernández *et al*., p. 279, fig. 93 P.
2013 *Weinkauffia turgidula* (Forbes, 1884 [*sic*]) – Chirli, p. 63, pl. 14, figs 3, 4.

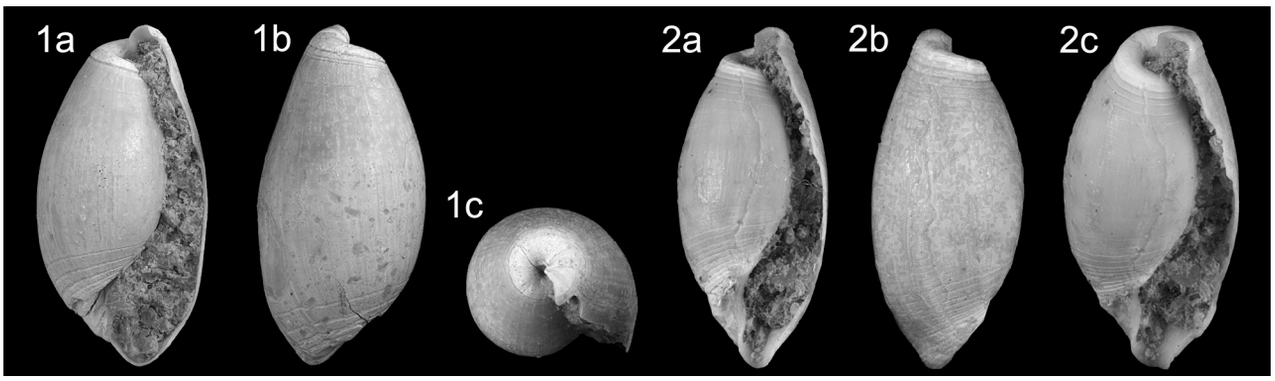

Plate 46. *Weinkauffia turgidula* (Forbes, 1844); 1. RGM.1404187, height 6.7 mm, width 3.4 mm. El Lobillo. 2. NHMW 2023/0076/0030, height 5.7 mm, width 2.5 mm (digital images), Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Material and dimensions – Maximum height 6.7 mm, width 3.4 mm. **CO**: NHMW 2023/0076/0030 (1). **EL**: RGM.1404187 (1).

Description – Shell small, medium-thickness, elongate ovate-subcylindrical, only last whorl visible. Last whorl elongate, somewhat inflated mid-whorl, rounded at base; apex narrowly truncated, umbilicus of mid-depth and width, delimited by round-edged elevated crest. Sculpture of a few spiral grooves just below apex weakening abapically, and over base, strengthening abapically. Aperture longer than shell, very narrow posterior and mid-section, widening anteriorly. Outer lip narrowly alate apically, extending some distance above apex, weakly convex below, roundly pointed abapically. Columella short, narrow, twisted by moderate fold abapically, bordering broad umbilical chink medially. Columellar and parietal callus not developed.

Discussion – *Weinkauffia turgidula* (Forbes, 1844) is extremely uncommon in the Estepona assemblages where it is found only in the shallow water deposits of Velerín conglomerates and El Lobillo. The specimens illustrated (Pl. 46, figs 1, 2) seem narrower than usual, but this is probably misleading, as in both specimens the last portion of the aperture is missing, which if complete would give the shell a more inflated aspect.
Today this species lives in littoral muddy sands between 10-40 m depth (Gofas *et al*., 2011).

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2013); central Mediterranean, Italy (Pavia, 1976a). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Aimone & Ferrero Mortara, 1983; Cavallo & Repetto, 1992). Present-day: Atlantic, Iberian Peninsula, Madeira, Canary Islands (Nordsieck & García-Talavera, 1979; Segers *et al*., 2009; Hernández *et al*., 2011), to Senegal (Ardovini & Cossignani, 2004) and Republic of Guinea (Nicklès , 1950), into entire Mediterranean (Cachia *et al*., 2001; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Superfamily Philinoidea Gray, 1850 (1815)
Family Philinidae Gray, 1850 (1815)
Subfamily Hermaniinae Chaban, Ekimova, Schepetov, Kohnert, Schrödl & Chernyshev, 2019
Genus *Hermania* Monterosato, 1884

Type species (by monotypy) – *Bulla scabra* Müller, 1784, present-day, Norway.

1884 *Hermania* Monterosato, p. 147.

***Hermania scabra* (Müller, 1784)**
Plate 47, fig. 1

*1784 *Bulla scabra* Müller, p. 90, figs 1-3.
1952 *Philine scabra* (Müller, 1776 [*sic*]) – Van der Burg, p. 52, pl. 3, figs 8-10.
1979 *Philine scabra* (O.F. Müller, 1776 [*sic*]) – Nordsieck & García-Talavera, p. 171, pl. 43, fig. 13.
2004 *Philine scabra* (Müller, 1784) – Campani, p. 7, unnumbered fig. bottom.
2011 *Philine scabra* (Müller, 1784) – Cossignani & Ardovini, p. 38, 378, unnumbered fig.
2011 *Philine scabra* (Müller, 1784) – Gofas *et al*., p. 411, unnumbered fig. bottom.
2013 *Philine scabra* (Müller, 1784) – Landau *et al*., p. 330, pl. 77, fig. 4 (*cum syn*.).
2016 *Philine scabra* (Müller, 1784) – Negri & Corselli, p. 84, figs 19k-n.
2022 *Philine catena* (Montagu, 1803) – Brunetti, p. 80, fig. 189 [*non* Montagu, 1803].

Material and dimensions – Maximum height 6.6 mm, width 3.8 mm. **VC**: RGM.1404247 (1), RGM.1404305 (10), NHMW 2023/0076/0138 (20). **CO**: RGM.1404248 (5), NHMW 2023/0076/0143 (11). **EL**: RGM.1404298 (5). **PA**: NHMW 2023/0076/0142 (3).

Description – Shell small, relatively solid for genus, subquadrate, with flattened spire. Last whorl inflated, subcylindrical, widening abapically, apex relatively narrowly and roundly truncated, whorl profile almost straight

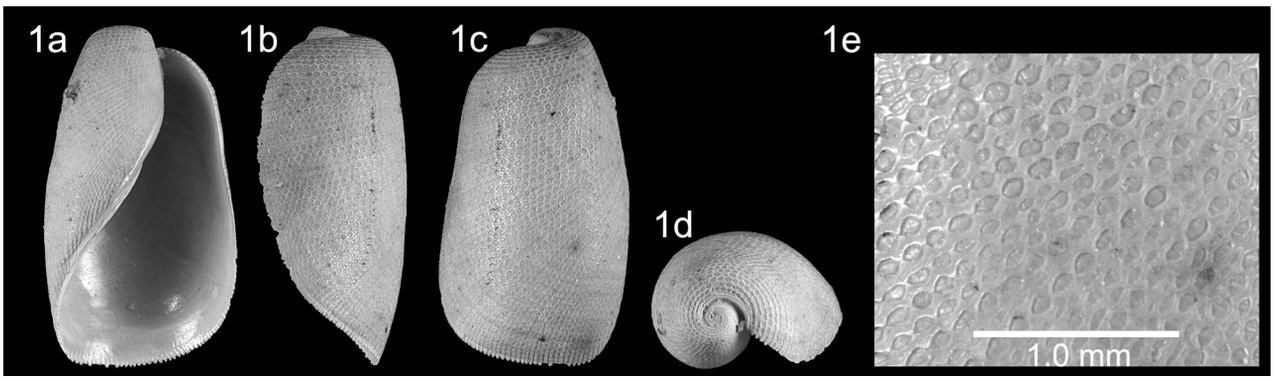

Plate 47. *Hermania scabra* (Müller, 1784); 1. RGM.1404247, height 6.6 mm, width 3.8 mm, 1e, detail of surface sculpture, (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

and widening below, squarely rounded at base. Sculpture of regular punctate spiral grooves; punctuations large, some disconnected, others connected by narrow groove. Aperture 92% of total length, moderately broad in upper quarter, widening abapically; outer lip not rising above apex, straight below, roundly angled abapically. Columella much reduced, narrow. Parietal callus very narrow.

Discussion – In their revision of the genus *Philine* Ascanius, 1772, using both anatomical and molecular data, Ohnheiser & Malaquias (2013, fig. 33) showed that there was no justification for considering *Hermania* Monterosato, 1884 a separate genus. However, based on molecular data Oskars *et al*. (2015) showed *Philine sensu lato* to be paraphyletic and later Chaban *et al*. (2015) based on the shell surface sculpture and anatomical characters reassigned *Philine scabra* to the genus *Hermania* arguing that the species was distinct from all other *Philine* species. More recently, Moles *et al*. (2019) using molecular phylogenetics confirmed this taxonomic assignment.
Hermania scabra (Müller, 1776) differs from *Philine catena* (Montagu, 1803) in having a slenderer shell and in its dorsal sculpture, which is composed of a fan of spiral dots rather than chains (Pl. 47, fig. 1e). For discussion on fossil populations see Landau *et al*. (2013, p. 330).
Today the species lives from the littoral zone in its more northern distribution to the bathyal zone in its southern distribution (Gofas *et al*., 2011). In Estepona it is found both in the shallow and deeper water assemblages.
Assignment of Middle Miocene shells from the Paratethys to this species by Berger (1953) will need confirmation as the specimens cannot, at present, be found.

Distribution – Middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (A.W. Janssen, 1984). Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953), Hungary (Csepreghy-Meznerics, 1952; Strausz, 1962, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): Cacela Basin, Portugal (NHMW collection). Lower Pliocene: North Sea Basin, England (S.V. Wood, 1848; Harmer, 1923), Belgium (Glibert, 1960b; Marquet, 1997b), The Netherlands (Van der Burg, 1952); northeastern Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011; Brunetti, 2022); western Mediterranean, NE Spain (Martinell, 1982), Roussillon Basin, France (Chirli & Richard, 2008), Tunisia (Fekih, 1975). Upper Pliocene: North Sea Basin, The Netherlands (Van der Burg, 1952); Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Chirli, 2013). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Present-day: northeastern Atlantic, Iceland, Norway, British Isles (T.E. Thompson, 1988), south to West Africa, Madeira, Canaries (Nordsieck & García-Talavera, 1979), Iceland (Poppe & Goto, 1991), entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011; Negri & Corselli, 2016).

Subfamily Philininae Gray, 1850 (1815)
Genus *Philine* Ascanius, 1772

Type species (by monotypy) – *Philine quadripartita* Ascanius, 1772, present-day, Norway.

1772 *Philine* Ascanius, p. 331.

For generic synonymy see Landau *et al*. (2020, p. 274), except the genus *Hermania* Monterosato, 1884 is removed from that synonymy (see above).

***Philine catena* (Montagu, 1803)**
Plate 48, figs 1-2

*1803 *Bulla catena* Montagu, p. 215, pl. 7, fig. 7.
1979 *Philine catena* (Montagu, 1803) – Nordsieck & García-Talavera, p. 171, pl. 43, fig. 15.
2001 *Philine* (*Hermania*) *catena* (Montagu, 1803) – Silva, p. 586, pl. 27, figs 17-19.
2004 *Philine catena* (Montagu, 1803) – Campani, p. 5, unnumbered fig. top.
2005 *Philine catena* (Montagu, 1803) – Repetto *et al*., p. 263, fig. 1166.

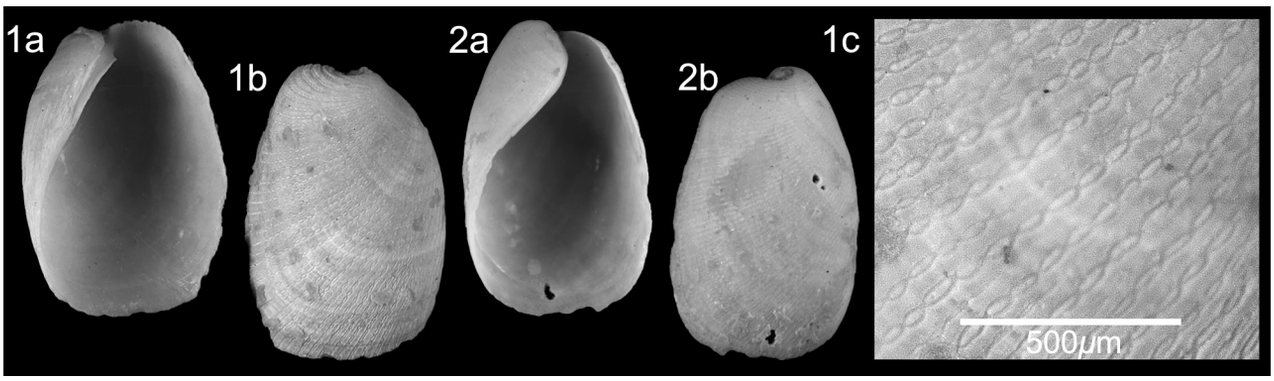

Plate 48. *Philine catena* (Montagu, 1803); 1. RGM.1404249, height 2.7 mm, width 1.8 mm, 1c, detail of surface sculpture; 2. NHMW 2023/0076/0137 (1), height 3.7 mm, width 2.4 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

2011 *Philine catena* (Montagu, 1803) – Cossignani & Ardovini, p. 38, 377, unnumbered fig.
2011 *Philine catena* (Montagu, 1803) – Gofas *et al*., p. 412, unnumbered fig. top.
2011 *Philine catena* (Montagu, 1803) – Hernández *et al*., p. 280, fig. 93 U.
2013 *Philine catena* (Montagu, 1803) – Landau *et al*., p. 329, pl. 77, fig. 2 (*cum syn*.).
2018 *Philine catena* (Montagu, 1803) – Trigo *et al*., p. 381, unnumbered fig.
2020 *Philine catena* (Montagu, 1803) – Landau *et al*., p. 275, pl. 21, figs 1, 2 (*cum syn*.).

non 2022 *Philine catena* (Montagu, 1803) – Brunetti, p. 80, fig. 189 [= *Philine scabra* (Müller, 1784)].

Material and dimensions – Maximum height 3.7 mm, width 2.4 mm. **EL**: RGM.1404249 (1), NHMW 2023/0076/0137 (1).

Description – Shell very small, relatively fragile, ovate, with flattened spire. Last whorl inflated, ovate, apex roundly truncated, whorl profile convex below, rounded at base. Sculpture of regular, chain-like spiral grooves; the links small, elongated and connected. Aperture total height of shell, moderately broad in upper quarter, widening abapically; outer lip rising slightly above apex to slightly below, convex below, rounded abapically. Columella much reduced, narrow. Parietal callus very narrow.

Discussion – *Philine catena* (Montagu, 1803) is easily distinguished by its oval shape and very distinctive sculpture, which consists of a fan of spiral chains, composed of interconnected links or rings. *Philine iris* Tringali, 2001 from the present-day western Mediterranean and adjacent Atlantic is closely similar but differs in having the chain-like sculpture composed of smaller, more rounded links.
Philine catena is uncommon in the Estepona assemblages and found only in the shallower water assemblage of El Lobillo. The shells are small, similar in size to other Pliocene fossil and present-day faunas (3.2-3.7 mm height).Today it seems to have a wide bathymetric range (low tide-2000m) (Ohnheiser & Malaquias, 2013, p. 280). The Middle Miocene Paratethyan record of Berger (1953, p. 114, pl. 18, fig. 82) needs confirmation, as we were not able to find Berger's material.

Distribution – *Distribution* – Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene (Tortonian): Atlantic, NW France (Landau *et al*., 2020). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848); western Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); central Mediterranean, Italy (Sacco, 1897; Chirli, 2013; Brunetti & Cresti, 2018). Lower Pleistocene: central Mediterranean, Italy (Ruggieri & Greco, 1965); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Lofoten, British Isles (T.E. Thompson, 1988), southwards along the entire coast of Norway (Høisæter *et al*., 2001; Ohnheiser & Malaquias, 2013), down to the British Isles, Bay of Biscay (Trigo *et al*., 2018), to Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*., 2009), Canary Islands (Nordsieck, 1972b; Nordsieck & García-Talavera, 1979; Van der Linden, 1995; Hernández *et al*., 2011), into western Mediterranean (Repetto *et al*., 2005; Gofas *et al*., 2011), central Mediterranean (Cossignani & Ardovini, 2011).

Philine condensa Van der Linden, 1995

Plate 49, fig. 1

*1995 *Philine condensa* Van der Linden, p. 71, figs 8, 9, 16.
?2001 *Philine condensa* Van der Linden, 1995 – Tringali, p. 219, 220, fig. 25.
2017 *Philine condensa* Van der Linden, 1995 – Crocetta & Tringali, p. 1500, fig. 3F.

Material and dimensions – Maximum height 3.2 mm, width 2.9 mm. **VC**: RGM.1404242 (1), NHMW 2023/0076/0084 (14).

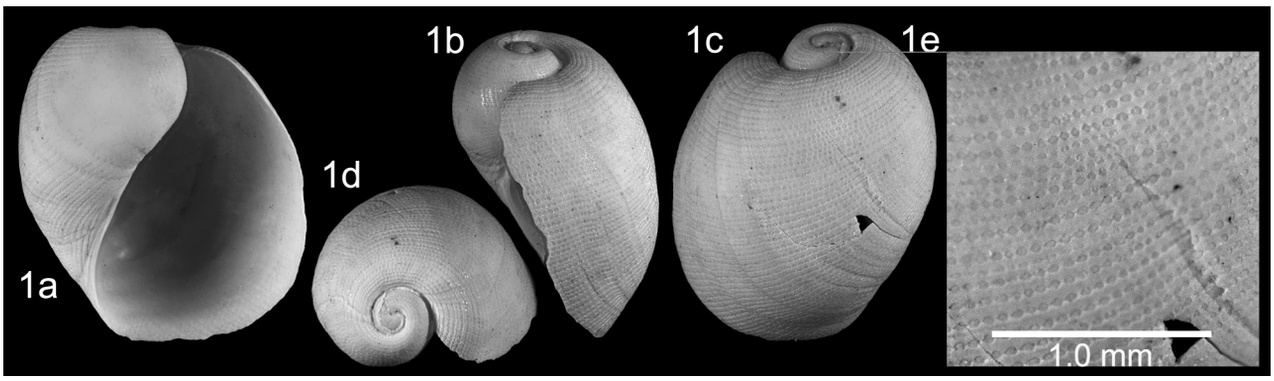

Plate 49. *Philine condensa* Van der Linden, 1995; 1. RGM.1404242, height 3.2 mm, width 2.9 mm, 1e, detail of surface sculpture (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Description – Shell very small, fragile, roundish-oval, with broad, flattened spire. Protoconch about 1.2 depressed whorls. Junction with teleoconch marked by scar and beginning of adult sculpture. Teleoconch of 1.25 rapidly expanding whorls separated by impressed, deeply and narrowly canaliculate suture. Last whorl entire length of shell, strongly inflated, evenly rounded, bearing sculpture of numerous, close-set pitted grooves, somewhat irregular in width, but roughly equal in width to their interspaces; punctuations small, oval, separated from each other by narrow groove. Aperture 90% of total height, moderately narrow in upper fifth, rapidly widening abapically; outer lip horizontal adapically, strongly convex below, expanded in abapical half. Columella much reduced, very narrow. No columellar or parietal callus developed.

Discussion – *Philine condensa* Van der Linden, 1995 is most like *P. striatula* Monterosato, 1874 from the present-day Mediterranean and Atlantic coast of West Africa, but that species differs in being slightly larger, the flattened apex in both species is narrower in *P. striatula*, and the grooves are finer, more numerous, with smaller punctuations (see Crocetta & Tringali, 2017, figs 3A-B). *Philine calva* Van der Linden, 1995, also described from the Azores and Canary Islands is considered a junior subjective synonym of *P. striatula* author, year (Segers *et al*., 2009; Crocetta & Tringali, 2017).
Philine condensa was described from deeper waters around the Canary Islands and Azores (330-620 m; Van der Linden, 1995, p. 71). Although it was reported from the present-day Mediterranean of Palermo based on four shells (Tringali, 2001), Crocetta & Tringali (2017) questioned this indentification based on the absence of follow-up records. In Estepona it is found in the deeper water assemblage of Velerín carretera. This is the first fossil record for the species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper). Present-day: Canary Islands, Azores (Van der Linden, 1995), ?central Mediterranean (Tringali, 2001; Crocetta & Tringali, 2017).

***Philine ligustica* (Sacco, 1897)**
Plate 50, fig. 1

*1897 *Philine* (*Hermania*) *ventrosa* var. *ligustica* Sacco, p. 54, pl. 4, fig. 45.
2020 *Philine ligustica* (Sacco, 1897) – Landau *et al*., p. 275, pl. 22, figs 1, 2 (*cum syn*.).

Material and dimensions – Maximum height 3.9 mm, width 2.7 mm. **VC**: RGM.1404303 (2), NHMW 2023/0076/0141 (7). **CO**: RGM.1404295 (1), NHMW 2023/0076/0085 (1). **EL**: RGM.1404195 (1), RGM.1404196 (1), NHMW 2023/0076/0139 (3). **VS**: NHMW 2023/0076/0140 (25).

Description – Shell very small, solid for genus, ovate, with relatively coarse chain-like sculpture in spiral lines, only last whorl visible. Last whorl inflated, apex broadly and roundly truncated with small shallow umbilicus, whorl profile slightly pinched just below apex, convex below, rounded at base. Sculpture of regular punctate spiral grooves; punctuations large, oval, separated from each other by narrow groove, narrower than ovals. Aperture length of shell, moderately narrow in upper quarter, widening abapically; outer lip not rising above apex, pinched in upper third, convex below, expanded abapically. Columella much reduced, narrow.

Discussion – For discussion see Landau *et al*. (2020, p. 275).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Landau *et al*., 2020). Lower Pliocene: central Mediterranean, Italy (Sacco, 1897; Brunetti & Cresti, 2018). Upper Pliocene: Atlantic, Mondego Basin, central-west Portugal (NHMW coll.); western Mediterranean, Estepona Basin, Spain (this paper).

***Philine rostrata* (Deshayes, 1830)**
Plate 51, figs 1-4

*1830 *Bullaea rostrata* Deshayes, p. 148.
1895 *Bullaea rostrata* Desh. – Cossmann, p. 127 [dis-

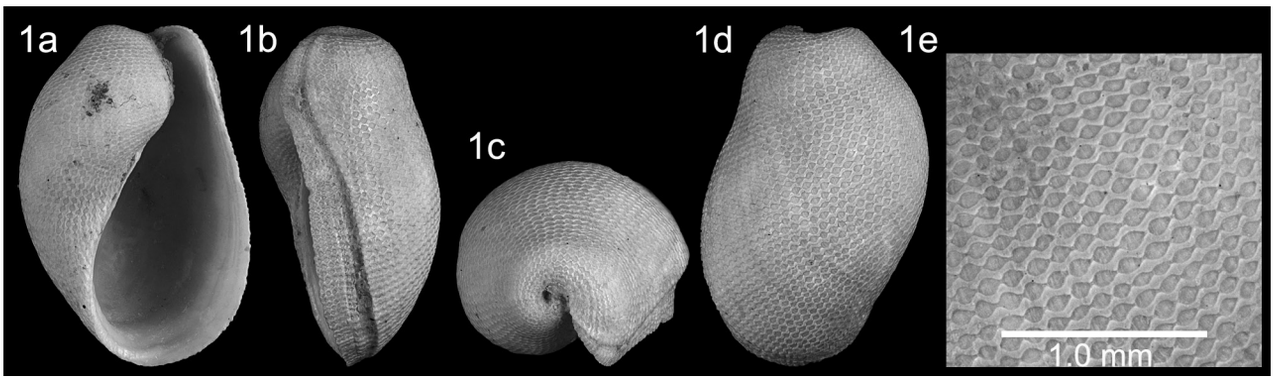

Plate 50. *Philine ligustica* (Sacco, 1897); 1. RGM.1404195, height 3.9 mm, width 2.7 mm, 1e, detail of surface sculpture (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

cussed under *Philine* (*Megistostoma*)].

1897 *Philine* (*Megistostoma*) *rostratum* (Desh.) – Sacco, p. 54, pl. 4, fig. 41.

2011 *Megistostoma rostratum* (Deshayes, 1830) – Sosso *et al*., p. 23, figs 2A-F

2020 *Philine rostrata* (Deshayes, 1830) – Landau *et al*., p. 276, pl. 23, figs 1, 2 (*cum syn*.).

Material and dimensions – Maximum diameter 11.2 mm. **VC**: RGM.1404318 (1), NHMW 2023/0076/0072-0074 (3), NHMW 2023/0076/0075 (2). **PQ**: NHMW 2023/0076/0156 (2).

Description – Shell medium sized, extremely fragile, rounded-auriculiform, dorso-ventrally flattened. Last whorl entire height of shell, rapidly expanding, roundly shouldered adapically, forming weak, rounded keel extending into wing of outer lip; venter greatly reduced to narrow rounded whorl in parietal area. Surface appears smooth, but fine, close-set axial riblets seen under magnification. Outer lip strongly alate apically, extending far above apex, rounded below. Columella and inner lip callus not developed.

Discussion – *Philine rostrata* (Deshayes, 1830) has seldom been recorded. We therefore repeat here the chresonymy and history of the species summarised in Landau *et al*. (2020, p. 276). Originally described by Deshayes (1830), it was based on material from the Piacenzian Pliocene and deposited in the collection of l'École des Mines di Parigi. Sacco (1897, p. 54) stated that the type was not in that collection, and illustrated a photograph sent to him by Cossmann of a specimen from the Pliocene of Gourbesville housed in the collection of l'École des Mines. Sosso *et*

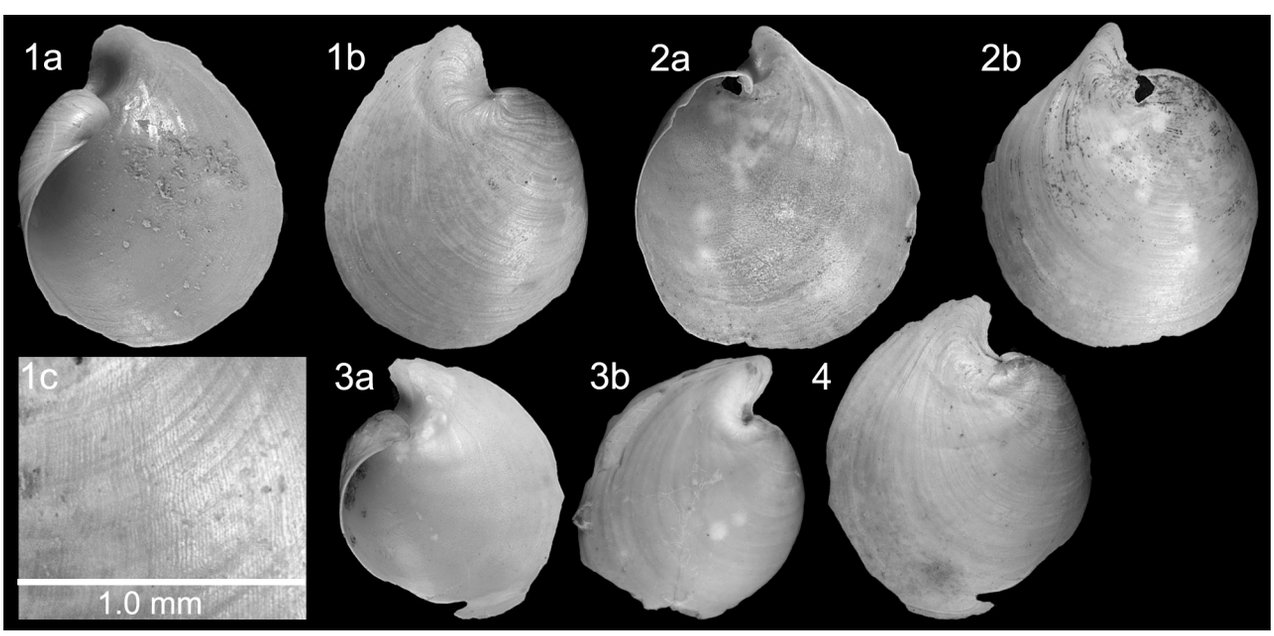

Plate 51. *Philine rostrata* (Deshayes, 1830); 1. NHMW 2023/0076/0072, maximum diameter 4.6 mm, 1c, detail of surface sculpture; 2. NHMW 2023/0076/0073, maximum diameter 11.2 mm; 3. RGM.1404318, maximum diameter 7.1 mm; 4. NHMW 2023/0076/0074, maximum diameter 7.1 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

al. (2011) rediscovered the species in the Zanclean Lower Pliocene deposits of Rio Torsero, Italy, confirming its presence in the Italian Pliocene. Landau *et al*. (2020, p. 276) recorded the species in the Atlantic Tortonian Upper Miocene of NW France). It is likely, therefore, that it is widely distributed in the eastern Atlantic and Mediterranean Upper Miocene and Pliocene, but probably underreported due to the extreme fragility of the shell.
The Estepona specimens are similar in size and profile to the specimen from Rio Torsero illustrated by Landau *et al*. (2020, pl. 23, fig. 2; height 8.8 mm). The axial riblets typical for the species are only preserved on part of the dorsum of one individual from Estepona (Pl. 51. fig. 1c).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Landau *et al*., 2020). Lower Pliocene: central Mediterranean, Italy (Sosso *et al*., 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper). Upper Pliocene-Pleistocene: Atlantic, NW France (Cossmann, 1895; Sacco, 1897).

Family Laonidae Pruvot-Fol, 1954
Genus *Laona* A. Adams, 1865

Type species (by monotypy) – *Laona zonata* A. Adams, 1865, present-day, Japan.

1865 *Laona* A. Adams, p. 324.
1870 *Utriculopsis* M. Sars, p. 177. Type species (by monotypy): *Bulla vitrea* M. Sars, 1866, present-day, Norway.
1884 *Ossiania* Monterosato, p. 147. Type species (by original designation): *Philine scutulum* Lovén, 1846, present-day.
1967 *Rhinodiaphana* Lemche, p. 208. Type species (by monotypy): *Amphisphyra ventricosa* Jeffreys, 1865b, present-day, British Isles.
2009 *Praephiline* Chaban & Soldatenko, p. 206. Type species (by original designation): *Philine finmarchica* M. Sars, 1859, present-day, Norway.

Note – Based on molecular data, Oskars *et al*. (2015) reinstated the family Laonidae Pruvot-Fol, 1954 and genus *Laona* A. Adams, 1865 for philinids with a net-like sculpture covering the dorsum and a parietal wall extending into the aperture.

***Laona quadrata* (S.V. Wood, 1839)**
Plate 52, figs 1-2

*1839 *Bullaea quadrata* S. Wood, p. 462, pl. 7, fig. 1.
1848 *Bullaea quadrata* S. Wood – S.V. Wood, p. 179, pl. 21, fig. 9.
1850 *Philine formosa* Stimpson, p. 334.
1887 *Philine polaris* Aurivillius, p. 371, 380, pl. 3, figs 21, 22, pl. 13, fig. 18.
1878 *Philine quadrata* Wood – G.O. Sars, p. 299, pl. 18, fig. 9, pl. 12, fig. 7.
1895 *Philine quadrata* S. Wood – Pilsbry, p. 19, pl. 5, figs 14-16, pl. 3, fig. 43.
1952 *Philine quadrata* (S. V. Wood, 1839) – Van der Burg, p. 52, pl. 3, fig. 11.
1953 *Philine* (*Ossiania*) *quadrata* (Wood) – Berger, p. 114, pl. 18, fig. 81.
1959 *Laona* (*Ossiania*) *quadrata* (S. Wood) – Zilch, p. 31, fig. 97.
1960 *Philine quadrata* Wood, 1839 – Glibert, p. 25, pl. 4, fig. 30.
1969 *Philine quadrata* (S. Wood, 1839) – Marcus & Marcus, `p. 12, figs 18, 19.
1972b *Laona* (*Ossiania*) *quadrata* (S. Wood, 1839) – Nordsieck, p. 22, pl. OIII, fig. 12.
1981 *Philine quadrata* (S. Wood, 1839) – Biondi & Di Paco, p. 274, pl. 2, fig. 15.
1988 *Philine quadrata* (S. Wood, 1839) – T.E. Thompson, p. 64, fig. 23.
1995 *Philine quadrata* (S. Wood, 1839) – Van der Linden, p. 75, figs 18, 22, 23.
2001 *Philine quadrata* (S.V. Wood, 1839) – Oliverio & Tringali, p. 137, figs 64a-c, 68.
2004 *Philine quadrata* (Wood, S., 1839) – Campani, p. 7, unnumbered fig. middle.
2005 *Philine quadrata* (Wood, S., 1839) – Repetto *et al*., p. 264, unnumbered fig. mid left.
2006 *Philine quadrata* (Wood, 1839) – Marquet & Landau, p. 42, fig. 10/1a-d.
2013 *Philine quadrata* (S. Wood, 1839) – Ohnheiser & Malaquias, p. 303, figs 20A-I, 21A-C.
2016 *Philine quadrata* (Wood, S., 1839) – Negri & Corselli, p. 82, figs 19g-j.

Material and dimensions – Maximum height 9.6 mm, width 6.3 mm. **VC**: RGM.1404244 (1), **CO**: RGM.1404295 (1), NHMW 2023/0076/0088 (20). **EL**: RGM.1404243 (2).

Description – Shell small, fragile, quadrate-oval, with fine chain-like sculpture in spiral lines, only last whorl visible. Last whorl strongly inflated, apex broadly and roundly truncated with small shallow umbilicus, whorl profile diagonally subquadrate with periphery mid-whorl. Sculpture of regular punctate spiral grooves; punctuations small, oval, separated from each other by very short narrow groove that varies from relatively wide to absent. Aperture length of shell, moderately broad in upper quarter, widening greatly abapically; outer lip not rising above apex, almost square in anterior view, roundly angled at periphery. Columella much reduced, very narrow, small protrusion of parietal wall over aperture covered in parietal callus.

Discussion – The specimen from Estepona undoubtedly represent *Laona quadrata* (S.V. Wood, 1839). That species was originally described from the Lower Pliocene North Sea Basin Coralline Crag of England. Marquet & Landau (2006, figs 10/1a-d) illustrated a complete, although slightly abraded specimen from the Lower Pliocene North Sea Basin of Belgium that is almost identical.
Ohnheiser & Malaquias (2013, p. 303, figs 20A-I, 21A-C) identified present-day shells as being conspecific and

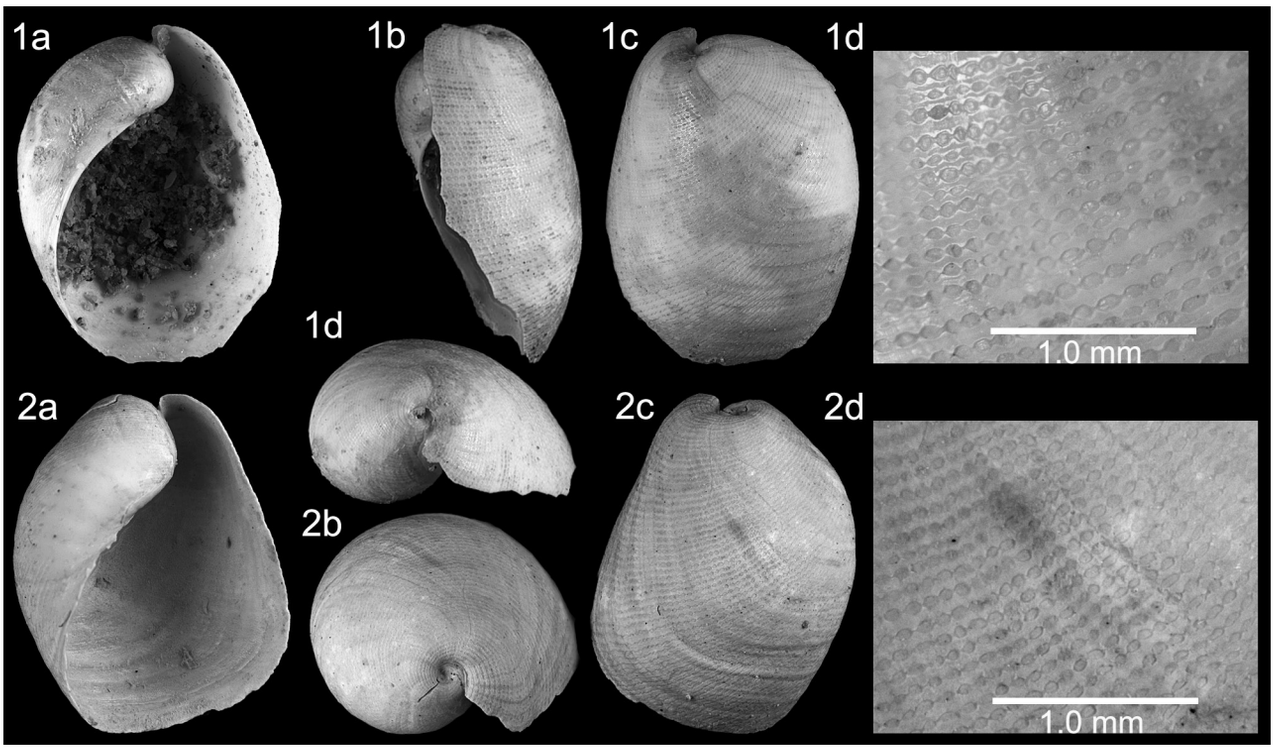

Plate 52. *Laona quadrata* (S.V. Wood, 1839); 1. RGM.1404243, height 7.3 mm, width 5.5 mm, 1e, detail of surface sculpture, El Lobillo. 2. RGM.1404244, height 5.0 mm, width 3.9 mm, 2d, detail of surface sculpture (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

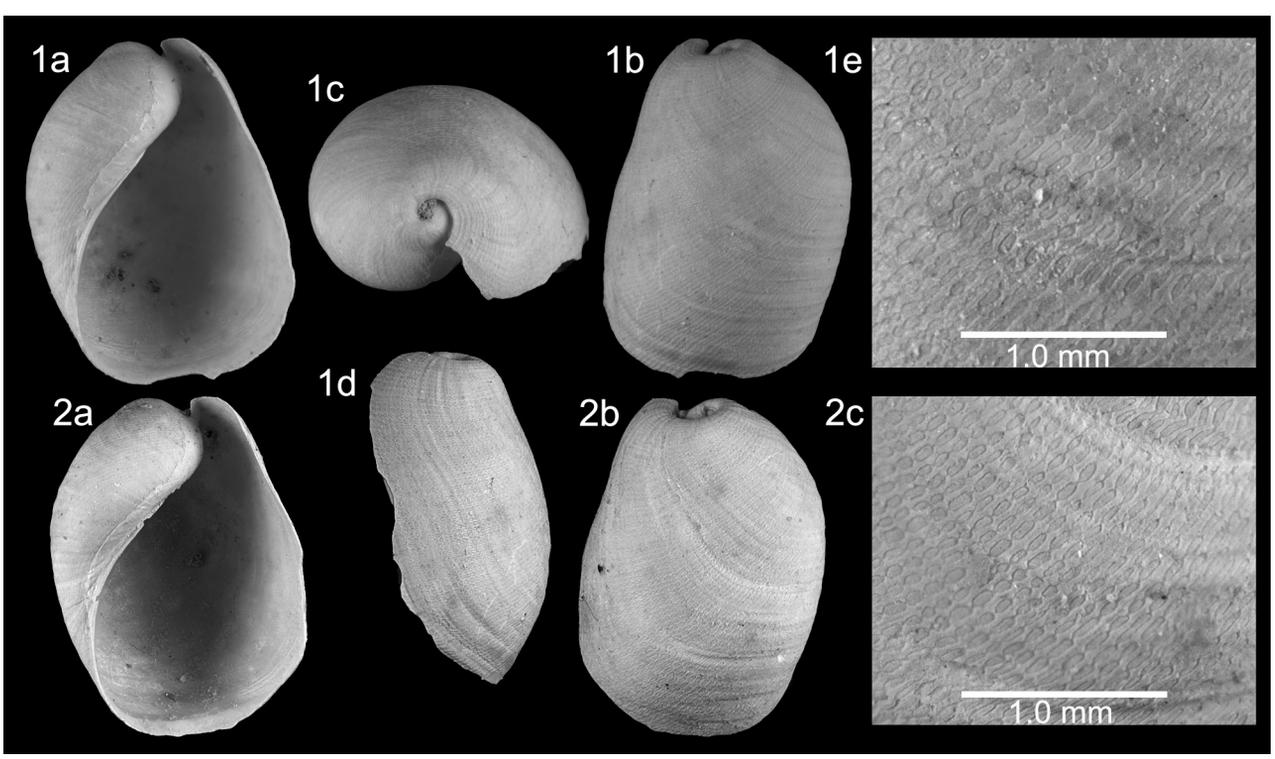

Plate 53. *Laona* cf. *quadrata* (S.V. Wood, 1839); 1. RGM.1404245, height 6.2 mm, width 4.8 mm, 1e, detail of surface sculpture; 2. RGM.1404246, height 5.4 mm, width 4.1 mm, 2d, detail of surface sculpture (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

illustrated a shell with similar quadrate-oval profile and sculpture of fine chains. It differs slightly in that the rows of chains are more widely spaced than in our fossil specimen, and the parietal wall that overhangs the aperture is much narrower in *L. quadrata*. However, there is some variability in these characters.
The Middle Miocene Paratethyan record of Berger (1953, p. 114, pl. 18, fig. 81) needs confirmation, as we were not able to find Berger's material.

Distribution – Middle Miocene: Paratethys, Austria (Berger, 1953). Lower Pliocene: North Sea Basin, Coralline Crag, England (S.V. Wood, 1848), Belgium (Glibert, 1960; Marquet & Landau, 2006). Upper Pliocene: North Sea Basin, The Netherlands (Van der Burg, 1952); western Mediterranean, Estepona Basin, Spain (this paper). Present-day: Amphiatlantic, New England, USA (Pilsbry, 1895; Marcus & Marcus, 1969), eastwards to Greenland and Iceland, the Barents and White Seas, Norway, the Faeroes, British Isles, southwards to Azores, Morocco, and St. Helena (T.E. Thompson, 1988; Van der Linden, 1995; Ohnheiser & Malaquias, 2013), into the Mediterranean (Biondi & Di Paco, 1981; Repetto *et al*., 2005; Negri & Corselli, 2016).

***Laona* cf. *quadrata* (S.V. Wood, 1839)**
Plate 53, fig. 1

Material and dimensions – Maximum height 9.7 mm, width 6.5 mm. **VC**: RGM.1404245-246 (2), RGM.1404308 (6), NHMW 2023/0076/0087 (1). **CO**: NHMW 2023/0076/0086 (7).

Discussion – A few specimens are closely similar in shell profile to *Laona quadrata* (S.V. Wood, 1839), possibly the last whorl is slightly constricted just below the apex, a feature not usually seen in *L. quadrata*, and the outer lip is slightly less expanded, especially in the adapical half. However, they seem to differ in their surface sculpture. *Laona quadrata* has pitted grooves, the punctuations small and rounded, whereas *L.* cf. *quadrata* has more chain-line spirals, the punctuations conspicuously elongated. We are unsure if these specimens fit within the rather wide intraspecific variability of *L. quadrata* or if they represent a separate species.

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

Family Alacuppidae Oskars, Bouchet & Malaqias, 2015
Genus *Roxania* Leach, 1847

Type species (by monotypy) – *Bulla cranchii* Fleming, 1828, present-day, British Isles.

1847 *Roxania* Leach, p. 268.

***Roxania semilaevis* (G. Seguenza, 1880)**
Plate 54, figs 1-2

*1880 *Bulla semilaevis* Jeffr. (M.S.) G. Seguenza, p. 251, pl. 16, fig. 5.
1880 *Diaphana gemma* Verrill, p. 399.
1889 *Bulla semilaevis* Seguenza – Dautzenberg, p. 24, pl. 1, fig. 5.
1897 *Bulla semilaevis* Jeffreys – Locard, p. 57, 60, pl. 1, figs 23-25.
1975 *Roxania* (*?*) *semilaevis* (Seguenza) 1880 – Bouchet, p. 358, pl. 2, fig. g.
1992 *Roxania semilaevis* (G. Seguenza, 1880 ex Jeffreys ms) – Gaglini, p. 167, p. 151, fig. 152.
2005 *Roxania semilaevis* (Seguenza, G. 1880) – Repetto *et al*., p. 267, fig. 1190.
2013 *Roxania semilaevis* (Seguenza, G. 1880) – Chirli, p. 41, pl. 10, figs 7-11.

Material and dimensions – Maximum height 6.0 mm, width 3.3 mm. **VC**: RGM.1404174-175 (2), RGM.1404176 (45), NHMW 2023/0076/0131 (50+). **CO**: RGM.1404283 (10), NHMW 2023/0076/0132 (40). **PA**: NHMW 2023/0076/0144 (9).

Description – Shell small, solid, ovate, only last whorl visible. Last whorl strongly globose, apex rounded, deeply and narrowly umbilicate, bearing punctate spiral cords

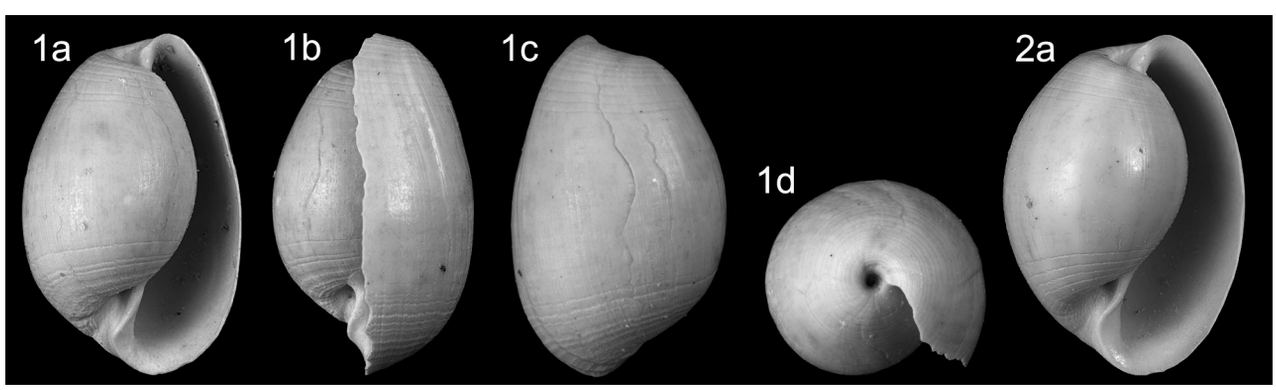

Plate 54. *Roxania semilaevis* (G. Seguenza, 1880); 1. RGM.1404174, height 5.0 mm, width 2.7 mm; 2. RGM.1404175, height 4.6 mm, width 3.2 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

at extremities, middle part of whorl smooth, surface glossy. Aperture entire length of shell, narrow adapical half, widening abapically. Outer lip narrowly alate adapically, extending above apex, convex below, slightly expanded abapically. Columella short, strongly thickened, everted, no parietal callus. Umbilicus deep, moderately wide, round edged.

Discussion – *Roxania semilaevis* (G. Seguenza, 1880) is characterised by its very solid, globose, glossy shell, with spirals restricted to the extremities. There is some variation in the inflation of the last whorl; some specimens evenly globose, others more inflated abapically. Sculpture is relatively constant, the middle two-thirds of the last whorl smooth in all specimens. This later character separates the species easily from *R. utriculus* (Brocchi, 1814) that usually has more of the surface of the last whorl spirally striate, and it also has a deeper, wider apical and basal umbilicus that *R. utriculus*. For discussion on type material see Gaglini (1992, p. 167).
Roxania semilaevis seems to be an uncommon species in both the Italian Plio-Pleistocene fossil assemblages and extant faunas. Today it is a bathyal species (Bouchet, 1975, p. 359) and in the Estepona deposits it is relatively abundant in the deeper water deposits.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper). Lower Pleistocene: central Mediterranean, Italy (Gaglini, 1992). Present-day: western Atlantic (Verrill, 1880), eastern Atlantic, British Isles to Morocco (Bouchet, 1975), Azores (Dautzenberg, 1889), into western Mediterranean (Repetto *et al*., 2005).

***Roxania utriculus* (Brocchi, 1814)**
Plate 55, figs 1-2

1814 *Bulla striata* Bruguiere – Brocchi, p. 276, pl. 1, fig. 6 (*non B. striata* Bruguière, 1792).
*1814 *Bulla utriculus* Brocchi, p. 633.
1845 *Bulla utricula* Br. – Nyst, p. 457, pl. 39, fig. 9.
1856 *Bulla utricula* Brocc. – Hörnes, p. 618 (*partim*) [*non* pl. 50, fig. 2 = *Sabatia callifera* (Boettger, 1907)].
1897 *Roxania utriculus* (Br.) – Sacco, p. 45, pl. 3, figs 127-129.
1897 *Roxania utriculus* var. *totornata* Sacco, p. 46, figs 130-132.
1904 *Roxania utriculus* Brocchi – Dollfus *et al*., p. 22, pl. 36, fig. 15.
1907 *Atys utriculus* Broc. – Ravn, p. 367, pl. 8, fig. 13.
1907 *Roxania utriculus* Brocchi – Almera, p. 207, pl. 15, fig. 28.
1910 *Roxania utriculus* Br. – Cerulli-Irelli, p. 36 [228], pl. 4 [35], figs 8, 9.
1936 *Sabatia utricula* Br. – Bogsch, p. 82, pl. 3, figs 43, 44.
1952a *Sabatia* (*Damoniella*) *utricula* Brocchi – Glibert, p. 397, pl. 15, fig. 9.
1952b *Sabatia* (*Damoniella*) *utricula* Brocchi 1814 – Glibert, p. 145, pl. 10, fig. 16.
1953 *Roxania* (*Roxania*) *utriculus utriculus* (Brocchi) – Berger, p. 111, pl. 18, figs 75, 76.
1953 *Roxania* (*Roxania*) *utriculus totornata* Sacco – Berger, p. 111, pl. 18, fig. 77.
1955 *Sabatia* (*Damoniella*) *utriculus* (Brocchi 1814) – Rossi Ronchetti, p. 337, fig. 182.
1958 *Roxania utriculus* (Brocchi) – Sorgenfrei, p. 350, pl. 76, fig. 260.
1963 *Roxania* (*Roxania*) *utriculus* (Br.) – Venzo & Pelosio, p. 137, pl. 37, fig. 24.
1964 *Roxania utriculus* (Brocchi 1814) – Anderson, p. 334, pl. 51, fig. 301.
1965 *Roxania utriculus* (Brocchi 1814) – Van Regteren Altena *et al*., p. 48, pl. 22, fig. 209.
1966 *Sabatia utriculus* Brocchi, 1814 – Strausz, p. 480, pl. 74, figs 36, 37.
1972a *Roxania utriculus* (Brocchi 1814) – Nordsieck, p. 123, fig. 214.
1975 *Roxania* (*Roxania*) *utriculus* (Brocchi) – Fekih, p. 145, pl. 42, fig. 11 (fig. 8 on plate, *lapsus*).
1978 *Bulla utriculus* Brocchi, 1814 – Pinna & Spezia, p. 134, pl. 15, fig. 2.
1979 *Roxania utriculus* (Brocchi 1814) – Nordsieck & García-Talavera, p. 170, pl. 43, fig. 11.
1982 *Roxania utriculus* (Brocchi 1814) – Martinell, p. 231, pl. 1, figs 24, 25.
1983 *Roxania utriculus* (Brocchi) – Macrì, p. 116, pl. 4, fig. 2.
1984 *Roxania* (*Roxania*) *utriculus* (Brocchi, 1814) – A.W. Janssen, p. 373, pl. 19, fig. 2.
1988 *Roxania utriculus* (Brocchi, 1814) – T.E. Thompson, p. 48, fig. 15.
1989 *Roxania utriculus* (Brocchi, 1814) – Moths, p. 112, pl. 22, fig. 117.
1992 *Roxania* (*Roxania*) *utriculus* (Brocchi, 1814) – Cavallo & Repetto, p. 168, fig. 487.
1997 *Roxania* (*R.*) *utriculus* (Brocchi, 1814) – Marquet, p. 115, pl. 11, fig. 9.
1998 *Roxania* (*R.*) *utriculus* (Brocchi, 1814) – Marquet, p. 219, fig. 192.
2001 *Roxania utriculus* (Brocchi, 1814) – Silva, p. 589, pl. 27, figs 9, 10.
2004 *Roxania* (*Roxania*) *utriculus* (Brocchi, 1814) – Ardovini & Cossignani, p. 43, 245, unnumbered fig.
2005 *Roxania* (*Roxania*) *utriculus* (Brocchi, 1814) – Schnetler, p. 164, pl. 9, fig. 20.
2005 *Roxania utriculus* (Brocchi, 1814) – Repetto *et al*., p. 267, fig. 1191.
2007 *Roxania utriculus* (Brocchi, 1814) – Wienrich, p. 776, pl. 171, figs 6, 7.
2008 *Roxania* (*Roxania*) *utriculus* (Brocchi, 1814) – Moths & Tüxen, p. 124, pl. 18, fig. 2.
2008 *Roxania utriculus* (Brocchi, 1814) – Chirli & Richard, p. 82, pl. 16, figs 9, 10.
2010 *Roxania utriculus* (Brocchi, 1814) – Moths *et al*., p. 91, pl. 25, fig. 9.

2011 *Roxania utriculus* (Brocchi, 1814) – Landau *et al*., p. 282, figs 94J-K.
2011 *Roxania utriculus* (Brocchi, 1814) – Hernández *et al*., p. 43, pl. 23, fig. 12.
2011 *Roxania utriculus* (Brocchi, 1814) – Cossignani & Ardovini, p. 38, 380, unnumbered fig.
2011 *Roxania utriculus* (Brocchi, 1814) – Gofas *et al*., p. 408, unnumbered fig. bottom.
2011 *Roxania utriculus* (Brocchi, 1814) – Chirli & Linse, p. 218, pl. 86, fig. 5.
2013 *Roxania utriculus* (Brocchi, 1814) – Chirli, p. 41, pl. 10, figs 12-16.
2013 *Roxania utriculus* (Brocchi, 1814) – Landau *et al*., p. 332, pl. 53, figs 1, 2.
2017 *Bullaria subampulla* d'Orbigny, 1852 [*sic*] – Büyükmeríç *et al*., p. 7, 9, fig. 5N [p. 7, 9 listed as *Bulla ampulla* Linnaeus, 1758, in fig. 7A1-A2 legend *B. ampulla*] [*non Bulla subampulla* d'Orbigny, 1852].
2018 *Roxania utriculus* (Brocchi, 1814) – Brunetti & Cresti, p. 120, fig. 432.
2018 *Roxania utriculus* (Brocchi, 1814) – Trigo *et al*., p. 387, unnumbered figs.
2018 *Roxania utriculus totornata* (Sacco, 1897) [*sic*] – Brunetti & Cresti, p. 120, fig. 432.

non 1938 *Roxania utriculus* Brocchi – Peyrot, p. 315 [= *Roxania labrella* (Férussac, 1822)].

Material and dimensions – Maximum height 10.9 mm, width 7.1 mm. **VC**: RGM.1404230 (13), NHMW 2023/0076/0129 (32). **CO**: RGM.1404227-228 (2), RGM.1404229 (10). **EL**: RGM.1404231 (1), NHMW 2023/0076/0130 (27).

Description – Shell small to medium sized, solid, ovate, only last whorl visible. Last whorl strongly globose, apex rounded, deeply and narrowly umbilicate, bearing punctate spiral cords at extremities extending a variable distance towards mid-whorl, middle part smooth in most specimens, surface glossy. Aperture entire length of shell, narrow adapically, widening abapically. Outer lip extending only slightly above apex adapically, convex below, rounded abapically. Columella short, narrowly thickened, bordering very narrow umbilical chink.

Discussion – Miocene to present-day shells of *Roxania utriculus* (Brocchi, 1814) typically have spiral sculpture on the last adult whorl restricted to the extremities, with the central portion of the whorl smooth. However, some Miocene specimens at hand have spiral sculpture extending across the entire last whorl. An Italian Pliocene specimen of this form was illustrated by Brunetti & Cresti (2018, fig. 432) under the name *Roxania utriculus totornata* (Sacco, 1897). In the Estepona material are also exceptional specimens with the last whorl if not completely striate, almost so. We therefore consider this character variable and not of subspecific value, as specimens with varying extension of the spiral striations coexist.
Today *R. utriculus* lives in sandy bottoms from the circalittoral zone from 30-200 m depth (Gofas *et al*., 2011; Trigo *et al*., 2018). In Estepona it is found in both the shallow and deeper water assemblages.

Distribution – Lower Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Denmark (Ravn, 1907; Moths & Tüxen, 2008), Germany (Sorgenfrei, 1958; Anderson, 1964; Moths, 1989; Wienrich, 2007; Moths *et al*., 2010), The Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984). Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856; Berger, 1953), Hungary (Bogsch, 1936; Strausz, 1966); Proto-Mediterranean (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: North Sea Basin (Tortonian): Denmark (Schnetler, 2005); northeastern Atlantic (Tortonian): Cacela Basin, Portugal (Dolfuss *et al*., 1904); Proto-Mediterranean (Tortonian and Messinian): Po Basin, Italy (Sacco, 1897; Venzo & Pelosio, 1963). Lower Pliocene: North Sea Basin: Belgium (Marquet, 1997, 1998); Atlantic, Santa Maria Island, Azores (this paper), Guadalquivir Basin, Spain (Landau *et al*., 2011); northeastern Spain (Almera, 1907; Martinell, 1982), Roussillon Basin, France (Chirli & Richard, 2008), Tunisia (Fekih, 1975); central Mediterranean, Italy (Cavallo & Repetto, 1992; Chirli, 2013; Brunetti & Cresti, 2018); eastern Mediterranean, Turkey (Büyükmeríç *et al*., 2017). Upper Pliocene: North Sea Basin, Belgium (Nyst, 1843; Marquet, 1997, 1998); Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin (NHMW collection); central Medi-

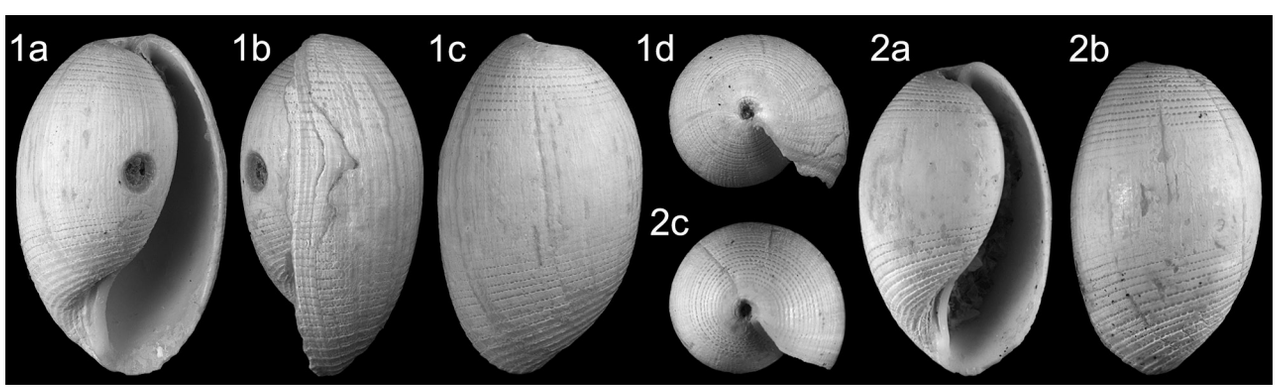

Plate 55. *Roxania utriculus* (Brocchi, 1814); 1. RGM.1404227, height 7.5 mm, width 4.6 mm; 2. RGM.1404228, height 6.4 mm, width 4.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

terranean, Italy (Sacco, 1897). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Macrì, 1983); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Scandinavia, Shetlands, British Isles (T.E. Thompson, 1988), Bay of Biscay (Trigo *et al*., 2018), Portugal, Canaries (Nordsieck & García-Talavera, 1979; Hernández *et al*., 2011), Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*., 2009), and entire Mediterranean (Ardovini & Cossignani, 2004; Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Family Scaphandridae G.O. Sars, 1878
Genus *Scaphander* de Montfort, 1810

Type species – Bulla lignaria Linnaeus, 1758, by original designation, present-day, Europe.

1810 *Scaphander* de Montfort, p. 334.

For generic synonymy see Ceulemans *et al*. (2018, p. 126).

***Scaphander lignarius* (Linnaeus, 1758)**
Plate 56, figs 1-2

*1758 *Bulla lignaria* Linnaeus, p. 727.
1976a *Scaphander* (*S.*) *lignarius lignarius* (Linné, 1758) – Pavia, p. 165, pl. 12, fig. 2.
1979 *Scaphander lignarius* (Linnaeus, 1758) – Nordsieck & García-Talavera, p. 171, pl. 43, fig. 12.
1983 *Scaphander lignarius* (L.) – Macrì, p. 116, pl. 4, fig. 1.
2005 *Scaphander lignarius* (Linné, 1758) – Repetto *et al*., p. 267, fig. 1192.
2011 *Scaphander lignarius* (Linnaeus, 1758) – Cossignani & Ardovini, p. 38, 380, unnumbered fig.
2011 *Scaphander lignarius* (Linnaeus, 1758) – Gofas *et al*., p. 408, unnumbered fig. top.
2011 *Scaphander lignarius* (Linnaeus, 1758) – Chirli & Linse, p. 219, pl. 86, fig. 6.
2011 *Scaphander lignarius* (Linnaeus, 1758) – Hernández *et al*., p. 282, fig. 94 I.
2018 *Scaphander lignarius* (Linneo, 1758) – Trigo *et al*., p. 386, unnumbered figs.
2018 *Scaphander lignarius* (Linnaeus, 1758) – Ceulemans *et al*., p. 126, pl. 7, fig. 13 (*cum syn*.).

Material and dimensions – Maximum height 39.8 mm, width 22.2 mm. **VC**: RGM.1404302 (6), NHMW 2023/0076/0116 (7). **CO**: RGM.1404232-233 (2), RGM.1404234 (5), NHMW 2023/0076/0114 (1). **EL**: RGM.1404235 (13), NHMW 2023/0076/0115 (3).

Description – Shell large to very large, relatively fragile, narrow posteriorly, expanding abapically, slightly anterodorsally compressed. Only last whorl visible; apex with narrow, shallow, round-margined umbilicus; sculpture of close-set, irregular, punctate spiral grooves, separated by gaps much wider than the grooves; punctuations small, rounded and fused within each groove. Aperture entire length of shell, narrow in apical third, widening greatly abapically. Outer lip alate apically, extending above apex, expanding and almost straight below, broadly rounded abapically. Columella narrow, broadly excavated. Columellar callus absent; parietal callus thin, narrow.

Discussion – Based on molecular studies, Eilertsen & Malaquias (2013) revised the present-day Atlantic *Scaphander* de Montfort, 1810 species, and concluded that four species occurred in the eastern Atlantic, of which only one is relatively shallow water: *S. lignarius* (Linnaeus, 1758). *Scaphander lignarius* is characterised by its relatively large (maximum height 70 mm) pyriform shell with the abapical part of the aperture flared. The adapical edge of the outer lip is rounded and usually does not protrude beyond the apex. The dorsum is covered by rounded punctuated striations, interconnected along the striae. The grooves formed by these striations are separated much wider than the grooves themselves.
Today *S. lignarius* lives in sandy and muddy bottoms from 30-200 m depth (Gofas *et al*., 2011; Trigo *et al*., 2018). In Estepona it is found in all assemblages, although specimens from the deeper water Velerín carretera do not reach the large size of those of the shallower water deposits.

Distribution – Lower Pliocene: North Sea Basin, Coral-

Plate 56. *Scaphander lignarius* (Linnaeus, 1758); 1. RGM.1404232, height 13.2 mm, width 7.2 mm; 2. RGM.1404233, height 15.2 mm, width 8.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

line Crag, England (S.V. Wood, 1848; Harmer, 1923), Kattendijk Formation, Belgium (Marquet, 1997, 1998); Atlantic, northwestern France (Brébion, 1964; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011); central Mediterranean, Italy (Sacco, 1897; Pavia, 1976a; Chirli, 2013). Upper Pliocene: North Sea Basin, Red Crag, England (S.V. Wood, 1848; Harmer, 1923), Oorderen Sands Formation, Belgium (Marquet, 1997, 1998); western Mediterranean, Estepona Basin (this paper), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1897; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Pliocene (indeterminate): North Sea Basin, The Netherlands (Van Regteren Altena *et al*., 1964). Upper Pliocene-Pleistocene: Atlantic, northwestern France (Brébion, 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Macrì, 1983); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Iceland, British Isles, European Atlantic frontage, Bay of Biscay (Trigo *et al*., 2018), and Canaries (Nordsieck & García-Talavera, 1979; T.E. Thompson, 1988; Hernández *et al*., 2011), Madeira (Nordsieck & García-Talavera, 1979; Segers *et al*. 2009), into entire Mediterranean (Repetto *et al*., 2005; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Sabatia* Bellardi, 1877

Type species (by monotypy) – *Sabatia isseli* Bellardi, 1877, Pliocene, Italy.

1877 *Sabatia* Bellardi, p. 209.

Note – Based on molecular evidence, Siegwald *et al*. (2022) showed that the genus *Sabatia* Bellardi, 1877 formed a well-supported clade, today with a predominantly Indo-West Pacific distribution, but with one lineage in the North Atlantic Ocean.

***Sabatia isseli* Bellardi, 1877**
Plate 57, figs 1-2

1842 *Bulla Plicata* Bell. – Sismonda, p. 26 (*nomen nudum*) (*non* Deshayes, 1824, *nec* T. Brown, 1827).
1847 *Bulla uniplicata* Bell. – Sismonda, p. 57 (*nomen nudum*) (*non* Dixon, 1850).
*1877 *Sabatia Isseli* Bellardi, p. 4, pl. C, figs 5-8.
1895 *Sabatia Isseli* Bell. – Cossmann, p. 88, pl. 2, figs 11, 12.
1897 *Sabatia uniplicata* (Bell.) – Sacco, p. 45, pl. 3, figs 116-126.
1959 *Roxania* (*Sabatia*) *isseli* (Bellardi) – Zilch, p. 27, fig. 83.
1968 *Roxania* (*Sabatia*) *isseli* (Bellardi, 1877) – Robba, p. 616, pl. 46, fig. 10.
1974 *Roxania* (*Sabatia*) *isseli* (Bellardi), 1877 – Caprotti, p. 35, pl. 4, fig. 16.
1992 *Roxania* (*Sabatia*) *isseli* (Bellardi, 1877) – Cavallo & Repetto, p. 168, fig. 488.

Material and dimensions – Maximum height 17.6 mm, width 12.0 mm. **VC**: NHMW 2023/0076/0051-0052 (2), NHMW 2023/0076/0053 (5).

Description – Shell medium sized, solid, ovate, broadening abapically. Protoconch visible in subadult specimens partially embedded in outer whorl, about 1.5 whorls with elevated nucleus. In fully adult specimens protoconch concealed, only last whorl visible forming entire height of shell. Last whorl with rounded apex, bearing moderately narrow, shallow umbilicus with flattened base, whorl swollen just below mid-height forming periphery, rounded at base. Sculpture of narrow, finely pitted grooves, more close-set at extremities, slightly more spaced mid-whorl. Aperture relatively narrow in apical third, widening greatly abapically. Outer lip not rising above apex, almost straight in upper half, strongly expaded and rounded abapically. Columella moderately excavated in lower half. Columellar callus greatly thickened, sharply delimited, expanded

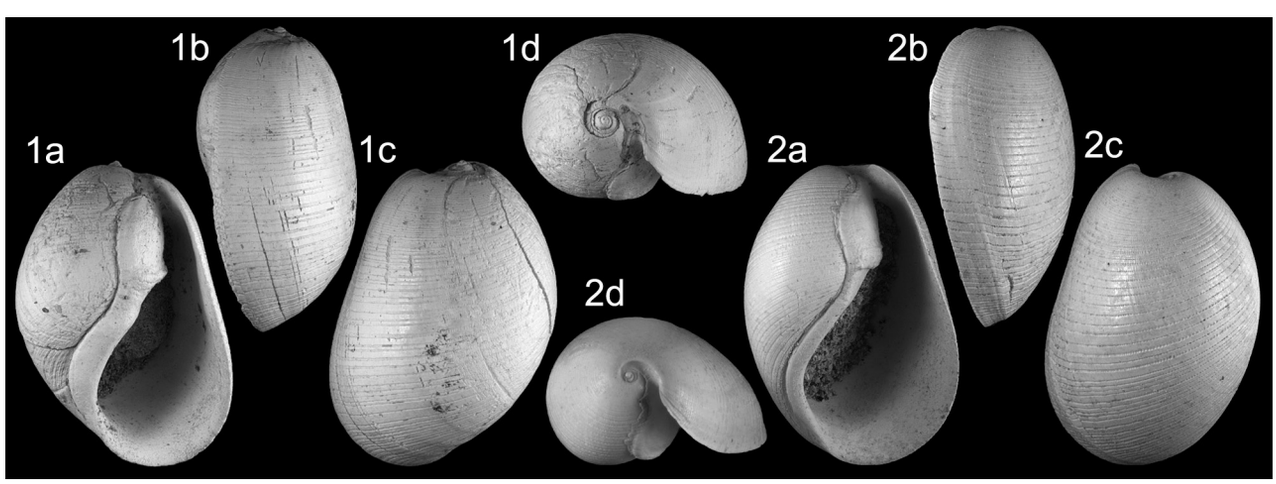

Plate 57. *Sabatia isseli* Bellardi, 1877; 1. NHMW 2023/0076/0051 (subadult), height 15.3 mm, width 10.2 mm; 2. NHMW 2023/0076/0052 (subadult), height 14.2 mm, width 9.7 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

over medial side of venter, continuous with even more expanded and thicker parietal callus bearing well developed parietal ridge at about two-thirds whorl height.

Discussion – *Sabatia isseli* disappeared from the Mediterranean at the end of the Pliocene. *Sabatia grandis* (Seguenza, 1880) from the Calabrian Pleistocene of Italy is larger, has a more regularly oval profile and the outer lip is more expanded, especially in the adapical half, resulting in a wider aperture adapical. The genus is not present in the Mediterranean today, but is represented in the Atlantic by *Sabatia bathymophila* (Dall, 1881) distributed from Delaware Bay, USA (Pilsbry, 1893) to Caribbean Sea and eastwards to the Azores (Eilertsen & Malaquias, 2013, p. 400) that differs in having a characteristic tuberculate parietal callus (see Eilertsen & Malaquias, 2013, fig. 2, 8A, 9A), whereas the parietal callus is smooth in the fossil species. Moreover, the aperture is more expanded abapically in *S. isseli*.
In Estepona this species is found only in the deeper water Velerín carretera assemblage.

Distribution – Upper Miocene: Proto-Mediterranean (Tortonian and Messinian), Italy (Sacco, 1897; Robba, 1968). Lower Pliocene: central Mediterranean, Italy (Sacco, 1897; Caprotti, 1974). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992).

Order Ellobiidae Pfeiffer, 1854 (1822)
Superfamily Ellobioidea Pfeiffer, 1854 (1822)
Family Ellobiidae Pfeiffer, 1854 (1822)
Subfamily Ellobiinae Pfeiffer, 1854 (1822)
Genus *Leucophytia* Winckworth, 1949

Type species (by typification of replaced name) – *Voluta bidentata* Montagu, 1808, present-day, British Isles.

1840 *Leuconia* Gray, p. 227. Type species (by subsequent designation, Herrmannsen, 1847): *Voluta bidentata* Montagu, 1808, present-day, British Isles. Junior homonym of *Leuconia* Grant, 1833 [Porifera]
1926 *Leucopepla* Peile, p. 75. Type species (by typification of replaced name): *Voluta bidentata* Montagu, 1808, present-day, British Isles. *Nom. nov. pro Leuconia* Gray, 1840, *non* Grant, 1833 [Porifera]. Junior homonym of *Leucopepla* Kirkaldy, 1907 [Hemiptera].
1949 *Leucophytia* Winckworth, p. 38. *Nom. nov. pro Leuconia* Gray, 1840, *non* Grant, 1833 [Porifera].

***Leucophytia bidentata* (Montagu, 1808)**
Plate 58, figs 1-3

*1808 *Voluta bidentata* Montagu, p. 100, pl. 30, fig. 2 (not pl. 29, fig. 3 as stated in text).
1819 *Voluta alba* Turton, p. 250 (*non* Montagu, 1803).
1830 *Auricula Erosa* Jeffreys, p. 369.
1841 *Auricula Bivonae* Philippi *in* Küster, p. 20, pl. 1 fig. 14-15.
1841 *Auricula Micheli* Mittre, p. 66.
1866 *Alexia Paivana* Pfeiffer, p. 146.
1890 *Alexia Kobelti* Caruana-Gatto, p. 210,
1897 *Leuconia Serresi* var. *parvulina* Sacco, p. 80, pl. 6, fig. 46.
1923 *Leuconia bidentata* (Montagu) – Harmer, p. 787, pl. 62, fig. 23.
1923 *Leuconia bidentata* var. *alba* (Turton) – Harmer, p. 787, pl. 62, fig. 24.
1950 *Ovatella Micheli* Mittre – Nicklès, p. 141, fig. 290.
1959 *Auriculinella* (*Leucophytia*) *bidentata* (Montagu) – Zilch, p. 75, fig. 244.
1965 *Ovatella* (*Myosotella*) *bidentata* (Montagu) – Ruggieri & Greco, p. 62, pl. 9, fig. 1.
1973 *Auriculinella* (*Leucophitia* [*sic*]) *bidentata* Montagu – Cesari, p. 186, pl. 1, figs 2-4.
1987 *Ovatella bidentata* (Montagu 1808) – Cuerda Barceló, p. 332, pl. 30, fig. 18.
1989 *Alexia Kobelti* Caruana-Gatto, 1989 – Sammut *et al*., p. 247, 249, figs 1-4.
2000 *Auriculinella bidentata* (Montagu, 1808) – Rolán & Templado, p. 92, figs 42, 43, 48-50.
2005 *Auriculinella erosa* (Jeffreys, 1830) – Repetto *et al*., p. 277, fig. 1253.
2008 *Auriculinella* (*Leucophytia*) *bidentata* (Montagu, 1808) – Cecalupo *et al*., p. 138, pl. 79, figs 1-5.
2011 *Auriculinella bidentata* (Montagu, 1808) – Cossignani & Ardovini, p. 48, 389, unnumbered fig.
2011 *Auriculinella bidentata* (Montagu, 1808) – Gofas *et al*., p. 537, unnumbered fig. bottom.
2011 *Auriculinella bidentata* (Montagu, 1808) – Hernández *et al*., p. 297, figs 99 P-T.
2013 *Ovatella bidentata* (Montagu, 1808) – Chirli, p. 74, pl. 16, figs 3-7.
2019 *Leucophytia bidentata* (Montagu, 1808) – Alonso Suárez *et al*., p. 46, fig. 1B.

Material and dimensions – Maximum height 9.3 mm, width 4.1 mm. **CO**: NHMW 2023/0076/0031-0033 (3), NHMW 2023/0076/0034 (3). **EL**: RGM.1404256 (1).

Description – Shell small, solid, elongate-ovate, with medium height conical spire. Protoconch abraded. Teleoconch of four whorls. Spire whorls straight sided, with periphery at abapical suture, separated by superficial, linear suture. Surface smooth, without sculpture. Last whorl about 80% of total height, regularly ovate, hardly constricted at base. Aperture about 50% of total height; anal canal narrow, V-shaped; siphonal canal short, open. Outer lip thickened by labial varix, bearing palatal swelling within placed mid-aperture. Columella with strong columellar fold and anterior parietal fold. Columellar callus strongly thickened, continuous with narrower parietal callus.

Discussion – Today the species lives under mid-sized and large stones in humid areas near the high-tide line (Rolán & Templado, 2000; Gofas *et al*., 2011).

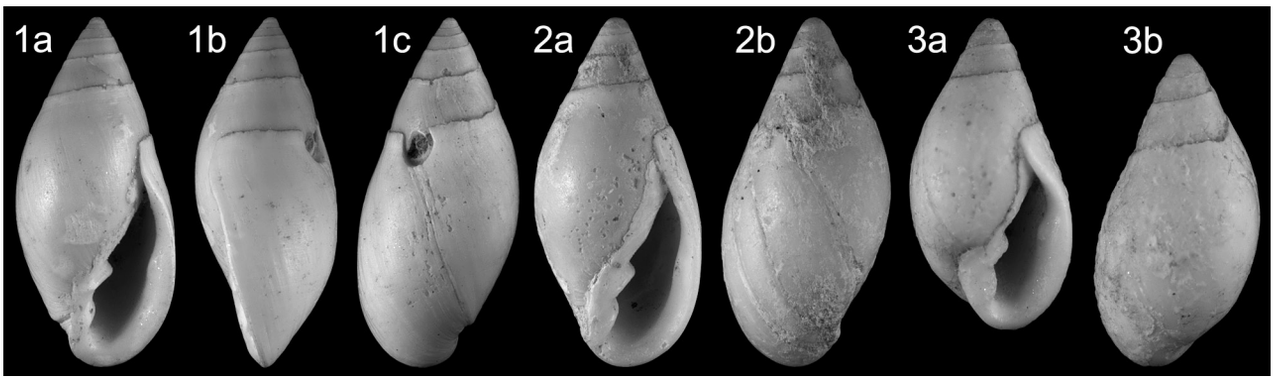

Plate 58. *Leucophytia bidentata* (Montagu, 1808); 1. NHMW 2023/0076/0031, height 10.3 mm, width 4.8 mm; 2. NHMW 2023/0076/0032, height 9.3 mm, width 4.1 mm; 3. NHMW 2023/0076/0033, height 8.3 mm, width 4.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1897). Lower Pleistocene: English Channel (Harmer, 1923); central Mediterranean (Ruggieri & Greco, 1985). Upper Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); Algeria (Lamothe, 1911). Present-day: Atlantic, British Isles, Bay of Biscay, Spain (Alonso Suárez *et al*., 2019) to Mauritania (Nicklès, 1950), Azores, Madeira (Rolán & Templado, 2000), Canary Islands (Hernández *et al*., 2011), western Mediterranean (Rolán & Templado, 2000), entire Mediterranean (Cesari, 1973; Repetto *et al*., 2005; Cecalupo *et al*., 2008; Cossignani & Ardovini, 2011; Gofas *et al*., 2011).

Genus *Pseudomelampus* Pallary, 1900

Type species (by subsequent designation, Westerlund, 1903) – *Melampus exiguus* Lowe, 1832, present-day, Madeira.

1900 *Pseudomelampus* Pallary, p. 240.

***Pseudomelampus exiguus* (Lowe, 1832)**
Plate 59, figs 1-2

*1832 *Melampus exiguus* Lowe, p. 291, pl. 13, figs 6, 7.
1900 *Alexia* (*Pseudomelampus*) *Kochi* Pallary, p. 241, pl. 6, fig. 10.
1900 *Alexia* (*Pseudomelampus*) *Jolyi* Pallary, p. 241, pl. 6, fig. 10.
1900 *Melampus biscayensis* H. Fischer, p. 67, 68, figs 1, 2.
1973 *Pseudomelampus kochi* (Pallary) – Cesari, p. 186, pl. 1, fig. 1.
1979 *Melampus canariensis* Nordsieck & García-Talavera, p. 193, pl. 46, fig. 2.
2000 *Pseudomelampus exiguus* (Lowe, 1832) – Rolán & Templado, p. 93, figs 31, 55-57.
2011 *Pseudomelampus exiguus* (Lowe, 1832) – Cossignani & Ardovini, p. 48, 390, unnumbered fig.
2011 *Pseudomelampus exiguus* (Lowe, 1832) – Gofas *et al*., p. 538, unnumbered fig. centre.
2011 *Pseudomelampus exiguus* (Lowe, 1832) – Hernández *et al*., p. 299, figs 100 K-N.
2019 *Pseudomelampus exiguus* (Lowe, 1832) – Alonso Suárez *et al*., p. 48, fig. 1E.

Material and dimensions – Maximum height 6.8 mm, width 3.5 mm. **EL**: RGM.1404250-251 (2), RGM.1404252 (15), NHMW 2023/0076/0078 (21).

Description – Shell small, cylindrical-ovate, with low, pointed spire. Protoconch heterostrophic, with axis perpendicular to axis of teleoconch, partially immersed in first teleoconch whorl. Teleoconch of about five whorls, separated by narrowly impressed suture. Spire whorls somewhat depressed, with periphery at abapical suture. Microsculpture of irregular spiral striae. Last whorl 86-90% of total height, rounded at high-placed shoulder, broadly convex below, not constricted at base, bearing 2-3 spiral grooves on the subsutural ramp and a few weaker spiral grooves over base. Aperture about 74% of total height, widening slightly abapically; outer lip simple; columella with strong columellar tooth, anterior parietal tooth strong, sharp, elevated, posterior parietal tooth weaker. Columellar callus thickened, expanded over base, continuous with thinner, narrower parietal callus.

Discussion – Today the species lives under mid-sized and large stones in humid areas near the high-tide line (Rolán & Templado, 2000; Gofas *et al*., 2011).

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: Atlantic, Bay of Biscay, Spain (Suárez *et al*., 2019), Madeira (Lowe, 1832; Rolán & Templado, 2000; Segers *et al*., 2009), Canary Islands, Cape Verde Archipelago (Hernández *et al*., 2011), into western Mediterranean (Cossignani & Ardovini, 2011; Gofas *et al*., 2011), central Mediterranean, Italy (Cesari, 1973).

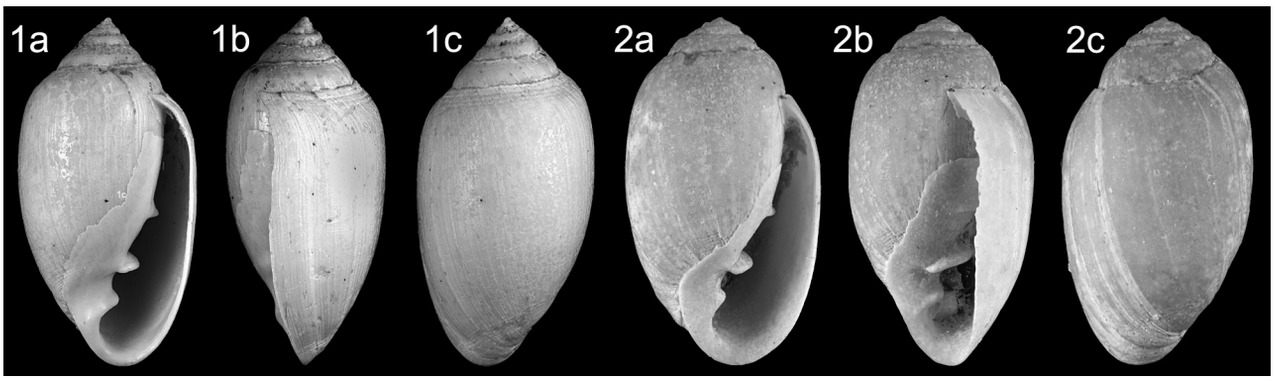

Plate 59. *Pseudomelampus exiguus* (Lowe, 1832); 1. RGM.1404250, height 6.4 mm, width 3.5 mm; 2. RGM.1404251, height 6.8 mm, width 3.5 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Subfamily Pythiinae Odhner, 1925
Genus *Ovatella* Bivona e Bernardi, 1832

Type species (by subsequent designation, Monterosato, 1906) – *Ovatella punctata* Bivona e Bernardi, 1832 [= *Ovatella firminii* (Payraudeau, 1827)], present-day, Italy.

1832 *Ovatella* Bivona e Bernardi, p. 58.
1855 *Monica* H. Adams & A. Adams, p. 247. Type species (by subsequent designation, Connolly, 1915): *Melampus aequalis* Lowe, 1832, present-day, Madeira.

***Ovatella aequalis* (Lowe, 1832)**
Plate 60, figs 1-2

*1832 *Melampus aequalis* Lowe, p. 288, pl. 13, figs 1-5.
1999 *Melampus aequalis* Lowe, 1832 – Martins, p. 73, fig. 2.
2000 *Ovatella aequalis* (Lowe, 1832) – Rolán & Templado, p. 90, figs 38-41.
2011 *Ovatella aequalis* (Lowe, 1832) – Gofas *et al*., p. 538, unnumbered fig. top.
2011 *Ovatella aequalis* (Lowe, 1832) – Hernández *et al*., p. 298, figs 100 F-J.
2019 *Ovatella aequalis* (Lowe, 1832) – Alonso Suárez *et al*., p. 47, figs 1F-G.

non 2020 *Ovatella aequalis* (Lowe, 1832) – Manousis *et al*., p. 31, fig. 9D [?= *O. vulcani* (Morelet, 1860)].

Material and dimensions – Height 15.4 mm, width 7.6 mm. **EL**: NHMW 2023/0076/0045 (1), NHMW 2023/0076/0083 (3).

Description – Shell medium sized, solid, elongate-ovate, with mid-height regularly conical spire. Protoconch abraded. Teleoconch of five low, straight-sided whorls with periphery at abapical suture; suture superficial, linear. Sculpture of spiral lines of fine pits, most strongly developed below suture, weakening towards lower suture and abapically. Last whorl 76% of total height, slightly concave in subsutural area, regularly convex below; only pitted spiral immediately below suture present; shallow umbilical chink. Aperture 47% of total height, pyriform. Outer lip bearing relatively prominent palatal swelling and strong tubercle just above mid-aperture, rounded abapically. Columellar tridentate: columellar tooth strong, oblique; parietal teeth lamellar, straight, of roughly equal strength, extending into and narrowing aperture, anterior tooth subhorizontal, posterior oblique. Columellar and parietal callus thickened, forming narrow, continuous, sharply delimited callus margin.

Discussion – The tridentate inner lip with the parietal teeth subequal in strength, if anything the posterior slightly stronger, and the presence of a strong palatal tubercle place this species in the genus *Ovatella* Bivona e Bernardi, 1832 rather than *Myosotella* Monterosato, 1906 (Martins, 1999).
Three species occur in the present-day European Atlantic and Mediterranean waters: *O. aequalis* (Lowe, 1832), *O. firminii* (Payraudeau, 1826), and *O. vulcani* (Morelet, 1860). Martins (1995) considered the sculpture of the protoconch and the first teleoconch whorls to be important specific characters in this group. Unfortunately, they are not well preserved in the material at hand. In Estepona this species is extremely uncommon, represented by a single adult and one subadult specimen. Nevertheless, the adult specimen illustrated (Pl. 60, fig. 1) has the parietal denticles of roughly equal size (the posterior possibly slightly longer), the posterior tooth is not curved abapically, and a single strong palatal tubercle within the outer lip; characters of *O. aequalis*. *Ovatella firminii* has more clearly defined rows of spiral pits, more strongly callused apertural armature, with the posterior parietal tooth usually longer than the anterior, the tip curved abapically, and two palatal tubercles. *Ovatella vulcani* is more difficult to separate from *O. aequalis* based on shell characters alone, although it has weaker apertural armature.
Today the species lives under mid-sized stones in humid areas, not close to sands (Rolán & Templado, 2000; Gofas *et al*., 2011). The scant material from Estepona suggests that this habitat is not well represented in the assemblage. We have not included the recent record for the eastern

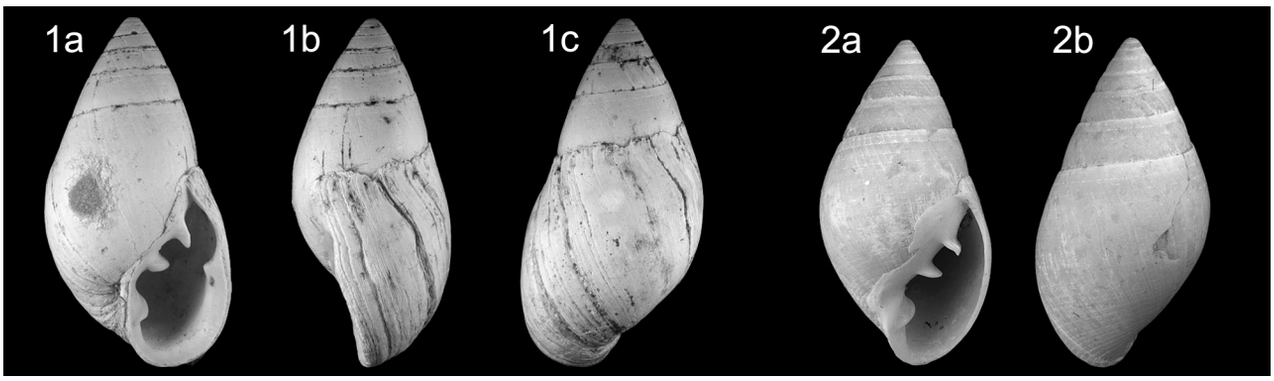

Plate 60. *Ovatella aequalis* (Lowe, 1832); 1. NHMW 2023/0076/0045, height 15.4 mm, width 7.6 mm; 2. RGM.1404208 (suadult), height 12.3 mm, width 6.5 mm (digital images) (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

Mediterranean of Manousis *et al*. (2020) which clearly has to palatal tubercles.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin (this paper). Present-day: Atlantic, Bay of Biscay (Alonso Suárez *et al*., 2019), Madeira (Lowe, 1832), southwards to Bay of Cadiz and Morocco (Gofas *et al*., 2011), Canary Islands (Hernández *et al*., 2011).

Discussion

In this paper 59 species are reviewed representing 37 genera from the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain (Figure 2). No species in the superfamilies reviewed are considered new.

Architectonicidae

In his discussion on the distribution of Architectonicidae of the western Atlantic Pliocene, Solsona & Martinell (1996) listed seven species from the 'Malaga' Basin [*A. simplex* (Bronn, 1831), *A. monilifer* (Bronn, 1831), *A. obtusa* (Bronn, 1831), *A. semisquamosa* (Bronn, 1831), *A. pseudoperspectiva* (Brocchi 1814), *A. millegrana* (Lamarck, 1822), and *A. contexta* (G. Seguenza, 1876)]. In this work, the generic framework given by Solsona & Martinell is updated, and we increase the number to twelve, representing nine genera, adding *Solatisonax pliohumilis* (Chirli, 2013), *Ammotectonica emiliae* (Semper, 1861), *Pseudotorinia architae* (O.G. Costa, 1841), *Pseudomalaxis aldrovandii* (Foresti, 1868), and *Spirolaxis clenchi* Jaume & Borro, 1946. *Architectonica obtusa* (Bronn, 1831) is recorded herein as *Heliacus fallaciosus* (Tiberi, 1872) (see discussion under *H. fallaciosus*).

This is similar in number to the eleven species (Melone & Taviani, 1985) present in the Mediterranean today within eight genera: *Discotectonica* Marwick, 1931, *Solatisonax* Iredale, 1931 (synonym: *Granoheliacus* Melone & Taviani, 1985; *Redivivus* Melone & Taviani, 1985), *Basisulcata* Melone & Taviani, 1985, *Philippia* Gray, 1847, *Heliacus* d'Orbigny, 1842 (synonyms: *Torinista* Iredale, 1936; *Gyriscus* Tiberi, 1867), *Redivivus* Melone & Taviani, 1985, *Pseudomalaxis* Fischer, 1885 and *Spirolaxis* Monterosato, 1913.

Solsona & Martinell (1996) postulated that based on their protoconch type, planktotrophic development could be inferred for Pliocene Mediterranean architetonicids, which would allow them to be widely distributed throughout their entire study are (the Mediterranean). The increase in known architectonicid diversity in the Estepona assemblages resulting from this study supports this hypothesis, as the assemblage is almost identical to that of the central Mediterranean Pliocene with no endemic species in Estepona. This contrasts sharply with other parts of this Estepona series in which endemic taxa are found in almost all groups (*e.g.*, Marginellidae, Cystiscidae, Landau *et al*., 2006; Nassariidae, Landau *et al*., 2009; *inter alia*).

Architectonicidae are well represented in the Estepona assemblages. This is undoubtedly explained at least in part by the presence of both deeper water clayey sediments and shallower water deposits. The resulting distribution of architectonicids given by Solsona & Martinell (1996) showing a heterogenous pattern of Mediterranean basins with high and low diversity is likely to be due to palaeoenvironmental conditions such as depth and sediment type as suggested by Solsona & Martinell (1996, p. 288) rather than endemism.

He suggested that the gradual drop of water temperatures during the Pliocene did not affect the assemblage greatly, but that the greater drop of water temperature at the end of the Pliocene caused the extinction of the majority of species, except two *A. contexta* and *A. obtusa* (Solsona & Martinell, 1996, p. 289).

In the light of this revision, these conclusions require amendment. *Solatisonax pliohumilis* (Chirli, 2013) and probably *Ammotectonica emiliae* are known only from MPPMU1 (roughly time equivalent to Zanclean and early Piacenzian) when fully tropical conditions prevailed in the Mediterranean. *Discotectonica pseudoperspectiva*, *D. semisquamosa*, *Granosolarium millegranum*, *Pseudomalaxis aldrovandii* and *Nipteraxis monilifer* disappeared at the end of the Pliocene. *Heliacus fallaciosus* and *Psilaxis simplex* survived into the Mediterranean early Pleistocene. *Solatisonax contexta* was found living

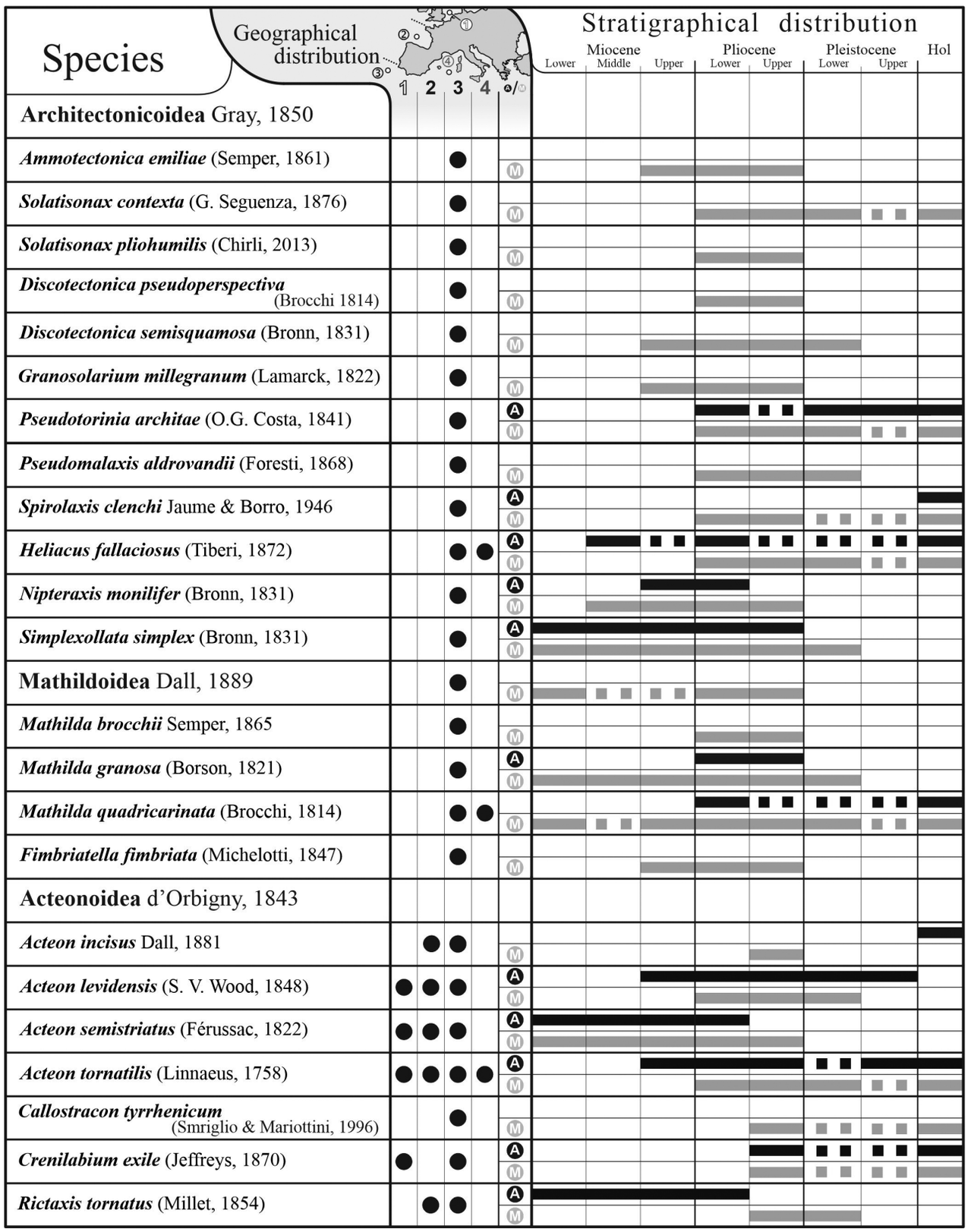

Figure 2. Geography, stratigraphy and distribution of species found in the Upper Pliocene Lower Piacenzian of the Estepona Basin, southern Spain. For present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan 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).

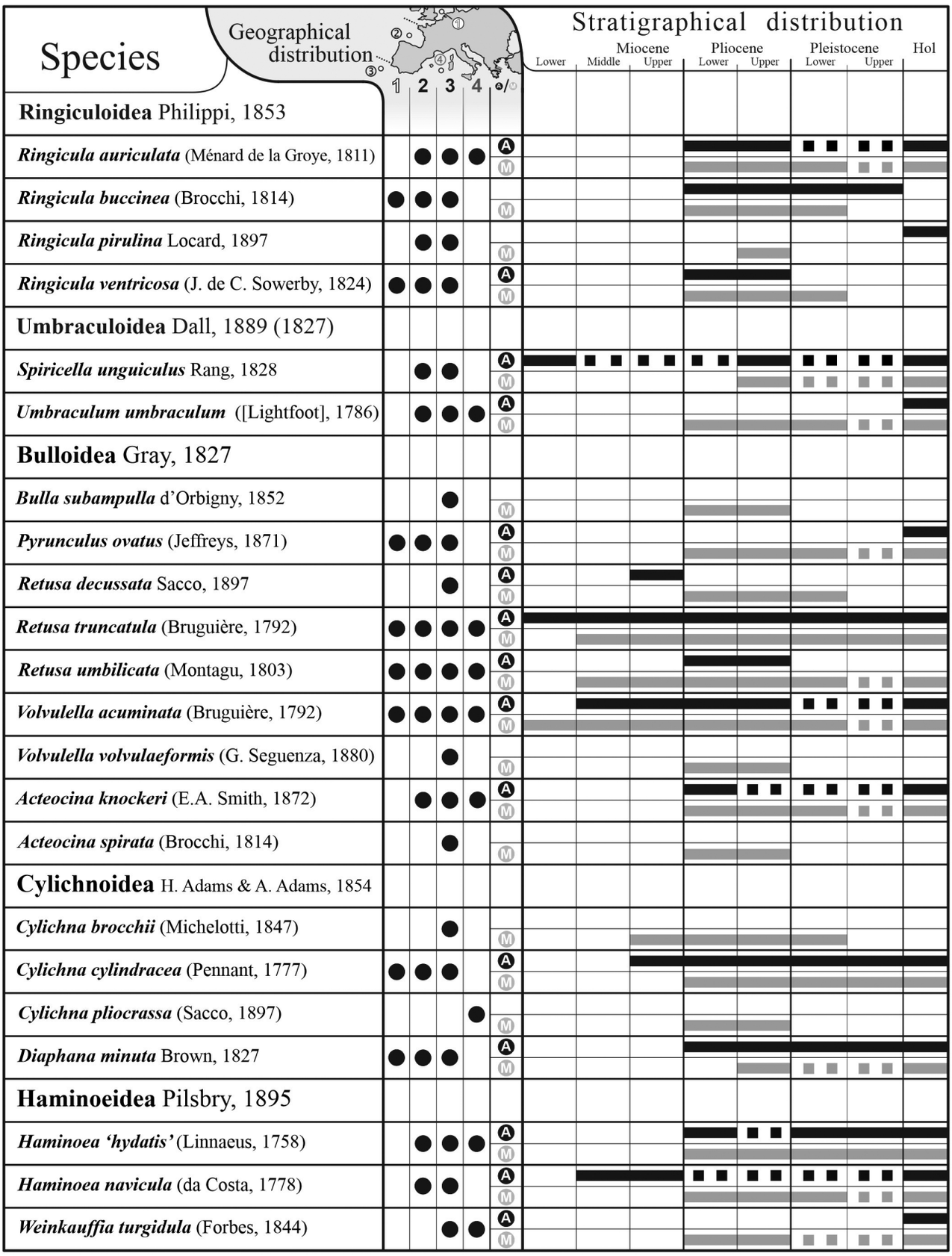

Figure 2, continued

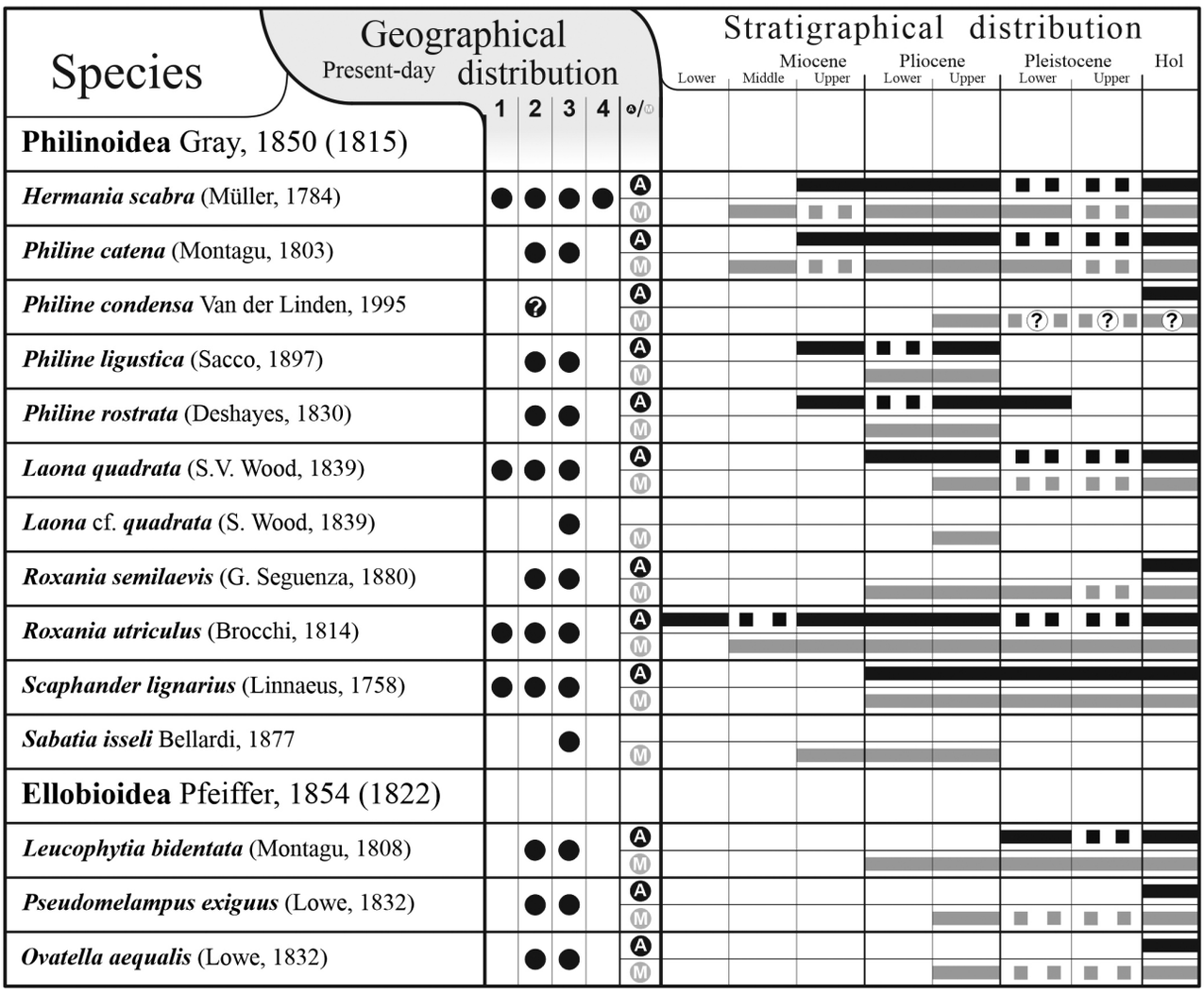

Figure 2, continued

in the Mediterranean (Melone & Taviani, 1982, 1985), and survived to the present day together with *Pseudotorinia architae* and *Spirolaxis clenchi*.
Therefore, although architectonicid diversity has not changed greatly in the Mediterranean since the Pliocene, the most thermophilic genus present in Estepona, *Granosolarium* Sacco, 1892 did not survive the cooling during the Pliocene, and *Psilaxis* Woodring, 1928, which is also relatively thermophilic, disappeared at the end of the Early Pleistocene. These two genera also represent the largest shelled species. Similar findings apply to the Italian architectonicid assemblages by Taviani & Melone (1986).

Mathildoidea, Acteonoidea, Ringiculoidea, Umbraculoidea, Bulloidea, Cylichnoidea, Haminoeidea, Philinoidea

These groups are all well represented in the Estepona assemblages. The Mathildoidea Dall, 1889 by two genera, four species, only one of which is still extant. The Acteonoidea d'Orbigny, 1843 by four genera, seven species, of which four are still extant. The Ringiculoidea Philippi, 1853 by one genus, four species of which two are still living. The Umbraculoidea Dall, 1889 (1827) by two genera, two species, both of which are still living. The Bulloidea Gray, 1827 by five genera, nine species of which five are still extant. The Cylichnoidea H. Adams & A. Adams, 1854 by two genera, four species of which two are still living. The Haminoeidea Pilsbry, 1895 by two genera, three species all of which are still extant. The Philinoidea Gray, 1850 (1815) by six genera, eleven species, seven of which are still living, one species is left in open nomenclature.
As can be seen from Figure 2, many of the species in these groups are unusually widely distributed geographically, present both in the Atlantic and the Mediterranean, and long lived stratigraphically compared to other groups already revised in this series. Within these groups, 40% of the species extend their range into the Miocene, 62% are still living, and no species are described as new.

Ellobiidae

The Ellobiidae Pfeiffer, 1854 (1822) are pulmonate gastropods that inhabit primarily the high intertidal zone in brackish water and terrestrial habitats, less often fully marine environments such as high intertidal boulder beaches (Rolán & Templado, 2000) . In the Estepona assemblages they are poorly represented by only three genera and one species in each genus, all of which survive today. As well as poor in species, they are not abundant, suggesting that intertidal and brackish habitats are poorly represented. Almost all specimens come from the El Lobillo deposits. *Pseudomelampus exiguus* (Lowe, 1832) is the only species that is relatively abundant.

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