The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 26: Conidae (Conoidea, Neogastropoda)

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In this paper we continue to review the Conoidea Fleming, 1822 of the Upper Zanclean, Lower Pliocene of Estepona, southern Spain, and review the family Conidae Fleming, 1822. Twenty-four species in eight genera are recorded, none of which are described as new. The assemblage is typical for the Conidae of the Pliocene Mediterranean during the tropical ecostratigraphic unit MPPMU1 at both species and genus level during which cone shells were diverse and plentiful in the Mediterranean, reaching sizes of over 100 mm in height. Conid diversity dropped drastically due to the cooling event at about 3 Ma that left only three cone species in the Mediterranean during MPPMU2.
Recent changes in conoidean supraspecific taxonomy have led to new combinations for most species. These new generic assignments drastically alter our understanding of conid palaeobiogeographical relationships for Pliocene Mediterranean cones. Affinities to Indo-West Pacific cones suggested by historical generic assignments is not supported, but instead there is strong correlation with present day West African faunas.

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

Introduction

In this paper we continue the revision of the diverse Pliocene assemblage of Estepona in south-western Spain and describe the family Conidae Fleming, 1822 (Conoidea). As with almost all Mediterranean Neogene molluscan studies, the centre of research has always been Italy. Italian Neogene cone shells number amongst the first species to be described in early works such as those of Brocchi (1814) and Borson (1820). The first major work at family level was that of Sacco (1893a, b), in which he described all cone shells from Italian Neogene deposits. True to that author's style, he also named every conceivable intraspecific variety. Hall (1964) produced an important revision of the Lower and Middle Miocene cones from Italy, and Davoli (1972) a revision of the Upper Miocene cones from the classic locality of Montegibbio. Cones have featured in almost every major publication on Italian Pliocene assemblages (*e.g.*, Malatesta, 1974; Pavia, 1976; Cavallo & Repetto, 1992; Chirli, 1997; Brunetti & Cresti, 2018; *inter alia*). A couple of papers dealing uniquely with Pliocene cones were published by Spadini (1990) and Paganelli (2014), however, these are rather brief and take the form of annotated lists rather than in depth revisions.
In the Iberian Pliocene, the Conidae from Estepona were described by Muñiz Solís (1999). That publication presented good descriptions of the forms found in Estepona, described the subsutural sinus, and gave a discussion and comparison for each species. Unfortunately, that publication suffers slightly from the relatively poor quality of the illustrations and the figures of the subsutural sinus and protoconchs are hand drawn. Nevertheless, it is a worthy paper, and we agree with the majority of the identifications therein. Cones from other Iberian localities were reported briefly by Martinell (1982) and Martinell & Domènech (1985) for the Barcelona area, Landau *et al.* (2013) for the Guadalquivir Basin, southwestern Spain, and Silva (2001) for the Mondego Basin of central-west Portugal, but all these assemblages are very poor in conid diversity compared to Estepona.
The Estepona Conidae are revisited herein and some of the identifications made in previous papers discussed and revised. Generic concepts in Conidae have changed drastically in the last 20 years following revisions based on shell characters, soft parts and molecular data (da Motta, 1991; Tucker & Tenorio, 2009; Puillandre *et al*., 2014a, b; Harzhauser & Landau, 2016), so that almost all species recorded by Muñiz Solís (1999) are here presented in new combinations (see Table 1, *hoc opus*). This has important implications for the palaeobiogeography, as will be discussed in the conclusions.

Age of the deposits

Prior to 2013 the age of the deposits was stated as Late Zanclean (late Early Pliocene) (for list of papers giving Zanclean age see Landau & Micali, 2021, p. 160) following Guerra Merchán *et al*. (2002). In our later works we have dated the assemblages as earliest Piacenzian, early Late Pliocene, an age corroborated by the assemblage of Euthecosomata (Janssen, 2004). Fresh samples from the various Estepona outcrops were collected by our team. Based on the calcareous nannofossils and planktonic foraminifera, a correlation of the Estepona assemblages with upper Zanclean biozones MNN14/NN15/CNPL3 (calcareous nannofossils) and MPl4a/upper PL2 to PL3 (planktonic foraminifera) was obtained, corresponding to an age of c. 4.0-3.8 Ma (Grunert, *et al*., 2025; this volume, pp. 17-23). Either way, they form part of the Mediterranean ecostratigraphic unit MPPMU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al*., 2011, text-fig. 9).

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL; 1997-2020) and by Henk Mulder between 2008-2023, to whom we are extremely grateful for his tireless efforts and generosity in making his collection available to us. For a map of localities see Landau *et al*. (2003, p. 4, text-fig. 1). The material is housed in the Natural History Museum Vienna (NHMW) and the collection of Henk Mulder (HM).

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

Shell terminology follows Smith (1930), Röckel *et al*. (1995) and Hendricks (2009).

Conidae vary little in shell characters but have varied and intricate colour patterns that help to identify modern species. Fossil cone shells are not easy to identify due to their rather conservative shell form and absence of sculpture. Moreover, shell height, width and spire height are quite variable within a species. Fortunately, many cones from Estepona retain remnants of their original colour pattern, although no further pattern was enhanced by ultraviolet light, except for in some specimens of *Kalloconus pulcher* ([Lightfoot], 1786). In this work colour pattern was extremely useful in separating cone species and relatively constant within a species. All colour patterns described are seen under natural light. Why UV light did not enhance any further pattern in such well preserved material is unclear and probably due to taphonomic processes.

Shell length: very small (<15 mm), small (15-25 mm), moderately small (25-35 mm), medium-sized (35-55 mm), moderately large (55-80 mm), large (>80 mm).

Measurements (see Harzhauser & Landau, 2016, p. 8, fig. 2):

SL: shell length
MD: maximum diameter
AH: aperture height
HMD: height of maximum diameter
SA: spire angle
AL: apertural length

In addition, we measured the angle of the last whorl (LWA). Ratios:

LW: length width ratio (SL/MD)
RD: relative diameter (MD/AH)
PMD: position of maximum diameter (HMD/AH)
RSH: relative height of spire [(SL-AH)/SL]
μ: mean
σ: standard deviation

The classification of the spire height and relative diameter proposed herein is: very low (RSH ≤ 0.1), low (RSH = 0.11–0.15), medium (RSH = 0.16–0.19), high (RSH ≥ 0.2–0.25, very high (≥ 0.26); elongate (RD ≤ 0.6), medium (RD 0.61–0.7), wide (RD > 0.7); we follow Cox (1960) who defined the shoulder of a gastropod shell as "*angulation of whorl forming abaxial edge of sutural ramp or shelf*". Thus, the shoulder is not necessarily the point of maximum diameter.

Almost all the Conidae in Estepona are found in the Velerín conglomerates assemblage, with a handful from El Lobillo and Velerín carretera. Numbers of specimens recorded in a collection do not reflect the number of cone shells in the assemblage. Muñiz Solís (1999, p. 87) also commented that more than 50% of the specimens were unidentifiable due to their poor state of conservation. Most living cones have a smooth polished surface that is abraded in the Estepona conglomerates material. The few specimens recovered from the Velerín carretera assemblage are better preserved, but only represent one or two species. As suggested by Muñiz Solís, some of the wear is due to transport, but it is also due to decalcification, with an adherent crystalline calcitic crust formed on the shell or the underside of the shell, depending on how it was deposited. This is most evident in large specimens like those of *Kalloconus pulcher* ([Lightfoot], 1786) (*e.g*., Pl. 6, figs 1-3).

In the material at hand, the protoconch is abraded in all subadult and adult specimens, as well as usually the early teleoconch whorls in adult specimens. A few protoconchs were preserved in the several hundred very juvenile specimens. Attribution of these juveniles is in some cases possible, others not (Pl. 1, figs 1-7). We note that our results do not always match those of Muñiz Solís (1999, p. 39, fig. 5). The illustrations given by that author are hand drawings of the protoconch without any detail of the early teleoconch whorls and are therefore difficult confirm.

Abbreviations:

CO: Velerín conglomerates; **VC**: Velerín carretera;
EL: El Lobillo; see Landau *et al*. (2003, p. 4, text-fig. 1).
HM coll. Henk Mulder collection, Monster, The Netherlands.
NHMW Natural History Museum Vienna (Austria)

Generic concepts

Following the advances in our understanding of supraspecific systematics in cone shell, controversy arose regarding genus and subgenus concepts. In summary, Tucker & Tenorio (2009) recognised two families and numerous genera, Puillandre *et al*. (2014a, b) chose to use *Conus* Fleming, 1822 as a genus along with three other genus-group names (*Profundiconus*, *Californiconus*, and *Conasprella*) and "downgraded" many of the genera discussed by Tucker & Tenorio (2009) to subgenera.

In our works we have preferred to follow Tucker & Tenorio's model. Reasons were discussed in full in Harzhauser & Landau (2016, p. 35). To summarise our reasoning, in our opinion, this approach firstly obfuscates smaller monophyletic groups of species, which can be distinguished both on shell features and soft tissue anatomy and are far more useful for understanding the evolution and palaeobiogeography of cone snails. Secondly, it supports the use of subgenera, which most modern authors, including those behind the on line WoRMS database, try to avoid. Thirdly, many of these genera can be traced back at least to Miocene times, when the Conidae experienced a first major radiation (Landau *et al*., 2016, p. 202).

Almost ten years later, justification for using the genus *Conus* with other groups as subgenera seems to be inconsistent with the approach to other equally ancient groups. For example, within the Mitroidea the broad genus concept of '*Mitra*' as proposed by Cernohorsky (1970, 1976, 1991) was not supported by molecular data, and Fedosov *et al*. (2018) expressed this pointedly as the "collapse of *Mitra*". Similar examples can be found within the Muricoidea (Russini *et al*., 2023), Buccinoidea (Kantor *et al*., 2021), Columbellidae (deMaintenon & Strong, 2022), Terebridae (Fedosov *et al*., 2020), plus the examples already given by Harzhauser & Landau (2016).

Systematic Palaeontology

Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822
Genus *Artemidiconus* da Motta, 1991

Type species (by original designation): *Conus selenae* Van Mol, Tursch & Kempf, 1967, present-day, Western Atlantic.

1991 *Artemidiconus* da Motta, p. 24.

Note – Tucker & Tenorio (2009, p. 134) characterised this genus as including small, squat, rounded shells with convex spire whorls with cords. Nodules on spire whorls are absent or become obsolete very early. The subsutural sinus is shallow and asymmetrical. Harzhauser & Landau (2016, p. 36) broadened the genus concept to include the presence of more or less prominent beads on the last whorl as a characteristic feature, being also present on

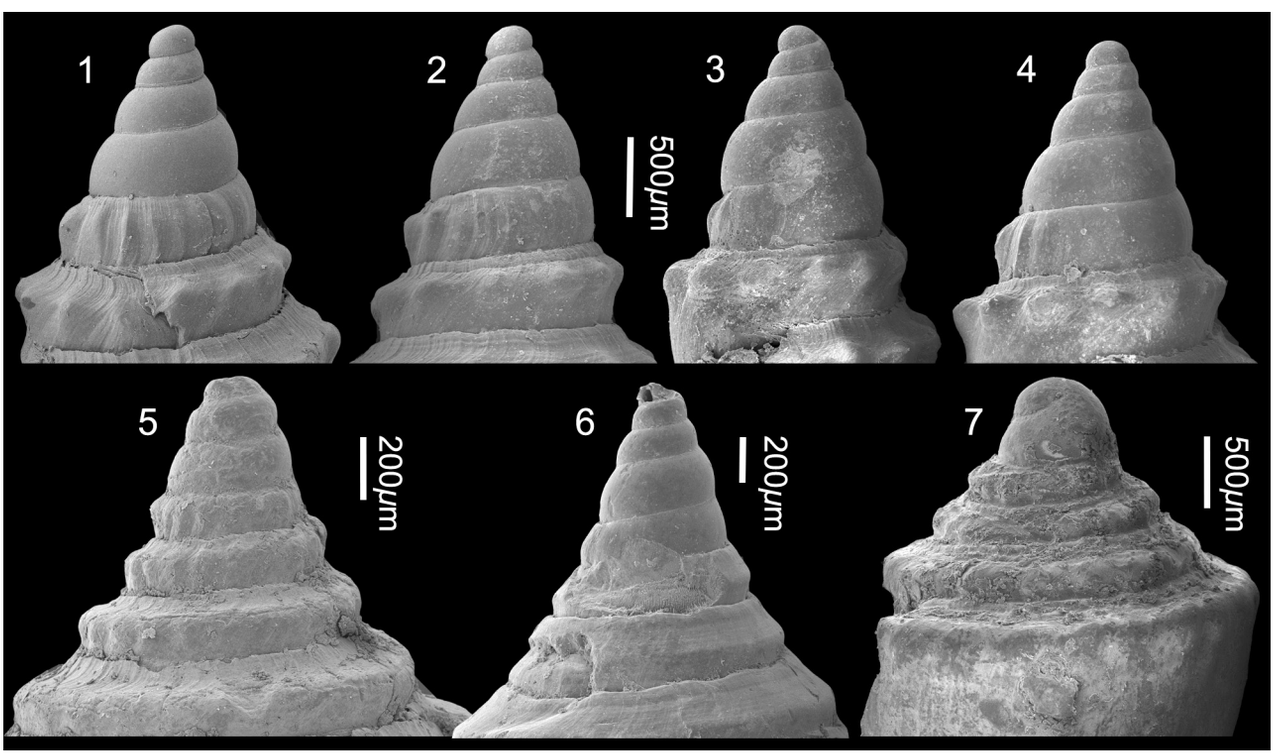

Plate 1. Protoconchs of Estepona Conidae. Figs 1-4. *Conilithes antidiluvianus* (Bruguière, 1792), NHMW 2024/0205/0116-0119 (juveniles). Velerín carretera. Fig. 5. *Conilithes brocchii* (Bronn, 1828), NHMW 2024/0205/0120 (juvenile); 6. *Pseudonoduloconus virginalis* (Brocchi, 1814), NHMW 2024/0205/0121 (juvenile); 7. *Varioconus striatulus* (Brocchi, 1814), NHMW 2024/0205/0122 (juvenile). Figs 5-7, Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

the type species. Those authors included *Conus granularis* Borson, 1820 in the genus *Artemidiconus* da Motta, 1991.

?*Artemidiconus* sp.
Plate 2, fig. 1

Material and dimensions – Height 19.9 mm, width 10.9 mm. **CO:** NHMW 2024/0205/0021(1).

Description – Shell small, with high conical spire, conical last whorl. Protoconch and earliest teleoconch whorls not preserved. Six teleoconch whorls preserved. Spire abraded, but clear opisthocline axial ridges or ribs preserved on the tops of the last two whorls. Suture deeply channelled. Last whorl with narrow subsutural ramp, weakly angled at shoulder, conical below with slightly convex sides, weakly constricted at base, periphery at about two thirds whorl height; siphonal fasciole hardly developed; sculpture of opisthocline ribs over subsutural ramp terminating in small tubercles at shoulder giving coronate appearance, spiral threads over entire whorl below shoulder, strengthening slightly abapically, overriding two rows of small coalescent tubercles placed at the periphery, horizontal band of short irregular axial ridges, placed at about one third whorl height, formed by coalescent tubercles.

Shell measurements and ratios – n = 1 specimen. SL: 19.9 mm, MD: 10.9 mm; spire angle: 92°; last whorl angle: 37°; LW: 2.0. RD: 0.7; PMD: 0.8; RSH: 0.24.

Discussion – Unfortunately only a single somewhat worn specimen of this intriguing little cone is at hand. If it does indeed represent an undescribed species of sculptured cone, it must be very uncommon considering that at least 3000 cones were examined in preparation of this work. Only a fraction is included in the material and methods due to the poor state of conservation of many of the specimens. We have not seen any other cone with this sort of sculpture, and we cannot exclude that the 'sculpture' is a result of decortication with areas of surface possibly bearing colour pattern somehow protected. Having raised this possibility, we do not recognise this colour pattern in any other Estepona cone. Because of its small size and granules over the last whorl we place it in *Artemidiconus* da Motta, 1991. The only similar species is *A. granularis* (Borson, 1820) that was unusually widespread in the Miocene of Europe, in the Lower Miocene Atlantic Aquitaine Basin of France (Peyrot, 1931; Lozouet *et al.* 2001), the Burdigalian to Tortonian Proto-Mediterranean (Sacco, 1893b, Hall, 1964; Davoli, 1972), and very widespread in the Middle Miocene Paratethys (Harzhauser & Landau, 2016). The last occurrence of that species is in the Pliocene Mediterranean of Italy (Borson, 1820; Sacco, 1893b). Numerous varieties of that species were illustrated by various authors. Although some are coronate (*e.g.*, var. *tauroscabricula* Sacco, 1893b, pl. 11, fig. 33) none have the tubercles coalescing into axial lines. We hope to be able to better characterise this species in the future.

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

Genus *Conasprella* Thiele, 1929

Type species (by subsequent designation, Tucker & Tenorio 2009): *Conus pagoda* Kiener, 1847, present-day, Philippines.

1929 *Conasprella* Thiele, p. 373.

Note – WoRMS (MolluscaBase, 2024) synonymises numerous conid genera with *Conasprella* Thiele, 1929 or consider them subgenera of it. We note that in the molecular phylogeny of Puillandre *et al.* (2014b, p. 295, fig. 2) some of these synonymised names fall into groups that they then lump under *Conasprella* (*e.g.*, *Kohniconus* Tucker & Tenorio, 2009, *Dalliconus* Tucker & Tenorio, 2009, *Fusiconus* da Motta, 1991, *Endemoconus* Iredale, 1931, *Boucheticonus* Tucker & Tenorio, 2009, and *Ximeniconus* W. K. Emerson & Old, 1962). For the reasons discussed in Harzhauser & Landau (2016, p. 35, 41) we prefer not to synonymise these genera, nor use them at subgeneric level until more detailed genetic data is available.

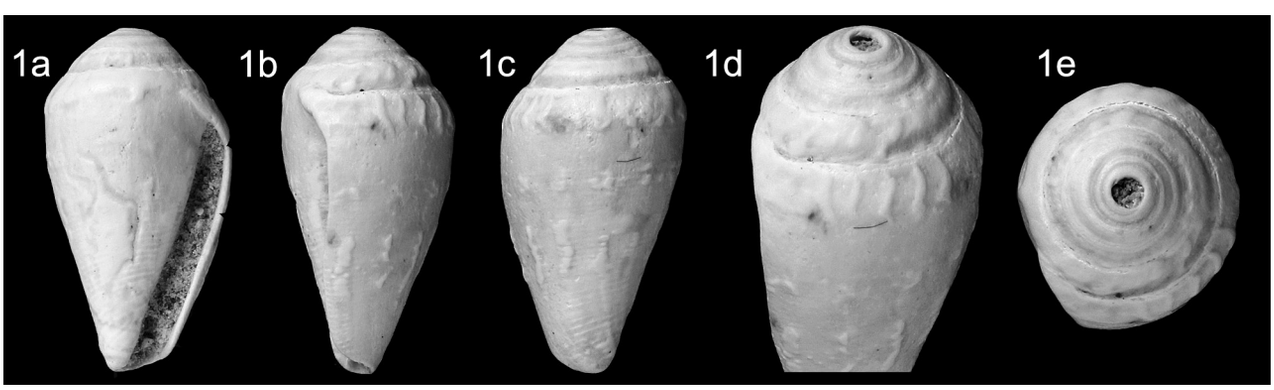

Plate 2. ?*Artemidiconus* sp.; 1. NHMW 2024/0205/0021, 19.9 mm, width 10.9 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

***Conasprella subbicrenulata* (Sacco, 1893)**
Plate 12, figs 1-3, Plate 17, fig. 1, Plate 18, fig. 1

1893b *Conus* (*Stephanoconus*) *subbigranosus* var. *subbicrenulata* Sacco, p. 120, pl. 11, fig. 26.
1893b *Conus* (*Stephanoconus*) *subbigranosus* var. *ligusticofusulata* Sacco, p. 120, pl. 11, fig. 27.
1893b *Conus* (*Stephanoconus*) *subbigranosus* var. *ligusticovulata* Sacco, p. 120, pl. 11, fig. 28.

Material and dimensions – Maximum height 22.3 mm, width 10.4 mm. **CO:** NHMW 2024/0205/0026-0028 (3), NHMW 2024/0205/0029 (1), HM coll. (2).

Description – Shell small, slender, with very high, weakly scalariform spire of up to nine teleoconch whorls. Spire whorls carinate just above suture, finely tuberculate; subsutural ramp weakly striate crossed by close-set comma-shaped growth lines giving faintly cancellate pattern over ramp. Suture impressed, linear, migrating slightly abapically on last two whorls, giving increasingly scalate aspect of spire, exposing a narrow portion of the preceding whorl below the shoulder. Subsutural sinus shallow, moderately curved, moderately asymmetrical. Last whorl with faintly concave, weakly striate subsutural ramp, angled at shoulder bearing very fine tubercles, hardly constricted at base; siphonal fasciole weakly developed; relatively prominent smooth cords over base, strengthening further over fasciole. Aperture narrow, with subparallel margins, siphonal canal moderate length. Colour pattern of alternating white and orange blotches on spire whorls, thin spirals lines and white mottling over beige background below shoulder on last whorl.

Shell measurements and ratios – n = 5 adult specimens; largest specimen: SL: 23.4 mm, MD: 10.5 mm, mean SL: 19.9 mm (σ = 3.0), mean MD: 9.3 (σ = 1.3); spire angle: μ = 74.4° (σ = 5.9°), last whorl angle: μ = 32.6° (σ = 2.7°), LW: μ = 2.1 (σ = 0.2), RD: μ = 0.65 (σ = 0.03), PMD: μ = 0.9 (σ = 0.01), RSH: μ = 0.3 (σ = 0.03), subsutural sinus (n=4): SSFD: shallow. μ = 2.1 (σ = 0.5), SSFd: moderately curved. μ = 5.3 (σ = 0.01), PV: moderately asymmetrical. μ = 0.5 (σ = 0.06).

Discussion – We have provisionally placed this species in the genus *Conasprella* Thiele, 1929 based on its finely tubercular spire whorls placed at the shoulder that extend to the last whorl. Species of *Artemidiconus* da Motta, 1991 differ in having a broader biconic profile and having the spire whorls smooth or tubercular only on the earliest whorls (see Harzhauser & Landau, 2016, key p. 36). It differs from typical *Conasprella* species in that the grooves on the last whorl are weaker than usual and present only over the base and fasciole, and the sinus is shallower that usual for *Conasprella*. The genus was recognised in the Middle Miocene Paratethys by Harzhauser & Landau (2016). This is the first Pliocene record for the genus.
A small number of specimens from Estepona agree with some of the Pliocene varieties of *Conus* (*Stephanoconus*) *subbigranosus* (Sacco, 1893) described by Sacco (1893b). *Conus* (*S.*) *subbigranosus* was described from the Upper Miocene of Stazzano, Italy. The original figure (Sacco, 1893b, pl. 20, fig. 24), a syntype figured by Ferrero Mortara *et al*. (1984, pl. 20, fig. 12), and the anomaly *bispirata* (Sacco, 1893b, pl. 20, fig. 25) all have far stronger and larger tubercles at the shoulder than any of the Pliocene forms and are therefore unlikely to be conspecific.
The Estepona material at hand is closely similar in size and sculpture to three of Sacco's Pliocene varieties (*subbicrenulata*, *ligusticofusulata*, and *ligusticovulata*) that probably represent a single species. The shells are slenderer and the tubercles in these forms are far finer than they are in *Conasprella subbigranosa*. As first revisors, we chose the first of these names in the combination *Conasprella subbicrenulata* (Sacco, 1893). We have not seen Pliocene specimens from Italy, nor has it been re-illustrated since its original description. The colour pattern has also not been described from the Pliocene forms.
Sacco's Pliocene variety *ligustoconica* (1893b, pl. 20, fig. 29; refigured in Ferrero Mortara *et al*., 1984, pl. 20, fig. 13) from the Lower Pliocene of Bussana, Italy is much lower spired and broader than the three other Pliocene varieties listed above and is probably not conspecific. Sacco's Pliocene variety *pliocoronaxoides* (1893b, pl. 11, fig. 30) might represent *Lautoconus subtextile* (Sacco, 1893b) (see discussion under than species). Similarly, the Estepona specimens illustrated by Muñiz Solís (1999, pl. 10J-L) as *Conus* (*S.*) *subbigranosus* are neither that species, nor *Conasprella subbicrenulata* (Sacco, 1893), but in our opinion also represent *L. subtextile*, with its very characteristic colour pattern although Sacco (1893b, p. 121) describes both forms *ligusticofusulata* and *ligusticoovulata* as being "…, *ornati*.", which we assume means they have a colour pattern, although it is ambiguous if he meant sculpture or colour.
Conasprella minitissima Harzhauser & Landau, 2016 from the Middle Miocene Paratethys is not unlike *C. subbicrenulata* in profile but has beaded cords that extend further over the abapical half of the last whorl.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (this paper); central Mediterranean, Italy (Sacco, 1893b).

Genus *Conilithes* Swainson, 1840

Type species (by monotypy): *Conus antidiluvianus* Bruguière, 1792, Pliocene, Italy.

1920 *Conilites* Schlotheim, p. 125. Invalid under Art. 20 of the Code (ICZN 1999).
1840 *Conilithes* Swainson, p. 311.
1847 *Conolithus* Herrmannsen, p. 295. Unjustified emendation of *Conilithes* Swainson, 1840.
1890 *Conospirus* De Gregorio, p. 21. Type species (by original designation): *Conus antidiluvianus* Bruguière, 1792, Pliocene, France. Junior objective synonym of *Conilithes* Swainson, 1840.
1896 *Conospira* Cossmann, p. 155. Unjustified emendation of *Conospirus* De Gregorio, 1890.

***Conilithes antidiluvianus* (Bruguière, 1792)**
Plate 3, figs 1-4, Plate 17, fig. 2, Plate 18, fig. 2

*1792 *Conus antidiluvianus* Bruguière, p. 637.
1814 *Conus antidiluvianus* Bruguiere [*sic*] – Brocchi, p. 291, pl. 11, fig. 11.
1845 *Conus antediluvianus* [*sic*] v. *Scalata* Grateloup, pl. 45, figs 13, 14.
1851 *Conus antediluvianus* [*sic*] Brug. – Hörnes, p. 38, pl. 5, figs 2a-e.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *dertonensis* Sacco, p. 41, pl. 4, fig. 29.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *compressospira* Sacco, p. 41, pl. 4, fig. 30.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *dertogranosa* Sacco, p. 41, pl. 4, fig. 31.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *turritospira* Sacco, p. 42, pl. 4, fig. 32.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *turripina* De Greg. – Sacco, p. 42, pl. 4, fig. 33.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *turripina* anom. *fusulatissima* Sacco, p. 42, pl. 4, fig. 34.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *fasciornata* Sacco, p. 42, pl. 4, fig. 35.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *dertoblita* Sacco, p. 43, pl. 4, fig. 36.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *crassogranosa* Sacco, p. 43, pl. 4, fig. 37.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *mioblita* Sacco, p. 43, pl. 4, fig. 38.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *tauroblitoides* Sacco, p. 43, pl. 4, fig. 39.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *taurascalarata* Sacco, p. 43, pl. 4, fig. 40.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *miosubagranosa* Sacco, p. 44, pl. 4, fig. 41.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *taurocatenatoides* Sacco, p. 44, pl. 4, fig. 42.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *empena* De Greg. – Sacco, p. 44, pl. 4, fig. 43.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *transiens* Sacco, p. 45, pl. 4, fig. 44.
1893a *Conus* (*Conospirus*) *antediluvianus* [*sic*] var. *subagranulata* Sacco, p. 45, pl. 4, fig. 45.
1896 *Conospira antediluvianus* [*sic*] Brug. – Cossmann, p. 155, pl. 8, figs 7, 8.
1904 *Conus* (*Conospirus*) *antediluvianus* [*sic*] (Brug.) – Sacco, p. 111, pl. 24, fig. 39.
1932 *Conus* (*Conospira*) *antediluvianus* mut. *scalata* Grateloup – Peyrot, p. 84, pl. 1, figs 21, 22.
1958 *Conus* (*Conospira*) *antediluvianus* [*sic*] Bruguière, 1792 – Erünal-Erentöz, p. 124, pl. 20, fig. 11.
1960 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière, 1792 – Kojumdgieva in Kojumdgieva & Strachimirov, p. 209, pl. 49, fig. 3.
1964 *Conus antidiluvianus* Bruguière, 1792 – Hall, p. 127 [17], pl. 22, fig. 7.
1966 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière, 1792 – Strausz, p 451, pl. 16, fig. 10, pl. 17, fig. 1.
1967 *Conus* (*Conolithus*) *antidiluvianus* Bruguière – Pelosio, p. 67, pl. 46, figs 16, 17, 19, pl. 47, figs 1-6.
1967 *Conus* (*Conolithus*) *antidiluvianus* Bruguière, 1792 – Palla, p. 1002, pl. 75, fig. 8.
1969 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière – Atanacković, p. 215, pl. 12, figs 14-15.
1969 *Conus* (*Conospirus*) *antediluvianus* [*sic*] Bruguière – Dermitzakis, pl. 78, fig. 7.
1969 *Conus* (*Conolithus*) *antidiluvianus* Bruguière – Mastrorilli, p. 121, pl. 11, fig. 4.
1972 *Conus* (*Lithoconus*) *antediluvianus* [*sic*] Bruguière – Csepreghy-Meznerics, p. 34, pl. 17, fig. 14.
1972 *Conus antidiluvianus* Bruguière – Davoli, p. 75, pl. 3, figs 1-5.
1973 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière – Steininger, p. 447, pl. 9, fig. 4 (strongly compressed specimen).
1974 *Conus* (*Conolithus*) *antidiluvianus* Bruguière, 1792 – Malatesta, p. 385, pl. 30, fig. 1.
1975 *Conus* (*Conolithus*) *antidiluvianus* Bruguière – Fekih, p. 139, pl. 41, fig. 8.
1976 *Conus antidiluvianus* Bruguière – Pavia, p. 114, pl. 9, fig. 4.
1976 *Conus antidiluvianus* Bruguière – Caprotti, p. 12, pl. 17, fig. 10.
1978 *Conus antidiluvianus* Bruguière – Cuscani Politi, p. 48, pl. 6, fig. 17.
1988 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguiere, 1792 – Chirli, p. 22, pl. 3, fig. 4.
1990 *Conus antidiluvianus* Bruguière, 1792 – Spadini, p. 30, pl. 1, figs 1-3.
1992 *Conus antidiluvianus* Bruguière, 1792 – Cavallo & Repetto, p. 126, fig. 326.
1997 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière, 1792 – Chirli, p. 11, pl. 3, figs 11-13.
1998 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière – Schultz, p. 72, pl. 29, fig. 9.
1999 *Conus* (*Conolithes*) *antidiluvianus* [*sic*] Bruguière, 1792 – Muñiz Solís, p. 69, figs 8O-Q.
2001 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguiere – Chira & Voia, p. 156, pl. 1, figs 6a-b.
2003 *Conus antidiluvianus* Bruguière, 1792 – Davoli, p. 446, pl. 1, fig. 8, pl. 2, fig. 11.
2009 *Conilithes antidiluvianus* (Bruguière, 1792) – Tucker & Tenorio, p. 136, unnumbered fig., p. 137, fig. 21.
2008 *Conus* (*Conolithes*) *antidiluvianus* Bruguière, 1792 – Chirli & Richard, p. 72, pl. 14, fig. 8.
2010 *Conus antidiluvianus* Bruguière, 1792 – Sosso & Dell'Angelo, p. 49, 64 unnumbered fig bottom row left.
2011 *Conolithus antidiluvianus* (Bruguière, 1792) – Harzhauser *et al*., p. 217, fig. 4.5.
2011 *Conilithes antidiluvianus* (Bruguière, 1792) – Landau *et al*., p. 32, pl. 16, fig. 10.
2013 *Conilithes antidiluvianus* (Bruguière, 1792) – Kovács & Vicián, p. 89, fig. 149.
2014 *Conus antidiluvianus* Bruguière, 1792 – Paganelli, p. 30, pl. 1, figs 1-3.

2015 *Conilithes antidiluvianus* (Bruguière, 1792) – Kovács & Balázs, p. 38, figs 95-96.
2016 *Conilithes antidiluvianus* (Bruguière, 1792) – Harzhauser & Landau, p. 46, figs 3C, $5J_1$-J_3, $5K_1$, $6A_1$-A_3.
2018 *Conus antidiluvianus* (Bruguière, 1792) – Brunetti & Cresti, p. 102, fig. 427.
2021 *Conilithes antidiluvianus* (Bruguière, 1792) – Psarras *et al*., p. 1321, fig. 11.

non 1831 *Conus antidiluvianus* Bruguière – Dubois de Montpéreux, p. 23, pl. 1, fig. 1 [= *Conilithes exaltatus* (Eichwald, 1830)].
?*non* 1853 *Conus antediluvianus* [*sic*] Brug. – Beyrich, p. 291, pl. 4, fig. 1.
?*non* 1907 *Conus antediluvianus* [*sic*] Bruguière – Ravn, p. 362, pl. 8, fig. 5.
non 1955 *Conus* (*Conuspira* [*sic*]) *antidiluvianus* Bruguière var. *buiturica* var. nov. – Moisescu, p. 162, pl. 14, figs 7-8 [= *Conilithes exaltatus* (Eichwald, 1830)].
?*non* 1964 *Conus* (*Conolithus*) *antediluvianus* [*sic*] (Bruguière, 1792) [*sic*] – Anderson, p. 317, pl. 45, figs 274, 274a, b.
non 1972 *Conus* (*Lithoconus*) *antediluvianus* [*sic*] *anomalus* n. spp. – Csepreghy-Meznerics, p. 34, pl. 17, figs 9-10 (*nomen nudum*) [= *Conilithes exaltatus* (Eichwald, 1830)].
?*non* 1984 *Conus* (*Conolithus*) *antediluvianus* [*sic*] Bruguière, 1792 – A.W. Janssen, p. 334, pl. 13, figs 18, 19, pl. 76, figs 4-9.

Material and dimensions – Maximum height 96.1 mm, width 35.9 mm. **CO:** NHMW 2024/0205/0009-0012 (4), NHMW 2024/0205/0013 (8), HM coll. (100+). **VC:** NHMW 2024/0205/0014 (4), NHMW 2024/0205/0116-0119 (4 juveniles), HM coll. (5). **EL**: HM coll. (2).

Description – See Harzhauser & Landau (2016, p. 47).

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 96.1 mm, MD: 40.3 mm, mean SL: 71.8 mm (σ = 15.0), mean MD: 28.7 (σ = 6.6); spire angle: μ = 66.6° (σ = 5.3°), last whorl angle: μ = 27.5° (σ = 2.8°), LW: μ = 2.45 (σ = 0.12), RD: μ = 0.58 (σ = 0.04), PMD: μ = 0.95 (σ = 0.02), RSH: μ = 0.29 (σ = 0.03). Subsutural sinus (n=3): SSFD: moderately deep, μ = 1.4 (σ = 0.4). SSFd: strongly curved, μ = 3.2 (σ = 0.2). PV: moderately asymmetrical, μ = 0.6 (σ = 0.1).

Discussion – For the complicated nomenclatural history surrounding this species see A.W. Janssen *et al*. (2014). This species was discussed by Harzhauser & Landau (2016, p. 47). We have endeavoured to give a more complete chresonymy herein than in the Paratethyan paper but have excluded the North Sea Basin references where specimens have a protoconch of 5.5 whorls (*e.g*., Anderson, 1964, pl. 45, figs 274a, b; A.W. Janssen, 2014, pl. 13, figs 18, 19) as opposed to the 3.5 whorls in the Pliocene and Paratethyan specimens. However, as discussed by Harzhauser & Landau (2016) they cannot be separated on shell morphometrics. We have included the Miocene references for the French Atlantic, although these require confirmation.
The Estepona specimens are highly variable in slenderness and in spire height. In some specimens the suture is placed just below the shoulder, whilst in others it is some

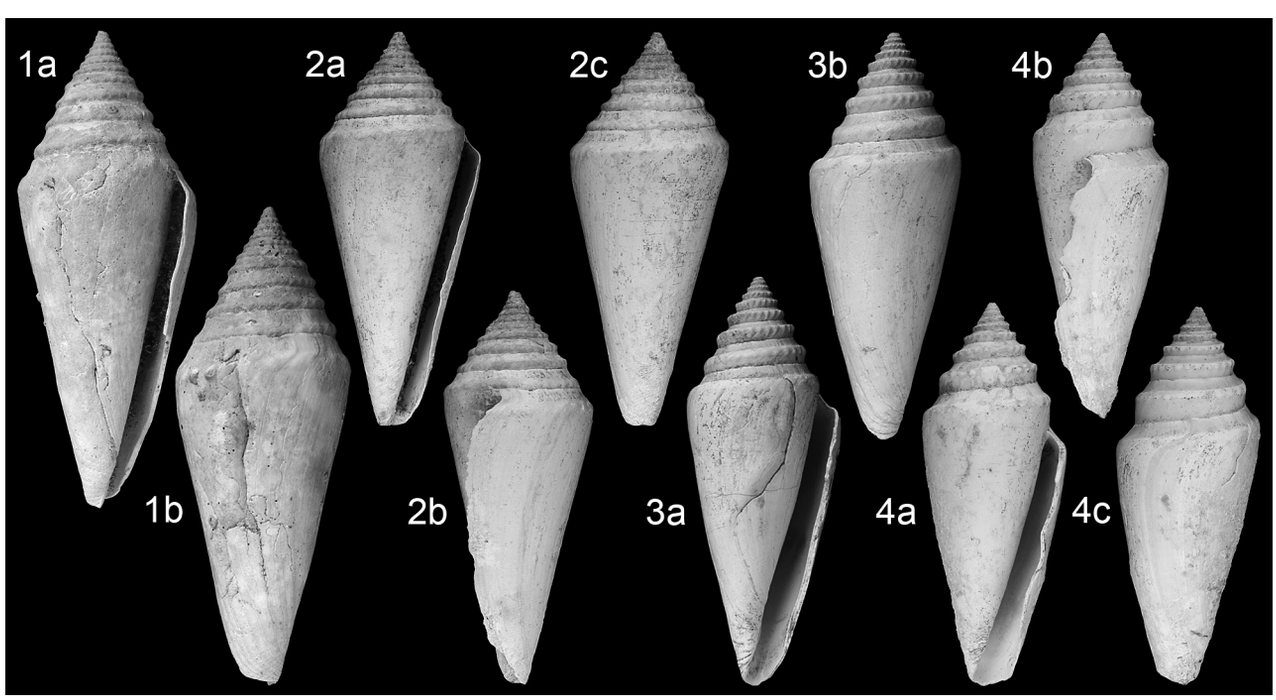

Plate 3. *Conilithes antidiluvianus* (Bruguière, 1792); 1. NHMW 2024/0205/0011, height 96.1 mm, width 35.9 mm; 2. NHMW 2024/0205/0010, height 69.7 mm, width 28.6 mm; 3. NHMW 2024/0205/0009, height 72.9 mm, width 27.7 mm; 4. NHMW 2024/0205/0012, height 59.2 mm, width 22.4 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

distance below, giving the spire a gradate appearance (Pl. 3, fig. 4). The strength and size of the shoulder tubercles is also variable tending to weaken on the last whorl. The shell ratios are comparable to specimens from the Paratethys, except they attain a greater maximum size (height 96.1 mm vs. 81.9 mm; Harzhauser & Landau, 2016, p. 47). No colour pattern was seen in the material described by Harzhauser & Landau (2016). Based on Upper Miocene eastern Proto-Mediterranean specimens from Crete, Psarras *et al*. (2021, fig. 11A3) detected a faint pattern of axially arranged, rectangular blotches along the posterior two-thirds of last whorl. We have not detected such colour pattern in the Estepona material.
In Estepona this species is found both in the shallow and deeper water Velerín conglomerates assemblage, which partly agrees with the observations of Harzhauser & Landau (2016) that the species is mainly found in offshore clays suggesting middle shelf to upper bathyal settings.

Distribution – Lower Miocene: Paratethys, Austria (Steininger, 1973), Slovakia (Harzhauser, *et al*., 2011); Proto-Mediterranean: Italy (Sacco, 1893a; Hall, 1964). Middle Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1932); Paratethys, Austria, Czech Republic (Hoernes & Auinger, 1879; Harzhauser & Landau, 2016); Hungary (Strausz, 1966; Csepreghy-Meznerics, 1972; Kovács & Vicián, 2013); Bosnia and Herzegovina (Atanacković, 1969); Romania (Chira & Voia, 2001; Kovács & Balázs, 2015; Harzhauser & Landau, 2016); Bulgaria (Kojumdgieva & Strachimirov, 1960). Upper Miocene: central Proto-Mediterranean: Italy (Sacco, 1893a; Davoli, 1972, 2003); eastern Proto-Mediterranean, Greece (Psarras *et al*., 2021), Crete (Dermitzakis, 1969). Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al*., 2011); western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), France (Cossmann, 1896); central Mediterranean, Italy (Sacco, 1893a; Pelosio, 1967; Pavia, 1976; Spadini, 1990; Chirli, 1997; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975); eastern Mediterranean, Turkey (Erünal-Erentöz, 1958). Upper Pliocene: western Mediterranean, France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1893a, 1904; Palla, 1967; Mastrorilli, 1969; Malatesta, 1974; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992; Paganelli, 2014).

Conilithes brocchii (Bronn, 1828)

Plate 4, figs 1-3, Plate 17, fig. 3, Plate 18, fig. 3

1814 *Conus deperditus* Bruguiere – Brocchi, p. 292, pl. 3, fig. 2 [*non Eoconus deperditus* (Bruguière, 1792)].
*1828 *Conus Brocchii* Bronn, p. 740 [*nom. nov. pro Conus deperditus* Brocchi, 1814 *non* Bruguière, 1792].
1831 *Conus Brocchii* Brn. – Bronn, p. 12.
1868 *Conus Brocchii* Bronn – Foresti, p. 56.
1880 *Conus brocchii* Bronn – Fontannes, p. 149, pl. 8, fig. 15.
1891 *Conus Brocchii* Bronn – Levy & Bergeron, p. 249, pl. O, fig. 1.
1893a *Conus* (*Leptoconus*) *Brocchii* (Bronn) – Sacco, p. 30, pl. 4, fig. 1.
1893a *Conus* (*Leptoconus*) *Brocchii* var. *excanaliculata* Sacco, p. 31.
1893a *Conus* (*Leptoconus*) *Brocchii* var. *antediluvianoides* Sacco, p. 31, pl. 4, fig. 2.
1893a *Conus* (*Leptoconus*) *Brocchii* var. *fusulospirata* Sacco, p. 31, pl. 4, fig. 3.
1893a *Conus* (*Leptoconus*) *Brocchii* var. *crassospirata* Sacco, p. 31, pl. 4, fig. 4.
1893a *Conus* (*Leptoconus*) *Brocchii* var. *brevidepressula* Sacco, p. 32, pl. 4, fig. 5.
1955 *Conus* (*Conospira*) *brocchii* Bronn 1831 – Rossi Ronchetti, p. 287, fig. 154.
1963 *Conus brocchii* Bronn – Caretto, p. 24, pl. 3, fig. 21.
1964 *Conus brocchii* Bronn, 1828 – Hall, p. 140 [30] (*partim*), pl. 23, figs 5, 6 (only).
1974 *Conus* (*Leptoconus*) *brocchii* Bronn, 1828 – Malatesta, p. 393, pl. 30, fig. 2.
1976 *Conus brocchii* Bronn – Caprotti, p. 12, pl. 17, fig. 7.
1978 *Conus brocchii* Bronn, 1831 [*sic*] – Pinna & Spezia, p. 136, pl. 18, fig. 3.
1990 *Conus brocchii* Bronn, 1831 [*sic*] – Spadini, p. 317, pl. 1, fig. 6.
1992 *Conus brocchii* Bronn, 1831 [*sic*] – Cavallo & Repetto, p. 126, fig. 330.
1997 *Conus* (*Leptoconus*) *brocchii* Bronn, 1831 [*sic*] – Chirli, p. 16, pl. 4, figs 9-10.
1999 *Conus* (*Leptoconus*) *brocchii* Bronn, 1831 [*sic*] – Muñiz Solís, p. 77, figs 9J-K.
2008 *Conus* (*Leptoconus*) *brocchii* Bronn, 1828 – Chirli & Richard, p. 73, pl. 14, fig. 9.
2009 *Conilithes brocchii* (Bronn, 1828) – Tucker & Tenorio, p. 137.
2010 *Conus brocchii* Bronn, 1831 [*sic*] – Sosso & Dell'Angelo, p. 49, 64 unnumbered fig. bottom row centre.
2014 *Conus brocchii* Bronn, 1828 – Paganelli, p. 31, pl. 3, figs 22, 23.

non 1964 *Conus brocchii* Bronn, 1828 [*sic*] – Hall, p. 140 [30] (*partim*), pl. 23, fig. 12 [= *Conilithes allioni* (Michelotti, 1847)].
non 2009 *Conus brochii* [*sic*] Bronn, 1828 [*sic*] – Zunino & Pavia, p. 365, pl. 2, fig.1[= *Conilithes allioni* (Michelotti, 1847)].
non 2014 *Conilithes brocchii* (Bronn, 1828) – Kovács & Vicián, p. 89, figs 150-151 [= *Conilithes* sp.].
non 2015 *Conilithes brocchii* (Bronn, 1828) – Kovács & Balázs, p. 39, figs 97-98 [= *Conilithes* sp.].

Material and dimensions – Maximum 67.4 mm, width 32.5 mm. **CO:** NHMW 2024/0205/0004-0006 (3), NHMW 2024/0205/0007 (5), NHMW 2024/0205/0120 (1 juvenile), HM coll. (41). **EL**: NHMW 2024/0205/0008 (2), HM coll. (1).

Description – Shell moderately large, medium width, with high, scalariform conical to coeloconoid spire and moderately long last whorl. Protoconch tall, multispiral of at least 3-3.5 smooth, convex whorls (apex of protoconch missing). Teleoconch of up to eight whorls. First three teleoconch whorls tuberculate, with tubercles placed mid-whorl. Later spire whorls with concave subsutural ramp bearing close-set, arcuate growth lines, delimited by sharp carina placed slightly below mid-whorl, no spiral sculpture. Subsutural sinus shallow, strongly curved, nearly asymmetrical. Last whorl strongly angular at shoulder, with maximum diameter at carina, represented by broad rounded cord in fully adult specimens, regularly conical and contracting below, hardly constricted at base, with moderately long, poorly delimited siphonal fasciole; 8-10 weak spiral cords over fasciole, strengthening slightly abapically. Aperture elongate, narrow, hardly widening abapically. Columella straight. No colour pattern preserved.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 59.5 mm, MD: 30.0 mm, mean SL: 46.4 mm (σ = 7.5), mean MD: 22.5 (σ = 3.8); spire angle: μ = 87.5° (σ = 8.1°), last whorl angle: μ = 33.6° (σ = 1.5°), LW: μ = 2.1 (σ = 0.1), RD: μ = 0.65 (σ = 0.03), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.25 (σ = 0.03). Subsutural sinus (n=4): SSFD: shallow, μ = 2.6 (σ = 0.6). SSFd: strongly curved, μ = 3.3 (σ = 0.3). PV: nearly symmetrical, μ = 0.7 (σ = 0.2).

Discussion – Hall (1964), synonymised *Conus allioni* Michelotti, 1847 with *Conus brocchii* Bronn, 1828. Harzhauser & Landau (2016) considered *Conilithes brocchii* to be a Pliocene species, differing in its larger size, higher and sometimes slightly coeloconoid spire, prominent carina and the broader last whorl, lacking the slight constriction of *C. allioni*, which has a low and sometimes cyrtoconoid spire.

The Estepona specimens are rather uniform in shape and sculpture. The sharp carina on early adult whorls becomes a rounded cord on later adult whorls that broadens and flattens with ontogeny but remains evident in even the largest specimens. The last whorl above the siphonal fasciole is smooth in most specimens, although occasionally a few narrow, irregular, subobsolete spiral cords may develop, mainly mid-whorl.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1893a; Pavia, 1976; Spadini, 1990; Chirli, 1997; Sosso & Dell'Angelo, 2010). Upper Pliocene: Atlantic, Mondego Basin, Portugal (NHMW coll.); western Mediterranean, France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1893a; Caretto, 1963; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992; Paganelli, 2014).

Genus *Kalloconus* da Motta, 1991

Type species (by original designation): *Conus pulcher* [Lightfoot], 1786, present-day, West Africa.

1991 *Kalloconus* da Motta, p. 12.

***Kalloconus pulcher* ([Lightfoot], 1786)**
Plate 5, figs 1-4, Plate 17, fig. 4, Plate 18, fig. 4

*1786 *Conus pulcher* [Lightfoot], p. 179.
1791 *Conus leoninus* Gmelin, p. 3386.
1798 *Cucullus Indiae* Röding, p. 43.
1807 *Conus gigas* Fischer von Waldheim, p. 140.
1817 *Conus fluctifer* Dillwyn, p. 382.
1823 *Conus grandis* G.B. Sowerby I, p. 16 [266], fig. 2.
1833 *Conus bicolor* G.B. Sowerby I, p. 28, fig. 18 [May, junior homonym of *Conus bicolor* G.B. Sowerby I, 1833, March).
1833 *Conus breviculus* G.B. Sowerby I, p. 37, fig. 55.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *canaliculatodepressa* Sacco, p. 19, pl. 2, fig. 13.
1893a *Conus* (*Lithoconus*) *antiquus* var. *percanaliculata* Sacco, p. 25, pl. 3, fig. 11.
1964 *Conus antiquus* Lamarck, 1810 – Hall, p. 128 [18] (*partim*), pl. 21, fig. 7 only.
1985 *Conus pulcher* Lightfoot, 1786 – Caretto, p. 185,

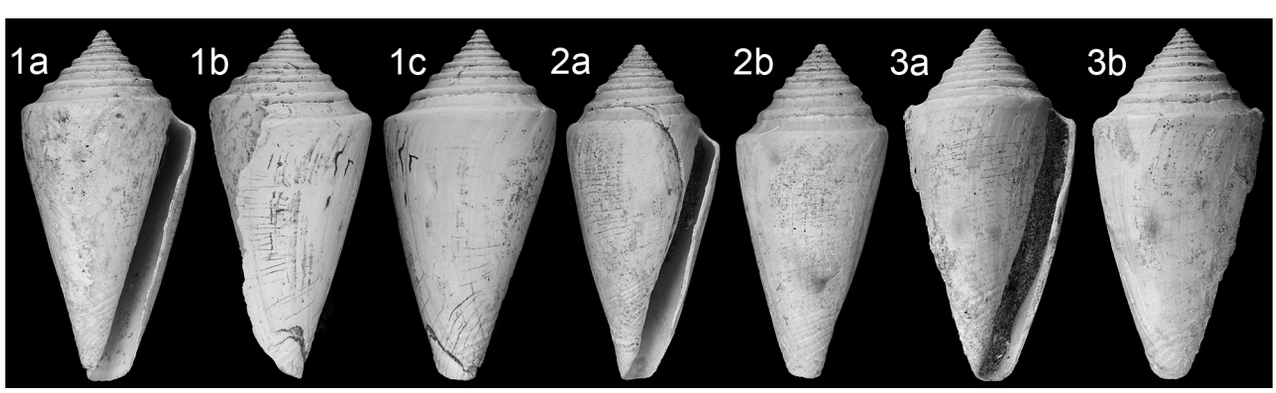

Plate 4. *Conilithes brocchii* (Bronn, 1828); 1. NHMW 2024/0205/0004, height 46.9 mm, width 23.6 mm; 2. NHMW 2024/0205/0005, height 51.2 mm, width 23.7 mm; 3. NHMW 2024/0205/0006, height 54.6 mm, width 26.7 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

figs 1-9.

1990 *Conus* cfr. *pulcher* Lightfoot, 1786 – Spadini, p. 320, pl. 3, figs 11-12.

1999 *Conus* (*Lithoconus*) *antiquus* Lamarck, 1810 – Muñiz Solíz, p. 79, figs 10A-C [*non Monteiroconus antiquus* (Lamarck, 1810)].

?1999 *Conus* (*Lithoconus*) *pulcher* Lightfoot, 1786 – Muñiz Solíz, p. 82, figs 9L-N.

2009 *Kalloconus pulcher* ([Lightfoot], 1786) – Tucker & Tenorio, p. 99.

2011 *Conus pulcher siamensis* Hwass, 1792 – Hernández *et al*., p. 235, figs 78C-E.

2020 *Conus pulcher siamensis* Hwass, 1792 – Alf *et al*., p. 214, pl. 175.

Material and dimensions – Maximum 111.0 mm, width 57.4 mm. **CO:** NHMW 2024/0205/0030-000033 (4), NHMW 2024/0205/0034 (9), HM coll. (12).

Description – Shell very large, with very low conical spire. Teleoconch of 8-9 whorls, whorl tops smooth except for close-set, comma-shaped growth lines, concave, delimited by shoulder raised very slightly above suture. Suture deeply impressed. Subsutural sinus deep, strongly curved, strongly asymmetrical. Last whorl with horizontal, concave subsutural platform, sharply angled at shoulder placed almost at suture, regularly conical below, position of maximum diameter close below shoulder, not constricted at base, Siphonal fasciole weakly developed; a few weak, widely spaced cords over base and fasciole, strengthening slightly abapically. Aperture relatively narrow with parallel sides, hardly widening abapically; siphonal canal short. Colour pattern poorly preserved but seems to consist of dark spiral lines and possibly broad horizontal bands just visible under UV light.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 102.4 mm, MD: 54.0 mm, mean SL: 86.2 mm (σ =11.8), mean MD: 46.5 (σ = 6.0); spire angle: μ = 147.7° (σ = 6.7°), last whorl angle: μ = 30.8° (σ = 1.0°), LW: μ = 1.8 (σ = 0.03), RD: μ = 0.6 (σ = 0.03), PMD: μ = 0.9 (σ = 0.03), RSH: μ = 0.1 (σ = 0.02), Subsutural sinus (n=4): SSFD: deep. μ = 1.2 (σ = 0.3), SSFd: strongly curved. μ = 3.5 (σ = 4.3), PV: strongly asymmetrical. μ = 0.3 (σ = 0.2).

Discussion – Kalloconus pulcher ([Lightfoot], 1786) is the largest living cone shell, attaining up to 222 mm in height. It is characterised by its very large size, flattened spire composed of concave whorl tops without spiral sculpture, sharply angled shoulder placed just below the apex, and regularly conical last whorl.
Caretto (1985) was the first to recognise its presence in

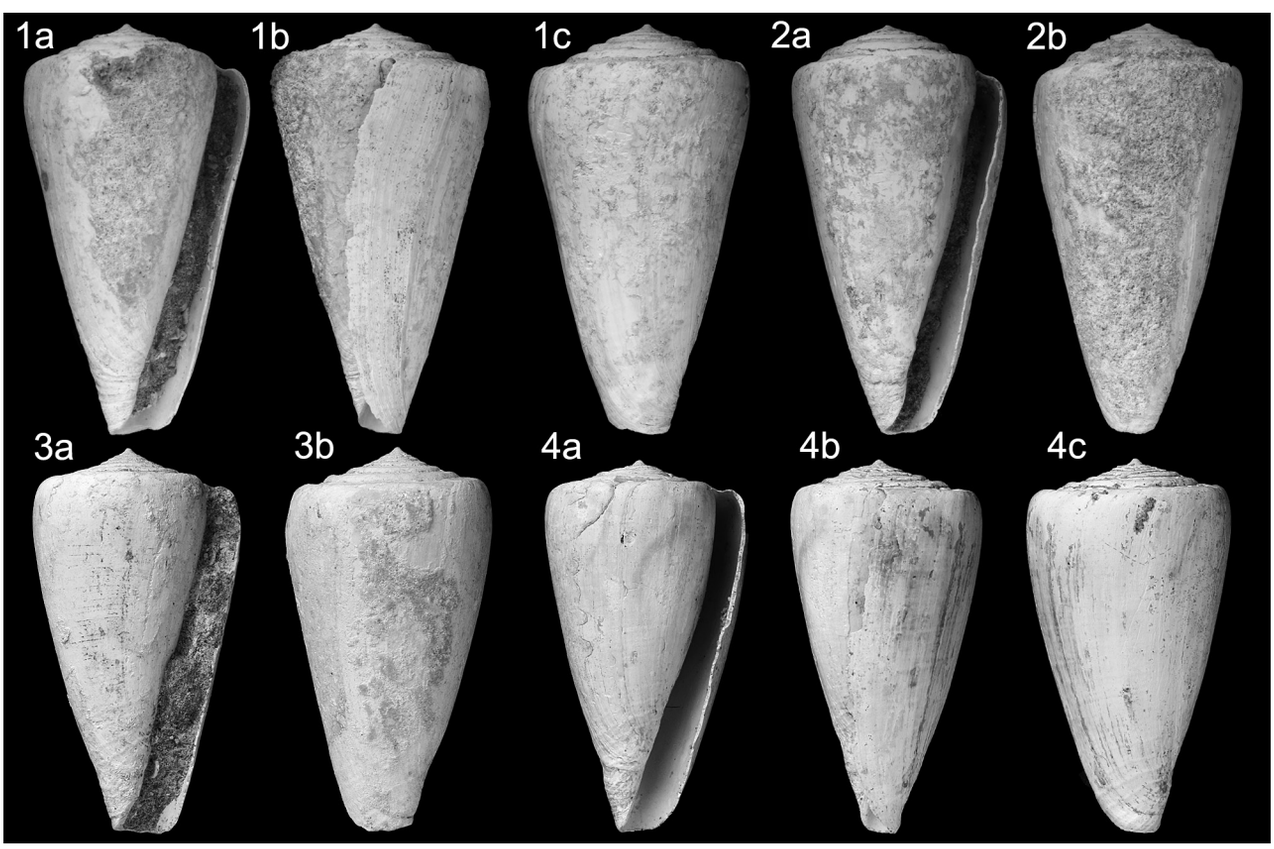

Plate 5. *Kalloconus pulcher* ([Lightfoot], 1786); 1. NHMW 2024/0205/0030, height 93.9 mm, width 51.6 mm; 2. NHMW 2024/0205/0031, height 102.4 mm, width 53.7 mm; 3. NHMW 2024/0205/0032, height 85.7 mm, width 45.7 mm; 4. NHMW 2024/0205/0033, height 62.4 mm, width 34.0 mm (subadult). Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

the Italian Upper Pliocene and discussed this fossil occurrence at length. The Estepona specimens fit within the range of variability of the Italian Pliocene specimens figured by authors and show some remnants of colour pattern consisting of fine dark spiral lines similar to that illustrated by Caretto (1985, fig. 4).
Muñiz Solís (1999, figs 9L-N) recorded this species in the Estepona assemblages and illustrated a shell 45 mm in height with a spire rather elevated for the species that might represent a juvenile specimen but misidentified adult specimens with a maximum height of 112 mm as *Conus* (*Lithoconus*) *antiquus* Lamarck, 1810 (Muñiz Solís, 1999, figs 10A-C). *Kalloconus antiquus* differs in having the last whorl slightly swollen below the shoulder and far more elongated and tapering below and has cords on the spire whorl tops (see Pereira da Costa, 1866, pl. 5, figs 1, 2, pl. 6, figs 1, 2, pl. 7, fig. 2; Sacco, 1893b, pl. 3, fig. 6; Hall, 1964, pl. 21, figs 5, 8, 9, 10 for typical specimens). We admit that some large specimens from Estepona are quite slender (Pl. 5, figs 1-2) and approximate to *K. antiquus*, but they lack the constriction at about two thirds whorl height seen in that species and have smooth concave whorl tops.
Caretto (1985) included in his chresonymy of *K. pulcher* Sacco's (1893) Pliocene form *Conus antiquus* var. *percanaliculata* (type re-illustrated by Hall, 1964, pl. 21, fig. 7). He also included *Conus antiquus* var. *percanaliculata* Sacco, 1893 from the Langhian Middle Miocene of Baldissero, Italy that also seems to represent *K. pulcher* and would signify the first occurrence of the species.
Today the species lives at greater latitudes, off the coast of West Africa, in tropical shallow subtidal coastal waters at about 20-30 m depth on sandy bottoms (Alf *et al*., 2020). In Italy it is also found in sandy facies (Caretto, 1985).

Distribution – Middle Miocene: central Proto-Mediterranean (Langhian), Italy (Sacco, 1893b; Hall, 1964). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893a; Caretto, 1985; Spadini, 1990). Present-day: Atlantic, Senegal, Cape Verde Islands (Caretto, 1985), Mauritania to Angola (Hernández *et al*., 2011; Alf *et al*., 2020).

Genus *Lautoconus* Monterosato, 1923

Type species (by original designation): *Conus mediterraneus* Hwass in Bruguière, 1792, present-day, Mediterranean.

1923 *Lautoconus* Monterosato, p. 11.

***Lautoconus bitorosus* (Fontannes, 1880)**
Plate 6, figs 1-5, Plate 17, fig. 5, Plate 18, fig. 5

*1880 *Conus bitorosus* Fontannes, p. 146, pl. 8, fig. 12.
1880 *Conus perpinianus* Fontannes, p. 148, pl. 8, fig. 14.
1893b *Conus* (*Chelyconus*) *bitorosus* (Font.) – Sacco, p. 108, pl. 10, fig. 19.
1893b *Conus* (*Chelyconus*) *bitorosus* var. *elatoastensis* Sacco, p. 109, pl. 10, fig. 21.
1893b *Conus* (*Chelyconus*) *bitorosus*? var. *crassovata* Sacco, p. 109, pl. 10, fig. 22.
1893b *Conus* (*Chelyconus*) *bitorosus* var. *exventricosa* Sacco, p. 109, pl. 10, fig. 22bis.
1893b *Conus* (*Chelyconus*) *bitorosus* var. *perpiniana* (Font.) – Sacco, p. 109, pl. 10, fig. 23.
1893b *Conus* (*Chelyconus*) *bitorosus* var. *pliotransiens* Sacco, p. 110, pl. 10, fig. 24.
1893b *Conus* (*Chelyconus*) *bitorosus*? var. *exilior* (Dod.) Sacco, p. 110, pl. 10, fig. 26.
1910 *Conus* (*Chelyconus*) *pelagicus* Br. – Cerulli-Irelli, p. 49 [241], pl. 4 [35], fig. 49 [*non Lautoconus pelagicus* (Brocchi, 1814)].
1972 *Conus bitorosus* Fontannes – Davoli, p. 87, pl. 3, figs 7-10, pl. 8, figs 11-15.
1974 *Conus* (*Chelyconus*) *bitorosus* Fontannes, 1880 – Malatesta, p. 378, pl. 30, fig. 12.
1976 *Conus bitorosus* Fontannes – Pavia, p. 114, pl. 9, fig. 6.
1990 *Conus bitorosus* Fontannes, 1880 – Spadini, p. 317, pl. 1, fig. 8.
1992 *Conus bitorosus* Fontannes, 1880 – Cavallo & Repetto, p. 126, fig. 329.
1997 *Conus* (*Chelyconus*) *bitorosus* Fontannes, 1880 – Chirli, p. 3, pl. 1, figs 1-3.
1999 *Conus* (*Chelyconus*) *bitorosus* Fontannes, 1880 – Muñiz Solíz, p. 38, figs 6E-H.
2014 *Conus bitorosus* Fontannes, 1880 – Paganelli, p. 32, pl. 4, figs 29, 30.

non 2013 *Lautoconus bitorosus* (Fontannes, 1880) – Landau *et al*., 239, pl. 38, figs 2-4, pl. 41, fig. 9, pl. 42, fig. 3, pl. 81, fig. 3 [= *Lautoconus miovoeslauensis* (Sacco, 1893)].

Material and dimensions – Maximum height 55.6 mm, width 31.0 mm. **CO:** NHMW 2024/0205/0015-0019 (5), NHMW 2024/0205/0020 (7), HM coll. (100+). **EL**: NHMW 2024/0205/0113 (1), HM coll. (3).

Description – Shell medium sized, robust, broad with medium height to low conical spire and ovate-conical last whorl. Protoconch not preserved. Teleoconch of up to eight whorls. Early spire whorls eroded in adult specimens, bearing 2-3 weak spiral cords in juvenile specimens, later spire whorls flattened, forming low conical spire, with weakly concave subsutural ramp on last 1-2 whorls; cords weakening further towards outer lip; last whorl with poorly defined groove placed adapical to mid subsutural ramp. Suture incised, not channelled. Subsutural sinus moderately deep, weakly curved, strongly asymmetrical. Last whorl barrel-shaped, with narrow, weakly concave subsutural ramp, weakly angled at shoulder, rounded below, position of maximum diameter slightly below shoulder, subcylindrical below with convex sides, moderately constricted at base, siphonal

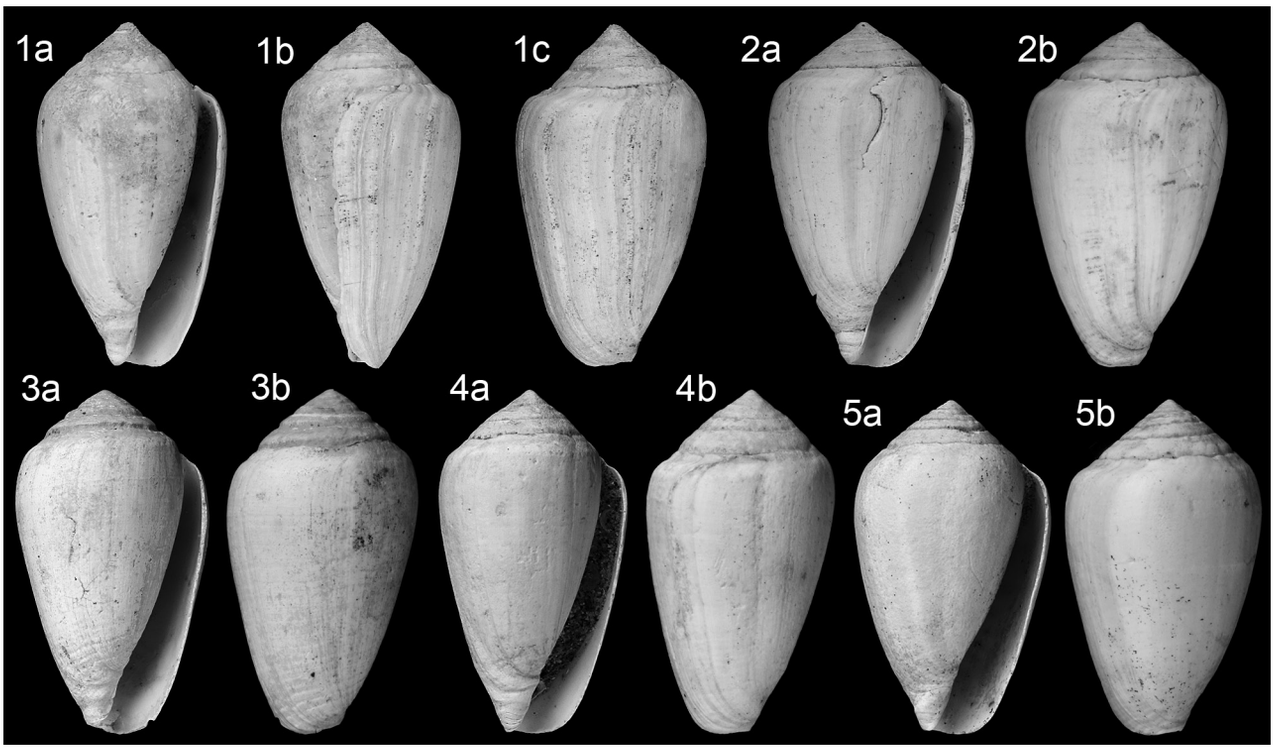

Plate 6. *Lautoconus bitorosus* (Fontannes 1880); 1. NHMW 2024/0205/0015, height 44.4 mm, width 24.4 mm; 2. NHMW 2024/0205/0016, height 49.1 mm, width 29.4 mm; 3. NHMW 2024/0205/0017, height 46.7 mm, width 26.0 mm; 4. NHMW 2024/0205/0018, height 44.1 mm, width 24.1 mm; 5. NHMW 2024/0205/0019, height 40.7 mm, width 24.6 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

fasciole short, up to ten weak flattened cords over base, strengthening slightly abapically. Aperture elongate, widening abapically, siphonal canal moderately twisted, short. No colour pattern preserved.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 49.1 mm, MD: 29.4 mm, mean SL: 43.1 mm (σ = 3.7), mean MD: 25.3 (σ = 2.3); spire angle: μ = 110.1° (σ = 10.0°), last whorl angle: μ = 41.9° (σ = 2.8°), LW: μ = 1.7 (σ = 0.1), RD: μ = 0.7 (σ = 0.03), PMD: μ = 0.8 (σ = 0.04), RSH: μ = 0.19 (σ = 0.02). Subsutural sinus (n=4): SSFD: moderately deep, μ = 1.2 (σ = 0.2). SSFd: weakly curved, μ = 9.0 (σ = 3.0). PV: strongly asymmetrical, μ = 0.3 (σ = 0.03).

Discussion – Following Hall (1964), Landau *et al.* (2013) adopted a wide species concept for *Lautoconus bitorosus* (Fontannes, 1880) which is probably incorrect. According to Harzhauser & Landau (2016), Middle Miocene specimens, including those from the eastern Proto-Mediterranean Karaman Basin, Turkey (see Landau *et al*., 2013), differ from the Pliocene *L. bitorosus* in their lower spires and more elongate shapes, and suggested it might be justified to separate the Miocene specimens as *Lautoconus miovoeslauensis* (Sacco, 1893), erected by Sacco for specimens from the Middle Miocene Paratethys (see Harzhauser & Landau, 2016, figs 17B, 18D_1-D_3, 18E_1-E_3, 18F_1-F_2). Harzhauser & Landau (2016) considered it likely that *L. bitorosus* applied to Pliocene specimens only, a position followed herein.

Together with *Varioconus striatulus* (Brocchi, 1814), this is one of the most abundant cones in the Estepona assemblages. *Lautoconus bitorosus* is similar in profile to *Lautoconus ventricosus* (Gmelin, 1791) (= *Conus mediterraneus* Hwass in Bruguìere, 1792) with which it co-occurs in the Estepona assemblages and still occurs today in the entire Mediterranean and the Atlantic coast of Morocco. However, *L. bitorosus* tends to be stockier, thicker shelled, more ovate, especially at the base, has smooth, convex spire whorls, whereas in *L. bitorosus* they are flattened, the last is slightly concave with a poorly defined sulcus placed slightly adapical of mid-whorl top, plus 2-3 fine spiral threads in some specimens. Muñiz-Solís (1999, figs 2B and 3A) suggested that they could easily be separated by the shape of their subsutural sinus, much shallower in *C. ventricosus*. In our material this difference is not so clear. Finally, *L. ventricosus* has a colour pattern that is highly variable, but usually consists of irregular reddish/brown blotches with a central lighter band, whereas no colour pattern is preserved in *L. bitorosus.*

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1893b; Pavia, 1976; Spadini, 1990; Chirli, 1997; Paganelli, 2014). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

***Lautoconus corynetes* (Fontannes, 1880)**
Plate 13, figs 4-6, Plate 17, fig. 6, Plate 18, fig. 6

*1880	*Conus corynetes* Fontannes, p. 146, pl. 8, fig. 13.
1990	*Conus belus* d'Orbigny, 1852 – Spadini, p. 319, pl. 1, figs 3-5 [*non Lautoconus belus* (d'Orbigny, 1852)].
1997	*Conus* (*Chelyconus*) *deshayesii* Bellardi & Michelotti, 1840 – Chirli, p. 5 (*partim*), pl. 1, figs 7, 8 [not fig. 9 = *Lautoconus deshayesii* (Bellardi & Michelotti, 1840)].
1999	*Conus* (*Dendroconus*) *belus* d'Orbigny, 1852 – Muñiz Solís, p. 71, figs 9A-B [*non Lautoconus belus* (d'Orbigny, 1852)].

Material and dimensions – Maximum height 35.9 mm, width 19.8 mm. **CO:** NHMW 2024/0205/0022-0024 (3), NHMW 2024/0205/0025 (8), HM coll. (28).

Description – Shell moderately small, broad with high mammillate spire and conical last whorl. Protoconch not preserved. Teleoconch of about seven whorls. Early spire whorls usually eroded in adult specimens, bearing very fine, weak spiral cords in juvenile specimens visible under magnification; later spire whorl tops smooth, weakly convex to almost flat sided forming broadly conical spire. Suture deeply incised, not channelled. Subsutural sinus moderately deep, weakly curved, moderately asymmetrical. Last whorl roundly angled at very high-placed shoulder, position of maximum diameter at about three quarters last whorl height, regularly conical below, almost straight-sided, evenly contracting in lower half of shell, not constricted at base, siphonal fasciole poorly developed, up to eight narrow cords over fasciole strengthening slightly abapically. Aperture elongate, moderately narrow, hardly widening abapically, siphonal canal weakly recurved, moderately long. Colour pattern of narrow, oblique flammules over entire spire and subsutural ramp, abruptly ending at or just below shoulder, below very fine, close-set and horizontal reddish/brown lines, narrower than their interspaces; colour pattern over cords on fasciole.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 33.8 mm, MD: 19.3 mm, mean SL: 30.1 mm (σ = 2.0), mean MD: 17.5 (σ = 1.4); spire angle: μ = 104.5° (σ = 7.2°), last whorl angle: μ = 39.9° (σ = 1.8°), LW: μ = 1.7 (σ = 0.05), RD: μ = 0.73 (σ = 0.03), PMD: μ = 0.9 (σ = 0.03), RSH: μ = 0.21 (σ = 0.03), Subsutural sinus (n=4): SSFD: moderately deep. μ = 1.7 (σ = 0.2), SSFd: weakly curved. μ = 7.0 (σ = 0.04), PV: moderately asymmetrical. μ = 0.5 (σ = 0.01).

Discussion – Muñiz Solís (1999, p. 71, figs 9A-B) identified these specimens as *Conus* (*Dendroconus*) *belus* d'Orbigny, 1852, probably influenced by Spadini (1990, p. 319, pl. 1, figs 3-5) who illustrated conspecific specimens from the Lower Pliocene Terre Rosse locality (Sienna, Italy) also as *C. belus*. *Conus belus* was introduced by d'Orbigny (1852, p. 11) for *C. pyrula* Grateloup (1847 pl. 44, figs 12, 13) *non* Brocchi, 1814, referring to a specimen from the Lower Miocene Aquitanian of Dax, Saubrigues, France. Sacco (1893b) and Hall (1964) identified specimens from the Lower Miocene Burdigalian Proto-Mediterranean of Italy as *C. belus*, or varieties thereof. Although the Italian specimens have spiral lines below the shoulder, we see no flammules over the spire and subsutural ramp, which is preserved in all the specimens from Estepona. Moreover, the stratigraphic gap between *L. belus* and the Estepona specimens make it very unlikely that they are conspecific.
Muñiz Solís (1999, p. 71) recognised the Estepona specimens to be the same species described by Fontannes (1880) as *Conus corynetes*. That author clearly described the colour pattern "*L'extrémité est entourée de cordons obliques, très déliés, inégaux, alternants; le reste de la surface est marqué de lignes en relief extrêmement fines, égales, équidistantes, assez rapprochées*, …[The end (apex) is surrounded by oblique, very slender, unequal, alternating cords; the rest of the surface is marked with extremely fine, equal, equidistant, fairly close lines…]" (Fontannes, p. 147). Muñiz Solís synonymised Fontannes' species with *C. belus*. However, as argued above, because of the lack of flammules over the apex in that species and the wide stratigraphic gap between them, we consider them separate species, the Pliocene specimens corresponding to *Lautoconus corynetes* (Fontannes, 1880).
There also seems to have been some confusion with *Lautoconus deshayesii* (Bellardi & Michelotti, 1840), with which it co-occurs in the Estepona assemblages. However, *L. corynetes* about half the maximum size (max height 35.9 mm herein, 37 mm in Muñiz Solís, 1999 vs. 66.5 mm herein, 49.6 mm in Muñiz Solís, 1999; Estepona specimens), the spire is lower and the last whorl less elongate, and the most obvious difference is in the colour pattern, having strongly preserved axial flammules over the entire spire extending to the shoulder. The whorl tops in *L. deshayesii* are a uniform light orange colour without flammules. Moreover, the spiral lines although fine and regular in both species are even finer and more numerous in *L. corynetes*. Some of the specimens from the Lower Pliocene of Tuscany identified as *L. deshayesii* by Chirli (1997, pl. 1, figs 7, 8) and the specimen from the Lower Pliocene of Sienna illustrated by Spadini (1990, pl. 1, figs 3-5) as *C. belus* both represent *L. corynetes*.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Spadini, 1990; Chirli, 1997).

***Lautoconus depressoastensis* (Sacco, 1893)**
Plate 7, figs 1-2, Plate 17, fig. 7, Plate 18, fig. 7

*1893a	*Conus* (*Dendroconus*) *Eschewegi* var. *depressoastensis* Sacco, p. 13, pl. 1, fig. 26.
1999	*Conus* (*Dendroconus*) *eschewegi* Da Costa, 1866 – Muñiz Solís, p. 73, figs 9C-E [*non Lautoconus eschewegi* (Pereira da Costa, 1866)].

Material and dimensions – Maximum height 37.8 mm, width 22.1 mm. **CO:** NHMW 2024/0205/0107-0108 (2), NHMW 2024/0205/0109 (3).

Description – Shell moderately small, solid, pyriform, with low to medium height pointed conical spire. Teleoconch of up to seven whorls. Surface of early whorls abraded giving apex exaggeratedly mucronate appearance; later spire low conical to cyrtoconoid with narrowly channelled suture; whorl tops slightly convex, bearing one or two spiral cords on adapical half of whorl top (abraded in most specimens); subsutural flexure very shallow, weakly curved, strongly asymmetrical. Last whorl with narrow, convex subsutural ramp, shoulder placed high, weakly subangulate, broadly rounded, conical below with weakly convex sides, maximum diameter placed at about two-thirds last whorl height, hardly constricted at base; siphonal fasciole swollen, sharply delimited; a few broad flattened cords over base. Aperture narrow, widening slightly abapically. No colour pattern preserved.

Shell measurements and ratios – n = 2 adult specimens; largest specimen: SL: 37.8 mm, MD: 22.1 mm, mean SL: 36.3 mm (σ =2.2), mean MD: 20.6 (σ = 2.1); spire angle: μ = 106.5° (σ = 9.2°), last whorl angle: μ = 38.5° (σ = 0.7°), LW: μ = 1.8 (σ = 0.1), RD: μ = 0.7 (σ = 0.05), PMD: μ = 0.8 (σ = 0.03), RSH: μ = 0.18 (σ = 0.04), Subsutural sinus (n=4): SSFD: very shallow, μ = 12.0 (σ = 1.1), SSFd: weakly curved, μ = 4.1 (σ = 1.2), PV: strongly asymmetrical, μ = 0.3 (σ = 0.1).

Discussion – We think this is the species identified by Muñiz Solís (1999, p. 73, figs 9C-E) as *Conus* (*Dendroconus*) *eschewegi* Da Costa, 1866. *Lautoconus eschewegi* (Pereira da Costa, 1866) was originally described based on material from the Upper Miocene Tortonian of Cacela Velha, southern Portugal. Subsequently, it has been recorded from Middle to Upper Miocene assemblages in the Proto-Mediterranean Sea (Sacco, 1893a; Davoli 1972; Ruggieri & Davoli 1984; *inter alia*) and Paratethys (Kovács & Vicián 2013; Harzhauser & Landau, 2016; *inter alia*).
The conspecificity of these Pliocene specimens was already questioned by Harzhauser & Landau, 2016, p. 77), who noted that the specimen illustrated by Muñiz Solís from Estepona had a broader, more conical last whorl than Miocene specimens of *L. eschewegi*. We have now compared these Spanish Pliocene shells directly with specimens from the Cacela assemblage and indeed the most notable difference is the shape of the shoulder on the last whorl which is more prominent and rounded in the Portuguese Miocene specimens and the profile of the last whorl below the shoulder is almost regularly conical with straight sides as opposed to more cylindrical in the Pliocene specimens. Moreover, the spiral sculpture is far stronger over the fasciole and extends further over the base in the Portuguese Miocene specimens. The subsutural flexure is similar in both forms. It is difficult to comment on the spire characters of Cacela cones. A taphonomic feature of the deposit, at least with Conidae, is that whilst the last whorl is beautifully preserved and retains its glossy surface, the spire of even the most juvenile specimens is eroded, giving a flattened aspect to the spire. As also noted by Harzhauser & Landau (2016, p. 77), we have no evidence of spiral sculpture on the spire whorls of *C. eschewegi*, which would place it in *Varioconus* da Motta, 1991. However, there is a hint of a couple of spiral cords on the spire whorl tops in the Spanish specimens (also described by Muñiz Solís, 1999, p. 73) and we therefore place it in *Lautoconus* Monterosato, 1923. However, we strongly suspect WoRMS to be correct in synonymising the two genera but refrain from doing so until supported by genetic data.
Sacco (1893a, p. 13) described *Conus eschewegi* var. *depressoastensis* from the Pliocene of Italy as being exceedingly uncommon and doubting that it was really *C. eschewegi*. The Pliocene form from Italy has not been illustrated or discussed since its original description and it is difficult to be certain that the figure given by Sacco is conspecific with the Estepona specimens. Subsequent authors have placed it rather uncritically or with a query in the synonymy of *C. eschewegi* (Davoli, 1972, p. 107-108; Ruggieri & Davoli, 1984, p. 73). It certainly seems to have a slightly more cylindrical last whorl than Portuguese specimens of *L. eschewegi*. We therefore provisionally use Sacco's name for this species.
In the Estepona assemblages it is most similar to small forms of *Lautoconus bitorosus* (Fontannes, 1880), but

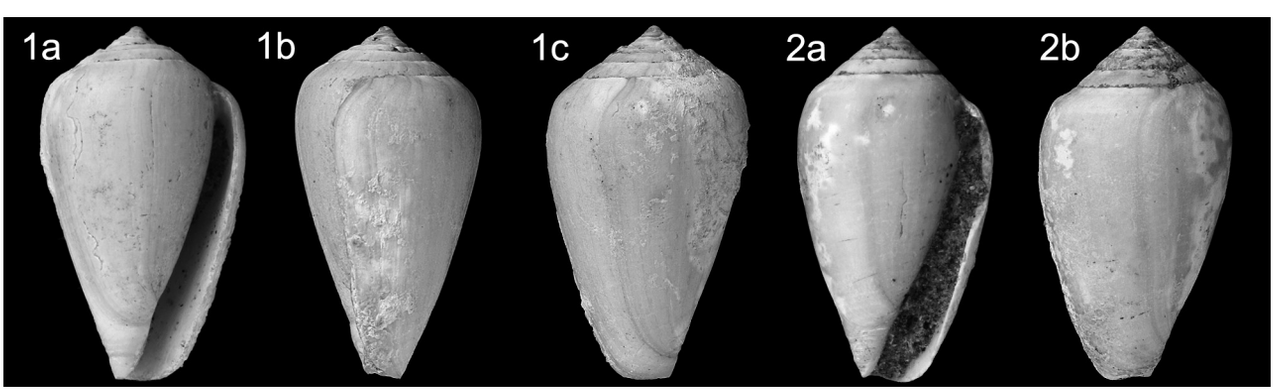

Plate 7. *Lautoconus depressoastensis* (Sacco, 1893); 1. NHMW 2024/0205/0107, height 37.8 mm, width 22.1 mm; 2. NHMW 2024/0205/0108, height 34.7 mm, width 19.1 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

that species is separated by having concave spire whorl tops on the last 2-3 whorls. It is also similar to the extremely variable *Lautoconus ventricosus* (Gmelin, 1791), with which it also co-occurs in the Velerín conglomerates, but that species is thinner shelled and usually has some trace of colour pattern.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893a).

***Lautoconus dertogibbus* (Sacco, 1893)**
Plate 13, figs 7-9, Plate 17, fig. 8, Plate 18, fig. 8

?1893b *Conus* (*Chelyconus*) *dertogibbus* Sacco, p. 64, pl. 6, fig. 17.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *tauroperlonga* Sacco, p. 64, pl. 6, fig. 18.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *semiovatospira* Sacco, p. 65, pl. 6, fig. 19.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *digitaloides* Sacco, p. 65, pl. 6, fig. 20.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *suturata* Sacco, p. 65, pl. 6, fig. 21.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *perovuloidea* Sacco, p. 65, pl. 6, fig. 22.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *depressogibba* Sacco, p. 65, pl. 6, fig. 23.
1893b *Conus* (*Chelyconus*) *dertogibbus* var. *ovatoastensis* Sacco, p. 65, pl. 6, fig. 24.
1984 *Chelyconus dertogibbus* Sacco, 1893 – Ferrero Mortara *et al*., p. 115, pl. 18, fig. 5.
1972 *Conus dertogibbus* Sacco – Davoli, p. 96, pl. 5, figs 1, 8, 9, 14-16, 19-21, 24-26, 35, 36, 40.
1997 *Conus* (*Chelyconus*) cf. *taurinensis* Bellardi & Michelotti, 1840 – Chirli, p. 11, pl. 3, fig. 8.
1999 *Conus* (*Chelyconus*) cfr. *taurinensis anomalomamillus* (Sacco, 1893) – Muñiz Solís, p. 37, figs 6A-D.
1999 *Conus* (*Clelyconus* [*sic*]) *dertogibbus* (Sacco, 1893) – Muñiz Solís, p. 46 (*partim*), figs 6P [not Q = ?*Varioconus striatulus* (Brocchi, 1814)].

Material and dimensions – Maximum height 30.8 mm, width 15.9 mm. **CO:** NHMW NHMW 2024/0205/0035-0037 (3), NHMW 2024/0205/0038 (10), HM coll. (44).

Description – Shell moderately small, solid, squat, with very high, broad, dome-shaped cyrtoconoid spire and relatively short conical last whorl. Protoconch and earliest teleoconch whorls not preserved. Six to seven teleoconch whorls preserved. Mid-spire whorls smooth, weakly convex, passing to weakly concave on the last 1-2 whorls. Suture deeply incised, not channelled. Subsutural sinus moderately deep, weakly curved, moderately asymmetrical. Last whorl with narrow, flattened to weakly convex subsutural ramp, roundly angled at high-placed shoulder, position of maximum diameter at or just below shoulder, conical below, almost straight-sided to weakly convex, not constricted at base, siphonal fasciole not developed, weak cords over base and siphonal fasciole, strengthening and closer-set abapically. Aperture elongate, moderately broad, widening abapically, siphonal canal short, straight. Colour pattern of blotches at shoulder on spire whorls and last whorl, fine, spiral reddish/brown lines, narrower than their interspaces, below shoulder.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 33.0 mm, MD: 16.5 mm, mean SL: 27.8 mm (σ = 6.9), mean MD: 14.7 (σ = 1.6); spire angle: μ = 82.4° (σ = 9.4°), last whorl angle: μ = 36.7° (σ = 2.2°), LW: μ = 1.9 (σ = 0.1), RD: μ = 0.72 (σ = 0.04), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.27 (σ = 0.03), Subsutural sinus (n=4): SSFD: moderately deep. μ = 1.9 (σ = 0.2), SSFd: weakly curved. μ = 9.7 (σ = 2.5), PV: moderately asymmetrical. μ = 0.5 (σ = 0.1).

Discussion – We agree with Muñiz Solís (1999, *partim*) that this species represents *Conus dertogibbus* Sacco, 1893. Sacco considered it a predominantly Upper Miocene species, but also recorded it from the Langhian Middle Miocene Baldissero Formation and the Pliocene of Asti of Italy. Subsequent to Sacco's record from the Italian Pliocene (var. *ovatoastensis*; 1893b) we can find no further mention of this species in the Italian Pliocene. Muñiz Solís (1999, figs 6A-D) figured two rather worn shells as *Conus* (*Chelyconus*) cfr. *taurinensis anomalomamillus* (Sacco, 1893) that in our opinion fit within the species concept of *Lautoconus dertogibbus* That author illustrated another two specimens under *Conus* (*Clelyconus* [*sic*]) *dertogibbus* of which one probably is that species (1999, 6P), whereas the other probably represents *Varioconus striatulus* (Brocchi, 1814).
Both Sacco (1893b) and Davoli (1972) considered *C. dertogibbus* to be highly variable as illustrated by the numerous forms figured by both authors. The Estepona specimens fit within this range of variability and show a colour pattern of reddish blotches of the spire and shoulder and fine horizontal spiral lines below the shoulder on the last whorl.
Although, we see no evidence of sculpture on the whorl tops in the material at hand, Sacco (1893b, p. 64), Davoli (1972, p. 96) and Muñiz Solís (1999, p. 46) described the spire whorls as being weakly striate. We therefore place this species in the genus *Lautoconus* Monterosato, 1923. Davoli (1972, p. 96) suggested that *Conus corynetes* Fontannes, 1880 might be a synonym. However, as interpreted here, we consider it a distinct species with a broader last whorl and narrow axial lines on the spire instead of blotches.

Distribution – Middle Miocene: central Proto-Mediterranean (Langhian), Italy (Sacco, 1893b). Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b; Davoli, 1972; Ferrero Mortara *et al*., 1984). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Proto-Mediterranean, Italy (Sacco, 1893b; Chirli, 1997). Upper Pliocene: central Proto-Mediterranean, Italy (Sacco, 1893b).

***Lautoconus deshayesii* (Bellardi & Michelotti, 1840)**
Plate 13, figs 10-12, Plate 17, fig. 9, Plate 18, fig. 9

*1840	*Conus deshayesii* Bellardi & Michelotti, p. 153, pl. 6, figs 6, 7.
1893b	*Conus* (*Chelyconus*) *Deshayesii* (Bell. Micht.) – Sacco, p. 73, pl. 7, fig. 14.
1893b	*Conus* (*Chelyconus*) *Deshayesii* var. *fusacuta* Sacco, p. 74, pl. 7, fig. 15.
1893b	*Conus* (*Chelyconus*) *Deshayesii* var. *conicoscalaris* Sacco, p. 74, pl. 7, fig. 16.
1893b	*Conus* (*Chelyconus*) *Deshayesii*? var. *ponderovata* Sacco, p. 74, pl. 7, fig. 17.
?1972	*Conus* sp. aff. *C. deshayesi* Bellardi & Michelotti – Davoli, p. 100, pl. 5, fig. 41.
1974	*Conus* (*Chelyconus*) *deshayesi* [*sic*] Bellardi, e Michelotti, 1840 – Malatesta, p. 379, pl. 30, figs 5, 9.
1976	*Conus deshayesi* [*sic*] Bellardi & Michelotti– Pavia, p. 114, pl. 9, fig. 9.
1984	*Chelyconus deshayesi* [*sic*] (Bellardi & Michelotti, 1840) – Ferrero Mortara *et al*., p. 119, pl. 19, fig. 4.
1990	*Conus deshayesi* [*sic*] Bellardi, e Michelotti, 1840 – Spadini, p. 317, pl. 1, figs 2, 7.
1992	*Conus deshayesi* [*sic*] Bellardi & Michelotti, 1840 – Cavallo & Repetto, p. 128, fig. 332.
1997	*Conus* (*Chelyconus*) *deshayesii* Bellardi & Michelotti, 1840 – Chirli, p. 5 (*partim*), pl. 1, fig. 9 [not figs 7, 8 = *Lautoconus corynetes* (Fontannes, 1880)].
1999	*Conus* (*Chelyconus*) *deshayesi* [*sic*] Bellardi y Michelotti, 1840 – Muñiz Solís, p. 47, figs 7A-B.
?non 2014	*Conus deshayesi* [*sic*] Orbigny, 1852 [*sic*] – Paganelli, p. 31, pl. 3, fig. 24, pl. 6, fig. 7.

Material and dimensions – Maximum height 66.5 mm, width 36.1 mm. **CO:** NHMW 2024/0205/0039-0041 (3), NHMW 2024/0205/0042 (2), HM coll. (28). **EL**: HM coll. (1).

Description – Shell moderately large, broad, with high mammillate spire and pyriform last whorl. Protoconch not preserved. Teleoconch of up to eight whorls. Early spire whorls usually eroded in adult specimens, bearing 3-4 weak spiral cords in juvenile specimens; later spire whorls smooth, very weakly convex to almost flat sided forming broadly conical spire. Suture deeply incised, not channelled. Subsutural sinus shallow, moderately curved, moderately asymmetrical. Last whorl with very weakly angled to rounded shoulder, position of maximum diameter slightly below shoulder, conical to slightly pyriform below with slightly convex sides, evenly contracting in lower half of shell, weakly constricted at base, siphonal fasciole poorly developed, up to eight narrow cords over fasciole strengthening slightly abapically. Aperture elongate, relatively broad, widening further abapically, siphonal canal weakly recurved, moderately long. Colour of light orange on spire and subsutural ramp on last whorl, and pattern only below shoulder on last whorl of very close-set and fine horizontal reddish/brown lines, roughly equal in width to their interspaces.

Shell measurements and ratios – n = 5 adult specimens; largest specimen: SL: 66.5 mm, MD: 36.1 mm, mean SL: 48.2 mm (σ = 10.3), mean MD: 26.8 (σ = 5.3); spire angle: μ = 98.4° (σ = 6.9°), last whorl angle: μ = 38.6° (σ = 2.3°), LW: μ = 1.8 (σ = 0.09), RD: μ = 0.69 (σ = 0.01), PMD: μ = 0.8 (σ = 0.01), RSH: μ = 0.2 (σ = 0.03), Subsutural sinus (n=4): SSFD: shallow μ = 3.6 (σ = 0.04), SSFd: moderately curved. μ = 6.3 (σ = 0.1), PV: moderately asymmetrical. μ = 0.6 (σ = 0.03).

Discussion – The rounded shoulder and weak cords on the early spire whorl tops place this species in the genus *Lautoconus* Monterosato, 1923. *Lautoconus deshayesii* (Bellardi & Michelotti, 1840) is immediately separated from most of its Mediterranean Pliocene congeners by its colour pattern of regular, narrow, slightly undulating horizontal stripes below the shoulder and solid light orange colour over the spire and subsutural ramp on the last whorl. The only species with which it can be confused is *Lautoconus corynetes* (Fontannes, 1880); for comparison see under that species.
We have not included in the chresonymy the Lower Miocene varieties *mioantiqua*, *taurosubscalaris* and *lineoclavata* Sacco, 1893 as we have not seen these specimens. We note that Hall (1964, p. 161) considered the variety *mioantiqua* to possibly represent a form of *Conus taurorectus* (Sacco, 1893). These Lower Miocene varieties have similar spiral lines, but according to Sacco (1893b, p. 74) the lines are white instead of reddish. The single specimen from the Upper Miocene of Italy illustrated by Davoli (1972, pl. 5, fig. 41) does seem to be this species and is included in the chresonymy, but also requires confirmation.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Davoli, 1972). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Pavia, 1976; Spadini, 1990; Chirli, 1997). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*., 1984; Cavallo & Repetto, 1992).

***Lautoconus laeviponderosus* (Sacco, 1893)**
Plate 14, figs 1-6, Plate 17, fig. 10, Plate 18, fig. 10

*1893b	*Conus* (*Chelyconus*) *laeviponderosus* Sacco, p. 82, pl. 8, fig. 25.
1893b	*Conus* (*Chelyconus*) *laeviponderosus* var. *perpupoides* Sacco, p. 83, pl. 8, fig. 27.
1893b	*Conus* (*Chelyconus*) *laeviponderosus* var. *brevipupoides* Sacco, p. 83, pl. 8, fig. 28.
1893b	*Conus* (*Chelyconus*) *laeviponderosus*? var. *mucronatina* Sacco, p. 83, pl. 8, fig. 29.
1893b	*Conus* (*Chelyconus*) *laeviponderosus* var. *perpyrulata* Sacco, p. 83, pl. 8, fig. 30.

1893b *Conus* (*Chelyconus*) *laeviponderosus*? var. *laevissima* Sacco, p. 83, pl. 8, fig. 31.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *gracilicaudata* Sacco, p. 83, pl. 8, fig. 32.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *fulminornata* Sacco, p. 84, pl. 8, fig. 33.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *perlineata* Sacco, p. 84, pl. 8, fig. 34.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *irregularilineata* Sacco, p. 84, pl. 8, fig. 35.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *ponderolineata* Sacco, p. 84, pl. 8, fig. 36.
1893b *Conus* (*Chelyconus*) *laeviponderosus* var. *lineofasciata* Sacco, p. 84, pl. 8, fig. 37.
1964 *Conus ponderosus* Brocchi, 1814 – Hall, p. 156 [46] (*partim*), pl. 28, figs 6-8, 10, 17 [*non Lautoconus ponderosus* (Brocchi, 1814)].
1974 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Malatesta, p. 382 (*partim*), pl. 30, fig. 3c [*non Lautoconus ponderosus* (Brocchi, 1814)].
1984 *Chelyconus laeviponderosus* Sacco, 1893 – p. 122, pl. 18, fig. 3.
1990 *Conus laeviponderosus* Sacco, 1893 – Spadini, p. 320, pl. 2, fig. 13, pl. 3, figs 1-3.
1992 *Conus laeviponderosus* Sacco, 1893 – Cavallo & Repetto, p. 128, fig. 334.
1997 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Chirli (*partim*), p. 7, pl. 2, figs 8-11 only [figs 6, 7 = *Lautoconus ponderosus* (Brocchi, 1814)].
1999 *Conus* (*Chelyconus*) cfr. *laeviponderosus* (Sacco, 1893) [*sic*] – Muñiz Solís, p. 51, figs 7K, L).
1999 *Conus* (*Chelyconus*) sp. 1 – Muñiz Solís, p. 68, figs 8M, N.
2014 *Conus laeviponderosus* Sacco, 1893 – Paganelli, p. 32, pl. 4, figs 34, 35.
2018 *Conus laeviponderosus* Sacco, 1893 – Brunetti & Cresti, p. 102, fig. 428.

non 1928 *Conus* (*Chelyconus*) cfr. *laeviponderosus* Sacco – Friedberg, p. 564, pl. 36, figs 32, 33.
non 1928 *Conus* (*Chelyconus*) *laeviponderosus* vars *perlineata*, *gracilicaudata* and *mucronatina* Sacco – Friedberg, p. 564-565, pl. 37, figs 1, 2.

Material and dimensions – Maximum height 58.2 mm, width 32.3 mm. **CO:** NHMW 2024/0205/0043-0048 (6), NHMW 2024/0205/0049 (14), HM coll. (72). **EL**: HM coll. (1).

Description – Shell moderately large, broad with medium height conical to mammillate spire and conical last whorl. Protoconch not preserved. Teleoconch of up to eight whorls. Early spire whorls usually eroded in adult specimens, bearing 2-3 weak spiral cords in juvenile specimens; later spire whorls weakly convex forming conical to cyrtoconoid spire, cords weakening further towards outer lip. Suture deeply incised, not channelled. Subsutural sinus moderately deep, weakly curved, strongly asymmetrical. Last whorl with weakly angled shoulder, position of maximum diameter slightly below shoulder, regularly conical below, evenly contracting in lower half of shell, not constricted at base, siphonal fasciole nearly absent, up to eight very weak flattened cords over base, strengthening slightly abapically. Aperture elongate, narrow, widening slightly abapically, siphonal canal weakly recurved, moderately short. Colour pattern of narrow axial lines on whorl tops; on last whorl three bands of narrow, irregular, wavey, close-set, reddish axial lines, in most specimens interrupted mid-whorl and above base by undecorated band; axial flammules cover entire last whorl in some specimens.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 58.2 mm, MD: 32.3 mm, mean SL: 47.6 mm (σ = 5.5), mean MD: 25.8 (σ = 2.9); spire angle: μ = 97.9° (σ = 7.9°), last whorl angle: μ = 34.8° (σ = 2.4°), LW: μ = 1.7 (σ = 0.3), RD: μ = 0.72 (σ = 0.01), PMD: μ = 0.9 (σ = 0.04), RSH: μ = 0.17 (σ = 0.1). Subsutural sinus (n=4): SSFD: moderately deep, μ = 1.8 (σ = 0.2). SSFd: weakly curved, μ = 9.8 (σ = 2.3). PV: strongly asymmetrical, μ = 0.2 (σ = 0.1).

Discussion – Hall (1964, p. 156) placed *Conus laeviponderosus* Sacco, 1893 as synonym of *Conus ponderosus* (Brocchi, 1814) considering there to be a complete gradation between the forms. However, we would agree with Spadini (1990, p. 320) who doubted they were conspecific and pointed out the consistent difference in colour pattern between the two. In Estepona almost all specimens of *Lautoconus laeviponderosus* have a strongly preserved colour pattern of narrow reddish axial lines on the whorl tops and the last whorl, usually interrupted by two undecorated bands. One of the specimens of *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 illustrated by Malatesta (1974, pl. 30, fig. 3c) shows a similar colour pattern and probably represents *L. laeviponderosus*. *Lautoconus ponderosus* has no colour pattern preserved. Moreover, *L. ponderosus* is much larger and usually had some spiral sculpture or a sulcus at the shoulder of the last whorl. Chirli (1997) again reunited the two species, but the differences described above are evident: Chirli (1997, pl. 2, figs 7, 8) represent *L. ponderosus* whilst (1997, pl. 2, figs 8-11) represent *L. laeviponderosus*.
As suggested by the numerous varieties described by Sacco, *L. laeviponderosus* is highly variable in profile; the spire can vary from low to relatively high conical, mammillate or low dome shaped. The last whorl is usually conical below the shoulder, although it may be slightly inflated in some specimens. The colour pattern is fairly consistent, although the two undecorated bands on the last whorl vary in width, and in occasional specimens the axial lines are continuous.
We have excluded from the synonymy the form *tauroperlata* Sacco, 1893 (refigured in Ferrero Mortara *et al*., 1984, pl. 19, fig. 7) from the Lower Miocene Burdigalian of Italy. We have included the Upper Miocene form *fulminornata* Sacco, 1893 that has a similar colour pattern.
Muñiz Solís (1999, figs 7K, L) recorded this species with some doubt as *Conus* (*Chelyconus*) cfr. *laeviponderosus* and also illustrated a low spired specimen as *Conus*

(*Chelyconus*) sp. 1 (1999, figs 8M, N) showing the typical colour pattern of *L. laeviponderosus*.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*., 1984; Spadini, 1990; Cavallo & Repetto, 1992; Chirli, 1997; Paganelli, 2014; Brunetti & Cresti, 2018).

***Lautoconus pelagicus* (Brocchi, 1814)**
Plate 14, figs 7-8, Plate 17, fig. 11, Plate 18, fig.11

*1814 *Conus pelagicus* Brocchi, p. 289, pl. 2, fig. 9.
1878a [*Chelyconus*] [*Conus*] *Mariae* Hoernes: 195 (*nomen nudum*).
1878b *Conus Mariae* Hoernes, p. 207 (*nomen nudum*).
1879 *Conus* (*Chelyconus*) *Mariae* Hoernes & Auinger, p. 49, pl. 6, fig.7.
1880 *Conus pelagicus* Brocchi – Fontannes, p. 143, pl. 8, fig. 10.
?1893b *Conus* (*Chelyconus*) *oboesus* var. *tauroconnectens* Sacco, p. 59, pl. 5, fig. 36.
1893b *Conus* (*Chelyconus*) *clavatus* var. *tauroclavatula* Sacco, p. 70, pl. 7, fig. 1.
?1893b *Conus* (*Chelyconus*) *Deshayesi* var. *taurosubscalaris* Sacco, p. 74, pl. 7, fig. 19.
?1893b *Conus* (*Chelyconus*) *Deshayesi* var. *lineoclavata* Sacco, p. 74, pl. 7, fig. 20.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *taurocrassa* Sacco, p. 78, pl. 8, fig. 3.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miosubtypica* Sacco, p. 78, pl. 8, fig. 6.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miofusuloides* Sacco, p. 79, pl. 8, fig. 7.
1893b *Conus* (*Chelyconus*) *pelagicus* (Br.) – Sacco, p. 90, pl. 9, fig. 17.
1893b *Conus* (*Chelyconus*) *pelagicus* anom. *monstruosa* Sacco, p. 91, pl. 9, fig. 18.
1893b *Conus* (*Chelyconus*) *pelagicus* subvar. *permaculata* Sacco, p. 92, pl. 9, fig. 19.
1893b *Conus* (*Chelyconus*) *pelagicus* subvar. *astensiscalaris* Sacco, p. 92, pl. 9, fig. 20.
1893b *Conus* (*Chelyconus*) *pelagicus* var. *taurogigantea* Sacco, p. 92, pl. 9, fig. 22.
1893b *Conus* (*Chelyconus*) *pelagicus* var. *acutiusculoides* Sacco, p. 92, pl. 9, fig. 23.
1893b *Conus* (*Chelyconus*) *pelagicus* var. *pseudopyrula* Sacco, p. 92, pl. 9, fig. 24.
1893b *Conus* (*Chelyconus*) *pelagicus* var. *depressoconica* Sacco, p. 93, pl. 9, fig. 26.
1893b *Conus* (*Chelyconus*) *pelagicus* var. *colorata* (Defr.) – Sacco, p. 93, pl. 9, fig. 28.
1893b *Conus* (*Chelyconus*) *parvus* var. *miofusuluvoides* Sacco, p. 97, pl. 9, fig. 45.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *taurovata* Sacco, p. 103, pl. 10, fig. 1.
1930 *Conus* (*Chelyconus*) *clavatulus* Lamarck – Peyrot, p. 105, no. 1176 (*partim*).
1931 *Conus* (*Chelyconus*) *clavatulus* Lamarck – Peyrot (*partim*, pl. 1, fig. 13 only).
1955 *Conus* (*Puncticulis*) (*Chelyconus*) *pelagicus* Brocchi 1814 – Rossi Ronchetti, p. 284, fig. 152.
1960 *Conus* (*Chelyconus*) *vindobonensis* var. *mariae* (Hoernes und Auinger 1879) – Kojumdgieva in Kojumdgieva & Strachimirov, p. 213, pl. 50, fig. 6.
1964 *Conus pelagicus* Brocchi, 1814 – Hall, p. 155 [45], pl. 27, figs 1-4, 7, 15, 16, 20-23.
1968 *Conus* (*Chelyconus*) *mariae* Hoernes et Auinger, 1879 – Hinculov, p. 150, pl. 37, figs 17a, b.
1974 *Conus* (*Chelyconus*) *pelagicus* Brocchi, 1814 – Malatesta, p. 381, pl. 30, figs 4, ?10.
1978 *Conus pelagicus* Brocchi, 1814 – Pinna & Spezia, p. 137, pl. 18, fig. 4.
1988 *Conus* (*Chelyconus*) *pelagicus* Brocchi, 1814 – Chirli, p. 22, pl. 9, fig. 1.
1990 *Conus pelagicus* Brocchi, 1814 – Spadini, p. 317, pl. 2, fig. 16.
1992 *Conus pelagicus* Brocchi, 1814 – Andreoli & Marsigli, p. 5, pl. 1, fig. 5.
1994 *Conus vindobonensis mariae* (Hoernes et Auinger) – Ionesi & Nicorici, p. 62, pl. 5, fig. 8.
1997 *Conus* (*Chelyconus*) *pelagicus* Brocchi, 1814 – Chirli, p. 7, pl. 1, fig. 17, pl. 2, figs 1-5.
1999 *Conus* (*Chelyconus*) *pelagicus* Brocchi, 1814 – Muñiz Solís, p. 55, figs 7Q, R.
2009 *Varioconus pelagicus* (Brocchi, 1814) – Tucker & Tenorio, p. 129.
2010 *Conus pelagicus* Brocchi, 1814 – Sosso & Dell'-Angelo, p. 49, 65 unnumbered figure top row left.
2013 *Varioconus pelagicus* (Brocchi, 1814) – Landau *et al*., p. 247, pl. 39, figs 6, 7, pl. 41, fig. 14, pl. 42, fig. 8, pl. 82, figs 1, 2.
2014 *Conus pelagicus* Brocchi, 1814 – Paganelli, p. 30, pl. 3, fig. 17, pl. 6, fig. 12.
2016 *Lautoconus pelagicus* (Brocchi, 1814) – Harzhauser & Landau, p. 84, figs 17J, 19A_1-A_4.

non 1845 *Conus pelagicus* Broc. – Grateloup, pl. 14, fig. 8 [= *Varioconus basteroti* (Mayer-Eymar, 1891a)].
non 1851 *Conus pelagicus* Brocc. – Hörnes, p. 31, pl. 3, figs 4a-d [= *Lautoconus ventricosus* (Gmelin, 1791)].
non 1910 *Conus* (*Chelyconus*) *pelagicus* Br. – Cerulli-Irelli, p. 49, pl. 4, fig. 49 [= *Lautoconus bitorosus* (Fontannes, 1880)].
non 2011 *Chelyconus pelagicus* (Brocchi, 1814) – Chirli & Linse, p. 165, pl. 56, figs 1a-d [= subspecies *L. ventricosus rhodesensis* Psarras, Merle, Moissette & Kodkeridou, 2024].
non 2013 *Varioconus pelagicus* (Brocchi, 1814)—Kovács & Vicián, p. 87, figs 131-137 [= *Leporiconus suessi* (Hoernes & Auinger, 1879)].
non 2015 *Varioconus pelagicus* (Brocchi, 1814) – Kovács & Balázs, p. 32, figs 71-74 [= *Leporiconus suessi* (Hoernes & Auinger, 1879)].

Material and dimensions – Maximum height 50.0 mm, width 24.1 mm. **CO:** NHMW 2024/0205/0050-0051 (2), NHMW 2024/0205/0102 (1).

Description – Shell medium sized, biconic, with high conical spire and elongate conical last whorl. Protoconch and early spire whorls eroded in all specimens. Teleoconch of 7-8 whorls. Spire whorls flat to weakly convex, very weakly striate. Suture narrow, deeply impressed. Subsutural sinus shallow, moderately curved, nearly symmetrical. Last spire whorl with weakly concave subsutural ramp, indistinct angled at shoulder. Last whorl with narrow, flattened to weakly concave subsutural ramp, rounded at shoulder, evenly conical below, with maximum diameter close below shoulder, weakly constricted at base; siphonal fasciole swollen, twisted; a few very weak spirals over base and fasciole. Aperture moderately narrow, hardly widening abapically; inner lip narrow, straight; siphonal canal moderately long, slightly reflected. Colour pattern of reddish flammules on spire to shoulder and reddish spiral rows of irregularly spaced short dots and dashes below shoulder on last whorl superimposed on 2-3 broad darker bands separated by broad lighter bands.

Shell measurements and ratios – n = 2 adult specimens; largest specimen: SL: 49.8 mm, MD: 25.0 mm, mean SL: 49.7 mm (σ = 0.2), mean MD: 25.8 (σ = 1.1); spire angle: μ = 92.0° (σ = 4.2°), last whorl angle: μ = 32.5° (σ = 2.1°), LW: μ = 2.1 (σ = 0.1), RD: μ = 0.6 (σ = 0.05), PMD: μ = 0.86 (σ = 0.02), RSH: μ = 0.22 (σ = 0.01), Subsutural sinus (n=4): SSFD: shallow. μ = 3.1 (σ = 0.1), SSFd: moderately curved. μ = 6.5 (σ = 0.2), PV: nearly symmetrical. μ = 1.5 (σ = 0.05).

Discussion – *Lautoconus pelagicus* (Brocchi, 1814) is a very characteristic species thanks to its colour pattern that is often preserved. The two specimens illustrated show some variability in broadness of the last whorl. Although Muñiz Solís (1999, p. 55) suggested that this species was common in Estepona, we have found very few specimens we can identify with confidence.
Landau *et al*. (2013) included *Conus lapugyensis* Hoernes & Auinger, 1879 and *C. ottiliae* Hoernes & Auinger, 1879 in their synonymy of *Lautoconus pelagicus* and Kovács & Vicián (2013) *C. suessi* Hoernes & Auinger, 1879. These were removed from synonymy by Harzhauser & Landau (2016) in the combinations *Plagioconus lapugyensis*, *Phasmoconus ottiliae* and *Leporiconus suessi*. For further discussion on all these Paratethyan species see Harzhauser & Landau (2016).

Distribution – Lower Miocene: Proto-Mediterranean (Burdigalian): Italy (Sacco, 1893b; Hall, 1964). Middle Miocene: northeastern Atlantic (Langhian): Aquitaine Basin, France (Mayer-Eymar, 1891a); Paratethys (Langhian-Serravallian): Austria, (Hörnes, 1851), Bulgaria (Kojumdgieva & Strachimirov 1960), Czech Republic (Hoernes & Auinger, 1879), Romania (Hoernes & Auinger, 1879; Hinculov 1968; Ionesi & Nicorici 1994; Kovács & Balázs, 2015; Harzhauser & Landau, 2016); eastern Proto-Mediterranean (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: central Proto-Mediterranean (Tortonian): Italy (Sacco, 1893b). Lower Pliocene: western Mediterranean, Estepona Basin, Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Andreoli & Marsigli, 1992; Chirli, 1988, 1997; Spadini, 1990; Sosso & Dell'Angelo, 2010). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Hall, 1964; Malatesta, 1974; Paganelli, 2014).

***Lautoconus ponderoglans* (Sacco, 1893)**
Plate 8, figs 1-3, Plate 17, fig. 12, Plate 18, fig. 12

1893b *Conus* (*Chelyconus*) *ponderoglans* Sacco, p. 76, pl. 7, fig. 28.
1893b *Conus* (*Chelyconus*) *ponderoglans* var. *mediosulcata* Sacco, p. 76, pl. 7, fig. 29.
1984 *Chelyconus ponderoglans* Sacco, 1893 – Ferrero Mortara *et al*., p. 120, pl. 18, fig. 6.
1984 *Chelyconus ponderoglans* var. *mediosulcata* Sacco, 1893 – Ferrero Mortara *et al*., p. 120, pl. 19, fig. 5.
1999 *Conus* (*Chelyconus*) *ponderoglans* (Sacco, 1893) – Muniz-Solís, p. 58, figs 7S, T.

Material and dimensions – Maximum height 47.2 mm, width 27.3 mm. **CO:** NHMW 2024/0205/0052-0054 (3), NHMW 2024/0205/0055 (1), HM coll. (1).

Description – Shell medium sized, relatively light-shelled, with low conical spire and broad conical last whorl. Protoconch not preserved. Teleoconch of up to seven whorls. Early spire whorls eroded; later spire whorls weakly convex, bearing weak spiral cords. Suture deeply incised, slightly undulating. Subsutural sinus shallow, weakly curved, moderately asymmetrical. Last whorl with rounded shoulder, position of maximum diameter slightly below shoulder, regularly conical below, evenly contracting in lower half of shell, not constricted at base, siphonal fasciole nearly absent, a few very weak flattened cords over base. Aperture elongate, relatively broad, widening abapically, siphonal canal weakly recurved, moderately short. No colour pattern preserved.

Shell measurements and ratios – n = 5 adult specimens; largest specimen: SL: 47.2 mm, MD: 27.3 mm, mean SL: 40.0 mm (σ = 4.7), mean MD: 23.5 (σ = 2.5); spire angle: μ = 108.0° (σ = 2.5°), last whorl angle: μ = 41.2° (σ = 1.8°), LW: μ = 1.7 (σ = 0.04), RD: μ = 0.73 (σ = 0.02), PMD: μ = 0.86 (σ = 0.02), RSH: μ = 0.122 (σ = 0.02), Subsutural sinus (n=4): SSFD: shallow. μ = 3.1 (σ = 0.7), SSFd: weakly curved. μ = 7.6 (σ = 0.5), PV: moderately asymmetrical. μ = 0.5 (σ = 0.03).

Discussion – This is a poorly defined species with no distinctive characters or colour pattern. Some specimens from Estepona (*e.g.*, Pl. 8, figs 1, 2) closely resemble the holotype from the Upper Miocene of Stazzano, Italy, illustrated by Ferrero Mortara *et al*. (1984, pl. 18, fig. 6). The Lower Pliocene var. *mediosulcata* Sacco, 1893 was said to differ in having a deep sulcus running below the

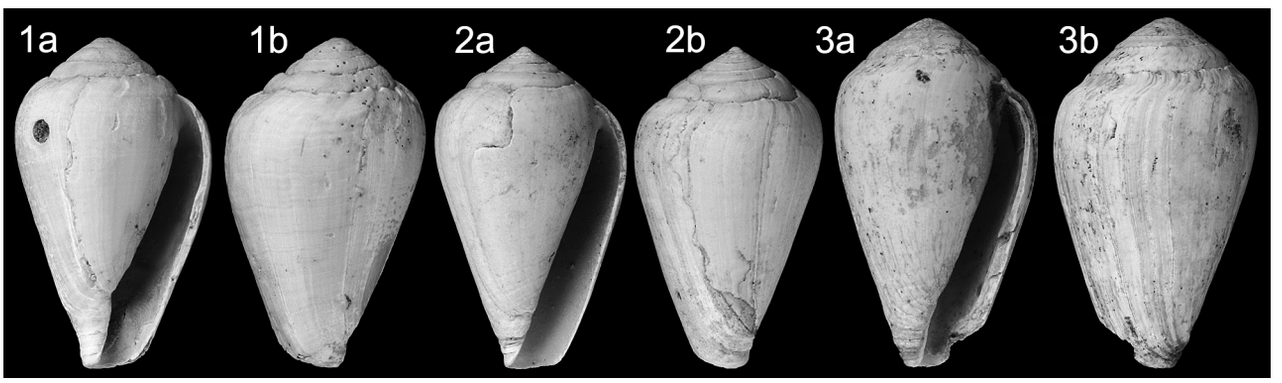

Plate 8. *Lautoconus ponderoglans* (Sacco, 1893); 1. NHMW 2024/0205/0052, height 39.7 mm, width 24.4 mm; 2. NHMW 2024/0205/0053, height 35.5 mm, width 20.7 mm; 3. NHMW 2024/0205/0054, height 47.2 mm, width 27.3 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

shoulder that is also clearly seen in the specimen illustrated by Ferrero Mortara *et al*. (1984, pl. 19, fig. 5). That sulcus is also seen in some specimens of *Lautoconus ponderosus* (Brocchi, 1814), although it runs at the shoulder rather than below. None of the Estepona specimens have this sulcus, nor is it described or illustrated by Muñiz Solís (1999, p. 58, figs 7S, T). All the Estepona specimens at hand are worn, and they may represent abraded, squat specimens of *Lautoconus laeviponderosus* (Sacco, 1893), but the shoulder is more rounded, they differ in the shape of their subsutural sinus and lack the distinctive colour pattern of that species. We list this species with some hesitation, as did Muñiz Solís.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz-Solís, 1999); central Mediterranean, Italy (Sacco, 1893b).

***Lautoconus ponderosus* (Brocchi, 1814)**

Plate 9, figs 1-4, Plate 17, fig. 13, Plate 18, fig. 13

*1814 *Conus ponderosus* Brocchi, p. 293, pl. 3, fig. 1.
1851 *Conus ponderosus* Brocc. – Hörnes, p. 26, pl. 2, figs 6a, b.
1885 *Conus ponderosus* f. *elmenus* De Gregorio, p 369 [*nov. nom. pro Conus ponderosus* in Hörnes 1851, pl. 2, fig. 6].
1893b *Conus* (*Chelyconus*) *ponderosus* (Br.) – Sacco, p. 77, pl. 8, fig. 1.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miopraecedens* Sacco, p. 78, pl. 8, fig. 2.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miosubmamillata* Sacco, p. 78, pl. 8, fig. 4.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miopermamillata* Sacco, p. 78, pl. 8, fig. 5.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *tauroponderosa* Sacco, p. 79, pl. 8, fig. 8.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *tauroperlaevis* Sacco, p. 79, pl. 8, fig. 9.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *miovulea* Sacco, p. 79, pl. 8, fig. 10.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *unisulcata* Sacco, p. 79, pl. 8, fig. 11.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *fusoclavata* Sacco, p. 80, pl. 8, fig. 12.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *laevimutinensis* Sacco, p. 80, pl. 8, fig. 13.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *compressospira* Sacco, p. 80, pl. 8, fig. 14.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *planoconvexospira* Sacco, p. 80, pl. 8, fig. 15.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *glandonoae* Sacco, p. 80, pl. 8, fig. 16.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *glandoasulcata* Sacco, p. 80, pl. 8, fig. 17.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *parvonoae* Sacco, p. 81, pl. 8, fig. 18.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *juventula* Sacco, p. 81, pl. 8, fig. 19.
1893b *Conus* (*Chelyconus*) *ponderosus* var. *juvenoasulcata* Sacco, p. 81, pl. 8, fig. 20.
1955 *Conus* (*Puncticulis*) (*Chelyconus*) *ponderosus* Brocchi 1814 – Rossi Ronchetti, p. 280, fig. 150.
1964 *Conus ponderosus* Brocchi, 1814 – Hall, p. 156 [46] (*partim*), pl. 28, figs 1-21 (not fig. 20).
1972 *Conus ponderosus* Brocchi – Davoli, p. 124, pl. 7, figs 1, 2, 6, 9-11.
?1974 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Malatesta, p. 382 (*partim*), pl. 30, figs 3a, b.
1976 *Conus ponderosus* Brocchi – Caprotti, p. 12, pl. 17, fig. 9.
1978 *Conus ponderosus* Brocchi, 1814 – Pinna & Spezia, p. 137, pl. 18, fig. 1.
1981 *Conus ponderosus* Brocchi, 1814 – Krach (*partim*), p. 77, pl. 20, figs 17-19, 21 [not fig. 20, pl. 21, figs 6–9].
1988 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Chirli, p. 22, pl. 9, fig. 2.
1990 *Conus ponderosus* Brocchi, 1814 – Spadini, p. 321, pl. 3, figs 8, 16.
1992 *Conus ponderosus* Brocchi, 1814 – Cavallo & Repetto, p. 128, fig. 337.

1997 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Bałuk, p. 62, pl. 22, fig. 9.
1997 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Chirli (*partim*), p. 7, pl. 2, figs 6-7 only [figs 8-11 = *Lautoconus laeviponderosus* (Sacco, 1893)].
1999 *Conus* (*Chelyconus*) *ponderosus* Brocchi, 1814 – Muñiz-Solís, p. 59, figs 8A-B.
2009 *Varioconus ponderosus* (Brocchi, 1814) – Tucker & Tenorio, p. 129.
2010 *Conus ponderosus* Brocchi, 1814 – Sosso & Dell'-Angelo, p. 49, 65 unnumbered figure top row middle.
2013 *Varioconus ponderosus* (Brocchi, 1814) – Kovács & Vicián, p. 87 (*partim*), fig. 139.
2014 *Conus ponderosus* Brocchi, 1814 – Paganelli, p. 31, pl. 3, fig. 18.
2016 *Lautoconus ponderosus* (Brocchi, 1814) – Harzhauser & Landau, p. 87, figs 19B_1-B_3, 19C_1–C_3

non 1879 *Conus* (*Rhizoconus*) *ponderosus* Brocc. Var. I – Hoernes & Auinger (*partim*), p. 39, pl. 5, fig. 4 [= *Lautoconus steinabrunnensis* (Sacco, 1893)].
non 1879 *Conus* (*Rhizoconus*) *ponderosus* Brocc. Var. II – Hoernes & Auinger (*partim*), p. 39, pl. 5, fig. 5 [= *Lautoconus steinabrunnensis* (Sacco, 1893)].
non 1879 *Conus* (*Rhizoconus*) *ponderosus* Brocc. Var. III – Hoernes & Auinger (*partim*), p. 39, pl. 5, fig. 6 [= *Kalloconus ponderoaustriacus* (Sacco, 1893)].
non 1955 *Conus* (*Lithoconus*) *ponderosus* Brocchi, 1814 – Moisescu, p. 164, pl. 14, figs 10, 11.
non 1959 *Conus ponderosus* Brocc. – Eremija, p. 187, pl. 1, figs 5-5a [= *Kalloconus ponderoaustriacus* (Sacco, 1893)].
non 1963 *Conus* (*Rhisoconus*) [*sic*] *ponderosus ponderosus* Brocchi – Atanacković, p. 79, pl. 15, fig. 1.
non 1966 *Conus* (*Chelyconus*) cfr. *ponderosus* Brocchi – Strausz, p. 463, pl. 69, fig. 11, pl. 70, fig. 1 [?= *Lautoconus pseudoponderosus* (Glibert, 1952)].
non 2001 *Conus* (*Chelyconus*) *ponderosus* Brocchi – Chira & Voia, p. 156, pl. 3, figs 1a, b [= ?*Kalloconus ponderoaustriacus* (Sacco, 1893)].

Material and dimensions – Maximum height 96.2 mm, width 51.2 mm. **CO:** NHMW 2024/0205/0056-0059 (4), NHMW 2024/0205/0060 (1), HM coll. (8). **EL**: HM coll. (1).

Description – Shell large, with medium height conical to slightly cyrtoconoid spire. Spire whorl tops initially weakly convex, passing to nearly flat on last 1-2 whorls, bearing faint irregular spiral threads. Suture incised. Subsutural sinus very shallow, weakly curved, moderately asymmetrical. Last whorl with almost flat sutural ramp, shoulder roundly angled, delimited by a cord or groove, below elongate conical, position of maximum diameter slightly below shoulder; base slightly constricted with bearing spiral grooves; weak siphonal fasciole, well demarcated from narrow inner lip. Siphonal canal moderately long, somewhat reflected. No colour pattern preserved.

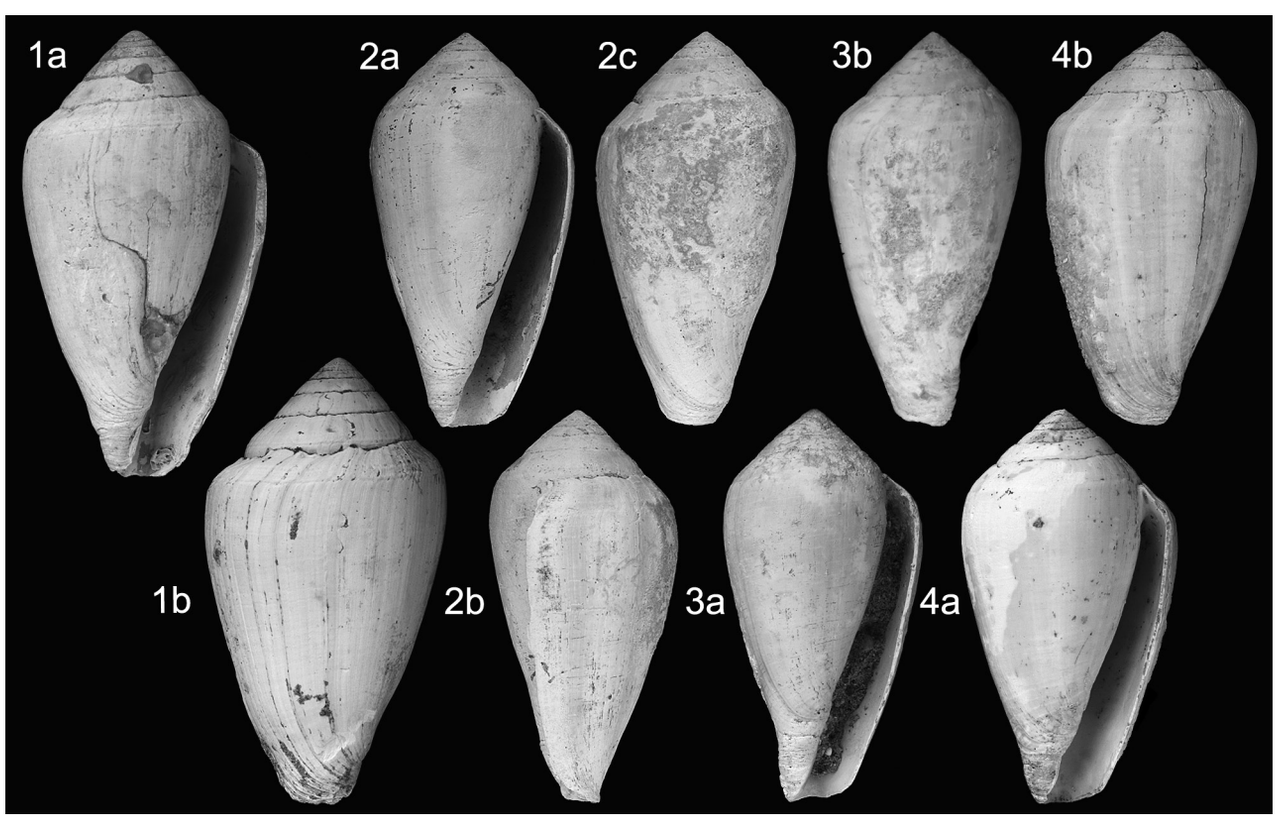

Plate 9. *Lautoconus ponderosus* (Brocchi, 1814); 1. NHMW 2024/0205/0056, height 96.2 mm, width 51.2 mm; 2. NHMW 2024/0205/0057, height 71.2 mm, width 38.2 mm; 3. NHMW 2024/0205/0058, height 77.4 mm, width 39.4 mm; 4. NHMW 2024/0205/0059, height 70.9 mm, width 38.1 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

Shell measurements and ratios – n = 5 adult specimens; largest specimen: SL: 96.2 mm, MD: 51.2 mm, mean SL: 76.6 mm (σ = 11.5), mean MD: 40.0 (σ = 6.7); spire angle: μ = 95.8° (σ = 4.6°), last whorl angle: μ = 35.2° (σ = 1.6°), LW: μ = 1.9 (σ = 0.08), RD: μ = 0.62 (σ = 0.04), PMD: μ = 0.8 (σ = 0.02), RSH: μ = 0.18 (σ = 0.03), Subsutural sinus (n=4): SSFD: very shallow. μ = 3.7 (σ = 0.6), SSFd: weakly curved. μ = 10.9 (σ = 1.2), PV: moderately asymmetrical. μ = 0.4 (σ = 0.09).

Discussion – We have adopted a stricter species concept for this species than Hall (1964) and Chirli (1997) and excluded *Conus laeviponderosus* Sacco, 1893 from the synonymy. As discussed under that species, *Lautoconus laeviponderosus* is smaller (Estepona specimens maximum height 58.2 mm vs. 96.2 mm), do not have a cord or groove delimiting the shoulder on the last whorl, and have a characteristic colour pattern of fine close-set axial lines over the spire and last whorl, usually interrupted in two undecorated bands on the last whorl placed below the shoulder. No colour pattern is preserved in Estepona specimens of *Lautoconus ponderosus* (Brocchi, 1814). Moreover, the subsutural sinus in *L. laeviponderosus* is moderately deep, weakly curved, and strongly asymmetrical as opposed to very shallow, weakly curved, and moderately asymmetrical in *L. ponderosus*. Having said that, we agree with all authors that *L. ponderosus* is a highly variable species with very broad forms (Pl. 9, fig. 1) to slenderer forms (Pl. 9, fig. 3) coexisting.
We agree with Sacco (1893b, p. 85), Davoli (1972, p. 89) and Spadini (1990, p. 321) that *Conus noae* (Brocchi, 1814) (for holotype see Pinna & Spezia, 1978, pl. 18, fig. 2) is probably an unusually slender and somewhat abnormal form of *L. ponderosus*. However, we do not formally synonymise them, which should be based on Italian material. We have not found any specimen that agrees with the *C. noae* morphotype in Estepona.

Distribution – Lower Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b; Hall, 1964). Middle Miocene: Paratethys, Austria (Hörnes, 1851; Harzhauser & Landau, 2016), Hungary (Kovács & Vicián, 2013), Poland (Bałuk, 1997). Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b; Davoli, 1972). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Chirli, 1988, 1997; Spadini, 1990; Sosso & Dell'Angelo, 2010; Paganelli, 2014). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; ?Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992).

***Lautoconus ponderovulatus* (Sacco, 1893)**
Plate 10, figs 1-3, Plate 17, fig. 14, Plate 18, fig. 14

1893b *Conus* (*Chelyconus*) *ponderovulatus* Sacco, p. 75, pl. 7, fig. 21.
1984 *Chelyconus ponderovulatus* Sacco, 1893 – Ferrero Mortara *et al*., p. 119, pl. 18, fig. 1.
1999 *Conus* (*Chelyconus*) *mucronatolaevis* (Sacco, 1893) – Muñiz Solís, p. 53, figs 7M, N [*non* Sacco 1893b].

Material and dimensions – Maximum height 48.1 mm, width 23.8 mm. **CO:** NHMW 2024/0205/0103-0105 (3), NHMW 2024/0205/0106 (1), HM coll. (6).

Description – Shell medium sized, with high conical spire and elongate conical-subcylinderical last whorl. Protoconch and early spire whorls eroded in all specimens. Spire whorls flat to weakly convex, very weakly striate. Suture narrowly impressed. Subsutural sinus shallow, weakly curved, strongly asymmetrical. Last whorl with moderate width, flattened to weakly concave subsutural ramp, broadly rounded at shoulder, conical-subcylindrical below, relatively strongly constricted at base, siphonal fasciole weakly developed, twisted; fine spirals over base and fasciole. Aperture moderately wide, widening considerably abapically; inner lip narrow, shallowly excavated in abapical portion; siphonal canal moderately long, slightly reflected.

Shell measurements and ratios – n = 3 adult specimens; largest specimen: SL: 41.1 mm, MD: 19.9 mm, mean SL: 38.6 mm (σ =2.2), mean MD: 19.1 (σ = 1.0); spire angle: μ = 78.7° (σ = 1.8°), last whorl angle: μ = 33.7° (σ = 1.5°),

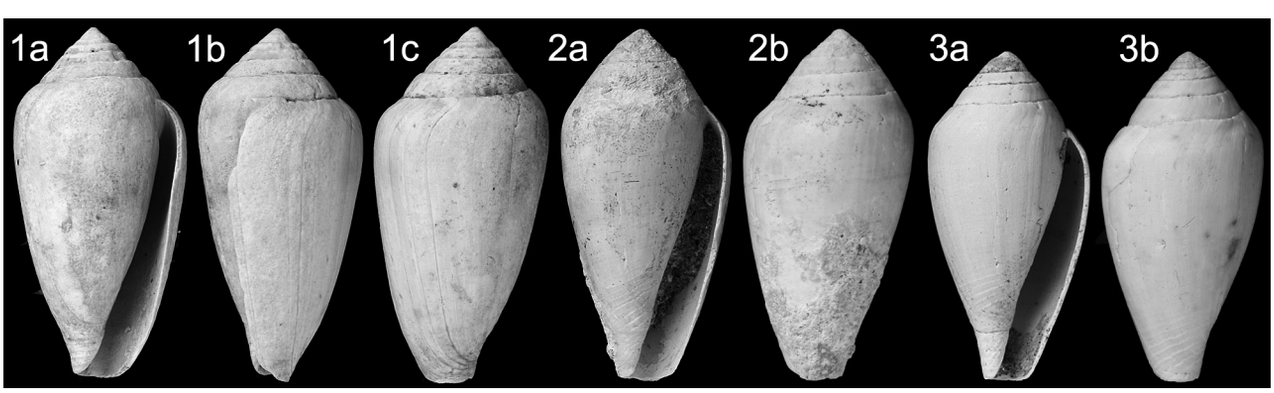

Plate 10. *Lautoconus ponderovulatus* (Sacco, 1893); 1. NHMW 2024/0205/0103, height 37.7 mm, width 19.3 mm; 2. NHMW 2024/0205/0104, height 41.1 mm, width 19.9 mm; 3. NHMW 2024/0205/0105, height 36.9 mm, width 18.0 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

LW: μ = 2.1 (σ = 0.05), RD: μ = 0.6 (σ = 0.01), PMD: μ = 0.9 (σ = 0.03), RSH: μ = 0.23 (σ = 0.02), Subsutural sinus (n=4): SSFD: shallow, μ = 2.1 (σ = 3.2), SSFd: weakly curved, μ = 13.6 (σ = 1.2), PV: strongly asymmetrical, μ = 0.4 (σ = 0.06).

Discussion – Muñiz Solís (1999, figs 7M, N) figured a specimen of this species as *Conus* (*Chelyconus*) *mucronatolaevis* (Sacco, 1893). That species is quite widespread in the Lower and Upper Miocene eastern Atlantic Frontage, Proto-Mediterranean and Paratethys, and is indeed similar but has a more mucronate spire and more evenly conical below the shoulder (see Ferrero Mortara *et al*., 1984, pl. 18, fig. 2; Harzhauser & Landau, p. 154, Figs 30S, 35H_1–H_3 , 35I_1–I_3 , 35J). In our opinion it seems closely similar to the Pliocene *Conus* (*Chelyconus*) *ponderovulatus* Sacco, 1893 (for syntype see Ferrero Mortara *et al*., 1984, pl. 18, fig. 1). They agree in the shape of the spire and the somewhat subcylindrical shape below the shoulder, which is more broadly rounded than in *Conus* (*s.l.*) *mucronatolaevis*. The channelled suture seen in the Italian syntype is not so clear in the Estepona specimens. We note that the mucronate apex seen in the specimen illustrated by Muñiz Solís is also seen in some of the Estepona specimens but is taphonomic artefact caused by erosion of the early whorls leaving the apex more prominent. In its elongate shape it is similar to *Lautoconus pelagicus* (Brocchi, 1814), but in that species has a shallow, moderately curved, nearly symmetrical subsutural sinus as opposed to shallow, weakly curved, and strongly asymmetrical in *Lautoconus ponderovulatus*.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (this paper); central Mediterranean, Italy (Sacco, 1893b). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*., 1984).

***Lautoconus pyrula* (Brocchi, 1814)**
Plate 14, figs 9-10, Plate 17, fig. 15, Plate 18, fig. 15

*1814	*Conus pyrula* Brocchi, p. 288, pl. 2, fig. 8.
1831	*Conus fulminans* Bronn, p. 13.
1893b	*Conus* (*Chelyconus*) *pyrula* (Br.) – Sacco, p. 88, pl. 9, fig. 4.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *circumangulata* Sacco, p. 88, pl. 9, fig. 5.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *fulminans* (Bronn) – Sacco, p. 88, pl. 9, fig. 6.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *longopyrulata* Sacco, p. 89, pl. 9, fig. 7.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *apiceperlonga* Sacco, p. 89, pl. 9, fig. 8.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *supraconvexulata* Sacco, p. 89, pl. 9, fig. 9.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *supradepressulata* Sacco, p. 89, pl. 9, fig. 10.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *perrubiginosa* Sacco, p. 89, pl. 9, fig. 11.
1893b	*Conus* (*Chelyconus*) *pyrula* var. *magnovata* Sacco, p. 89, pl. 9, fig. 12.
1910	*Conus* (*Chelyconus*) *pyrula* Br. – Cerulli-Irelli, p. 49 [241], pl. 4 [35], fig. 48.
1955	*Conus* (*Puncticulis*) (*Chelyconus*) *pyrula* (Brocchi 1814) – Rossi Ronchetti, p. 286, fig. 153.
1958	*Conus* (*Chelyconus*) *pyrula* Brocchi – Erünal-Erentöz, p. 120, pl. 20, figs 2, 3.
1974	*Conus* (*Chelyconus*) *pyrula* Brocchi, 1814 – Malatesta, p. 383, pl. 30, fig. 8.
1976	*Conus pyrula* Brocchi – Pavia, p. 114, pl. 9, figs 3, 8.
1978	*Conus pyrula* Brocchi, 1814 – Pinna & Spezia, p. 137, pl. 24, fig. 1.
1988	*Conus* (*Chelyconus*) *pyrula* Brocchi, 1814 – Chirli, p. 22, pl. 9, fig. 3.
1990	*Conus pyrula* Brocchi, 1814 – Spadini, p. 317, pl. 3, figs 13-15.
1992	*Conus pyrula* Brocchi, 1814 – Cavallo & Repetto, p. 128, fig. 338.
1997	*Conus* (*Chelyconus*) *pyrula* Brocchi, 1814 – Chirli, p. 8, pl. 12, figs 12-17.
?1999	*Conus* (*Dendroconus*) *pyrula* Brocchi, 1814 – Muñiz Solís, p. 74, figs 9F-G.
2009	*Lautoconus pyrula* (Brocchi, 1814) – Tucker & Tenorio, p. 104.
2014	*Conus pyrula* Brocchi, 1814 – Paganelli, p. 31, pl. 2, figs 12-16, pl. 6, figs 9, 10.
non 1970	*Conus* (*Chelyconus*) *pyrula* Brocchi – Greco, p. 292, pl. 6, figs 4-7 [= *Conilithes canaliculatus* (Brocchi, 1814)].
non 1997	*Conus* (*Chelyconus*) *pyrula* Brocchi, 1814 – Bałuk, p. 63, pl. 21, figs 5,6 [= *Conus* s.l. *vindobonensis* Hoernes & Auinger, 1879].
non 2013	*Lautoconus pyrula* (Brocchi, 1814) – Kovács & Vicián, p. 71, figs 7, 62.65 [= *Lautoconus eschewegi* (Pereira da Costa, 1866)].

Material and dimensions – Height 29.7 mm, width 15.1 mm. **CO:** NHMW 2024/0205/0099 (1), ?NHMW 2024/0205/0100 (1).

Description – Shell moderately small, relatively slender, with high coeloconoid spire. Surface of apex and earliest spire whorls abraded giving apex exaggeratedly mucronate appearance. Teleoconch of eight whorls. Spire whorl tops weakly convex, with 1-2 very faint irregular spiral threads seen on tangential light. Suture incised. Subsutural sinus moderately deep, weakly curved, strongly asymmetrical. Last whorl with narrow, convex sutural ramp, shoulder placed high, roundly angled, below elongate conical with convex sides, position of maximum diameter slightly below shoulder; base not constricted with bearing spiral grooves; siphonal fasciole not developed. Siphonal canal moderately short. Colour pattern of fine, reddish, straight to slightly irregular axial lines over spire and entire last whorl.

Shell measurements and ratios – n = 2 adult specimen; SL: 29.7 mm, MD: 15.1 mm; spire angle: 76.5°, last whorl

angle: 34°, LW: 2.0, RD: 0.7, PMD: 0.9, RSH: 0.26, Subsutural sinus (n=4): SSFD: moderately deep, μ = 1.8 (σ = 6.2), SSFd: weakly curved, μ = 14.6 (σ = 4.2), PV: strongly asymmetrical, μ = 0.3 (σ = 0.5).

Discussion – Only one specimen from the Estepona assemblage is attributed to *Lautoconus pyrula* (Brocchi, 1814) with certainty (Pl. 14, fig. 9). Muñiz Solís (1999, pl. 9F, G) illustrated a specimen as *Conus pyrula* from Estepona that might rather represent *Lautoconus laeviponderosus* (Sacco, 1893). It is much broader that *L. pyrula* and the photographs suggest the reddish lines are interrupted by two whitish bands below the shoulder on the last whorl, typical for that species (see Pl. 13, figs 1-6). The second specimen figured here (Pl. 14, fig. 2) probably represents *L. pyrula*, subsutural sinus and colour pattern match, but differs in being more regularly conical below the shoulder on the last whorl. *Lautoconus pyrula* is one of the most abundant cones in coeval Italian Pliocene deposits. Its scarcity in the Estepona assemblage is unexpected.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Sacco, 1893b). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Greco, 1970; Pavia, 1976; Chirli, 1988, 1997; Spadini, 1990; Paganelli, 2014); eastern Mediterranean, Turkey (Erünal-Erentöz, 1958). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

***Lautoconus spongiopictus* (Sacco, 1893)**
Plate 14, figs 11-13, Plate 17, fig. 16, Plate 18, fig. 16

*1893b	*Conus* (*Chelyconus*) *spongiopictus*	Sacco, p. 107, pl. 10, fig. 16.
1984	*Chelyconus spongiopictus*	Sacco, 1893 [*sic*] – Ferrero Mortara *et al*., p. 131, pl. 20, fig. 1.
1990	*Conus spongiopictus*	Sacco, 1893 – Spadini, p. 321, pl. 2, fig. 12.
1992	*Conus* cf. *spongiopictus*	Sacco, 1893 – Cavallo & Repetto, p. 128, fig. 339.
1997	*Conus* (*Chelyconus*) *spongiopictus*	Sacco, 1893 – Chirli, p. 9, pl. 3, fig. 1.
1999	*Conus* (*Chelyconus*) *spongiopictus*	Sacco, 1893 – Muñiz Solís, p. 61, figs 8C-D.
2014	*Conus spongiopictus*	Sacco, 1893 – Paganelli, p. 32, pl. 4, figs 35, 36, pl. 6, fig. 8.

Material and dimensions – Maximum height 44.9 mm, width 25.3 mm. **CO:** NHMW 2024/0205/0061-0063 (3), NHMW 2024/0205/0064 (12), HM coll. (9).

Description – Shell medium sized, of medium thickness, broad with high mammillate spire and weakly convex last whorl. Protoconch not preserved. Teleoconch of 6-7 whorls. Early teleoconch whorls bearing three spiral cords in adapical half in juvenile specimens, cords weaken and fade on later whorl tops, eroded in most adult shells; later spire whorls weakly convex to almost straight-sided and smooth, forming broadly conical spire; suture deeply incised, not channelled. Subsutural sinus shallow, weakly curved, moderately asymmetrical. Last whorl with narrow, weakly concave subsutural ramp, rounded at high-placed shoulder, position of maximum diameter at about three quarters last whorl height, weakly convex and evenly contracting below, weakly to moderately constricted at base, siphonal fasciole relatively long, poorly delimited; surface smooth except for a few weak few weak spirals over base, strengthening slightly over fasciole. Aperture elongate, relatively broad, widening further abapically, siphonal canal weakly recurved, moderately long. Colour pattern of brownish lines and large blotches with sponge-painted appearance.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 44.9 mm, MD: 24.6 mm, mean SL: 38.3 mm (σ = 4.6), mean MD: 20.5 (σ = 1.9); spire angle: μ = 86.4° (σ = 19.0°), last whorl angle: μ = 42.2° (σ = 1.6°), LW: μ = 1.7 (σ = 0.6), RD: μ = 1.2 (σ = 1.9), PMD: μ = 0.85 (σ = 0.02), RSH: μ = 0.23 (σ = 0.02), Subsutural sinus (n=4): SSFD: shallow. μ = 3.3 (σ = 0.08), SSFd: weakly curved. μ = 7.2 (σ = 0.1), PV: moderately asymmetrical. μ = 0.5 (σ = 0.08).

Discussion – Tucker & Tenorio (2009) did not mention this species in their revision of the group. However, in one exceptionally well-preserved specimen three spiral cords are present on the first three teleoconch whorl tops, suggesting placement in *Lautoconus* Monterosato, 1923. With colour pattern preserved, *L. spongiopictus* (Sacco, 1893) is easily recognised by its colour pattern of brownish lines and blotches that have a sponge-painted appearance that accounts for the apply given name. Without its colour pattern and with the early spire whorls abraded, it differs from *Varioconus pecchioli* (Crosse, 1865) in being slenderer, the last whorl less inflated below the shoulder and having a longer siphonal canal. The shell is also slightly less solid than that of *V. pecchioli*. *Lautoconus spongiopictus* is uncommon in the Estepona assemblages.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Spadini, 1990; Chirli, 1997; Paganelli, 2014). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*., 1984; Cavallo & Repetto, 1992).

***Lautoconus subtextile* (d'Orbigny, 1852)**
Plate 15, figs 1-6, Plate 17, fig. 17, Plate 18, fig. 17

1840	*Conus textile* Lin. – Bellardi & Michelotti, p. 152 [*non Cylinder textile* (Linnaeus, 1758)].	
*1852	*Conus subtextile* d'Orbigny, p. 172. [*Nom. nov. pro Conus textile* Bellardi & Michelotti, 1840, *non* Linnaeus, 1758].	

1893b *Conus* (*Cylindrus*?) *subtextilis* [*sic*] (D'Orb.) – Sacco, p. 112, pl. 10, fig. 30.
1893b *Conus* (*Cylindrus*?) *subtextilis* [*sic*] var. *parvoligustica* Sacco, p. 113, pl. 10, fig. 31.
1893b *Conus* (*Cylindrus*?) *subtextilis* [*sic*] var. *ovatoligustica* Sacco, p. 113, pl. 10, fig. 32.
1893b *Conus* (*Cylindrus*?) *subtextilis* [*sic*] var. *conoligustica* Sacco, p. 113, pl. 10, fig. 33.
?1893b *Conus* (*Stephanoconus*) *subbigranosus* var. *pliocoronaxoides* Sacco, p. 121, pl. 11, fig. 30.
1984 *Cylindrus*? *subtextilis* [*sic*] (d'Orbigny, 1852) – Ferrero Mortara *et al*., p. 133, pl. 20, fig. 4.
1990 *Conus subtexilis* [*sic*] D'Orbigny, 1852 – Spadini, p. 322, pl. 2, fig. 11, pl. 3, figs 9, 10.
1997 *Conus* (*Cylindrus*?) *subtextilis* [*sic*] D'Orbigny, 1852 – Chirli, p. 13, pl. 3, figs 15-20.
1999 *Conus* (*Chelyconus*) *subtexilis* [*sic*] D'Orbigny, 1852 – Muñiz Solís, p. 63, figs 8E, F.
1999 *Conus* (*Stephanoconus*) *subbigranosus* (Sacco, 1893) [*sic*] – Muñiz Solís, p. 86, figs 10J-L [*non Stephanoconus subbigranosus* (Sacco, 1893)].
2009 *Varioconus subtextile* (Orbigny, 1852) – Tucker & Tenorio, p. 129.
2014 *Conus subtextile* Orbigny, 1852 – Paganelli, p. 31, pl. 3, figs 25, 26, pl. 6, fig. 11.

Material and dimensions – Maximum height 51.5 mm, width 27.0 mm (*fide* Muñiz Solís, 1999, p. 64). **CO:** NHMW 2024/0205/0065-0070 (6), NHMW 2024/0205/0071 (10), HM coll. (7). **EL:** NHMW 2024/0205/0114 (1).

Description – Shell moderately small to medium sized, solid, very high broad to moderately broad coeloconoid spire and weakly convex last whorl. Protoconch not preserved (paucispiral of 1.5-2 whorls; *fide* Muñiz Solís, 1999, p. 63). Teleoconch of about seven whorls. Spire whorls with 4-5 fine spiral cords present on adapical half of whorl top. Apical angle rapidly increasing on last two whorls and whorl tops flattening abapically. In some specimens poorly delimited tubercles develop at the shoulder, especially on the last 3-4 whorls. Suture superficial, irregularly undulating, not channelled. Subsutural sinus very shallow, weakly curved, nearly symmetrical. Last whorl smooth, with weakly angled shoulder, position of maximum diameter slightly below shoulder, weakly convex below, evenly contracting in lower half of shell, weakly constricted at base, siphonal fasciole nearly absent; a few very weak cords grooves over fasciole. Aperture elongate, narrow, widening slightly abapically, siphonal canal weakly recurved, moderately short. Colour pattern of irregular reddish axial intersecting zig-zag lines.

Shell measurements and ratios – n = 12 adult specimens; largest specimen: SL: 38.5 mm, MD: 20.9 mm, mean SL: 86.2 mm (σ =11.8), mean MD: 15.7 (σ = 2.8); spire angle: μ = 82.8° (σ = 8.9°), last whorl angle: μ = 37.4° (σ = 2.4°), LW: μ = 2.0 (σ = 0.1), RD: μ = 0.7 (σ = 0.04), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.27 (σ = 0.03), Subsutural sinus (n=4): SSFD: very shallow. μ = 8.1 (σ = 8.1), SSFd: weakly curved. μ = 14.3 (σ = 1.2), PV: nearly symmetrical. μ = 1.7 (σ = 0.09).

Discussion – This species is placed in the genus *Lautoconus* Monterosato, 1923 based on the presence of cords on the spire whorls. *Lautoconus subtextile* (d'Orbigny, 1852) is a very characteristic species with its very tall spire, rounded shoulder and shallow subsutural sinus.
This species is unusual in that poorly developed tubercles develop at the shoulder on the last 3-4 whorls most evidently seen in juvenile and subadult specimens (Pl. 15, figs 4-6). As the shell becomes fully adult the last two whorls rapidly expand, and the tubercles become obsolete. Forms with these vague tubercles were illustrated by Sacco as vars *parvoligustica* and *ovatoligustica* (1893b; pl. 10, figs 31 and 32 respectively). Note that as with the Estepona specimens, these tubercular forms are much smaller (30 mm and 23 mm height respectively) than the fully adult type (45-58 mm) illustrated by Sacco (1893b, pl. 10, fig. 30, also Ferrero Mortara *et al*., 1984, pl. 20, fig. 4). The presence of these tubercles led Muñiz Solís (1999, p. 86, figs 10J-L) to identify them as *Conus* (*Stephanoconus*) *subbigranosus* (Sacco, 1893) [*sic*]. The two specimens illustrated by that author are small (22.7 and 20.2 mm height) and show tubercles at the periphery similar to those illustrated here. Muñiz Solís (1999, p. 87) noted that the colour pattern was identical to that of *Conus subtextilis* [*sic*] but did not consider it to signify a taxonomic relationship. *Conasprella subbigranosus* does not occur in Estepona, but *Conasprella subbicrenulata* (Sacco, 1893) does and neither have the same colour pattern. For discussion see under that species.
As discussed above, the colour pattern of zigzag lines is very characteristic. Another species with a similar pattern is *Conus planiligusticus* Sacco, 1893 from the Lower Pliocene of Albenga (Italy). Sacco's illustration (1893b, pl. 10, fig. 34) shows a shell with a lower spire than any we have seen in *L. subtextile* but shares the smooth spire whorl tops and the shallow subsutural sinus. The holotype was refigured by Ferrero-Mortara *et al*. (1984, pl. 20, fig. 8). In these photographs it is difficult to see the whorl tops and it could be that the spire is a little abraded apically. We have not seen any further reports for this species, and it might represent a specimen of *L. subtextile* with an unusually flattened spire. *Conus* (*Stephanoconus*) *subbigranosus* var. *pliocoronaxoides* Sacco, 1893 from the Pliocene of Asti, Italy is similar in profile to *L. subtextile* and at 23 mm height probably represents subadult form. We have not seen this specimen, nor was it refigured by Ferrero Mortara *et al*. (1984). Therefore, we include it in the chresonymy with some reservation.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Spadini, 1990; Chirli, 1997). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*., 1984; Paganelli, 2014).

***Lautoconus ventricosus* (Gmelin, 1791)**
Plate 15, figs 7-10, Plate 17, fig. 18, Plate 18, fig. 18

*1791 *Conus ventricosus* Gmelin, p. 3397.
1792 *Conus mediterraneus* Hwass in Brugière, p. 701.
1792 *Conus Jamaïcensis* Hwass in Brugière, p. 700.
1792 *Conus madurensis* Hwass in Brugière, p. 709.
1792 *Conus ignobilis*, Olivi, p. 133.
1801 *Conus cinctus* Bosc, p. 140.
1810 *Conus Adansonii* Lamarck, p. 424.
1810 *Conus intermedius* Lamarck, p. 441.
1826 *Conus postdiluvianus* Risso, p. 229.
1834 *Conus glaucescens* G.B. Sowerby I, p. 54, fig. 60.
1836 *Conus ignobilis* var. *rufa* Scacchi, p. 9.
1836 *Conus mediterraneus* vars *ater*, *marmoratus* Philippi, p. 238.
1846 *Conus Cailliaudii* Jay, p. 169, pl. 10, fig. 8.
1847 *Conus Pallans* Nardo, p. 39, 40.
1847 *Conus Thuscus* Nardo, p. 39, 40.
1847 *Conus Adriaticus* Nardo, p. 39, 40.
1847 *Conus Cretheus* Nardo, p. 41, 42.
1847 *Conus Phegeus* Nardo, p. 41, 42.
1847 *Conus Stercutius* Nardo, p. 41, 42.
1847 *Conus Amazonicus* Nardo, p. 41, 42.
1847 *Conus Istriensis* Nardo, p. 41, 42.
1847 *Conus Chersoideus* Nardo, p. 41, 42.
1847 *Conus Herillus* Nardo, p. 41, 42.
1847 *Conus Clodianus* Nardo, p. 41, 42.
1847 *Conus Epaphus* Nardo, p. 41, 42.
1848 *Conus Mediterraneus* vars *Obtusa*, *Acuta*, *Subconcolor*, *Marmorata*, *Fasciata* Requien, p. 86.
1849 *Conus inaequalis* Reeve, pl. 7, sp. 270.
1853 *Conus Grossii* Maravigna, p. 137.
1857 *Conus Hanleyi* G.B. Sowerby II, p. 20
1860 *Conus Guestieri* Lorois, p. 329, pl. 12, fig. 5.
1878 *Conus Mediterraneus* var. *minor* Monterosato, p. 107.
1880 *Conus ventricosus* Bronn – Fontannes, p. 144, pl. 8, fig. 11.
1882 *Conus mediterraneus* vars *major*, *oblonga*, *elongata*, *carinata*, *pallida*, *fusca*, *caerulescens*, *flammulata*, *rubens*, *lutea*, *albina* Bucquoy, Dautzenberg & Dollfus, p. 82-84
1885 *Conus mediterraneus* vars *alalmus*, *amigus*, *elpus*, *emisus*, *Pereirae*, *rufatra*, *subviridis* De Gregorio, p. 105-113.
1885 *Conus ventricosus* var. *empismus* De Gregorio, p. 106.
1886 *Conus submediterraneus* Locard, p. 99.
1886 *Conus galloprovincialis* Locard, p. 100.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *subalpina* Sacco, p. 105, pl. 10, fig. 7.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *depressissima* Sacco, p. 105, pl. 10, fig. 8.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *pseudoventricosa* Sacco, p. 105.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *intermedia* (Lk.) – Sacco, p. 105, pl. 10, fig. 9.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *plioventrosa* Sacco, p. 106, pl. 10, fig. 10.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *ovatoventrosa* Sacco, p. 106, pl. 10, fig. 11.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *conoangulata* Sacco, p. 106, pl. 10, fig. 12.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *ligusticomamilla* Sacco, p. 106, pl. 10, fig. 13.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *plioficoides* Sacco, p. 106, pl. 10, fig. 14.
1893b *Conus* (*Chelyconus*) *mediterraneus* var. *fusoficoides* Sacco, p. 107, pl. 10, fig. 15.
1900 *Conus galloprovincialis* vars *lineolata* and *minor* Locard & Caziot, p. 227.
1904 *Conus mediterraneus* var. *altoconica* Pallary, p. 217.
1910 *Conus* (*Chelyconus*) *mediterraneus* Brug. – Cerulli-Irelli, p. 50 [242], pl. 4 [35], figs 52-54.
1911 *Conus mediterraneus* var. *scalare* Dautzenberg, p. 209, pl. 10, fig. 8.
1917 *Conus Vayssierei* var. *ossea* Monterosato, p. 23.
1917 *Conus Mediterraneus* vars *arenaria*, *pretunculus*, *debilis*, *trunculus* Monterosato, p. 23-24, pl. 1, figs 23-26.
1933 *Conus mediterraneus* vars *alba*, *castanea*, *flavescens* Coen p. 70-71.
1933 *Conus galloprovincialis* vars *producta*, *interrupta*, *turrita* Coen, p. 175.
1974 *Conus* (*Lautoconus*) *mediterraneus* (Hwass ms) Bruguière, 1792 – Malatesta, p. 389, pl. 31, fig. 11.
1976 *Conus ventricosus* Gmelin – Pavia, p. 114, pl. 9, figs 7, 10.
1978 *Conus mediterraneus* f. *gaudiosus* Nicolay, p. 18.
1987 *Conus* (*Lautoconus*) *mediterraneus* Bruguière, 1792 – Cuerda Barceló, p. 310, pl. 28, figs 16-22.
1990 *Conus ventricosus* Brocchi, 1814 – Spadini, p. 317, pl. 1, fig. 15.
1992 *Conus mediterraneus* Hwass in Bruguière, 1792 – Cavallo & Repetto, p. 128, fig. 335.
1999 *Conus* (*Chelyconus*) *ventricosus* Gmelin, 1791 – Muñiz Solís, p. 65, figs 8K, L.
2011 *Chelyconus pelagicus* (Brocchi, 1814) – Chirli & Linse, p. 165, pl. 56, figs 1a-d [*non Lautoconus pelagicus* (Brocchi, 1814)] [subspecies *L. ventricosus rhodesensis* Psarras, Merle, Moissette & Kodkeridou, 2024].
2011 *Chelyconus striatulus* (Brocchi, 1814) – Chirli & Linse, p. 165, pl. 56, figs 2a-d [*non Varioconus striatulus* (Brocchi, 1814)] [subspecies *L. ventricosus rhodesensis* Psarras, Merle, Moissette & Kodkeridou, 2024].
2011 *Lautoconus mediterraneus* (Hwass in Bruguière, 1792) – Chirli & Linse, p. 166, pl. 56, figs 3a-d.
2014 *Conus ventricosus* Gmelin, 1791 – Paganelli, p. 30, pl. 1, figs 4, 5.
2018 *Conus* cf. *ventricosus* Gmelin, 1791 – Brunetti & Cresti, p. 102, fig. 430.
2020 *Conus ventricosus* Gmelin, 1791 – Alf *et al*., p. 214, pls 176, 177.

non 1851 *Conus ventricosus* Bronn – Hörnes, p. 32 (*partim*), pl. 3, figs 5, 7 [= *Conus* s.l. *vindobonensis* Hoernes & Auinger, 1879].
non 1851 *Conus ventricosus* Bronn – Hörnes 1851, p 32 (*partim*), pl. 3, fig. 6 [= *Lautoconus miovoeslau-*

ensis (Sacco, 1893)].
non 1851 *Conus ventricosus* Bronn – Hörnes, p. 32 (*partim*), pl. 3, fig. 8 [= *Kalloconus ponderovagus* (Sacco, 1893)].
non 1879 *Conus* (*Chelyconus*) *ventricosus* Bronn – Hoernes & Auinger, p. 49 (*partim*), pl. 6, fig. 6 [= *Lautoconus miovoeslauensis* (Sacco, 1893)].
non 1879 *Conus* (*Chelyconus*) *ventricosus* Bronn – Hoernes & Auinger, p. 49 (*partim*), pl. 1, figs 6–7, pl. 6, fig. 5 (same specimen as pl. 1 fig. 7) [= *Lautoconus magnolapugyensis* (Sacco, 1893)].
non 1879 *Conus* (*Chelyconus*) *mediterraneus* Hwass – Hoernes & Auinger, p. 51, pl. 6, figs 9-11 [= *Conus* s.l. *vindobonensis* Hoernes & Auinger, 1879].
non 1908 *Conus* (*Chelyconus*) *ventricosus* Bronn – Schaffer, p. 98, pl. 10, fig. 15 [= *Lautoconus magnolapugyensis* (Sacco, 1893)].
non 1911 *Conus ventricosus* Bronn – Friedberg, p. 60 (*partim*), text-fig. 14 [= *Kalloconus berghausi* (Michelotti, 1847)].
non 1911 *Conus ventricosus* Brocc. – Friedberg, p. 60, pl. 3, fig. 4 [= *Lautoconus magnolapugyensis* (Sacco, 1893)].
?*non* 2001 *Conus ventricosus* Bronn – Chira & Voia, p. 156, pl. 1, figs 1, 4.

Material and dimensions – Maximum height 32.7 mm, width 17.4 mm. **CO:** NHMW 2024/0205/0095-0098 (4), NHMW 2024/0205/0101 (1), HM coll. (2).

Description – Shell moderately small, broad with high mammillate spire and conical last whorl. Protoconch and early teleoconch whorls not preserved. Later spire whorls weakly convex to almost straight-sided and smooth, forming broadly mammillate spire; suture deeply incised, not channelled. Subsutural shallow, weakly curved, strongly asymmetrical. Last whorl with narrow, weakly convex subsutural ramp, roundly angled at high-placed shoulder, position of maximum diameter just below shoulder, weakly convex and evenly contracting below, not or hardly constricted at base, siphonal fasciole relatively short, poorly delimited; surface smooth except for a few weak spirals over base, strengthening slightly over fasciole. Aperture elongate, relatively broad, widening further abapically, siphonal canal hardly recurved, moderately short. Colour pattern of irregular brownish blotches over subsutural ramp and two white bands; one placed at shoulder, second broader placed just below mid-whorl height.

Shell measurements and ratios – n = 3 adult specimens; largest specimen: SL: 33.0 mm, MD: 17.0 mm, mean SL: 31.9 mm (σ =1.5), mean MD: 17.8 (σ = 2.8); spire angle: μ = 94.3° (σ = 5.1°), last whorl angle: μ = 36.3° (σ = 1.5°), LW: μ = 1.9 (σ = 0.08), RD: μ = 0.7 (σ = 0.03), PMD: μ = 0.9 (σ = 0.03), RSH: μ = 0.26 (σ = 0.01), Subsutural sinus (n=4): SSFD: shallow, μ = 2.3 (σ = 3.2), SSFd: weakly curved, μ = 10.7 (σ = 4.2), PV: strongly asymmetrical, μ = 0.3 (σ = 0.7).

Discussion – *Lautoconus ventricosus* (Gmelin, 1791) is an enormously variable species, as is suggested by the long list of synonyms and varieties that have been described. The chresonymy above lists synonyms of both extant and fossil forms but concentrates on the fossil record. Not all present-day records are given.
Estepona specimens ascribed to this species are almost invariably worn. The spire is mammillate probably due to wear and a colour pattern of two white bands is preserved at the shoulder and just below mid-whorl. The colour pattern seen in fresh specimens is slightly different, the bands not so clearly defined, but the Estepona specimens match perfectly images of abraded extant specimens (see http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/picture?id=920). This is the only species of cone shell in the Estepona assemblage still living today in the entire Mediterranean and possibly along the subtropical coast of West Africa in shallow subtidal habitats on sandy bottoms (Alf *et al*., 2020).
Abalde *et al*. (2023) found evidence of at least three mitochondrial '*Conus ventricosus*' clades corresponding to three cryptic species, and provisionally named those clades based on their colour patterns. Psarras *et al*. (2024) described a new subspecies from the Pleistocene of Rhodes Island, Greece based on a differing colour pattern than those seen in the Mediterranean today. Unfortunately, the Estepona material is too poorly preserved to identify further than *L. ventricosus* s.l.
We have excluded from the chresonymy the Lower and Middle Miocene forms described by Sacco (1893b) that require confirmation of synonymy.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1893b; Pavia, 1976; Spadini, 1990; Paganelli, 2014; Brunetti & Cresti, 2018). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: entire Mediterranean and possibly subtropical West Africa (Alf *et al*., 2020).

Genus *Monteiroconus* da Motta, 1991

Type species (by original designation): *Conus ambiguus* Reeve, 1844, present-day, West Africa.

1991 *Monteiroconus* da Motta, p. 13.

***Monteiroconus mercati* (Brocchi, 1814)**
Plate 11, figs 1-4, Plate 17, fig. 19, Plate 18, fig. 19

*1814 *Conus Mercati* Brocchi, p. 287, pl. 2, fig. 6.
1814 *Conus turricula* Brocchi, p. 288, pl. 2, fig. 7.
1820 *Conus Baldichieri* Borson, p. 193, pl. 1, fig. 1.

1880 *Conus Mercatii* [*sic*] var. *funiculigera* Fontannes, p. 140, pl. 8, fig. 8.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] – Sacco, p. 14, pl. 2, fig. 1.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] anom. *crasselabiata* Sacco, p. 15, pl. 2, fig. 2.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *elogatofusula* Sacco, p. 17, pl. 2, fig. 5.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *depressulospira* Sacco, p. 17, pl. 2, fig. 6.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *longoastensis* Sacc., Sacco, p. 17, pl. 2, fig. 7.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *Baldichieri* (Bors.) – Sacco, p. 18, pl. 2, fig. 8.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *fusuloidea* Sacc., Sacco, p. 18, pl. 2, fig. 9.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *crassovata* Sacc., Sacco, p. 18, pl. 2, fig. 10.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *turricula* (Br.) – Sacco, p. 19, pl. 2, fig. 12.
1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *suprainflata* Sacco, p. 20, pl. 2, fig. 14.
?1893a *Conus* (*Lithoconus*) *Mercatii* [*sic*] var. *acanaliculata* Sacco, p. 21, pl. 2, fig. 18.
1910 *Conus* (*Lithoconus*) *Mercatii* [*sic*] Br. – Cerulli-Irelli, p. 48 [240], pl. 4 [35], fig. 47.
1955 *Conus* (*Lithoconus*) *mercatii* [*sic*] Brocchi 1814 – Rossi Ronchetti, p. 292, fig. 156.
1955 *Conus* (*Lithoconus*) *mercatii* [*sic*] var. *turricula* Brocchi 1814 – Rossi Ronchetti, p. 293, fig. 157.
1964 *Conus mercati* Brocchi, 1814 – Hall, p. 127 [17], pl. 20, figs 6, 7.
1967 *Conus* (*Lithoconus*) *mercati* Brocchi 1814 – Palla, p. 1003, pl. 75, fig. 11.
1972 *Conus mercati* Brocchi – Davoli, p. 119, pl. 1, figs 2, 3, 5-9.
1974 *Conus* (*Lithoconus*) *mercati* Brocchi 1814 – Malatesta, p. 391, pl. 30, fig. 16.
1975 *Conus* (*Lithoconus*) *mercati* Brocchi – Fekih, p. 137, pl. 41, fig. 1.
1976 *Conus mercatii* [*sic*] Brocchi – Pavia, p. 114, pl. 9, fig. 2.
1978 *Conus mercati* Brocchi, 1814 – Pinna & Spezia, p. 136, pl. 20, fig. 2.
1978 *Conus turricula* Brocchi, 1814 – Pinna & Spezia, p. 138, pl. 22, fig. 1.
1981 *Conus mercati* Brocchi, 1814 – Meco, p. 608, pl. 6, fig. 21.
1984 *Lithoconus mercatii* [*sic*] var. *baldichieri* (Borson, 1820) – Ferrero Mortara *et al*., p. 103, pl. 16, fig. 6.
1985 *Conus mercati* Brocchi – Caretto, fig. 10.
1988 *Conus* (*Lithoconus*) *mercati* Brocchi, 1814 – Chirli, p. 22, pl. 10, fig. 3.
1990 *Conus mercati* Brocchi, 1814 – Spadini, p. 317, pl. 3, figs 3-5.
1992 *Conus mercati* Brocchi, 1814 – Cavallo & Repetto, p. 128, fig. 336.
1992 *Conus* (*Lithoconus*) *mercanti* [*sic*] – González-Delgado, p. 50, pl. 6, figs 3-5.
1997 *Conus* (*Lithoconus*) *mercati* Brocchi, 1814 – Chirli, p. 17 (*partim*, pl. 4, figs 11-16 only).
1999 *Conus* (*Lithoconus*) *mercatii* [*sic*] Brocchi, 1814 – Muñiz Solís, p. 80, figs 10D-F.
2004 *Conus antiquus* Lamarck 1810 – İslamoğlu, p. 162, pl. 4, figs 5, 6 [*non Monteiroconus antiquus* (Lamarck, 1810)].
2009 *Monteiroconus mercati* (Brocchi, 1814) – Tucker & Tenorio, p. 110.
2011 *Monteiroconus mercati* (Brocchi, 1814) – Landau *et al*., p. 32, pl. 16, fig. 8.
2013 *Monteiroconus mercati* (Brocchi, 1814) – Landau *et al*., p. 244, pl. 39, figs 2-4, pl. 41, fig. 12, pl. 42, fig. 6, pl. 81, figs 7, 8.
2014 *Conus mercati* Brocchi, 1814 – Paganelli, p. 30, pl. 2, figs 9-10.

non 1851 *Conus Mercati* Brocc. – Hörnes (*partim*), p. 23, pl. 2, figs 1a-b [= *Monteiroconus mojsvari* (Hoernes & Auinger, 1879)].
non 1851 *Conus Mercati* Brocc. – Hörnes (*partim*), p. 23, pl. 2, figs 2a-b [= *Monteiroconus supracompressus* (Sacco, 1893)].
non 1851 *Conus Mercati* Brocc. – Hörnes (*partim*), p. 23, pl. 2, figs 3a-c [= *Monteiroconus conicomaculatus* (Sacco, 1893)].
non 1866 *Conus Mercati* Brocc. in Hörnes – Pereira da Costa (*partim*), p. 11, pl. 3, fig. 3 (only) [= *Monteiroconus daciae* (Hoernes & Auinger, 1879)].
non 1930 *Conus* (*Lithoconus*) *Mercati* var. *vasconiensis* Peyrot, p. 93, no. 1167 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].
non 1931 *Conus* (*Lithoconus*) *Mercati* var. *vasconiensis* Peyrot, pl. 2, figs 9, 13, 14 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].
non 1938 *Conus* cf. *Mercati* var. *ligeriana* Peyrot, p. 257, pl. 4, figs 31, 40 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].
non 1952 *Conus mercati sharpeanus* Costa, 1866 – Glibert, p. 372, pl. 12, fig. 13 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].
non 1952 *Conus mercati vasconiensis* Peyrot, 1931 – Glibert, p. 373, pl. 13, fig. 1 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].
non 1952 *Conus mercati daciae* Hoernes & Auinger, 1879 – Glibert, p. 374, pl. 12, fig. 12 [*non Monteiroconus daciae* (Hoernes & Auinger, 1879)].
non 1952 *Conus mercati austriacus* Hoernes & Auinger, 1879 – Glibert, p. 374, pl. 13, fig. 2 [= *Pseudonoduloconus austriacus* (Hoernes & Auinger, 1879)].
non 1961 *Conus* (*Lithoconus*) *mercati* Brocc. – Florei, p. 688, pl. 9, fig. 66 [= *Monteiroconus mojsvari* (Hoernes & Auinger, 1879)].
non 1973 *Conus* (*Lithoconus*) *mercati sharpeanus* (Costa) 1866 – Bohn-Havas, p. 1123, pl. 7, fig. 9 [= *Monteiroconus mojsvari* (Hoernes & Auinger, 1879)].
non 1998 *Conus* (*Lithoconus*) *mercati* Brocchi—Schultz, p. 72, pl. 29, figs 12a-b [= *Monteiroconus daciae* (Hoernes & Auinger, 1879)].

non 2010 *Conus mercati* Brocchi, 1814 – Vaessen, p. 8, figs 9, 10B, 11-13 [= *Monteiroconus sharpeanus* (Pereira da Costa, 1866)].

non 2011 *Lithoconus mercati* (Brocchi, 1814) – Chirli & Linse, p. 166, pl. 57, figs 1a-d [= *Monteiroconus tsampikaensis* Psarras, Merle, Moissette & Kodkeridou, 2024].

non 2013 *Monteiroconus mercati* (Brocchi, 1814) – Kovács & Vicián (*partim*), p. 78, figs 87-88 [= *Lautoconus* sp.].

non 2013 *Monteiroconus mercati* (Brocchi, 1814) – Kovács & Vicián (*partim*), p. 78, figs 89-91 [= *Monteiroconus mojsvari* (Hoernes & Auinger, 1879)].

Material and dimensions – Maximum height 93.6 mm, width 47.7 mm (fragmentary specimens suggest larger maximum size). **CO:** NHMW 2024/0205/0072-0075 (4), NHMW 2024/0205/0076 (2), NHMW 2024/0205/0090 (4), HM coll. (37). **EL**: HM coll. (2).

Description – Shell moderately large to large (maximum height at least 93.6 mm), solid. Protoconch and early teleoconch whorls worn. Teleoconch of up to eight whorls. Spire depressed to moderately elevated, when elevated last spire whorls weakly gradate; whorl tops smooth, flat to concave. Suture incised, not channelled. Subsutural sinus moderately deep, strongly curved, moderately asymmetrical. Last whorl broad, almost no subsutural ramp, shoulder placed just below suture, rounded, almost straight-sided below, evenly contracting, hardly constricted at base; position of maximum diameter slightly below shoulder; siphonal fasciole broad, poorly delimited; many specimens bear weak, widely spaced, irregular grooves over last whorls, closer set and slightly stronger over fasciole. Aperture wide, broadening further abapically, insertion of outer lip well below rounded shoulder. Siphonal canal short, straight, wide. No colour pattern preserved.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 90.3 mm, MD: 50.9 mm, mean SL: 64.8 mm (σ = 10.0), mean MD: 37.9 (σ = 5.4); spire angle: μ = 123.2° (σ = 10.6°), last whorl angle: μ = 38.9° (σ = 4.4°), LW: μ = 1.7 (σ = 0.2), RD: μ = 0.76 (σ = 0.05), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.21 (σ = 0.04). Subsutural sinus (n=4): SSFD: moderately deep, μ = 1.9 (σ = 0.2). SSFd: strongly curved, μ = 4.0 (σ = 1.8). PV: moderately asymmetrical, μ = 0.6 (σ = 0.07)

Discussion – *Monteiroconus mercati* (Brocchi, 1814) is one of the largest cones in the Estepona assemblage. The maximum height given is certainly an underestimate, as incomplete specimens suggest an even larger size, probably similar to the size of the Middle Miocene eastern Proto-Mediterranean specimens from the Karaman Basin, Turkey (maximum height 100 mm; Landau *et al*., 2013). The species is highly variable in spire height, some specimens have depressed spires, whereas in others the

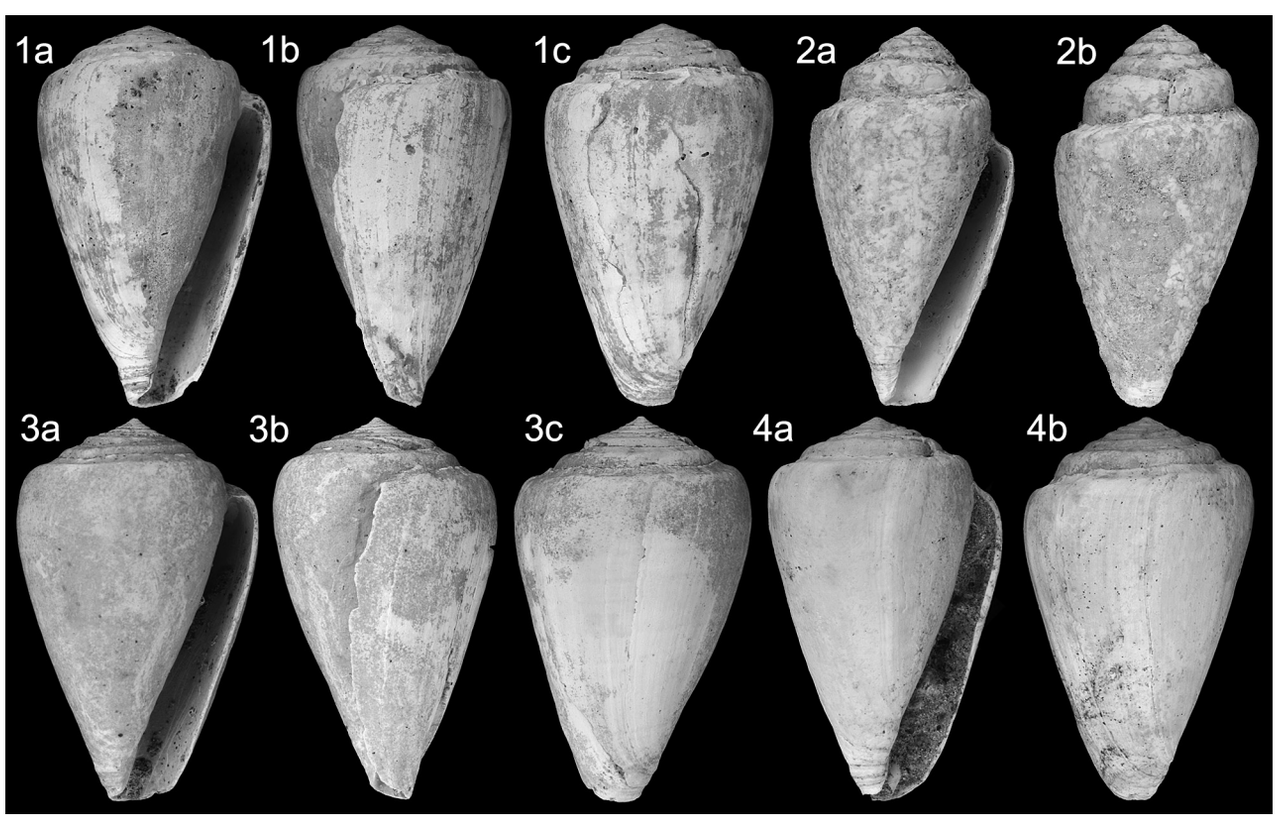

Plate 11. *Monteiroconus mercati* (Brocchi, 1814); 1. NHMW 2024/0205/0072, height 63.1 mm, width 38.5 mm; 2. NHMW 2024/0205/0073, height 60.6 mm, width 32.7 mm; 3. NHMW 2024/0205/0074, height 57.1 mm, width 35.7 mm; 4. NHMW 2024/0205/0075, height 63.6 mm, width 38.3 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

last two spire whorls become more elevated giving the last portion of the spire a gradate appearance. Sculpture on the last whorl is also variable ranging from smooth to having broadly spaced weak grooves over the entire last whorl that strengthen and become closer set over the siphonal fasciole. This variation in sculpture is also seen in Sacco's (1893a) 'varieties', although none of the Estepona specimens are as pronounced as his anom. *anomalosulcata* (Sacco, 1893a, pl. 2, fig. 2[bis]) which probably also represents this species, but is so deformed that we have excluded it from the chresonymy. The colour pattern described by Landau *et al*., 2013, p. 245, pl. 81, figs 7, 8) is not preserved in the Estepona specimens at hand but was described by Muñiz-Solís (1999) as broad, irregular, reddish, arcuate axial lines, more or less consistent with the pattern seen in the Karaman specimens.

As discussed by Landau *et al*. (2013, p. 245), we disagree with Glibert (1952, p. 372) who considered all species within the '*Conus mercati* group' to have three spiral cords on the spire whorls. Neither the holotype figured by Rossi Ronchetti (1955, fig. 156) nor any of the Pliocene Italian or Estepona specimens have spiral sculpture on the spire whorls. Landau *et al*. restrict *M. mercati* to forms with smooth spire whorl tops. We have therefore excluded from the chresonymy the Atlantic Middle Miocene specimens from the Loire and Aquitaine basins that have cords on the spire whorl tops as described and illustrated by Vaessen (2010, p. 9, fig 10B). These might represent *Monteiroconus sharpeanus* (Pereira da Costa, 1866), originally described from the Upper Miocene of Portugal that is very similar to *M. mercati*, but with cords on the whorl tops. Middle Miocene Paratethyan forms recorded as *M. mercati* by authors are also not this species (see chresonymy herein and Harzhauser & Landau, 2016).

Distribution – Middle Miocene: Proto-Mediterranean (Langhian): Kasaba Basin (İslamoğlu, 2004), (Serravallian): Karaman Basin, Turkey (Fischer, 1866; Landau *et al*., 2013). Upper Miocene: Proto-Mediterranean (Tortonian): Italy (Davoli, 1972). Lower Pliocene: Atlantic, Canary Islands (Meco, 1981), Guadalquivir Basin, SW Spain (González-Delgado, 1992; Landau *et al*., 2011); western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1893a; Pavia, 1976; Chirli, 1988, 1997; Spadini, 1990), Tunisia (Fekih, 1975). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893a; Palla, 1967; Malatesta, 1974; Ferrero Mortara *et al*., 1984; Cavallo & Repetto, 1992; Paganelli, 2014). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

Genus *Pseudonoduloconus* Tucker & Tenorio, 2009

Type species (by original designation): *Conus carnalis* G.B. Sowerby III, present-day, Angola.

1991 *Pseudonoduloconus* Tucker & Tenorio, p. 114.

***Pseudonoduloconus virginalis* (Brocchi, 1814)**
Plate 12, figs 1-3, Plate 17, figs 20, 21, Plate 18, fig. 20

*1814 *Conus virginalis* Brocchi, p. 290, pl. 2, fig. 10.
1840 *Conus bisulcatus* Bellardi & Michelotti, p. 154, pl. 6, figs 9-10.
1893b *Conus* (*Rhizoconus*?) *virginalis* (Br.) – Sacco, p. 113, pl. 11, fig. 1.
1893b *Conus* (*Rhizoconus*?) *virginalis* anom. *percingulellata* Sacco, p. 113, pl. 11, fig. 2.
1893b *Conus* (*Rhizoconus*?) *virginalis* var. *conicoligustica* Sacco, p. 113, pl. 11, figs 3, 3[bis].
1893b *Conus* (*Rhizoconus*?) *virginalis* var. *fusuloligustica* Sacco, p. 113, pl. 11, fig. 4.
1893b *Conus* (*Rhizoconus*?) *virginalis* var. *inflatulospira* Sacco, p. 114, pl. 11, fig. 5.
1893b *Conus* (*Rhizoconus*?) *virginalis* var. *planulatospira* Sacco, p. 114, pl. 11, fig. 6.
1893b *Conus* (*Rhizoconus*?) *virginalis* var. *perstriatula* Sacco, p. 114, pl. 11, fig. 7.
1955 *Conus* (*Lithoconus*) *virginalis* Brocchi 1814 – Rossi-Ronchetti, p. 289, fig. 155.
1974 *Conus* (*Lithoconus*) *virginalis* Brocchi, 1814 – Malatesta, p. 392, pl. 30, fig. 13.
1975 *Conus* (*Lithoconus*) *virginalis* Brocchi – Fekih, p. 138, pl. 41, fig. 2.
1976 *Conus virginalis* Brocchi – Caprotti, p. 12, pl. 17, fig. 8.
1978 *Conus virginalis* Brocchi, 1814 – Pinna & Spezia, p. 138, pl. 20, fig. 2.
1984 *Rhizoconus*? *virginalis* var. *planulatospira* Sacco, 1893 [*sic*] – Ferrero Mortara *et al*., p. 133, pl. 20, fig. 6.
1990 *Conus virginalis* Brocchi, 1814 – Spadini, p. 317, pl. 2, fig. 9.
1997 *Conus* (*Lithoconus*) *virginalis* Brocchi, 1814 – Chirli, p. 18, pl. 5, fig. 4.
1999 *Conus* (*Rhizoconus*) *virginalis* Brocchi, 1814 – Muñiz Solís, p. 84, figs 10G-I.
2009 *Pseudonoduloconus virginalis* (Brocchi, 1814) – Tucker & Tenorio, p. 115.
2010 *Conus virginalis* Brocchi, 1814 – Sosso & Dell'-Angelo, p. 50, 65 unnumbered figures middle row centre and right.
2014 *Conus virginalis* Brocchi, 1814 – Paganelli, p. 31, pl. 3, fig. 20.

Material and dimensions – Maximum height 48.5 mm, width 28.0 mm. **CO:** NHMW 2024/0205/0091-0093 (3), NHMW 2024/0205/0094 (4), NHMW 2024/0205/0115 (1 juvenile), NHMW 2024/0205/0121 (1 juvenile), HM coll. (29).

Description – Shell medium sized, with low to medium height coeloconoid spire, angular last whorl, regularly conical below. Teleoconch of up to nine weakly gradate whorls. Early spire whorls bearing 2-3 fine spiral cords on adapical half of whorl, undulating at periphery giving aspect of tubercles; on later spire whorls spiral cords weaken and disappear, tubercles at suture weaken, al-

though indistinct nodes can persist at shoulder in some specimens (Pl. 12, fig. 3). Subsutural sinus very shallow, moderately curved, moderately asymmetrical. Last whorl with narrow, weakly concave subsutural ramp bearing close-set comma shaped growth lines, angled at shoulder placed just below suture, position of maximum diameter short distance below shoulder, regularly conical below, hardly constricted at base; siphonal fasciole indistinct; relatively prominent narrow spiral cords over base and fasciole. Aperture narrow, widening slightly abapically. No colour pattern preserved.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 55.0 mm, MD: 27.7 mm, mean SL: 39.2 mm (σ =6.4), mean MD: 22.9 (σ = 3.4); spire angle: μ = 108.6° (σ = 8.1°), last whorl angle: μ = 33.7° (σ = 2.3°), LW: μ = 1.8 (σ = 0.1), RD: μ = 0.7 (σ = 0.05), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.16 (σ = 0.03), Subsutural sinus (n=4): SSFD: very shallow, μ = 3.9 (σ = 4.3), SSFd: moderately curved, μ = 5.8 (σ = 2.3), PV: moderately asymmetrical, μ = 0.6 (σ = 1.1).

Discussion – The shell characters of the genus *Pseudonoduloconus* Tucker & Tenorio, 2009 are "*Whorl tops have false nodes formed by elevations at the junction of the shoulder and major growth lines; the early whorls are not nodulose; the anal notch is shallow; the protoconch is paucispiral*." (Tucker & Tenorio, 2009, p. 114). In *Pseudonoduloconus virginalis* (Brocchi, 1814) these false nodes are rather poorly defined and irregular, although they persist on the shoulder of the last whorl in some gerontic specimens (Pl. 12, fig. 3). There is some variability as to the shell width and spire height.

Most of the specimens from Estepona do not have the 'nodes' extending to the last whorl, but only have the early whorls tubercular, similar to those figured by Sacco (1893b, p. 11, figs 1, 2). These specimens were identified by *Conus* (*Chelyconus*) *gallicus* Mayer-Eymar, 1890b by Muñiz Solís, 1999, p. 49). The identity of these Estepona specimens is revealed in the description "…, *las primeras ligeramente escalonadas, granulosas y después planas, ornadas con 2-3 cordoncillos más o menos visibles subsuturales y líneas de crecimiento curvas irregulares que marcan el seno anal* […, the first gradate, granulose and later flattened, bearing 2-3 cords in the subsutural area and curved growth lines marking the subsutural sinus]". In *Kalloconus gallicus* the whorl tops are smooth (see Harzhauser & Landau, 2016, p. 60, figs 3K, $10A_1$-A_6).

Meco *et al.* (2002, p. 201) listed but did not illustrate this species from the Lower Pleistocene of the Canary Islands. This record needs to be confirmed. Couffon & Dollfus (1928, p. 423) listed *C. virginalis* from the 'Redonian' of Anjou. This record probably refers to *Eoconus cambieni* Landau, Van Dingenen & Ceulemans, 2020 or *E. vanhoutenae* Landau, Van Dingenen & Ceulemans, 2020 both of which have 'false nodes' on the later spire whorls but differ from *Pseudonoduloconus* in having tubercles on the earliest spire whorls.

Pseudonoduloconus gastaldii (Michelotti, 1847) from the Lower Miocene Atlantic of France and Proto-Mediterranean of Italy and Middle Miocene Paratethys is closely similar and undoubtedly a predecessor of the Pliocene species (see Harzhauser & Landau, 2016, p. 142, figs $33F_1$–F_3). They are of about the same size and have a similar profile. The nodules on the last spire whorl seem somewhat coarser than those seen in any specimen of *P. virginalis*. Unfortunately, the material available is all relatively poorly preserved making further comparison difficult, but it is unlikely they are the same species. Two further congeners occur in the Paratethyan Middle Miocene; *P. austriacus* (Hoernes & Auinger, 1879) differs in its much broader conical profile and *P. wagneri* (Boettger, 1902) is much smaller with a more elevated spire. A further congener was described from the Miocene of Madeira, *P. reissi* (Mayer, 1864, pl. 8, fig. 59) that has weak nodules on the spire and differs from its congeners in having a more pyriform profile, somewhat constricted mid-last whorl.

Today the genus is represented in the West African fauna by *P. carnalis* (G.B. Sowerby III, 1879) which is slightly more rounded at the shoulder and has very weak nodules on the top of the last whorl.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Sacco, 1893b; Ferrero Mortara *et al*.,

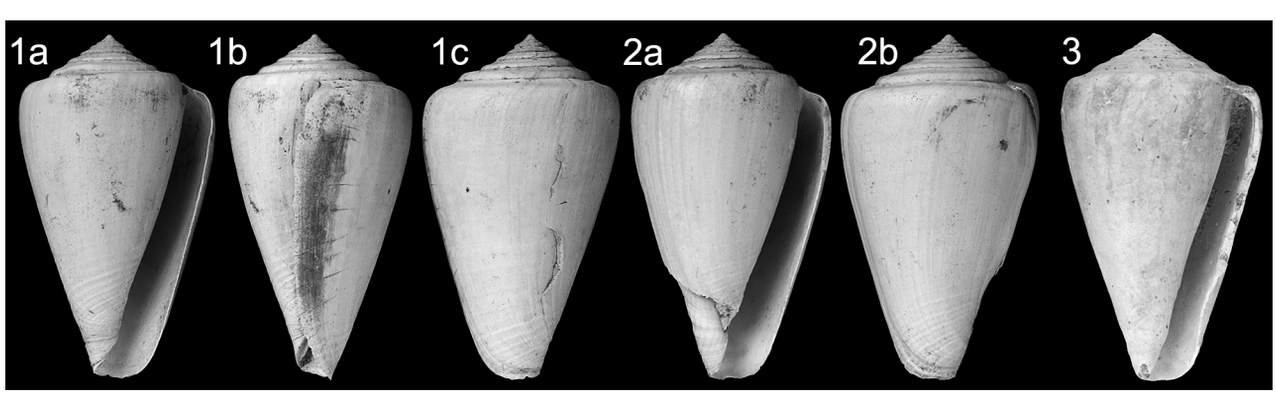

Plate 12. *Pseudonoduloconus virginalis* (Brocchi, 1814); 1. NHMW 2024/0205/0091, height 39.5 mm, width 19.7 mm; 2. NHMW 2024/0205/0092, height 37.5 mm, width 21.4 mm; 3. NHMW 2024/0205/0093, height 48.5 mm, width 28.0 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

1984; Spadini, 1990; Chirli, 1997; Sosso & Dell'Angelo, 2010), Tunisia (Fekih, 1975). Upper Pliocene: central Mediterranean, Italy (Sacco, 1893b; Malatesta, 1974; Caprotti, 1976; Paganelli, 2014).

Genus *Varioconus* da Motta, 1991

Type species (by original designation): *Conus variegatus* Kiener, 1848, present-day, West Africa.

1991 *Varioconus* da Motta, p. 34.

Note – Based on molecular data, Puillandre *et al*. (2014a, b) synonymised *Varioconus* da Motta, 1991 with *Lautoconus* Monterosato, 1923. According to Tucker & Tenorio (2009) the genus *Varioconus* da Motta, 1991 is characterised by shells with smooth spire whorls, a rounded, indistinct shoulder, a shallow subsutural sinus, and a paucispiral protoconch. For their molecular phylogeny Puillandre *et al*. (2014a, b) analysed numerous species, traditionally placed in *Lautoconus* but only two species, which are listed as *Varioconus* by Tucker & Tenorio (2009) (*Conus xicoi* Röckel, 1987 and *C. franciscoi* Rolán & Röckel, 2000). Unfortunately, *Conus variegatus* Kiener, 1845, the type species of *Varioconus*, is missing from their analysis. Therefore, the synonymy remains debateable (Harzhauser & Landau, 2016, p. 72). According to Tucker & Tenorio (2009, p. 103) *Lautoconus* species have cords that reach mid-spire whorls and usually persist, absent in *Varioconus*. We have used this character to assign species to one or another genus. However, after describing the numerous *Lautoconus* species from the Estepona assemblage, the presence/absence of cords on the spire whorls is sometimes very subtle, the spiral threads only just visible under tangential light or magnification in some species, obvious in others. We suspect that Puillandre *et al*. (2014a, b) were correct to synonymise the two genera, however, until further genetic information is available concerning the type species, we keep them separate.

***Varioconus clavatulus* (d'Orbigny, 1852)**
Plate 16, figs 1-6, Plate 17, fig. 22, Plate 18, fig. 21

1823 *Conus Noae* Brocc. – Brongniart, p. 61, pl. 3, fig. 2 [*non Lautoconus noae* (Brocchi, 1814)].
1845 *Conus clavatus* var. C Lamarck – Grateloup (*partim*), pl. 44, fig. 4 [*non* Lamarck, 1810].
1845 *Conus Nöe* Brocc. – Grateloup, pl. 43, fig. 10.
*1852 *Conus clavatulus* d'Orbigny, p. 11 [*nom. nov. pro Conus clavatus* Grateloup, 1845, fig. 4 only].
1852 *Conus Baldus* d'Orbigny, p. 11 [*nom. nov. pro Conus noae* Grateloup, 1845, *non* Brocchi, 1814].
1880 *Conus noae* var. *ruscinensis* Fontannes, p. 142, pl. 8, fig. 9.
?1893b *Conus Marii* var. *perglandiformis* Sacco, p. 63, pl. 4, fig. 9.
1895 *Conus Noe* Br. – Cossmann, p. 160, pl. 8, figs 20-22.
1931 *Conus* (*Chelyconus*) *clavatulus* D'Orbigny – Peyrot, p. 115, pl. 1, fig. 13, pl. 4, figs 1, 3, 5, 20.
1964 *Conus clavatulus* Orbigny, 1852 – Hall, p. 143 [33], pl. 24, figs 17-19, 21-24.
?1972 *Conus* cf. *clavatulus* Orbigny – Davoli, p. 89, pl. 4, figs 5, 15-17.
1990 *Conus* cfr. *clavatulus* d'Ornigny, 1852 – Spadini, p. 320, pl. 1, figs 9, 10.
1997 *Conus clavatus* Lamarck, 1810 – Chirli, p. 4, pl. 1, figs 4, ?5.
1999 *Conus* (*Dendroconus*) sp. 2 – Muñiz Solís, p. 76, figs 9H, I (juvenile form).
2014 *Conus clavatulus* Orbigny, 1852 – Paganelli, p. 31, pl. 3, fig. 23 (not 24 as stated in text; *lapsus*).

non 1992 *Conus clavatus* (Lamarck, 1810) [*sic*] – Cavallo & Repetto, p. 126, fig. 331 [*non Lautoconus clavatus* (Lamarck, 1810)].
?*non* 1999 *Conus* (*Chelyconus*) *clavatulus* D'Orbigny, 1852 – Muñiz Solís, p. 42, figs 6K-M.

Material and dimensions – Maximum height 87.9 mm, width 45.9 mm. **CO:** NHMW 2024/0205/0077-0082 (6), NHMW 2024/0205/0083 (5), HM coll. (18).

Description – Shell large, with medium height dome-shaped cyrtoconoid spire. Teleoconch of up to eight whorls. Spire whorl tops weakly convex, smooth. Suture moderately incised. Subsutural sinus very shallow, weakly curved, nearly symmetrical. Last spire whorl with steep, flattened to weakly concave sutural ramp, shoulder broadly and roundly angled, elongate conical below with slightly convex sides, position of maximum diameter about three quarter whorl height; base slightly to moderately constricted bearing broad flattened spiral cords, strengthening towards fasciole; moderately developed siphonal fasciole. Aperture moderately wide, widening further abapically. Siphonal canal moderately long, somewhat reflected. Colour pattern of flammules on whorl tops, fine reddish spiral lines below shoulder on last whorl narrower than their interspaces over light orange background.

Shell measurements and ratios – n = 12 adult specimens; largest specimen: SL: 90.2 mm, MD: 45.1 mm, mean SL: 72.8 mm (σ =10.4), mean MD: 37.4 (σ = 5.3); spire angle: μ = 100.6° (σ = 8.6°), last whorl angle: μ = 37.8° (σ = 0.9°), LW: μ = 2.0 (σ = 0.04), RD: μ = 0.6 (σ = 0.6), PMD: μ = 0.8 (σ = 0.02), RSH: μ = 0.19 (σ = 0.03), Subsutural sinus (n=4): SSFD: very shallow, μ = 3.9 (σ = 0.03), SSFd: weakly curved, μ = 7.2 (σ = 1.1), PV: nearly symmetrical, μ = 2.3 (σ = 0.1).

Discussion – *Conus clavatulus* Orbigny, 1852 is characterised by its medium height dome-shaped spire, smooth spire whorl tops, broadly rounded shoulder on the last whorl, slightly convex whorl profile below and widely spaced flattened cords over the base and fasciole. Apart for the features highlighted above, the Estepona specimens have a colour pattern preserved of broad reddish

flammules over the whorl tops and subsutural ramp of the last whorl and fine spiral lines below on the last whorl, narrower than their interspaces. The reddish lines are rather variable in their spacing, but always wider apart than in *Lautoconus corynetes* (Fontannes, 1880) or *Lautoconus deshayesii* (Bellardi & Michelotti, 1840), the other two Estepona cones with spiral lines below the shoulder on the last whorl.

We note important change in shell profile with ontogeny. Subadult specimens tend to have a comparatively lower spire and more angular shoulder (Pl. 16, figs 3-6) than fully adult specimens (Pl. 16, figs 1-3). We are fairly certain they represent the same species as the subsutural sinus is the same.

This species has been confused with *C. clavatus* Lamarck, 1810 (*e.g.*, Chirli, 1997). However, according to Peyrot (1931, p. 116), *Conus clavatus* Lamarck 1810 is a Lower Miocene Burdigalian species that differs from *C. clavatulus* d'Orbigny, 1852 in being smaller (54 mm vs. 68 mm height; *fide* Peyrot, 1931), by having fine cords on the spire whorl tops, and by its more rounded shoulder on the last whorl. The presence of cords on the spire whorls places it in *Lautoconus* Monterosato, 1923 rather than *Varioconus* da Motta, 1991. We note a *lapsus* in Harzhauser & Landau (2016) where *C. clavatulus* was placed in the genus *Lautoconus* (p. 129), *Plagioconus* Tucker & Tenorio, 2009 (p. 131), and *Varioconus* (p. 155). The dome-shaped spire in this species is indeed reminiscent of *Plagioconus* (type species, by original designation, *Conus elatus* Michelotti, 1847, Miocene, Europe), species in that genus have an even higher, slightly scalate dome-shaped spire and a very elongated last whorl. We place it in *Varioconus* based on the absence of cords on the spire whorls.

Its large size and rounded shoulder make it similar to *C. noae* Brocchi, 1814, which is even slenderer and has a groove running along the shoulder, although this might just represent an unusually elongated slender specimen of *Lautoconus ponderosus* (Brocchi, 1814). It could also be argued that these specimens are *L. ponderosus* without a groove along the periphery. However, that species usually has a lower spire, some spiral sculpture, albeit weak on the spire whorls that place it in *Lautoconus* rather than *Varioconus*, a clearly concave subsutural platform on the last whorl, lacks the flattened spiral cords over the base and fasciole, and has no traces of colour pattern.

The largest specimen from Estepona is almost identical to the large specimen illustrated by Spadini (1990, pl. 1, fig. 10) and he also described the fine reddish spiral lines seen on the last whorl that can also be clearly seen in his illustration. In Paganelli (2014, p. 31) the numbers and specimens have become confused. *Conus clavatulus* is discussed on p. 24, and stated being illustrated on pl. 3, fig. 24. On the plate caption p. 33 it is fig. 23 that shows a juvenile form with a relatively angled shoulder similar to those illustrated herein (Pl. 16, figs 4-6). The text states "*No trace of colour pattern*", but this is a *lapsus* as spiral lines are clearly seen in his photograph. The specimen illustrated by Cavallo & Repetto (1992, fig. 331) as *Conus clavatus* (Lamarck, 1810) is small, has a far lower spire than *V. clavatulus*, a more angular and higher placed shoulder, and fine spiral cords over the base and fasciole, far more crowded than seen in the Estepona specimens of *V. clavatulus*.

The specimen illustrated by Muñiz Solís (1999, figs 6K-M) as *Conus* (*Chelyconus*) *clavatulus* from Estepona is included in the chresonymy with some hesitation. In his material the maximum size was 58 mm in height and the specimen illustrated has a lower spire, less rounded shoulder, and the profile is more regularly conical below. That author describes spiral cords on the early spire whorls that we do not see in our material. Therefore, the somewhat abraded shell illustrated probably represents a species of *Lautoconus*.

The Italian Lower Miocene specimens illustrated by Hall (1964, pl. 24, figs 17-19, 21-24) seem to be conspecific. We have not compared them directly, but if the Pliocene specimens were a separate species, the name *L. ruscinensis* Fontannes, 1880 would be available.

Distribution – Lower Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b; Hall, 1964). Middle Miocene: central Proto-Mediterranean, Italy (Hall, 1964). Upper Miocene: Aquitaine Basin (Tortonian), France (Cossmann, 1895; Peyrot, 1931); central Proto-Mediterranean, Italy (Davoli, 1972). Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (?Muñiz Solís, 1999; this paper); central Mediterranean, Italy (Spadini, 1990; ?Cavallo & Repetto, 1992; Chirli, 1997; Paganelli, 2014).

***Varioconus pecchioli* (Crosse, 1865)**

Plate 15, figs 11, 12, Plate 17, fig. 23, Plate 18, fig. 22

1864	*Conus pulchellus* Pecchioli, p. 514, pl. 5, figs 15, 16.
*1865	*Conus pecchioli* Crosse, p. 95. [*Nom. nov. pro Conus pulchellus* Pecchioli, 1864, *non* Linnaeus, 1758].
1990	*Conus pecchioli* Crosse, 1865 – Spadini, p. 321, pl. 2, figs 4-6.
1997	*Conus* (*Chelyconus*) *pecchioli* Crosse, 1865 – Chirli, p. 6, pl. 1, figs 11-16.
1999	*Conus* (*Chelyconus*) cfr. *fuscocingulatus* Bronn in Hörnes, 1856 – Muñiz Solís, p. 48, figs 7E-H [*non Phasmoconus fuscocingulatus* (Hörnes, 1851)].
2009	*Lautoconus pecchiolii* [*sic*] (Crosse, 1865) – Tucker & Tenorio, p. 104.
2014	*Conus pecchioli* Crosse, 1865 – Paganelli, p. 32, pl. 4, figs 27, 28, pl. 5, figs 5, 6.

Material and dimensions – Maximum height 44.0 mm, width 25.3 mm. **CO:** NHMW 2024/ 0205/0001-0002 (2), NHMW 2024/0205/0003 (9), HM coll. (35).

Description – Shell medium sized, solid, broad with high mammillate spire and convex last whorl. Protoconch not preserved. Teleoconch of up to eight whorls. Early spire whorls eroded in adult specimens, smooth in juveniles; later spire whorls weakly convex and smooth, forming

broadly conical spire; suture deeply incised, not channelled. Subsutural sinus shallow, moderately curved, strongly to moderately asymmetrical. Last whorl smooth, with weakly angled shoulder, position of maximum diameter slightly below shoulder, weakly inflated below, evenly contracting in lower half of shell, weakly constricted at base, siphonal fasciole nearly absent. Aperture elongate, narrow, widening slightly abapically, siphonal canal weakly recurved, moderately short. Colour pattern of short axial flammules on whorl tops, below shoulder on last whorl horizontal rows of small reddish/brown dots.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 44.0 mm, MD: 25.2 mm, mean SL: 38.2 mm (σ = 3.8), mean MD: 21.1 (σ = 2.9); spire angle: μ = 102.3° (σ = 9.7°), last whorl angle: μ = 44.5° (σ = 2.4°), LW: μ = 1.75 (σ = 0.08), RD: μ = 0.73 (σ = 0.05), PMD: μ = 0.9 (σ = 0.02), RSH: μ = 0.21 (σ = 0.03). Subsutural sinus (n=6): SSFD: shallow, μ = 2.5 (σ = 0.4). SSFd: moderately curved, μ = 6.6 (σ = 2.4). PV: strongly to moderately asymmetrical, μ = 0.4 (σ = 0.1).

Discussion – Tucker & Tenorio (2009, p. 104) placed this species in the genus *Lautoconus* Monterosato, 1923. However, all specimens lack cords on the tops of the spire whorls, suggesting placement in *Varioconus* da Motta, 1991. The rounded shoulder and shallow subsutural sinus are also characters of that genus.
Varioconus pecchioli (Crosse, 1865) is easily recognised by its colour pattern of close set rows of small axially elongated reddish dots. Muñiz Solís (1999) left this species in open nomenclature and considered it to be similar to *Conus* (*Chelyconus*) cfr. *fuscocingulatus* Bronn in Hörnes, 1856 [*sic*]. However, as revised by Harzhauser & Landau (2016) Hörnes' figures correspond to more than one species. Hörnes (1851, pl. 1, fig. 5) is *Phasmoconus fuscocingulatus* (Hörnes, 1851), which differs in having beaded early spire whorls and a colour pattern of horizontal lines instead of dots. Hörnes (1851, pl. 1, fig. 4) is *Kalloconus moravicus* (Hoernes & Auinger, 1879), which differs in being lower spired, broader at the shoulder, and having coloured lines instead of dots. In the Paratethyan assemblage, it is most similar in colour pattern to *Kalloconus berghausi* (Michelotti, 1847), but again that species differs in the generic characters of *Kalloconus* da Motta, 1991, a low spire and broad shoulder. In the Estepona assemblage all specimens have their colour pattern preserved separating it from all other Estepona cone shells.

Distribution – Lower Pliocene: western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999); central Mediterranean, Italy (Pecchioli, 1864; Spadini, 1990; Chirli, 1997; Paganelli, 2014).

***Varioconus striatulus* (Brocchi, 1814)**
Plate 16, figs 7-11, Plate 17, fig. 24, Plate 18, fig. 23

*1814 *Conus striatulus* Brocchi, p. 294, pl. 3, fig. 4.
1873 *Conus lineolatus* Cocconi, p. 152, pl. 4, figs 4-6.
1880 *Conus striatulus* Brocchi – Fontannes, p. 150, pl. 8, fig. 16.
1891 *Conus Caroli* Fucini, p. 60, pl. 2, fig. 1.
1893b *Conus* (*Chelyconus*) *striatulus* (Br.) – Sacco, p. 93, pl. 9, fig. 30.
1893b *Conus* (*Chelyconus*) *striatulus* subvar. *cingulellata* Sacco, p. 94, pl. 9, fig. 31.
1893b *Conus* (*Chelyconus*) *striatulus* var. *anomalospira* Sacco, p. 94, pl. 9, fig. 32.
1893b *Conus* (*Chelyconus*) *striatulus* var. *ductifera* Sacco, p. 95, pl. 9, fig. 33.
1893b *Conus* (*Chelyconus*) *striatulus* var. *compressoconica* Sacco, p. 95, pl. 9, fig. 34.
1893b *Conus* (*Chelyconus*) *striatulus* var. *pagodinflata* Sacco, p. 95, pl. 9, fig. 35.
1893b *Conus* (*Chelyconus*) *striatulus* var. *clavinflata* Sacco, p. 95, pl. 9, fig. 36.
1893b *Conus* (*Chelyconus*) *striatulus* var. *fusulobronnioides* Sacco, p. 95, pl. 9, fig. 37.
1893b *Conus* (*Chelyconus*) *striatulus* var. *fusulovoides* Sacco, p. 96, pl. 9, fig. 38.
1893b *Conus* (*Chelyconus*) *striatulus* var. *ocreocingulellata* Sacco, p. 96, pl. 9, fig. 39.
1910 *Conus* (*Chelyconus*) *striatulus* Br. – Cerulli-Irelli, p. 49 [241], pl. 4 [35], figs 50, 51.
1955 *Conus* (*Puncticulis*) (*Chelyconus*) *striatulus* Brocchi 1814 – Rossi Ronchetti, p. 279, fig. 149.
1959 *Conus striatulus* Brocchi – Zbyszewski, p. 102, pl. 11, figs 43, 45.
1964 *Conus striatulus* Brocchi, 1814 – Hall, p. 159 [49], pl. 27, figs 8-9.
1972 *Conus striatulus* Brocchi, 1814 – Davoli, p. 130, pl. 8, figs 3-10.
1973 *Conus* (*Chelyconus*) *striatulus* Brocchi – Caprotti & Vescovi, p. 182, pl. 3, fig. 6.
1974 *Conus* (*Chelyconus*) *canaliculatus* Brocchi, 1814 – Malatesta, p. 386, pl. 30, fig. 14 [*non Conilithes canaliculatus* (Brocchi, 1814)].
1976 *Conus* (*Chelyconus*) *striatulus* Brocchi – Marasti & Raffi, p. 197, pl. 2, fig. 26.
1976 *Conus striatulus* Brocchi, 1814 – Pinna & Spezia, p. 137, pl. 22, fig. 2.
1976 *Conus striatulus* Brocchi – Caprotti, p. 12, pl. 17, fig. 6.
1982 *Conus* (*Chelyconus*) *striatulus* Brocchi, 1814 – Martinell, p. 359, pl. 36, figs 1, 2.
1984 *Conus striatulus* Brocchi, 1814 – Ruggieri & Davoli, p. 73, pl. 5, figs 11-13.
1985 *Conus* (*Chelyconus*) *striatulus* Brocchi, 1814 – Martinell & Domènech, pl. 4, fig. 9.
1990 *Conus striatulus* Brocchi, 1814 – Spadini, p. 317, pl. 2, fig. 7.
1992 *Conus striatulus* Brocchi, 1814 – Cavallo & Repetto, p. 128, fig. 340.
1997 *Conus* (*Chelyconus*) *striatulus* Brocchi, 1814 – Chirli, p. 10, pl. 3, figs 2-7.
1997 *Conus* (*Conolithus*) *canaliculatus* Brocchi, 1814 – Chirli, p. 12, pl. 3, figs 9-10 [*non Conilithes canaliculatus* (Brocchi, 1814)].

1999 *Conus* (*Chelyconus*) *parvecatenatus* (Sacco, 1893) – Muñiz Solís, p. 54, figs 7O, P. [*non* Sacco, 1893].
1999 *Conus* (*Chelyconus*) *canaliculatus* Brocchi, 1814 – Muñiz Solís, p. 40, figs 6I-J [*non Conilithes canaliculatus* (Brocchi, 1814)].
1999 *Conus* (*Chelyconus*) *taurinensis* (Bellardi y Michelotti, 1840) – Muñiz Solís, p. 64, figs 8G, H [*non Lautoconus taurinensis* (Bellardi & Michelotti, 1840).
1999 *Conus* (*Chelyconus*) *striatulus* Brocchi, 1814 – Muñiz Solís, p. 61, figs 8I-J.
2001 *Conus striatulus* Brocchi, 1814 – Silva, p. 517, pl. 23, figs 7, 8, 12, 13.
2009 *Varioconus striatulus* (Brocchi, 1814) – Tucker & Tenorio, p. 129.
2010 *Conus striatulus* Brocchi, 1814 – Sosso & Dell'-Angelo, p. 49, 65 unnumbered figure top row right.
2011 *Varioconus striatulus* (Brocchi, 1814) – Landau *et al*., p. 32, pl. 16, fig. 9.
2014 *Conus canaliculatus* Brocchi, 1814 – Paganelli, p. 30, pl. 1, figs 7, 8, pl. 5, fig. 3 [*non Conilithes canaliculatus* (Brocchi, 1814)].
2014 *Conus striatulus* Brocchi, 1814 – Paganelli, p. 31, pl. 3, fig. 19, pl. 5, fig. 4.
2018 *Conus striatulus* (Brocchi, 1814) [*sic*] – Brunetti & Cresti, p. 102, fig. 429.

non 2011 *Chelyconus striatulus* (Brocchi, 1814) – Chirli & Linse, p. 165, pl. 56, figs 2a-d [= subspecies *L. ventricosus rhodesensis* Psarras, Merle, Moissette & Kodkeridou, 2024].

Material and dimensions – Maximum height 32.8 mm, width 18.8 mm. **CO:** NHMW 2024/0205/0084-0088 (5), NHMW 2024/0205/0089 (36), NHMW 2024/0205/0122 (1 juvenile), HM coll. (200+). **EL**: HM coll. (7).

Description – Shell moderately small, biconic, with very high spire and regularly conical last whorl. Protoconch not preserved. Early spire whorls usually eroded in adult specimens, smooth in juveniles; later spire whorls flat and smooth, forming conical spire; suture deeply incised, placed at or just below shoulder, not channelled; in gerontic specimens suture migrates slightly below suture on last two whorls giving them weakly gradate appearance. Subsutural sinus shallow, strongly curved, moderately asymmetrical. Last whorl with narrow, weakly concave to flattened subsutural ramp, angled at high placed shoulder, position of maximum diameter just below shoulder, evenly conical and contracting below, hardly constricted at base, siphonal fasciole nearly absent, a few very weak spiral cords over base strengthening slightly abapically. Aperture elongate, narrow, hardly widening abapically; siphonal canal very weakly recurved, moderate length. Colour pattern of reddish/brown blotches or flammules on spire and fine interrupted spiral lines below shoulder on last whorl, lines narrower than their interspaces.

Shell measurements and ratios – n = 10 adult specimens; largest specimen: SL: 31.3 mm, MD: 12.9 mm, mean SL: 27.3 mm (σ = 2.4), mean MD: 13.9 (σ = 1.1); spire angle: μ = 82.2° (σ = 6.1°), last whorl angle: μ = 38.1° (σ = 1.1°), LW: μ = 1.9 (σ = 0.1), RD: μ = 0.74 (σ = 0.03), PMD: μ = 0.9 (σ = 0.01), RSH: μ = 0.3 (σ = 0.02). Subsutural sinus (n=4): SSFD: shallow, μ = 2.1 (σ = 0.1). SSFd: strongly curved, μ = 3.9 (σ = 0.6). PV: moderately asymmetrical, μ = 0.4 (σ = 0.1).

Discussion – *Varioconus striatulus* (Brocchi, 1814) is the most abundant cone shell in the Estepona assemblages. It is fairly consistent is shell characters, although spire height is a little variable; the last two whorls tend to become taller on fully adult specimens due to the suture migrating abapically, revealing more whorl below the shoulder carina. The shoulder is invariably angled but not accentuated by a shoulder cord.

Muñiz-Solís (1999) recorded both *Conus striatulus* and *Conus canaliculatus* Brocchi, 1814 from these Estepona assemblages. In our opinion, there has been some confusion over the identity of *V. striatulus* and *Conilithes canaliculatus* (Brocchi, 1814) by some workers describing Pliocene assemblages. The holotype of *Conilithes canaliculatus* is missing according to Rossi Ronchetti (1955, p. 5). Hall (1964, p. 142, pl. 24, figs 6, 7) chose a neotype from the Upper Pliocene of Valle d'Andona (Italy), 21.7 mm in height (missing tip of aperture) with a tall, scalate spire, the carina strongly angular, marked by a cord, and deep spiral grooves on the lower half of the last whorl. The various Burdigalian and Tortonian forms figured by Hall (1964, pl. 24, figs 3-5, 8, 9) all show these characters, with the spiral grooves extending along the entire last whorl in one specimen. The two specimens identified as *C. canaliculatus* by Muñiz-Solís (1999, figs 6I, J) have a raised spire, but not as scalate as in *C. canaliculatus*, they lack the well-defined carinal cord and the fine grooves seen over the fasciole are quite unlike the deep, widely spaced grooves seen in the lower half of the last whorl in *C. canaliculatus*. *Varioconus striatulus* (Brocchi, 1814) can also have an elevated spire as seen most extremely in Sacco's variety *fusulovoides* (Sacco, 1893b, pl. 9, fig. 38) and in the specimen illustrated by Brunetti & Cresti (2018, fig. 429), but the spire whorls are never as scalate as they are in *C. canaliculatus*. This form with an elevated spire is also found in Estepona (Pl. 16, fig. 5) with many varieties between this and a relatively flattened spire. Davoli (1972) came to a similar conclusion whilst working on specimens from the Upper Miocene of Montegibbio (Italy), that all specimens in their collection from that locality identified by Doderlein as *C. canaliculatus* fell within the variability of *C. striatulus*. Italian Pliocene cones identified as *C. canaliculatus* by Chirli (1997, pl. 3, figs 9-10) and Paganelli (2014, pl. 1, figs 7, 8, pl. 5, fig. 3) are, in our opinion also *V. striatulus*. Indeed, apart from the illustrations of the neotype chosen by Hall from Valle Andona (reillustrated by Pinna & Spezia, 1976, pl. 19, fig. 2) we struggle to find any reliable illustrations of *C. canaliculatus* from Pliocene strata, except for the specimens illustrated by Greco (1970, pl. 6,

figs 4-7) from the Upper Pliocene of Serradifalco, Sicily as *Conus* (*Chelyconus*) *pyrula* Brocchi which, in our opinion, represent *C. canaliculatus*.

Sacco (1893b) and Hall (1964) recorded *Conus striatulus* from the 'Middle Miocene' of Italy. Hall recorded it without stating any locality and figured the Pliocene holotype from the Brocchi collection. We have not seen any specimens from these strata, and therefore its presence in the Lower-Middle Miocene Proto-Mediterranean needs to be confirmed.

Muñiz Solís (1999, figs 7O, P) illustrated a shell from Estepona identified as *Conus* (*Chelyconus*) *parvecatenatus* (Sacco, 1893) that in our opinion is a typical *V. striatulus*. The author said it differed from *V. striatulus* in having a more convex spire that becomes concave near the apex (a separation taken from Hall, 1964, p. 155), and in having a multispiral as opposed to paucispiral protoconch in *V. striatulus*. The number of protoconch described and attributed to specific species by Muñiz Solís is problematic. In our material, including several thousand cones, not one adult specimen has its protoconch preserved. We have some juveniles that can be relatively easily attributed (Pl. 1, fig. 7), and *V. striatulus* is one of them. All the juvenile specimens at hand of this species have a multispiral protoconch similar to that figured by Muñiz Solís (1999, fig. A), attributed by that author to *C.* (*C.*) *parvecatenatus*. *Conus parvecatenatus* is known only from the Burdigalian of Italy (Hall, 1964, p. 155).

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1893b; Davoli, 1972; Ruggieri & Davoli, 1984). Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al*., 2011); western Mediterranean, Estepona Basin, S. Spain (Muñiz Solís, 1999), NW Spain (Martinell, 1982; Martinell & Domènech, 1985), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1893b; Spadini, 1990; Chirli, 1997; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: Atlantic, Mondego Basin, central-west Portugal (Zbyszewski, 1959; Silva, 2001); central Mediterranean, Italy (Sacco, 1893b; Caprotti & Vescovi, 1973; Malatesta, 1974; Marasti & Raffi, 1976; Caprotti, 1976; Cavallo & Repetto, 1992; Paganelli, 2014).

Plate 13

1-3. *Conasprella subbicrenulata* (Sacco, 1893); 1. NHMW 2024/0205/0026, height 17.5 mm, width 7.9 mm; 2. NHMW 2024/0205/0027, height 23.4 mm, width 10.5 mm; 3. NHMW 2024/0205/0028, height 19.8 mm, width 10.0 mm.

4-6. *Lautoconus corynetes* (Fontannes, 1880); 4. NHMW 2024/0205/0022, height 33.8 mm, width 19.3 mm; 5. NHMW 2024/0205/0023, height 29.7 mm, width 17.7 mm; 6. NHMW 2024/0205/0024, height 25.7 mm, width 14.6 mm (juvenile).

7-9. *Lautoconus dertogibbus* (Sacco, 1893); 7. NHMW 2024/0205/0035, height 27.3 mm, width 14.2 mm; 8. NHMW 2024/0205/0036, height 25.1 mm, width 13.5 mm; 9. NHMW 2024/0205/0037, height 33.0 mm, width 16.5 mm.

10-12. *Lautoconus deshayesii* (Bellardi & Michelotti, 1840); 10. NHMW 2024/0205/0039, height 43.8 mm, width 22.8 mm; 11. NHMW 2024/0205/0040, height 66.5 mm, width 36.1 mm; 12. NHMW 2024/0205/0041, height 43.2 mm, width 25.2 mm.

Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

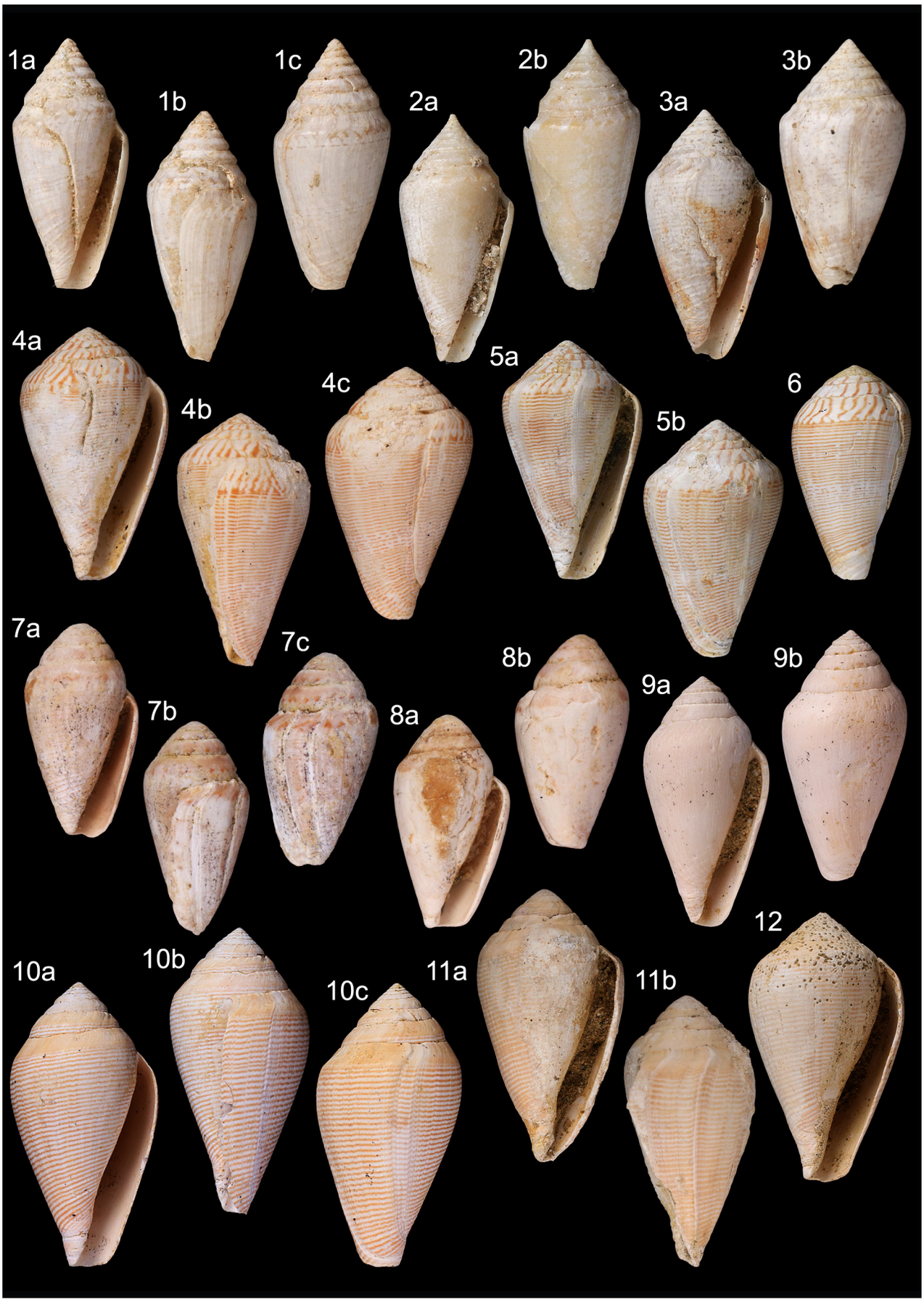
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Plate 13

Plate 14

1-6. *Lautoconus laeviponderosus* (Sacco, 1893); 1. NHMW 2024/0205/0043, height 50.4 mm, width 26.7 mm; 2. NHMW 2024/0205/0044, height 58.2 mm, width 32.3 mm; 3. NHMW 2024/0205/0045, height 34.5 mm, width 19.1 mm; 4. NHMW 2024/0205/0046, height 45.3 mm, width 25.1 mm; 5. NHMW 2024/0205/0047, height 48.2 mm, width 27.0 mm; 6. NHMW 2024/0205/0048, height 43.5 mm, width 24.2 mm.

7-8. *Lautoconus pelagicus* (Brocchi, 1814); 7. NHMW 2024/0205/0050, height 49.8 mm, width 25.0 mm; 8. NHMW 2024/0205/0051, height 49.5 mm, width 26.5 mm.

9. *Lautoconus pyrula* (Brocchi, 1814), NHMW 2024/0205/0099, height 29.7 mm, width 15.1 mm;

10. ?*Lautoconus pyrula* (Brocchi, 1814), NHMW 2024/0205/0100, height 40.7 mm, width 19.7 mm.

11-13. *Lautoconus spongiopictus* (Sacco, 1893); 11. NHMW 2024/0205/0061, height 38.0 mm, width 20.1 mm; 12. NHMW 2024/0205/0062, height 39.2 mm, width 21.6 mm; 13. NHMW 2024/0205/0063, height 37.4 mm, width 18.9 mm.

Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.


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Plate 14

Plate 15

1-6. *Lautoconus subtextile* (d'Orbigny, 1852); 1. NHMW 2024/0205/0065, height 38.5 mm, width 20.9 mm; 2. NHMW 2024/0205/0066, height 31.3 mm, width 14.8 mm; 3. NHMW 2024/0205/0067, height 32.7 mm, width 16.3 mm; 4. NHMW 2024/0205/0068, height 24.8 mm, width 12.7 mm; 5. NHMW 2024/0205/0069, height 29.8 mm, width 15.0 mm; 6. NHMW 2024/0205/0070, height 34.6 mm, width 17.6 mm.

7-10. *Lautoconus ventricosus* (Gmelin, 1791); 7. NHMW 2024/0205/0095, height 30.2 mm, width 20.9 mm; 8. NHMW 2024/0205/0096, height 32.5 mm, width 15.6 mm; 9. NHMW 2024/0205/0097, height 33.0 mm, width 17.0 mm; 10. NHMW 2024/0205/0098, height 30.9 mm, width 16.7 mm.

11-12. *Varioconus pecchioli* (Crosse, 1865); 11. NHMW 2024/0205/0001, height 38.7 mm, width 21.6 mm; 12. NHMW 2024/0205/0002, height 31.3 mm, width 14.8 mm.

Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

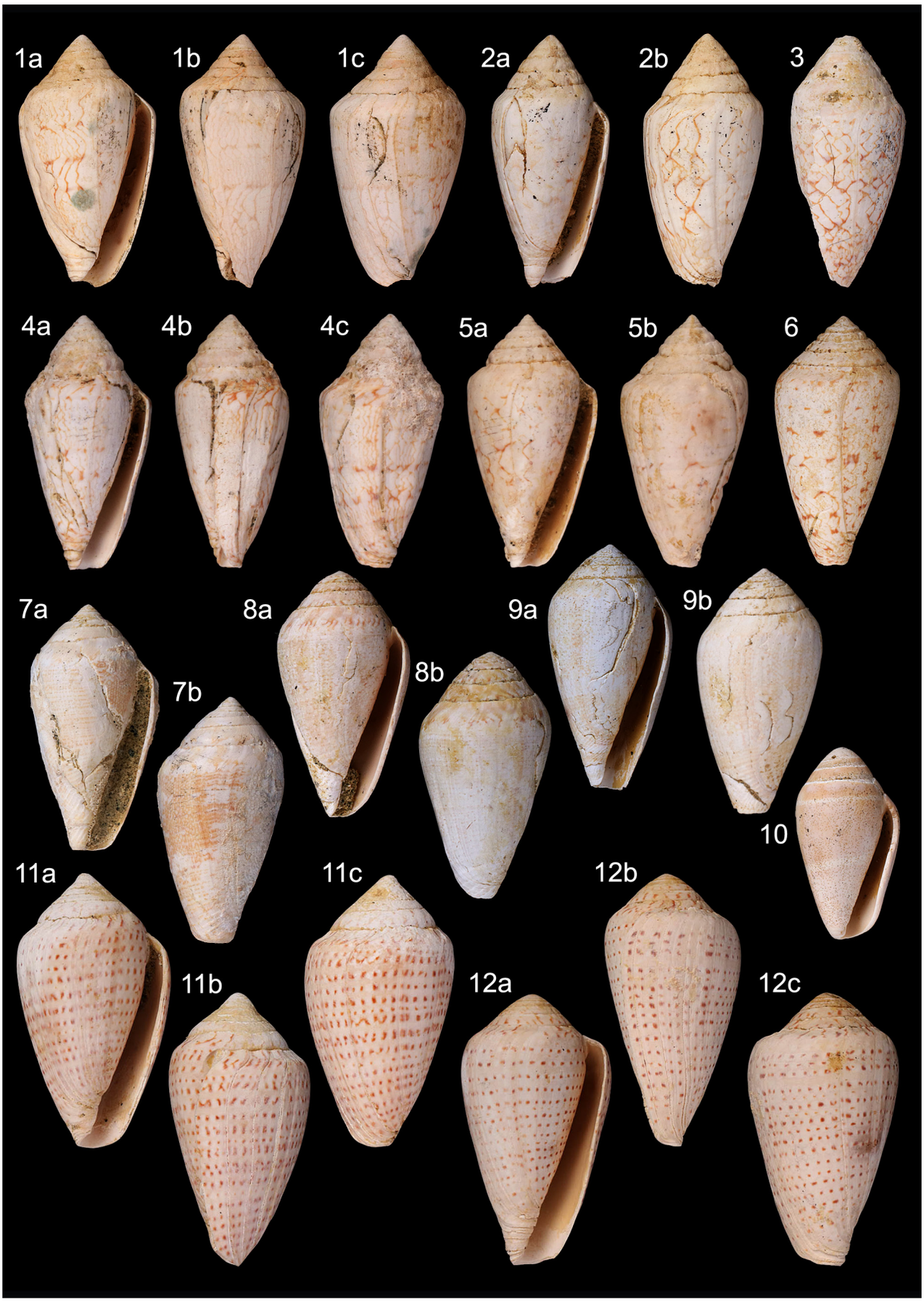
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Plate 15

Plate 16

1-6. *Varioconus clavatulus* (d'Orbigny, 1852); 1. NHMW 2024/0205/0077, height 87.8 mm, width 45.1 mm; 2. NHMW 2024/0205/0078, height 80.3 mm, width 40.0 mm; 3. NHMW 2024/0205/0079, height 75.3 mm, width 37.9 mm; 4. NHMW 2024/0205/0080, height 46.9 mm, width 25.6 mm; 5. NHMW 2024/0205/0081, height 46.9 mm, width 24.7 mm; 6. NHMW 2024/0205/0082, height 38.6 mm, width 21.1 mm.

7-11. *Varioconus striatulus* (Brocchi, 1814); 7. NHMW 2024/0205/0084, height 30.1 mm, width 14.6 mm; 8. NHMW 2024/0205/0085, height 31.3 mm, width 16.0 mm; 9. NHMW 2024/0205/0086, height 30.1 mm, width 14.6 mm; 10. NHMW 2024/0205/0087, height 30.1 mm, width 14.6 mm; 11. NHMW 2024/0205/0088, height 30.1 mm, width 14.6 mm.

Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

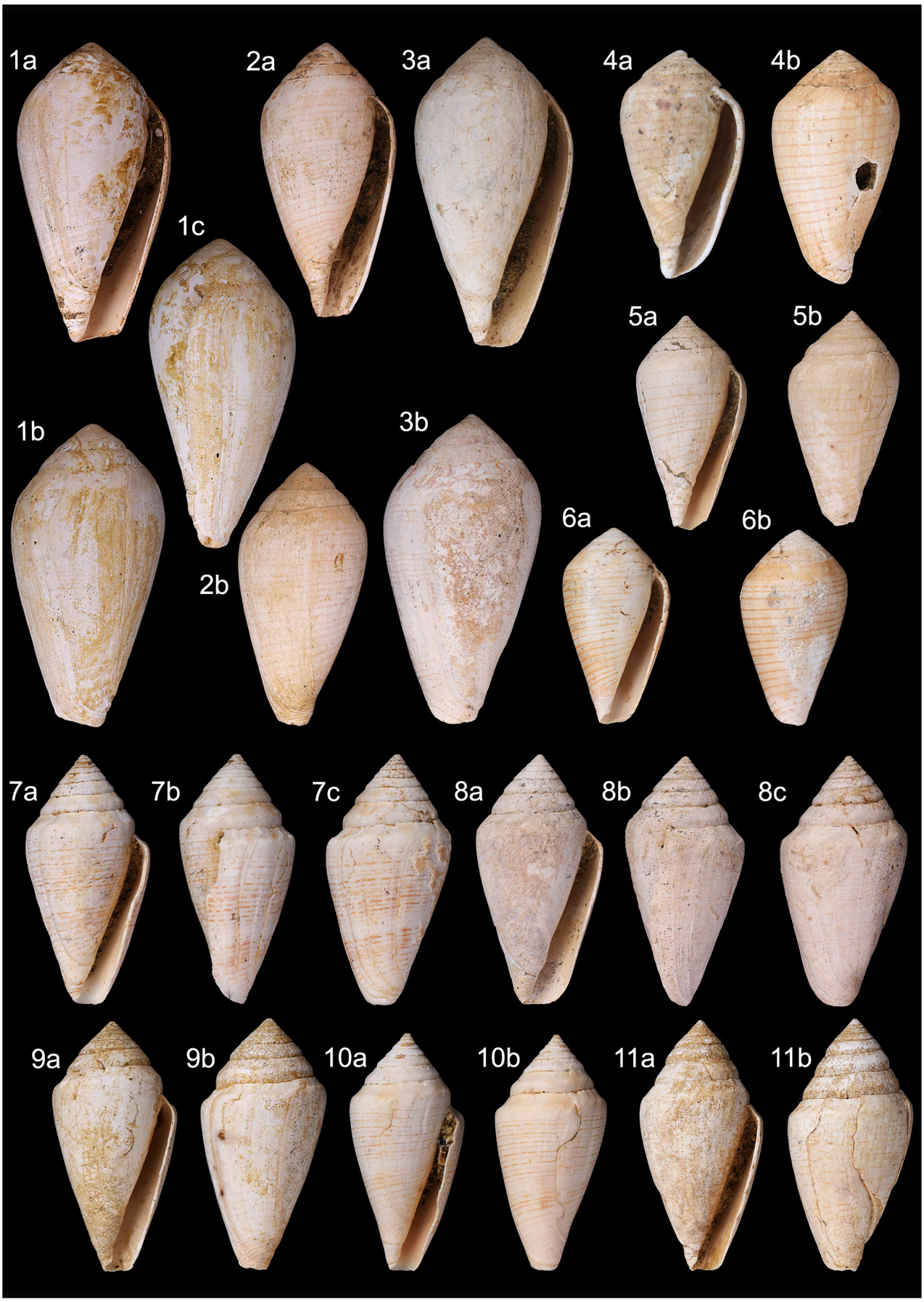
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Plate 16

Plate 17. Conidae from Estepona, apical views.

1. *Conasprella subbicrenulata* (Sacco, 1893), NHMW 2024/0205/0026, height 17.5 mm, width 7.9 mm.
2. *Conilithes antidiluvianus* (Bruguière, 1792), NHMW 2024/0205/0010, height 69.7 mm, width 28.6 mm.
3. *Conilithes brocchii* (Bronn, 1828), NHMW 2024/0205/0004, height 46.9 mm, width 23.6 mm.
4. *Kalloconus pulcher* ([Lightfoot], 1786), NHMW 2024/0205/0033, height 62.4 mm, width 34.0 mm (subadult).
5. *Lautoconus bitorosus* (Fontannes, 1880), NHMW 2024/0205/0016, height 49.1 mm, width 29.4 mm.
6. *Lautoconus corynetes* (Fontannes, 1880), NHMW 2024/0205/0023, height 29.7 mm, width 17.7 mm.
7. *Lautoconus depressoastensis* (Sacco, 1893), NHMW 2024/0205/0107, height 37.8 mm, width 22.1 mm.
8. *Lautoconus dertogibbus* (Sacco, 1893), NHMW 2024/0205/0035, height 27.3 mm, width 14.2 mm.
9. *Lautoconus deshayesii* (Bellardi & Michelotti, 1840), NHMW 2024/0205/0039, height 43.8 mm, width 22.8 mm.
10. *Lautoconus laeviponderosus* (Sacco, 1893), NHMW 2024/0205/0043, height 50.4 mm, width 26.7 mm.
11. *Lautoconus pelagicus* (Brocchi, 1814), NHMW 2024/0205/0051, height 49.5 mm, width 26.5 mm.
12. *Lautoconus ponderoglans* (Sacco, 1893), NHMW 2024/0205/0053, height 35.5 mm, width 20.7 mm.
13. *Lautoconus ponderosus* (Brocchi, 1814), NHMW 2024/0205/0056, height 96.2 mm, width 51.2 mm.
14. *Lautoconus ponderovulatus* (Sacco, 1893), NHMW 2024/0205/0103, height 37.7 mm, width 19.3 mm.
15. *Lautoconus pyrula* (Brocchi, 1814), NHMW 2024/0205/0099, height 29.7 mm, width 15.1 mm.
16. *Lautoconus spongiopictus* (Sacco, 1893), NHMW 2024/0205/0061, height 38.0 mm, width 20.1 mm.
17. *Lautoconus subtextile* (d'Orbigny, 1852), NHMW 2024/0205/0065, height 38.5 mm, width 20.9 mm.
18. *Lautoconus ventricosus* (Gmelin, 1791), NHMW 2024/0205/0095, height 30.2 mm, width 20.9 mm.
19. *Monteiroconus mercati* (Brocchi, 1814), NHMW 2024/0205/0075, height 63.6 mm, width 38.3 mm.
20. *Pseudonoduloconus virginalis* (Brocchi, 1814), NHMW 2024/0205/0093, height 48.5 mm, width 28.0 mm.
21. *Pseudonoduloconus virginalis* (Brocchi, 1814), NHMW 2024/0205/0115, height 20.5 mm, width 15.0 mm.
22. *Varioconus clavatulus* (d'Orbigny, 1852), NHMW 2024/0205/0079, height 75.3 mm, width 37.9 mm.
23. *Varioconus pecchioli* (Crosse, 1865), NHMW 2024/0205/0002, height 31.3 mm, width 14.8 mm.
24. *Varioconus striatulus* (Brocchi, 1814), NHMW 2024/0205/0084, height 30.1 mm, width 14.6 mm.

Plate 17

Plate 18. Conidae from Estepona, apical views with subsutural sinus.

1. *Conasprella subbicrenulata* (Sacco, 1893), NHMW 2024/0205/0026, height 17.5 mm, width 7.9 mm.
2. *Conilithes antidiluvianus* (Bruguière, 1792), NHMW 2024/0205/0010, height 69.7 mm, width 28.6 mm.
3. *Conilithes brocchii* (Bronn, 1828), NHMW 2024/0205/0004, height 46.9 mm, width 23.6 mm.
4. *Kalloconus pulcher* ([Lightfoot], 1786), NHMW 2024/0205/0033, height 62.4 mm, width 34.0 mm (subadult).
5. *Lautoconus bitorosus* (Fontannes, 1880), NHMW 2024/0205/0016, height 49.1 mm, width 29.4 mm.
6. *Lautoconus corynetes* (Fontannes, 1880), NHMW 2024/0205/0023, height 29.7 mm, width 17.7 mm.
7. *Lautoconus depressoastensis* (Sacco, 1893), NHMW 2024/0205/0107, height 37.8 mm, width 22.1 mm.
8. *Lautoconus dertogibbus* (Sacco, 1893), NHMW 2024/0205/0035, height 27.3 mm, width 14.2 mm.
9. *Lautoconus deshayesii* (Bellardi & Michelotti, 1840), NHMW 2024/0205/0039, height 43.8 mm, width 22.8 mm.
10. *Lautoconus laeviponderosus* (Sacco, 1893), NHMW 2024/0205/0043, height 50.4 mm, width 26.7 mm.
11. *Lautoconus pelagicus* (Brocchi, 1814), NHMW 2024/0205/0051, height 49.5 mm, width 26.5 mm.
12. *Lautoconus ponderoglans* (Sacco, 1893), NHMW 2024/0205/0053, height 35.5 mm, width 20.7 mm.
13. *Lautoconus ponderosus* (Brocchi, 1814), NHMW 2024/0205/0056, height 96.2 mm, width 51.2 mm.
14. *Lautoconus ponderovulatus* (Sacco, 1893), NHMW 2024/0205/0103, height 37.7 mm, width 19.3 mm.
15. *Lautoconus pyrula* (Brocchi, 1814), NHMW 2024/0205/0099, height 29.7 mm, width 15.1 mm.
16. *Lautoconus spongiopictus* (Sacco, 1893), NHMW 2024/0205/0061, height 38.0 mm, width 20.1 mm.
17. *Lautoconus subtextile* (d'Orbigny, 1852), NHMW 2024/0205/0065, height 38.5 mm, width 20.9 mm.
18. *Lautoconus ventricosus* (Gmelin, 1791), NHMW 2024/0205/0095, height 30.2 mm, width 20.9 mm.
19. *Monteiroconus mercati* (Brocchi, 1814), NHMW 2024/0205/0075, height 63.6 mm, width 38.3 mm.
20. *Pseudonoduloconus virginalis* (Brocchi, 1814), NHMW 2024/0205/0093, height 48.5 mm, width 28.0 mm.
21. *Varioconus clavatulus* (d'Orbigny, 1852), NHMW 2024/0205/0079, height 75.3 mm, width 37.9 mm.
22. *Varioconus pecchioli* (Crosse, 1865), NHMW 2024/0205/0002, height 31.3 mm, width 14.8 mm.
23. *Varioconus striatulus* (Brocchi, 1814), NHMW 2024/0205/0084, height 30.1 mm, width 14.6 mm.

Plate 18

Doubtful or unidentified specimens

A single strongly worn specimen (Pl. 19, fig. 1) seems to represent a form broader and squatter than any species we recognise from Estepona, with a broad, high-placed, rounded shoulder. The profile is highly reminiscent of *Kalloconus berghausi* (Michelotti, 1847), a species widespread in the northeastern Atlantic, Proto-Mediterranean and Paratethys (see Harzhauser & Landau, 2016, p. 55). However, the specimen is far too abraded to make any firm conclusions. Chirli (1997, pl. 4, figs 1, 2) also illustrated a severely abraded specimen from the Italian Pliocene as *Conus* (*Dendroconus*) *berghausi*, again this identification is speculative.

This specimen (Pl. 19, fig. 2) is undoubtedly conspecific with that illustrated by Muñiz Solís (1999, fig 8G) as *Conus* (*Chelyconus*) *taurinensis* (Bellardi & Michelotti, 1840), which was itself originally described as a variety of the Pliocene *C. striatulus* Brocchi, 1814 from the Lower Miocene of the Proto-Mediterranean. In our opinion this is an unusual form of *Varioconus striatulus* and has the same colour pattern of fine red stripes. Hall (1964, p. 159) considered *C. taurinensis* a valid species restricted to the Lower Miocene, although he offered no comparison to Brocchi's species.

A single specimen (Pl. 19, fig. 3) shows a cone shell with a high scalate spire, deep suture, a shallow, moderately curved, moderately asymmetrical subsutural sinus, a last whorl with a high placed rounded shoulder, regularly conical below, and a relatively wide aperture. Remnants of colour pattern are preserved consisting of irregular reddish axial stripes. We cannot match these shell characters to any of the species described above.

Discussion

In this paper 24 species are described from the Pliocene assemblages of Estepona, Spain, representing eight genera, one is left in open nomenclature. No species are described as new (Figure 1). This is significantly less than the 33 species recorded by Muñiz Solís (1999) from the same assemblages, of which five were left in open nomenclature. However, in our opinion some of those identifications are incorrect, some species were described twice under different names [*e.g.*, *Kalloconus pulcher* ([Lightfoot], 1786), *Lautoconus dertogibbus* (Sacco, 1893), *Lautoconus laeviponderosus* (Sacco, 1893), *Pseudonoduloconus virginalis* (Brocchi, 1814), *Varioconus striatulus* (Brocchi, 1814)], and some identifications were based on poor material that cannot be confirmed [*e.g.*, *Conus* (*Chelyconus*) *conoponderosus* (Sacco, 1893)].

Although he majority of the species identifications in Muñiz Solís are confirmed herein, generic concepts have changed drastically since that paper was published, resulting in almost none of the species retaining the same combination (see Table 1).

At species level, the species list presented by Muñiz Solís (1999) included typical Pliocene species, but also nine (27%) typically Miocene species [*e.g.*, *Conus* (*Chelyconus*) *conoponderosus* (Sacco, 1893), *C.* (*Chelyconus*) cfr. *fuscocingulatus* Bronn in Hórnes, 1856, *C.* (*Chelyconus*) *gallicus* Mayer-Eymar, 1890, *C.* (*Chelyconus*) *gastriculus* Coppi, 1876, *Conus* (*Chelyconus*) *mucronatolaevis* (Sacco, 1893), *Conus* (*Chelyconus*) *parvecatenatus* (Sacco, 1893), *Conus* (*Chelyconus*) *taurinensis* (Bellardi y Michelotti, 1840), *Conus* (*Dendroconus*) *eschewegi* Da Costa, 1866, *Conus* (*Lithoconus*) *antiquus* Lamarck, 1810 (generic combinations as given by Muñiz Solís)]. The presence of none of these Miocene species is confirmed in this paper. Twelve species (50%) present in Estepona are distributed both in the Miocene and Pliocene, but these are all species that had previously been recorded from the Italian Pliocene.

Results of this revision suggest that at species level the assemblage is typical for the Mediterranean tropical Pliocene ecostratigraphic unit MPPMU1 (Mediterranean Plio-Pleistocene Molluscan Unit 1) (see Raffi & Monegatti, 1993; Monegatti & Raffi, 2001; Landau *et al*., 2013; *inter alia*). MPPMU1 was in place at the beginning of the Pliocene and continued until the major cooling event at about 3.0 Ma. One notable absence is that of the large cone *Kalloconus betulinoides* (Lamarck, 1810), widespread in the Italian Pliocene (Pavia, 1976; Chirli, 1988, 1997; Cavallo & Repetto, 1992; *inter alia*), which was not recorded by Muñiz Solís (1999), nor the present authors.

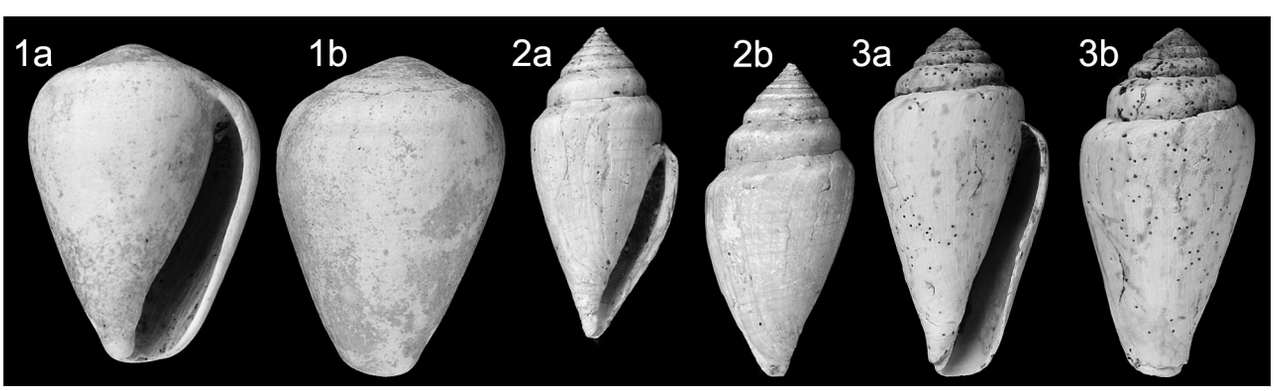

Plate 19. 1. NHMW 2024/0205/0110, height 34.4 mm, width 25.4 mm; 2. NHMW 2024/0205/0111, height 25.5 mm, width 11.7 mm; 3. NHMW 2024/0205/0112, height 42.7 mm, width 21.5 mm. Velerín conglomerates, Velerín, Estepona, Upper Zanclean, Lower Pliocene.

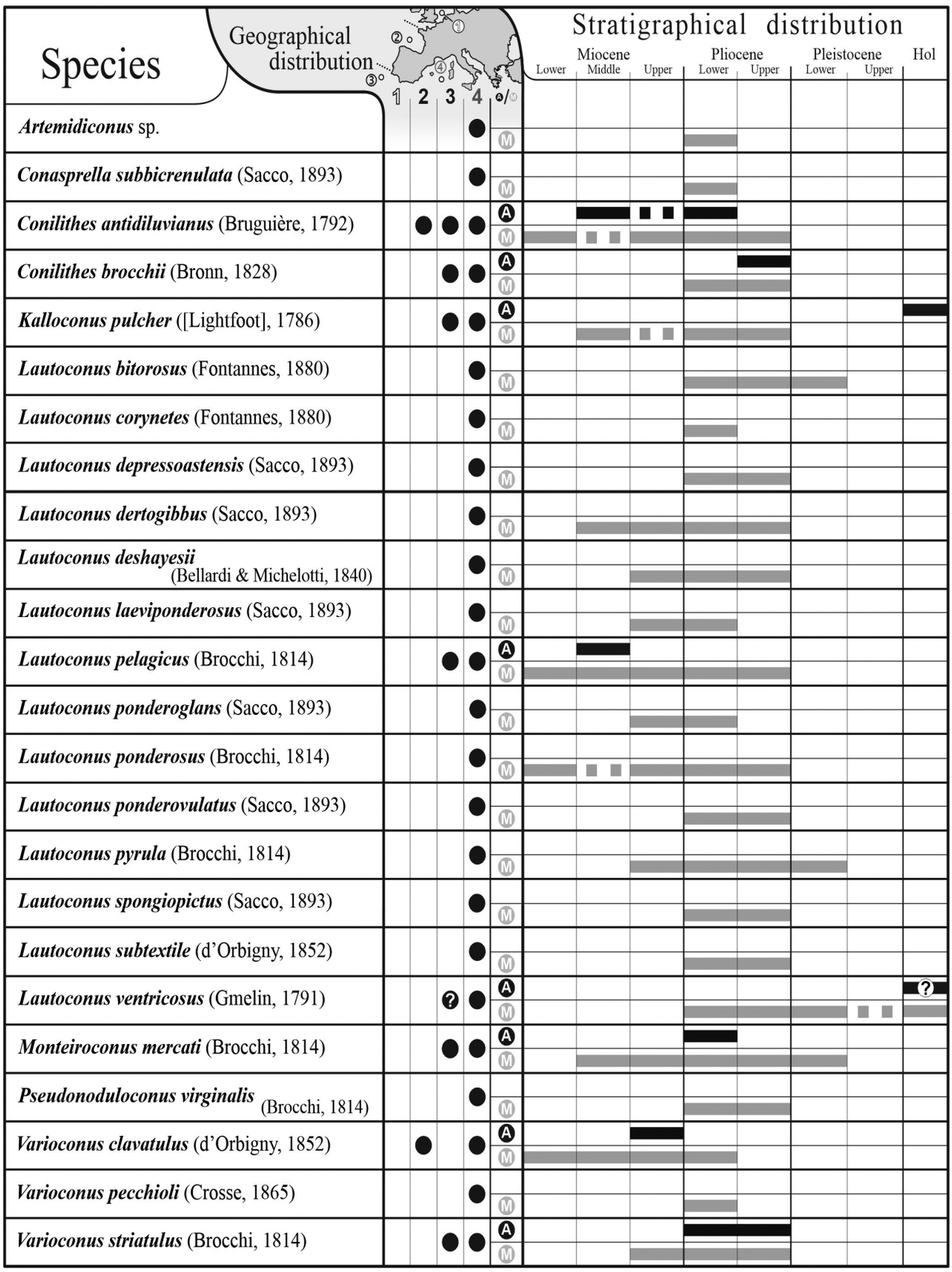

Figure 1. Geography, stratigraphy and distribution of species found in the Lower Pliocene Upper Zanclean of the Estepona Basin, southern Spain. For present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan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

Table 1. Estepona Conidae. Identification in Muñiz Solís (1999) (left) against identification or interpretation herein (right).

Muñiz Solís (1999)	This paper
Conus (*Chelyconus*) cfr. *anomalomamillus* (Sacco, 1893)	*Lautoconus dertogibbus* (Sacco, 1893)
Conus (*Chelyconus*) *bitorosus* Fontannes, 1880	*Lautoconus bitorosus* (Fontannes, 1880)
Conus (*Chelyconus*) *canaliculatus* Brocchi, 1814	*Varioconus striatulus* (Brocchi, 1814)
Conus (*Chelyconus*) *clavatulus* D'Orbigny, 1852	*Varioconus clavatulus* (d'Orbigny, 1852)
Conus (*Chelyconus*) *conoponderosus* (Sacco, 1893)	Muñiz Solís (1999, figs 6N, O) illustrated a rather abraded specimen. It has a more elongated profile than the syntype illustrated by Ferrero Mortara *et al*. (1984, pl. 18, fig. 10). This is an Upper Miocene species discussed at length by Davoli (1972). The Tortonian specimens illustrated are also broader and stockier. We do not recognise any specimens from Estepona that can be identified as *Lautoconus conoponderosus*
Conus (*Clelyconus*) *dertogibbus* (Sacco, 1893)	*Lautoconus dertogibbus* (Sacco, 1893)
Conus (*Chelyconus*) *deshayesi* Bellardi y Michelotti, 1840	*Lautoconus deshayesii* (Bellardi & Michelotti, 1840)
Conus (*Chelyconus*) cfr. *fuscocingulatus* Bronn in Hórnes, 1856	*Varioconus pecchioli* (Crosse, 1865)
Conus (*Chelyconus*) *gallicus* Mayer-Eymar, 1890b	*Pseudonoduloconus virginalis* (Brocchi, 1814)
Conus (*Chelyconus*) *gastriculus* Coppi, 1876	Davoli (1972) illustrated a rather abraded lectotype to replace the lost holotype, which show a small ovate shell, with a low spire and a clearly channelled suture and concave subsutural ramp. In our opinion they do not agree with the figures given by Muñiz Solís. *Conus gastriculus* remains a poorly characterised species, records are predominantly Lower and Middle Miocene and its presence in the Pliocene requires conformation.
Conus (*Chelyconus*) cfr. *laeviponderosus* (Sacco, 1893)	*Lautoconus laeviponderosus* (Sacco, 1893)
Conus (*Chelyconus*) *mucronatolaevis* (Sacco, 1893)	*Lautoconus ponderovulatus* (Sacco, 1893)
Conus (*Chelyconus*) *parvecatenatus* (Sacco, 1893)	*Varioconus striatulus* (Brocchi, 1814)
Conus (*Chelyconus*) *pelagicus* Brocchi, 1814	*Lautoconus pelagicus* (Brocchi, 1814)
Conus (*Chelyconus*) *ponderoglans* (Sacco, 1893)	*Lautoconus ponderoglans* (Sacco, 1893)
Conus (*Chelyconus*) *ponderosus* Brocchi, 1814	*Lautoconus ponderosus* (Brocchi, 1814)
Conus (*Chelyconus*) *spongiopictus* (Sacco, 1893)	*Lautoconus spongiopictus* (Sacco, 1893)
Conus (*Chelyconus*) *subtextilis* d'Orbigny, 1852	*Lautoconus subtextile* (d'Orbigny, 1852)
Conus (*Chelyconus*) *striatulus* Brocchi, 1814	*Varioconus striatulus* (Brocchi, 1814)
Conus (*Chelyconus*) *taurinensis* (Bellardi y Michelotti, 1840)	*Varioconus striatulus* (Brocchi, 1814)
Conus (*Chelyconus*) *ventricosus* Gmelin, 1791	*Lautoconus ventricosus* (Gmelin, 1791)
Conus (*Chelyconus*) sp. 1	*Lautoconus laeviponderosus* (Sacco, 1893)
Conus (*Conolithes*) *antidiluvianus* Bruguiére, 1792	*Conilithes antidiluvianus* (Bruguière, 1792)
Conus (*Dendroconus*) *belus* d'Orbigny, 1852	*Lautoconus corynetes* (Fontannes, 1880)
Conus (*Dendroconus*) *eschewegi* Da Costa, 1866	*Lautoconus depressoastensis* (Sacco, 1893)
Conus (*Dendroconus*) *pyrula* Brocchi, 1814	*Lautoconus pyrula* (Brocchi, 1814)
Conus (*Dendroconus*) sp. 2	*Varioconus clavatulus* (d'Orbigny, 1852), juvenile form
Conus (*Leptoconus*) *brocchii* Bronn, 1831	*Conilithes brocchii* (Bronn, 1828)
Conus (*Lithoconus*) *antiquus* Lamarck, 1810	*Kalloconus pulcher* ([Lightfoot], 1786)
Conus (*Lithoconus*) *mercatii* Brocchi, 1814	*Monteiroconus mercati* (Brocchi, 1814)
Conus (*Lithoconus*) *pulcher* Lightfoot, 1786	*Kalloconus pulcher* ([Lightfoot], 1786)
Conus (*Rhizoconus*) *virginalis* Brocchi, 1814	*Pseudonoduloconus virginalis* (Brocchi, 1814)
Conus (*Stephanoconus*) *subbigranosus* (Sacco, 1893)	*Lautoconus subtextile* (d'Orbigny, 1852)

Conid diversity is particularly important, as it was singled out by Raffi & Monegatti (1993) and Monegatti & Raffi (2001), together with Terebridae and the presence of *Strombus* (s.l.), as particularly important markers of tropicality. In order to ascertain how many species survived into MPPMU2, works dealing with these MPPMU2 assemblages (as defined by Monegatti & Raffi, 2001, fig 1) were consulted (*i.e*., Marasti & Raffi, 1976, 1977; Gasperi *et al*., 1982; Monegatti & Raineri, 1987), together with works of Mediterranean Pleistocene assemblages. Of these, Cerulli-Irelli's (1910) work on Monte Mario has the most conid species (5). The Monte Mario Formation is considered to be of Early Pleistocene age (Milli, 1997). Only three cone species are listed in MPPMU2 deposits: *Conilithes antidiluvianus* (Bruguière, 1792), *Lautoconus ventricosus* (Gmelin, 1791) and *Varioconus striatulus* (Brocchi, 1814). Cerulli-Irelli (1910) reported *C. mercati*, *C. pelagicus* (herein reassigned to *Lautoconus bitorosus*), *C. pyrula*, *C. striatulus*, and *C. mediterraneus* (= *Lautoconus ventricosus*). Therefore, six species survived after MPPMU1, although we have found records of three of these (*Lautoconus bitorosus*, *L. pyrula* and *Monteiroconus mercati*) only in the Monte Mario deposits. Therefore, 75% of the cone species present during MPPMU1 did not survive into MPPMU2, confirming that cone diversity is a good indicator for tropicality in the Pliocene Mediterranean and conid diversity can be used for dating Pliocene assemblages before or after the 3 Ma cooling event.

At genus level, the Pliocene cone shells have historically been attributed to the genera *Chelyconus* Mörch, 1852 and *Stephanoconus* Mörch, 1852, both Tropical American genera, and *Dendroconus* Swainson, 1840, *Leptoconus* Swainson, 1840 *Lithoconus* Mörch, 1852, and *Rhizoconus* Mörch, 1852, all Indo-Pacific genera. This would suggest predominantly affinities with Indo-West Pacific and Tropical American faunas.

The reinterpretation of generic shell characters and new combinations resulting thereof clearly suggest a strong affinity between the Estepona conid fauna and that of West Africa today. Twenty of the 24 species (83%) represent the genera *Lautoconus* Monterosato, 1923, *Varioconus* da Motta, 1991 [*Lautoconus* may be a synonym of *Varioconus*, but we have separated them based on the presence of spirals on the early whorls of *Lautoconus*, absent in *Varioconus*, however, in some species these spirals are very weak and may not be of generic value. Living species of both genera were not included in the molecular studies of Puillandre *et al*., 2014a, b, and we await further molecular data.], *Kalloconus* da Motta, 1991 and *Monteiroconus* da Motta, 1991, all of which are exclusively West African genera today. *Lautoconus ventricosus* (Gmelin, 1791) is the only conid survivor in the Mediterranean today. *Artemidiconus* da Motta, 1991 represented in Estepona by a single specimen is a Western Atlantic genus but has also been reported in the Middle Miocene Paratethys (Harzhauser & Landau, 2016). *Conilithes* Swainson, 1840 is represented by two species. This is a European and North American genus that disappeared at the end of the Pliocene. *Conasprella* Thiele, 1929 represented by one species in Estepona is an Indo-West Pacific genus today but has also been recognised in the Middle Miocene Paratethys (Harzhauser & Landau, 2016). Therefore, the overwhelming influence is West African and not Indo-West Pacific. The affinity of European Neogene conid assemblages with the recent Indo-West Pacific conid faunas, assumed in the historical literature, was already comparatively low in the Miocene Paratethys (Harzhauser & Landau, 2016) and eastern Middle Miocene Proto-Mediterranean (Landau *et al*., 2013). Other European Neogene assemblages are still in need of generic revisions.

Although cone shells were diverse and plentiful during tropical MPPMU1 in the Mediterranean, there was still an important reduction of diversity in the Early Pliocene compared to the European Miocene, with the disappearance of the genera *Leporiconus* Iredale, 1930 and *Phasmoconus* Mörch, 1852 that are today Indo-West Pacific genera, and the extinct genus *Plagioconus* Tucker & Tenorio, 2009. Conid species diversity was roughly three times as high in the Miocene Paratethys (44 species in the Middle Miocene Pannonian, Transylvanian and Vienna basins) (Harzhauser & Landau, 2016). The Miocene Proto-Mediterranean diversity is also undoubtedly extremely rich but requires revision at both species and genus level. Only the eastern Proto-Mediterranean Karaman Basin of Turkey has been revised, and although plentiful in cones, less diverse with only 13 species recorded by Landau *et al*., (2013).

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