The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 15: Borsoniidae, Clathurellidae, Mitromorphidae, Pseudomelatomidae (Gastropoda, Conoidea)

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Received 14 February 2022, revised version accepted 30 July 2022.

In this paper we review the Borsoniidae, Clathurellidae, Mitromorphidae, and Pseudomelatomidae of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. 15 species of Borsoniidae are recorded, of which two are left in open nomenclature. One species is described as new: *Microdrillia plioserratula* nov. sp. *Aphanitoma pliocenica* Vera-Peláez, 2002 is considered a junior subjective synonym of *Aphanitoma elegans* (D'Ancona, 1872). *Genota lusitaniae* Vera-Peláez & Lozano-Francisco, 2001 is considered a junior subjective synonym of *G. bonnanii* Bellardi, 1877. Five species of Clathurellidae are recorded. The genus *Comarmondia* Monterosato, 1884 is considered a junior subjective synonym of *Pleurotomoides* Bronn, 1831. Two Mitromorphidae are recorded, one is described as new: *Mitromorpha* (*Mitrolumna*) *velerinensis* nov. sp. *Anarithma*? *multigranosa* Vera-Peláez, 2002 is removed from the family and placed in the family Costellariidae MacDonald, 1860. Five species of Pseudomelatomidae Morrison, 1965 are recorded.

Key words: southern Spain, Upper Pliocene, Gastropoda, Borsoniidae, Clathurellidae, Mitromorphidae, Pseudomelatomidae, Conoidea

Introduction

In this paper we continue to revise the turrids found in the astoundingly diverse Pliocene assemblage of Estepona in south-western Spain (see Landau & Micali, 2021, p. 160 for other references to this series; Landau *et al*., 2022 for Clavatulidae Gray, 1853).

The Borsoniidae Bellardi, 1875, Clathurellidae H. Adams & A. Adams, 1858, Mitromorphidae Casey, 1904, and Pseudomelatomidae Morrison, 1965 from Estepona were initially discussed in a doctoral thesis submitted to the University of Malaga (date of thesis 1996 or 1997; both dates quoted in the taxonomic chresonymies of Vera -Peláez, 2002, but dated 1996 in the references section of that paper; the year 1996 used herein, which is the date on the front page of the copy available to the present authors). Subsequently his findings were published in Vera-Peláez (2002), which covers all turrid families, except the Clavatulidae and the genus *Genota* in the Borsoniidae, which were published together with his wife (Vera-Peláez & Lozano-Francisco 2001a, b).

Unfortunately, Vera-Peláez (2002) seems to have been hastily prepared, the chresonymy and distributions are randomly selected and very incomplete. These shortcomings are accentuated by rather 'unattractive' typesetting and topped by dreadful printing, in which the photographs, many of which were printed in colour, are blurred. Colour photographs of fossil taxa are, in the present authors' opinion, not helpful, as contrast is diminished, and thus shell features are less clear. Moreover, the taphonomic processes dictate the colour of fossils, unless, of course, some shell pattern is preserved, and the author's intention is to illustrate this. Even so, the preserved colour may not reflect the original colour, and black and white photography usually illustrates these patterns perfectly adequately. The photography in Vera-Peláez (2002) is so poorly reproduced that species interpretation in some instances is unclear. In view of these shortfalls, together with numerous corrections to these papers, additions of species not included by Vera-Peláez and co-workers, and the important change in supragenerIc taxonomy following Puillandre (2014a, b) and Fassio *et al*. (2019), we find it useful to offer a complete revision and update of this spectacularly diverse assemblage.

Age of the deposits

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

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL; 1997–2020) and by Henk Mulder between 2008–2021, 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: 4, text-fig. 1). The material is housed in the Natural History Museum Vienna (NHMW).
A comprehensive chresonymy and distribution is given for each species, concentrating on fossil records, in which only illustrated records are included. For extant species a selection of references is given representing the species' geographical and/or ecological extension. In most turrids, both the protoconch and teleoconch are highly and complexly sculptured. We therefore find it useful to offer a species description for each species, especially as this is the first English language description for most of these taxa, in a field dominated by non-Anglo-Saxon literature. The descriptions for each species are based on the Estepona material.

We have also partly adopted the shell terminology used by Harzhauser *et al*. (2022, p. 8). No colour pattern was observed under UV light.

Abbreviations:
CO: Velerín conglomerates; **PA**: Rio del Padrón; **VC**: Velerín carretera; **VA**: Velerín Antena; **PQ**: Parque Antena; **EL**: El Lobillo; see Landau *et al*. (2003, p. 4, text-fig. 1).
NHMW Natural History Museum Vienna (Austria)
MMPE Museo Municipal de Paleontología de Estepona (Málaga).

Protoconch measurements:
dp = diameter protoconch, **hp** = height protoconch, **dp/hp** = diameter/height protoconch, **dV1** = diameter first protoconch whorl, **n** = diameter nucleus.

Systematics

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

Family Borsoniidae Bellardi, 1875

For borsoniids the shells are categorised as small (<10 mm), medium (10-25 mm) large (>25-40 mm), very large (>40 mm), breadth is described as very broad (SL/MD <2.0), broad (SL/MD 2.0-2.5), moderately broad, (SL/MD = >2.5-2.7), moderately slender (SL/MD = >2.7-3.3), slender (SL/MD >3.3).

(= Pseudotominae Bellardi, 1875; = Zemaciinae Sysoev *in* Medinskaya & Sysoev, 2003)

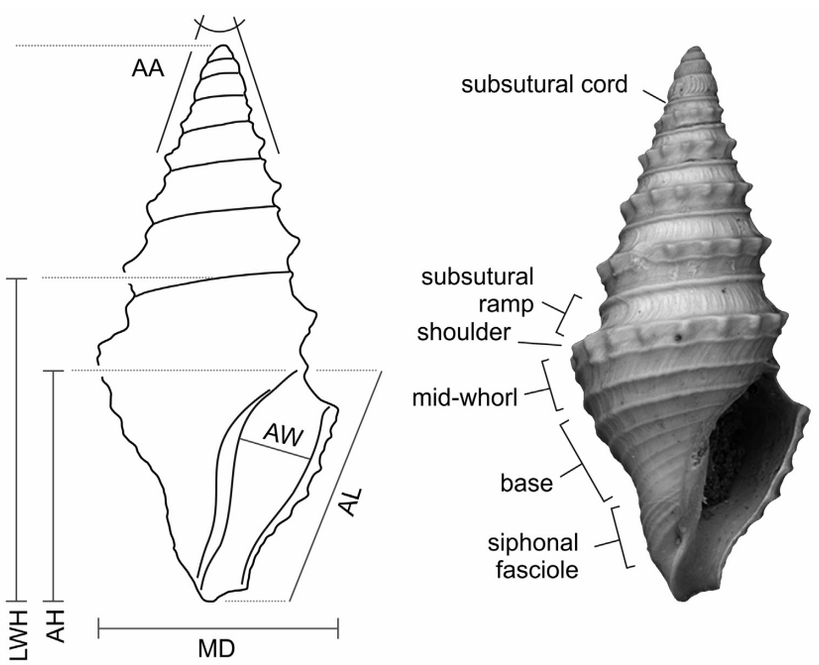

Figure 1. Descriptive terms used in descriptions and measurements to shell morphology, whorl profiles and anal sinus. SL: shell length, MD: maximum diameter, AA: apical angle, LWH: last whorl height, AH: aperture height, AL: aperture length, AW: aperture width (adapted from Harzhauser *et al*. (2022).

The molecular phylogeny of Puillandre *et al*. (2011) found the family Borsoniidae as a clade not to be strongly supported. Bouchet *et al*. (2011) highlighted the rather heterogenous character of this group and diagnosed the family as having shells that were: "*small to large (5-80 mm), fusiform to biconic, sometimes with strong to obsolete columellar pleats. Sculpture usually well developed, axial ribs sometimes obsolete to absent. Siphonal canal short to moderately long. Anal sinus on subsutural ramp, deep. Protoconch when multispiral with up to five whorls, initially smooth and then with arcuate axial riblets, when paucispiral up to two smooth whorls*." (Bouchet *et al*., 2011, p. 276).

More recent work by Uribe *et al*. (2018) placed the family in "Clade B" (together with Conidae, Clathurellidae, Mangeliidae, Raphitomidae, and Mitromorphidae) and sister to the genus *Profundiconus* Kuroda, 1956.

Many groups within the Borsoniidae are amongst the most ancient conoideans, known since the Palaeocene (*Zemacies* Finlay, 1926, *Borsonia* Bellardi, 1839, *Tomopleura* Casey, 1904) or Eocene (*Bathytoma* Harris & Burrows, 1891, *Genota* H. Adams & A. Adams, 1853, *Microdrillia* Casey, 1903).

Genus *Aphanitoma* Bellardi, 1875

Type species – Turbinella labellum Bellardi & Michelotti, 1841, by original designation, Upper Miocene, Italy.

1875 *Aphanitoma* Bellardi, p. 22.

Note – Aphanitoma Bellardi, 1875 species form an easily distinguishable group characterised by their narrow ovate-fusiform shape, tall spire composed of weakly convex or shouldered whorls, and long slender last whorl hardly or weakly constricted at the base. Axial sculpture is usually predominant, but not in all species, and composed of long ribs that usually weaken on the last whorl, overridden by spiral cords. The aperture is narrow-elongate, the outer lip not thickened and lirate within in some species, the anal sinus is broad and shallow, and the inner lip callus is narrow, the columella bearing two oblique folds placed about mid-aperture.

Powell (1966, p. 65) included a paucispiral protoconch to the generic description, but as with many other turrids, protoconch type is not a constant generic character, and species with multispiral protoconchs occur (see Della Bella & Scarponi, 2007). In the Estepona Pliocene all species are paucispiral. Powell (1966, p. 65) described the sinus as being very shallow and "*almost sutural*", however, in some of the species described herein the sinus, although indeed shallow, the apex is placed on the ramp or close to the shoulder [*i.e*.: *A. aplicata* Vera-Peláez, 2002, *A. elegans* (D'Ancona, 1872)].

The number of *Aphanitoma* species present in the Estepona assemblages is difficult to assess due to their scarcity and hence a poor understanding of their intraspecific variability. Vera-Peláez (2002) recorded four species: *A. aplicata*, *A. elegans*, *A. pliocenica* Vera-Peláez, 2002, which is considered a junior subjective synonym of *A. elegans* herein, and *A. pecchiolii* Bellardi, 1877, which is here recorded as *Aphanitoma* sp. 1. We add to this *A. pluriplicata* Bellardi, 1877 and *Aphanitoma* sp. 2.

***Aphanitoma aplicata* Vera-Peláez, 2002**
Plate 1, fig. 1

*2002 *Aphanitoma aplicata* Vera-Peláez, p. 190, pl. 2, figs E, F, pl. 17, figs C, D.

Material and dimensions – Maximum height 12.7 mm, width 4.3 mm. **VC**: NHMW 2020/0171/0385 (1), NHMW 2020/0171/0387 (1).

Description – Shell medium-sized, relatively solid, moderately slender, narrow ovate-fusiform (apical angle 39°). Protoconch paucispiral, dome-shaped, of 1.8 smooth whorls, with a large nucleus (dp = 425 μm, hp = 475 μm, dp/hp = 0.89, dV1 = 350 μm, dn = 250 μm). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of up to six angular whorls, with broad, steeply sloping, slightly concave subsutural ramp, sharply delimited by angular shoulder cord, weakly convex below, separated by narrowly impressed weakly undulating suture. Axial sculpture predominant, of very narrow, opisthocline, slightly sinuous ribs, twelve on penultimate whorl, about

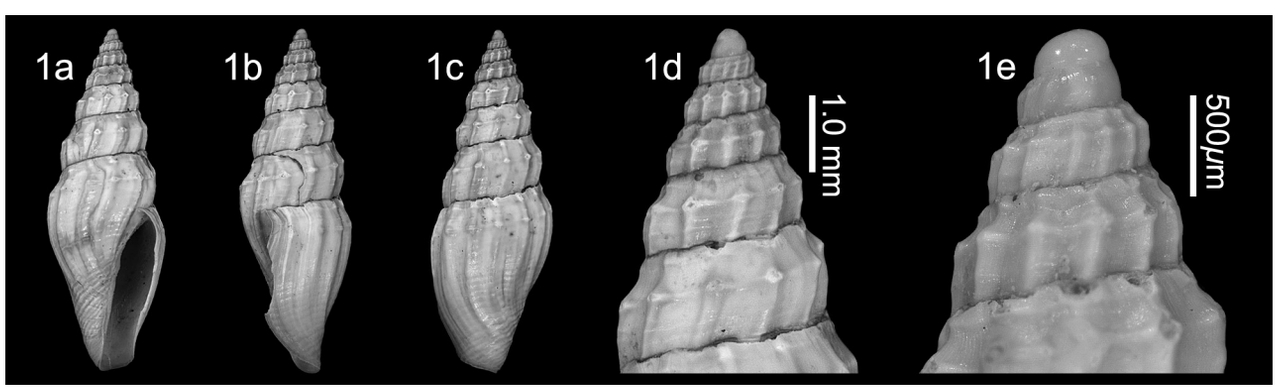

Plate 1. *Aphanitoma aplicata* Vera-Peláez, 2002; 1. NHMW 2020/0171/0385, height 12.7 mm, width 4.3 mm, 1d, detail of early teleoconch whorls, 1e, detail of protoconch (digital image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

one-quarter width of their interspaces. Spiral sculpture subobsolete on spire whorls. Last whorl about 63% of total height, subsutural ramp weakly concave, sharply delimited by weakly angular shoulder, broadly rounded mid-whorl, weakly constricted at base, siphonal fasciole weakly delimited, slightly swollen; axial ribs persist strong to outer lip and over base, spirals weakly developed below shoulder, stronger over siphonal fasciole. Aperture 46% of total height, narrow-elongate, outer lip simple, smooth within; anal sinus very shallow U-shaped with apex mid-ramp; siphonal canal moderate length, open, slightly recurved and twisted to the right, unnotched. Columella weakly excavated in upper third, straight below, bearing two weak, oblique folds mid-aperture. Columellar and parietal callus forming narrow callus rim.

Discussion – According to the original description and figure, *Aphanitoma aplicata* Vera-Peláez, 2002 is characterised by a paucispiral protoconch, adult sculpture composed of 12 narrow, opisthocline, axially aligned ribs, and 6-12 weak, widely spaced spiral cords. The subsutural ramp on the last whorl is concave, with weak spiral sculpture in some specimens, the shoulder sharp, siphonal fasciole short for the genus, outer lip bearing 6-7 lirae within (no lirae seen in illustration of holotype), columella with two weak, oblique folds.
Vera-Peláez (2002, p. 190 under "*Material tipo*") stated that the holotype of *A. aplicata* was adult and perfectly preserved. The size of the holotype and two of the paratypes is between 6.5 and 8.1 mm, which is small for an *Aphanitoma* species. In the description section the author states that in three of the four specimens no folds are present on the columella. The small size, shell profile and absence of folds might suggest that the holotype is not fully adult. It is likely that only paratype 3 (height 14.25 mm) is adult, however, this specimen is not figured. We have interpreted Vera-Peláez's species as the fully adult specimen illustrated (Plate 1, fig. 1).
Della Bella & Scarponi (2007) illustrated a poorly known congener from the Italian Pliocene: *A. targioniana* (D'Ancona, 1872). The authors state "*...si osservano individui con pliche columellari e apertura stretta, ed esemplari privi di pliche con apertura larga e guscio più sottile* [some specimens have columellar folds and a narrower aperture, whilst others have no folds, a wider aperture and thinner shelled]" (Della Bella & Scarponi, 2007, p. 43). In the series illustrated it can be seen that the specimen without folds is the smallest and we interpret these observations as changes in shell character related to ontogeny. *Aphanitoma aplicata* differs from *A. targioniana* in having stronger axial ribs and the sculpture on the early spire whorls is different, with a wider subsutural ramp in *A. aplicata* (compare Plate 1, fig. 1d vs. Della Bella & Scarponi, 2007, fig. 80). However, both species: *A. aplicata* and *A. targioniana* are uncommon and intraspecific variability is poorly known.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

***Aphanitoma elegans* (D'Ancona, 1872)**
Plate 2, figs 1-2

*1872	*Turbinella elegans* D'Ancona, p. 206, pl. 11, figs 3, 4.
?1997	*Aphanitoma elegans* (D'Ancona, 1872) – Chirli, p. 33, pl. 9, fig. 6.
1996	*Aphanitoma elegans* (d'Ancona, 1873 [*sic*]) – Vera-Peláez, p. 289, pl. 18, figs 3, 4, 7-10.
2002	*Aphanitoma elegans* (d'Ancona, 1873 [*sic*]) – Vera-Peláez, p. 189, pl. 1, figs X, Y, pl. 17, figs E, F.
2002	*Aphanitoma pliocenica* Vera-Peláez, p. 191, pl. 2, figs C, D, pl. 17, figs A, B.
2007	*Aphanitoma elegans* (D'Ancona, 1872) – Della Bella & Scarponi, p. 38, figs 69-71.
2018	*Aphanitoma elegans* (D'Ancona, 1872) – Brunetti & Cresti, p. 90, fig. 366.

Material and dimensions – Maximum height 14.5 mm, width 4.5 mm. **VC**: NHMW 2020/0171/0391-0392 (2), NHMW 2020/0171/0393 (2).

Description – Shell medium-sized, relatively solid, moderately slender, narrow ovate-fusiform (apical angle 32°). Protoconch paucispiral, tall dome-shaped, of 1.8 smooth whorls, with a large nucleus (Estepona specimen: dp = 570 μm, hp = 980 μm, dp/hp = 0.58, dV1 = 420 μm, dn = 290 μm). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of up to six weakly convex whorls, with broad, steeply sloping, poorly delimited subsutural ramp, weakly rounded at shoulder, convex below, separated by narrowly impressed undulating suture. Axial sculpture predominant, of narrow, opisthocline ribs, 8-9 on penultimate whorl, about one-third width of their interspaces. Spiral sculpture of close-set, low, narrow cords separated by narrow grooves; cords weak to subobsolete in axial interspaces, slightly swollen over the ribs. Last whorl about 62% of total height, subsutural ramp weakly concave, poorly delimited by subobsolete shoulder, weakly rounded mid-whorl, below mid-whorl profile straight, not constricted at base, siphonal fasciole weakly delimited, slightly swollen; axial ribs weaken towards outer lip and over base, regular sculpture of fine spirals persists over base and fasciole. Aperture 45% of total height, narrow-elongate, outer lip simple, lirate deep within aperture; anal sinus very shallow U-shaped; siphonal canal short, open, unnotched. Columella weakly excavated in upper third, straight below, bearing two oblique folds just above mid-aperture. Columellar and parietal callus forming narrow callus rim.

Discussion – For discussion, see under *A. pluriplicata* Bellardi, 1877. This species has only been found in the deeper water Velerín carretera assemblage, which coincides with the deep circalittoral and epibathyal habitat given by Della Bella & Scarponi (2007, p. 39). Della Bella & Scarponi (2007, p. 38) considered the Estepona specimen illustrated by Vera-Peláez (2002, pl. 1, figs X, Y, pl. 17, figs E, F) to represent *A. pluriplicata* rather than *A. elegans*. In either case, both species co-occur in the Estepona assemblages.

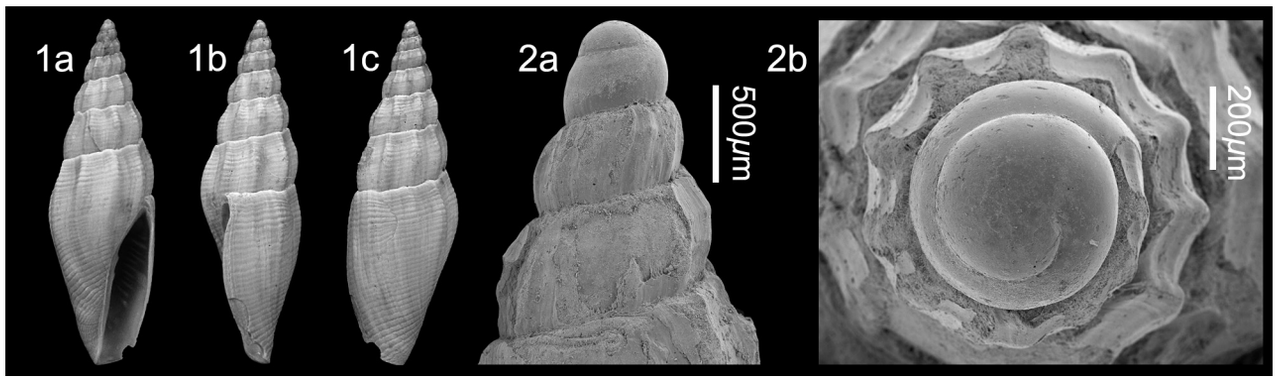

Plate 2. *Aphanitoma elegans* (D'Ancona, 1872); 1. NHMW 2020/0171/0391, height 14.5 mm, width 4.5 mm (digital image); 2. NHMW 2020/0171/0392, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Aphanitoma pliocenica Vera-Peláez, 2002 is based on a single specimen from the deeper water Velerín carretera assemblage. We can see no difference between the holotype figured by that author and the specimen illustrated here from the same locality (Plate 2, fig. 1). Vera-Peláez (2002, p. 191) compares his species with *A. arctata* Bellardi 1877 and *A. pecchiolii* Bellardi, 1877, from which it clearly differs, but did not compare it to *Aphanitoma elegans* (D'Ancona, 1872). He commented that the paucispiral protoconch was very small and especially the nucleus that was "*diminuto* [minute]". However, no protoconch measurements are given and in the figure caption of the crude drawing of the nucleus the author states "*el núcleo esta roto* [the nucleus is broken]" (Vera-Peláez, 2002, p. 262). Moreover, a paucispiral protoconch with a minute protoconch would be unusual. Paucispiral protoconchs imply species with direct development in which the nucleus is usually medium to large sized to accommodate a large amount of yolk to feed the developing shell. Therefore *A. pliocenica* Vera-Peláez, 2002 is herein considered a junior subjective synonym of *Aphanitoma elegans* (D'Ancona, 1872).

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1997; Della Bella & Scarponi, 2007; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

***Aphanitoma pluriplicata* Bellardi, 1877**
Plate 3, figs 1-2

*1877	*Aphanitoma pluriplicata* Bellardi, p. 244, pl. 7, fig. 30.
1981	*Aphanitoma pluriplicata* Bellardi, 1877 – Ferrero Mortara *et al*., p. 85, pl. 17, fig. 14.
2007	*Aphanitoma pluriplicata* Bellardi, 1877 – Della Bella & Scarponi, p. 41, figs 76-79.

Material and dimensions – Maximum height 12.5 mm, width 4.3 mm. **VC**: NHMW 2020/0171/0388-0389 (2), NHMW 2020/0171/0390 (4).

Description – Shell medium-sized, solid, moderately slender, narrow ovate-fusiform (apical angle 35°). Protoconch paucispiral, dome-shaped, of two smooth whorls, with a large nucleus (Estepona specimen: dp = 575 μm, hp = 575 μm, dp/hp = 1, dV1 = 390 μm, dn = 210 μm). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of up to 5.5 weakly angular whorls, with steeply sloping, slightly concave subsutural ramp placed at two-thirds whorl height, moderately delimited by weakly angular shoulder, weakly convex below, separated by narrowly impressed weakly undulating suture. Axial sculpture of low, rounded, weakly opisthocline ribs, 8-9 on penultimate whorl, one-third width of their interspac-

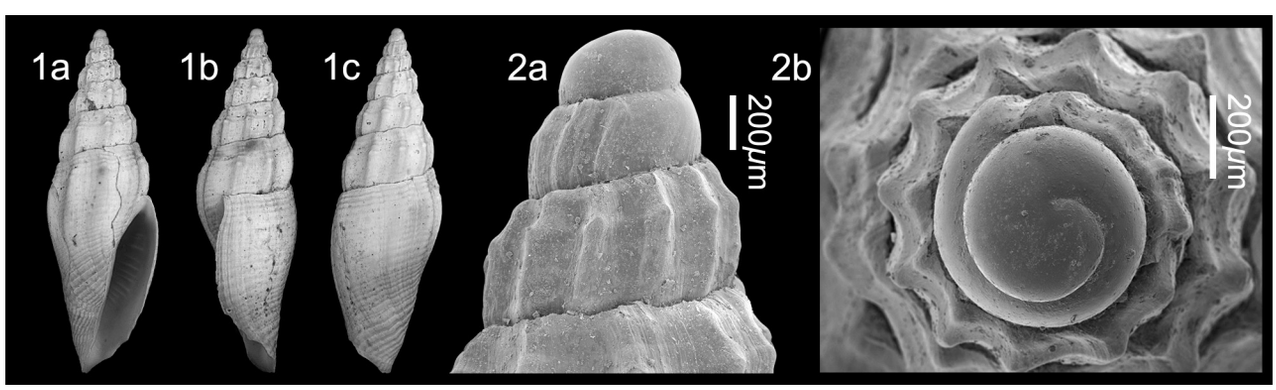

Plate 3. *Aphanitoma pluriplicata* Bellardi, 1877; 1. NHMW 2020/0171/0388, height 12.5 mm, width 4.3 mm (digital image); 2. NHMW 2020/0171/0389, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

es, crossed by very weak spirals; spirals on subsutural ramp slightly stronger, shoulder spiral weakly spinous over ribs. Last whorl about 66% of total height, subsutural ramp weakly concave, moderately delimited by slightly angular shoulder, weakly rounded mid-whorl, hardly constricted at base, siphonal fasciole not delimited, slightly swollen; axial ribs broaden and weaken towards outer lip, and not persisting over base, spirals weakly developed below shoulder, slightly stronger over siphonal fasciole. Aperture 50% of total height, narrow-elongate, outer lip simple, lirate deeply within; anal sinus very shallow U-shaped with apex mid-ramp; siphonal canal moderately short, open, slightly twisted to left, unnotched. Columella weakly excavated in upper third, straight below, bearing two stout, oblique folds mid-aperture. Columellar and parietal callus forming narrow callus rim.

Discussion – *Aphanitoma pluriplicata* Bellardi, 1877 is closely similar to the Pliocene Mediterranean *A. elegans* (d'Ancona, 1872), but differs in having a sharply delimited subsutural ramp on late adult whorls, absent in *A. elegans*, and broader axial ribs. Another similar Pliocene Mediterranean species, *A. imperati* (Scacchi, 1835) is closely similar in sculpture, but the spiral sculpture and especially shoulder cord are more strongly developed, the ribs are much narrower and sharper than in *A. pluriplicata*, and the aperture is relatively shorter than it is in either *A. pluriplicata* or *A. elegans*.
Aphanitoma aplicata Vera-Peláez, 2002 is separated from *A. pluriplicata* by its more numerous (12 vs. 8-9), narrower and more elevated ribs, its sharper shoulder and weaker spiral sculpture, the base is more constricted, and the outer lip is smooth within, as opposed to lirate in *A. pluriplicata*.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Lower Pliocene: central Mediterranean, Italy (Della Bella & Scarponi, 2007). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

Aphanitoma sp. 1

2002 *Aphanitoma pecchiolii* Bellardi, 1877 – Vera-Peláez, p. 189, pl. 2, figs A, B, pl. 17, figs G, H (*non* Bellardi, 1877).

Material and dimensions – Velerín Antena: 1 specimen, height 9.0 mm, width 2.9 mm (MMPE coll.) (figured: Vera-Peláez, pl. 2, figs A, B, pl. 17, figs G, H).

Description – "*concha pequeña (H. medida: 9.00 mm; A. medida: 2.90 mm), bicónica-fusiforme, estrecha, de 6 vueltas de espira. Las vueltas son levemente convexas. Desarrollo larvario no planctotrófico. Protoconcha paucispiral, pequeña (H. de protoconcha: 0.45 mm; A. de protoconcha: 0.35 mm), lisa, pulida, globosa, algo más alta que ancha, aplanada apicalmente, de 1 y $^{3}/_{4}$ vueltas. Núcleo amplio, aplanado apicalmente. Sutura embrionaria poco profunda. Escultura de la teleoconcha doble: axial y espiral. La axial consta de 8-10 cóstulas varicosas que se prolongan de sutura a sutura. La escultura espiral consta de 4-6 cordones espirales anchos, planos y muy espaciados entre sí. Líneas de crecimiento opistoclinas. Sutura sinuosa, cubierta por un cordón ancho. La última vuelta ocupa $^{2}/_{3}$ de la altura total de la concha, de perfil fusiforme, consta de numerosos cordones epsirales planos, anchos y regularmente espaciados y cóstulas axiales que desaparecen con la ontogenia y se atenúan abapicalmente. Abertura angosta y larga. Labro extremo recto. Seno anal superficial, en forma de C sobre la rampa sutural. Canal sifonal breve, indiferenciado, ancho y recto. Bordes columelar y parietal rectos, cubiertos por un callo engrosado. No se aprecian pliegues columelares*" (Vera-Peláez, 2002, p. 189).

Discussion – The strongly spirally sculptured specimen illustrated by Vera-Peláez (2002, pl. 2, figs A, B, pl. 17, figs G, H) as *Aphanitoma pecchiolii* Bellardi, 1877 is characterised by its paucispiral protoconch, very strong, rounded spiral cords, strengthened shoulder cord, and lack of axial sculpture on the last two whorls. On the last whorl there is a strong subsutural cord, narrow subsutural ramp bearing two weaker cords, and a further 15 rounded cords below the poorly delimited shoulder.
In the discussion Vera-Peláez wrote: "*Escultura de la teleoconcha doble: axial y espiral. La axial consta de 8-10 cóstulas varicosas que se prolongan de sutura a sutura* [Both axial and spiral teleoconch sculpture. Axial sculpture of 8-10 varicose ribs that extend between the sutures] … *La última vuelta... y cóstulas axiales que desaparecen con la ontogenia y se atenúan abapicalmente* [The last whorl... and axial ribs that disappear with ontogeny and weaken abapically]" (Vera-Peláez, 2002, p. 189). This description must pertain to Italian specimens, as no ribs are seen on the last two adult whorls in the Estepona specimen illustrated, and a range of 8-10 ribs cannot refer to a single specimen.
The holotype of *A. pecchiolii* from the Upper Miocene Tortonian of Italy was figured by A.W. Janssen (1972, pl. 9, fig 7) and Ferrero Mortara *et al*. (1981, pl. 15, fig. 11). It differs from the Estepona specimen in having axial ribs persisting onto the last whorl. We hesitate to consider them conspecific, and with no further specimens at hand from Estepona we cannot comment further. Unfortunately, all *Aphanitoma* species are exceedingly uncommon in the Estepona assemblages making intraspecific variability difficult to assess.
Several of the Italian records for *A. pecchiolii* (Montanaro, 1937; Pelosio, 1967) were shown to represent *A. arcata* Bellardi, 1877. *Aphanitoma arcata*, originally described from the Lower Pliocene of Italy, was described based on a shell without protoconch. However, Della Bella & Scarponi (2007, p. 37) attributed a typically planktotrophic type multispiral protoconch of three whorls to that species. Therefore, despite having similar teleoconch sculpture to the Estepona specimen, it can be immediately separated by its protoconch type.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

***Aphanitoma* sp. 2**
Plate 4, fig. 1

Material and dimensions – Maximum height 24.5 mm, width 12.0 mm. **VC**: NHMW 2020/0171/0386 (1).

Description – Shell medium-sized, solid, moderately slender, narrow ovate-fusiform (apical angle 38°). Protoconch paucispiral, tall dome-shaped, of two smooth whorls, with a large nucleus (Estepona specimen: dp = 550 μm, hp = 675 μm, dp/hp = 0.81, dn = damaged). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of five weakly angular whorls, with steeply sloping, slightly concave subsutural ramp placed at two-thirds whorl height, well delimited by weakly angular shoulder, weakly convex below, separated by narrowly impressed, undulating suture. Axial sculpture of low, rounded, weakly opisthocline ribs, nine on penultimate whorl, half width of their interspaces, overrun by strong spirals, seven on penultimate whorl, separated by narrower interspaces; subsutural and shoulder spirals strengthened, shoulder spiral forming small tubercles over ribs. Last whorl about 66% of total height, subsutural ramp weakly concave, well delimited by angular shoulder, broadly rounded mid-whorl, weakly constricted at base, siphonal fasciole not delimited, slightly swollen; axial ribs broaden and weaken towards outer lip, and not persisting over base, spirals strong over entire last whorl. Aperture 48% of total height, narrow-elongate, outer lip simple, lirate deeply within; anal sinus very shallow U-shaped with apex mid-ramp; siphonal canal moderately length, open, slightly twisted to left, unnotched. Columella weakly excavated in upper third, straight below, bearing two stout, oblique folds mid-aperture. Columellar and parietal callus forming narrow callus rim.

Discussion – *Aphanitoma* sp. 2 is more strongly shouldered than *A. elegans* (D'Ancona, 1872). The specimen might represent a more strongly spirally sculptured specimen of *A. pluriplicata* Bellardi, 1877, but the profile of the last whorl is more inflated in *Aphanitoma* sp. 2 and the protoconch seems more elevated. *Aphanitoma* sp. 1 has far stronger spiral sculpture, lacks axial ribs on the last two whorls, and is less inflated midwhorl resulting in the base being hardly constricted.
In the Italian Pliocene, *Aphanitoma* sp. 1 of Della Bella & Scarponi (2007, figs 84-87) is immediately separated by its multispiral protoconch. *Aphanitoma* sp. 2 of Della Bella & Scarponi (2007, figs 88-91) is closely similar, although the apex and protoconch seem less elevated (compare Plate 4, fig. 1e vs. fig. 88 in Della Bella & Scarponi, 2007). With the scant material available we leave this species in open taxonomy.

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

Genus *Asthenotoma* Harris & Burrows, 1891

Type species – *Pleurotoma meneghinii* Mayer, 1868, by typification of replaced name, Miocene, Italy.

1875 *Oligotoma* Bellardi, p. 21. Type species (by original designation): *Pleurotoma meneghinii* Mayer, 1868, Miocene, Italy (*non* Westwood, 1836 [Insecta, Embioptera]).
1891 *Asthenotoma* Harris & Burrows, p. 113. *Nom. nov. pro Oligotoma* Bellardi, 1875, *non* Westwood, 1836 [Insecta, Embioptera].

***Asthenotoma orcianensis* Gatto, 1997**
Plate 5, figs 1-4

1996 *Oligotoma* sp. – Vera-Peláez, p. 293, pl. 19, figs 1-6.
*1997 *Asthenotoma orcianensis* Gatto, p. 51, pl. 5, figs 1-10, pl. 8, figs 1-3.
2002 *Asthenotoma pannus* (Basterot, 1825) – Vera-Peláez, p. 191, pl. 1, fig. B', pl. 10, figs C, D [*non Asthenotoma pannus* (de Basterot, 1825)].
2007 *Asthenotoma orcianensis* Gatto, 1997 – Della Bella & Scarponi, p. 19, figs 13-16.
2018 *Asthenotoma orcianensis* Gatto, 1997 – Brunetti & Cresti, p. 90, fig. 360.

Material and dimensions – Maximum height 10.0 mm,

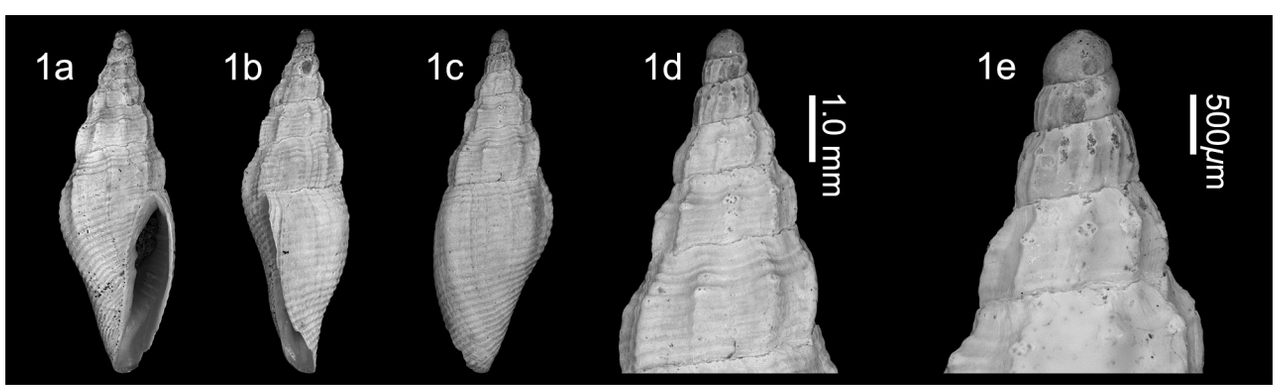

Plate 4. *Aphanitoma* sp. 2; 1. NHMW 2020/0171/0386, height 11.1 mm, width 3.7 mm, 1d, detail of early teleoconch whorls, 1e, detail of protoconch (digital image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

width 3.5 mm. **CO**: NHMW 2020/0171/0433-0436 (1), NHMW 2020/0171/0437 (4).

Description – Shell small, solid, broad biconic fusiform, with moderately tall, regularly conical spire (apical angle 38.6-40.6°). Protoconch paucispiral, composed of 1.25-1.75 convex whorls, with medium-sized nucleus (Estepona specimen: dp = 610 μm, hp = 750 μm, dp/hp = 0.81, dV1 = 470 μm, dn = 210 μm). Transition to teleoconch gradual, marked by sinusigera. Teleoconch of up to five almost straight-sided whorls, with periphery at abapical suture, separated by narrowly impressed linear suture. Spiral sculpture of four primary cords, initially narrow, separated by wider interspaces, broadening abapically, cut by sinuous flattened axial ribs (T2 = 10-12, TP = 14-15), giving cords flattened tubercular appearance; by second whorl two adapical cords narrower and more finely beaded than two abapical ones. Last whorl 57-61% of total height, subsutural ramp slightly concave, poorly delimited by weak shoulder, broadly rounded mid-whorl, weakly constricted at base; on subsutural ramp one secondary spiral appears above each primary forming beaded cords of alternate strength; mid-whorl two broader rows of larger, flattened, square tubercles, below a further 6-8 irregular coarsely beaded spirals; siphonal fasciole with eight narrower smooth cords. Aperture 41-42% of total height, narrow, elongate; outer lip sharp, smooth within; anal sinus relatively deep and broadly U-shaped, with apex on abapical half of ramp; siphonal canal short, bent abaxially and recurved, notched at tip. Columella moderately excavated in upper third, strongly twisted at fasciole, bearing broad fold just below mid-aperture. Columellar callus thickened, extending over medial side of siphonal fasciole, parietal callus hardly developed.

Discussion – *Asthenotoma orcianensis* Gatto, 1997 exhibits similar sculpture to the Middle and Upper Miocene *A. falunica* Peyrot, 1938 from NW France (see Landau *et al*., 2020, p. 12, pl. 7), with two rows of smaller tubercles adapically and two rows coarser tubercles abapically, but in that species the tubercles are more rounded, also the number of axials is far greater in *A. falunica*. Vera-Peláez (2002, p. 191) identified this species as the Atlantic Lower Miocene *A. pannus* (de Basterot, 1825) from the Aquitaine Basin of France. The complications surrounding that species were discussed in length by Gatto (1997, p. 45). Suffice to say that *A. pannus* differs from most of its congeners in having a planktotrophic type multispiral protoconch (Gatto, 1997, pl. 7, figs 2, 3), and is therefore not the same as the Estepona species that has a typical non-planktotrophic protoconch, as described also by Vera-Peláez (2002, p. 192).

Distribution – Lower Pliocene: central Mediterranean, Italy (Della Bella & Scarponi, 2007; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 1996, 2002); central Mediterranean, Italy (Gatto, 1997).

Genus *Bathytoma* Harris & Burrows, 1891

Type species – *Murex cataphractus* Brocchi, 1814, by typification of replaced name, Pliocene, Italy.

1875 *Dolichotoma* Bellardi, p. 21. Type species (by original designation): *Murex cataphractus* Brocchi, 1814, Pliocene, Italy. Junior homonym of *Dolichotoma* Hope, 1839 [Coleoptera].

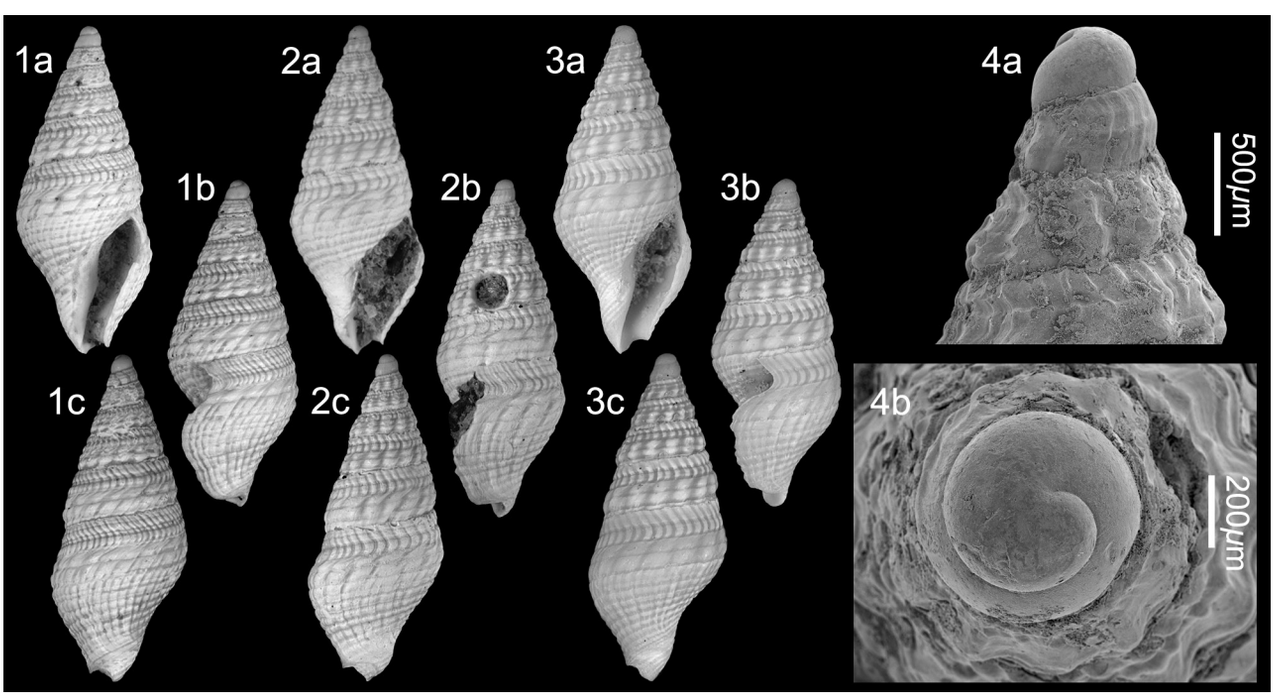

Plate 5. *Asthenotoma orcianensis* Gatto, 1997; 1. NHMW 2020/0171/0433, height 9.3 mm, width 3.8 mm; 2. NHMW 2020/0171/0434, height 9.5 mm, width 3.9 mm; 3. NHMW 2020/0171/0435, height 7.0 mm, width 3.0 mm (digital images); 4. NHMW 2020/0171/0436, detail of protoconch (SEM image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1891 *Bathytoma* Harris & Burrows, p. 113. *Nom. nov. pro Dolichotoma* Bellardi, 1875, *non* Hope, 1839 [Coleoptera].
1936 *Micantapex* Iredale, p. 319. Type species (by original designation): *Bathytoma agnata* Hedley & Petterd, 1906, present-day, New South Wales, Australia.
1951 *Riuguhdrillia* Oyama, p. 1, 3, 4. Type species (by monotypy): *Pleurotoma engonia* Watson, 1881, present-day, Japan.
1961 *Parabathytoma* Shuto, p. 87. Type species (by original designation): *Pleurotoma striatotuberculata* Yokoyama, 1928, Pliocene, Japan.

***Bathytoma cataphracta* (Brocchi, 1814)**
Plate 6, fig. 1

*1814 *Murex cataphractus* Brocchi, p. 427, pl. 8, fig. 16.
1829 *Pleurotoma cataphracta* Brocc. – de Serres, p. 112, pl. 2, figs 3, 4.
1841 *Pleurotoma polita* Münster – Münster *in* Goldfuss, p. 20, pl. 171, fig. 4 [*non* Link, 1807].
1845 *Pleurotoma cataphracta* var. *Aquensis* Grateloup, pl. 20, figs 41, 43, pl. 21, fig. 20.
1845 *Pleurotoma cataphracta* var. *Burdigalensis* Grateloup, pl. 20, figs 41, 43, pl. 21, fig. 21.
1847 *Pleurotoma cataphracta* Brocchi (*Murex*) – Bellardi, p. 20, pl. 1, fig. 14.
1852 [*Pleurotoma*] *cataphracta* – Naumann, pl. 70, fig. 2.
1854 *Pleurotoma cataphracta* Brocc. – Hörnes, p. 333, pl. 36, figs 5-9.
1856 *Pleurotoma cataphracta* Brocc. – Bronn, p. 539, pl. 41, fig. 12.
1859 *Pleurotoma cataphracta* Brocchi – Chenu, p. 145, fig. 637.
1867 *Pleurotoma cataphracta* Brocchi – Pereira da Costa, p. 214, pl. 26, fig. 6.
1877 *Dolichotoma cataphracta* (Brocch.) vars B-D – Bellardi, p. 230, pl. 7, figs 20a-d.
1880 *Dolichotoma cataphracta* Brocchi – Fontannes, p. 259, pl. 12, figs 32, 33.
1890 *Dolichotoma cataphracta* var. *appenninica* Sacc. – Sacco, p. 279.
1890 *Dolichotoma cataphracta* var. *dertogranosa* Sacc. – Sacco, p. 279.
1891 *Pleurotoma* (*Dolichotoma*) *cataphracta* Brocch. – Hoernes & Auinger, p. 379, pl. 50, figs 15-22.
1896 *Bathytoma cataphracta* (Brocchi) – Cossmann, p. 101, pl. 6, fig. 19, pl. 8, figs 12, 14.
1904 *Bathytoma cataphracta* (Br.) – Sacco, p. 50, pl. 13, figs 21, 22.
1904 *Bathytoma cataphracta* var. *apenninica* [*sic*] Sacco, p. 50, pl. 13, fig. 23.
1912 *Bathytoma cataphracta* Brocch. – Friedberg, p. 224, pl. 14, fig. 5.
1914 *Bathytoma cataphracta* Brocchi – Cipolla, p. 134, pl. 13, fig. 1.
1932 *Bathytoma cataphracta* var. *dertogranosa* Sacco – Peyrot, p. 16, no. 1279, pl. 8, figs 45, 47.
1932 *Bathytoma cataphracta* mut. *burdigalica* Peyrot, no. 1280, pl. 8, fig. 50.
1932 *Bathytoma cataphracta* mut. *pyrenaica* Peyrot, no. 1280, pl. 8, fig. 51.
1937 *Bathytoma cataphracta* (Br.) – Montanaro, p. 162 [132], pl. 7 [10], figs 51, 52, 57-60.
1937 *Bathytoma cataphracta* var. *taurodenticulata* Montanaro, p. 163 [133], pl. 7 [10], fig. 54.
1937 *Bathytoma cataphracta* nov. var. Montanaro, p. 164 [134], pl. 7 [10], figs 55, 56.
1944 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi) – Wenz, p. 1421, fig. 4013.
1952 *Bathytoma cataphracta* Brocchi – Lecointre, p. 137, pl. 18, fig. 8.
1953 *Moniliopsis* (*Bathytoma*) *cataphracta orientalis* Csepreghy-Meznerics, p. 16, pl. 3, figs 19-20.
1953 *Moniliopsis* (*Bathytoma*) *cataphracta dertogranosa* Sacco – Csepreghy-Meznerics, p. 16, pl. 3, figs 21-22.
1955 *Moniliopsis* (*Bathytoma*) *cataphracta* (Brocchi 1814) – Rossi Ronchetti, p. 329, fig. 177.
1958 *Moniliopsis* (*Bathytoma*) *cataphracta* (Brocchi) – Erünal-Erentöz, p. 107, pl. 16, figs 14-16.
1959 *Bathytoma cataphracta* (Brocchi) – Ruggieri & Curti, p. 118, pl. 30, fig. 168.
1959 *Bathytoma cataphracta pliodebilis* Ruggieri & Curti, p. 119, pl. 29, fig. 167.
1960 *Bathytoma* (*Bathytoma*) *cataphracta* var. *dertogranosa* (Sacco 1890) – Kojumdgieva, p. 196, pl. 47, figs 4, 5.
1960 *Bathytoma* (*Bathytoma*) *cataphracta* var. *orientalis* Meznerics, 1953 – Kojumdgieva, p. 197, pl. 47, fig. 6.
1962 *Bathytoma subdenticulata* (v. Münster in Goldfuss 1834/40) – Hölzl, p. 195, pl. 10, fig. 12.
1962 *Moniliopsis* (*Bathytoma*) *cataphracta* Brocchi – Strausz, p. 67, pl. 18, figs 11-15.
1962 *Moniliopsis* (*Bathytoma*) *cataphracta orientalis* Csepreghy-Meznerics – Strausz, p. 67, pl. 19, figs 1-6.
1963 *Bathytoma cataphracta subdenticulata* Münst. – Báldi, p. 95, pl. 7, fig. 7.
1963 *Moniliopsis cataphracta* (Br.) – Caretto, p. 24, pl. 3, fig. 20.
1966 *Bathytoma cataphracta* (Brocchi, 1814) – Powell, p. 63, pl. 9, fig. 13.
1966 *Moniliopsis* (*Bathytoma*) *cataphracta* Brocchi, 1814 – Strausz, p. 428, pl. 18, figs 11-15.
1966 *Moniliopsis* (*Bathytoma*) *cataphracta orientalis* Csepreghy-Meznerics, 1953 – Strausz, p. 429, pl. 19, figs 1-6.
1967 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi) – Pelosio, p. 164 [64], pl. 46, figs 20-22.
1967 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – Palla, p. 1001, pl. 75, fig. 13.
1968 *Bathytoma cataphracta* (Brocchi, 1814) – Zelinskaya *et al*., p. 220, pl. 50, figs 14, 15.
1973 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi), 1814 – Caprotti & Vescovi, p. 180, pl. 3, fig. 19.

1972 *Moniliopsis* (*Bathytoma*) *cataphracta* (Brocchi) – Csepreghy-Meznerics, p. 33, pl. 16, figs 28, 33.
1973 *Bathytoma cataphracta* (Brocchi, 1814) – Báldi, p. 317, pl. 49, fig. 6.
1973 *Epalxis* (*Bathytoma*) *cataphracta dertogranosa* (Sacco, 1904 [*sic*]) – Steininger, p. 443, pl. 9, fig. 3.
1974 *Bathytoma* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – Malatesta, p. 416, pl. 31, fig. 24a-c.
1976 *Epalxis cataphracta* (Brocchi) – Caprotti, p. 48, pl. 17, fig. 19.
1978 *Murex cataphractus* Brocchi, 1814 – Pinna & Spezia, p. 146, pl. 30, fig. 3.
1978 *Bathytoma cataphracta* Brocchi [*sic*] – Cuscani Politi, p. 37, 43, pl. 4, figs 9-10.
1984 *Bathytoma cataphracta* (Brocchi) – Bernasconi & Robba, p. 297, pl. 6, figs 1, 2.
1984 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi) – Ruggieri & Davoli, p. 69, pl. 4, fig. 24.
1986 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi) – Martinell & Domènech, p. 119, pl. 1, fig. 9.
1988 *Bathytoma cataphracta* (Brocchi, 1814) – Chirli, p. 24, pl. 11, fig. 16.
1990 *Bathytoma cataphracta* (Brocchi, 1814) – Davoli, p. 96, pl. 8, fig. 25.
1990 *Epalxis* (*Bathytoma*) *cataphracta* (Br.) – Brambilla *et al*., p. 42, pl. 10, fig. 1.
1992 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – Cavallo & Repetto, p. 130, fig. 345.
1993 *Epalxis* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – González Delgado, p. 34, pl. 3, figs 4-5.
1996 *Bathytoma* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – Vera-Peláez, p. 197, pl. 8, figs 1-9.
1997 *Epalxis cataphracta* (Brocchi) – Ruiz Muñoz, p. 184, pl. 39, figs 13-14.
1997 *Bathytoma cataphracta* (Brocchi, 1814) – Chirli, p. 33, pl. 9, figs 7-9.
1998 *Epalxis* (*Bathytoma*) *cataphracta dertogranosa* (Sacco) – Schultz, p. 76, pl. 31, fig. 7
2002 *Bathytoma* (*Bathytoma*) *cataphracta* (Brocchi, 1814) – Vera-Peláez, p. 192, pl. 2, figs G. H, pl. 10, figs E, F.
2003 *Bathytoma cataphracta* (Brocchi, 1814) – Bałuk, p. 53, pl. 17, figs 2-4.
2003 *Clavatula cataphracta* (Brocchi) – Mikuž, p. 308, pl. 10, fig. 31.
2007 *Bathytoma cataphracta* (Brocchi, 1814) – Della Bella & Scarponi, p. 13, figs 1-8.
2008 *Bathytoma cataphracta* (Brocchi, 1814) – Chirli & Richard, p. 61, pl. 12, fig. 3.
2009 *Bathytoma cataphracta* (Brocchi, 1814) – Zunino & Pavia, p. 359, pl. 2, fig. 2.
2009 *Epalxis* (*Bathytoma*) *cataphracta dertogranosa* (Sacco, 1890) – Mikuž, p. 30, pl. 10, fig. 129.
2010 *Bathytoma cataphracta* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 46, unnumbered fig. p. 61 bottom row right.
2011 *Bathytoma cataphracta* (Brocchi, 1814) – Landau *et al*., p. 32, pl. 16, fig. 12.
2013 *Bathytoma cataphracta* (Brocchi, 1814) – Landau *et al*., p. 256, pl. 42, fig. 14.
2016 *Bathytoma cataphracta* (Brocchi) – Kovács & Vicián, pl. 5, fig. 9.
2018 *Bathytoma cataphracta* (Brocchi, 1814) – Brunetti & Cresti, p. 90, fig. 359.
2019 *Bathytoma cataphracta* (Brocchi, 1814) – Cárdenas *et al*., p. 213, fig. 7g.
2021 *Bathytoma cataphracta* (Brocchi, 1814) – Kovács & Vicián, p. 140, fig. 13.

non 1861 *Pleurotoma cataphracta* Brocchi – Nyst, p. 14, no. 44 [= *Bathytoma jugleri* (Philippi, 1847)].
non 1907 *Pleurotoma cataphracta* Brocchi – Ravn, p. 350, pl. 7, fig. 12 [= *Bathytoma mioturbida* (Kautsky, 1925)].
non 1925 *Bathytoma cataphracta* Brocch. – Kautsky, p. 179, pl. 11, fig. 33 [= *Bathytoma jugleri* (Philippi, 1847)].
non 1937 *Bathytoma cataphracta* var. *dertogranosa* Sacco – Montanaro, p. 163, pl. 7, fig. 53 [= *Bathytoma pagoda* Della Bella & Scarponi, 2007].
non 1956 *Bathytoma cataphracta* (Brocchi) – Rasmussen, p. 91, pl. 9, fig. 3 [= *Bathytoma mioturbida* (Kautsky, 1925)].
non 1958 *Bathytoma cataphracta* (Brocchi) – Rasmussen, p. 260, pl. 54, fig. 179 [= *Bathytoma mioturbida* (Kautsky, 1925)].

Material and dimensions – Maximum height 24.5 mm, width 12.0 mm. **VC**: NHMW 2020/0171/0349 (1), NHMW 2020/0171/0350 (1).

Description – Shell very large and solid, broadly biconic, pagodiform profile, with weakly gradate spire (apical angle 44.8-54.3°). Protoconch large, dome-shaped, multispiral, of 3.5 strongly convex whorls, with small nucleus, last whorl shouldered, bearing axial riblets (Estepona specimen: dp = 1325 μm, hp = 600 μm, dp/hp = 2.2, dV1 = 400 μm, dn = 250 μm). Teleoconch of up to eight angular whorls, with concave subsutural ramp, almost vertical on early whorls, less steep abapically, angular at shoulder, weakly convex below, separated by deeply impressed suture. Sculpture on first whorl of row of small subsutural beads and row of larger narrow, axially-elongated tubercles mid-whorl. Secondary spirals appear on second whorl. From third whorl spirals on abapical half of ramp finer than those on adapical half, all finely beaded, spirals at shoulder and below overrunning axial tubercles, forming small tubercles at intersections. Later whorls carinate, carina composed of about three cords, cords above and below carina of roughly equal strength, of alternating strength, finely beaded. Last whorl, about 65% of total height, with concave subsutural ramp, angled at elevated shoulder carina, weakly rounded below, weakly to moderately constricted at base, siphonal fasciole relatively well delimited rounded, bearing fine spirals. Aperture subrectangular, elongate, 47% of total height, outer lip sharp, bearing fine lirae within; anal sinus deep, narrow V-shaped, with apex at shoulder carina; siphonal canal moderate length, bent to right and slightly recurved, unnotched. Columella moderately excavated mid-height, twisted at fasciole, bearing broad fold mid-aperture. Col-

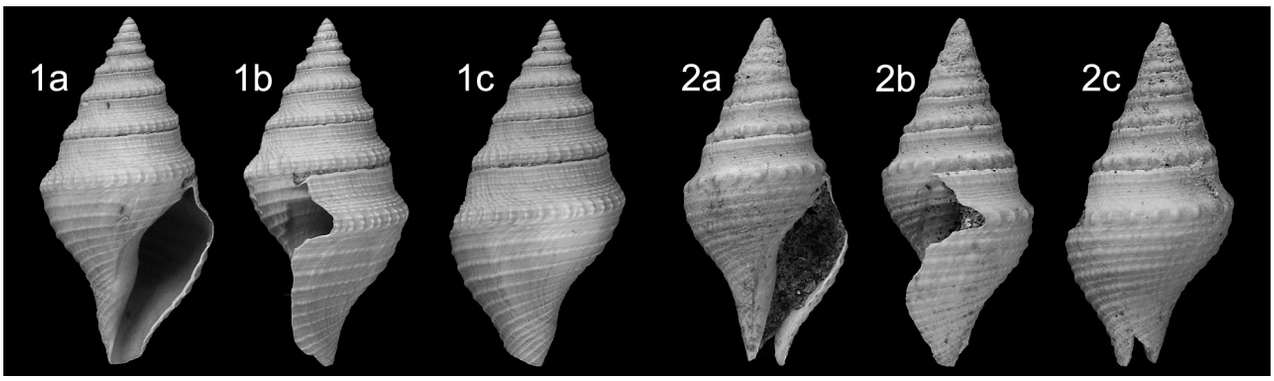

Plate 6. *Bathytoma cataphracta* (Brocchi, 1814); 1. **NHMW 2020/0171/0349 (subadult), height 19.4 mm, width 10.0 mm. Velerín carretera.** 2. NHMW 2020/0171/0350 (subadult), height 24.5 mm, width 12.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

umellar and parietal callus slightly thickened, closely adherent, forming moderately wide callus margin extending over medial side of venter bordered by indented groove.

Discussion – The European Miocene species of *Bathytoma* have been recorded by most authors as conspecific with or as subspecies of *Bathytoma cataphracta* (Brocchi, 1814), which was originally described from the Pliocene of Italy. As pointed out by Della Bella & Scarponi (2007, p. 16), this position cannot be supported, as the early–middle Miocene North Sea Basin species *Bathytoma jugleri* (Philippi, 1847) and the late Miocene North Sea Basin species *Bathytoma mioturbida* (Kautsky, 1925) both have protoconchs consisting of five whorls, whereas the protoconch of Pliocene specimens of *B. cataphracta* has only three. The two North Sea Basin species are easily separated from each other by their shape, *B. jugleri* being slenderer with a taller spire, and sculpture, which is much finer in *B. jugleri* and the row of nodules at the carina is far less strongly developed. Having distinguished the North Sea Basin species, the late Oligocene–Pliocene species *Bathytoma cataphracta* is extremely variable in both shape and sculpture. This variability was illustrated by Della Bella & Scarponi (2007, figs 2-4, 6-8).

Della Bella & Scarponi (2007) described a second species from the Pliocene of Italy, *Bathytoma pagoda*, which was said to differ from *B. cataphracta* in having a smaller protoconch, also composed of three whorls, in having a more irregular suture, in having a more strongly concave subsutural area and in having a single secondary spiral thread in the interspaces between the primary cords below the shoulder on the last teleoconch whorl as opposed to *B. cataphracta*, in which most specimens have two threads in each interspace. *Bathytoma pagoda* occurs in the Upper Miocene (Tortonian) and Lower Pliocene (Zanclean) of Italy. We have not found this form in the Estepona deposits. *Bathytoma cataphracta* inhabited the infralittoral to upper bathyal zone (Della Bella & Scarponi, 2007, p. 16). In the Estepona assemblages this species is found in both the shallow and deeper water deposits but is extremely uncommon. Only two juvenile specimens are at hand, although Vera-Peláez (1996, p. 198) recorded three adults from Velerín.

Distribution – Upper Oligocene: Atlantic (Chattian): Aquitaine Basin, France (Peyrot, 1932); Proto-Mediterranean, Italy (Bernasconi & Robba, 1984). Lower Miocene: Atlantic (Burdigalian): Aquitaine Basin, France (Peyrot, 1932); Paratethys, Austria (Steininger, 1973). Proto-Mediterranean (Burdigalian): Colli Torinesi, Italy (Bellardi, 1847, 1877; Sacco, 1904; Zunino & Pavia, 2009), Mut Basin, Turkey (MH personal observation); Paratethys (Aquitanian): Hungary (Báldi, 1963, 1973). Middle Miocene: Atlantic (Langhian-Serravallian): Aquitaine Basin, France (Peyrot, 1932); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1854; Schultz, 1998), Bulgaria (Kojumdgieva in Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1962, 1966; Csepreghy-Meznerics, 1966, 1972), Poland (Friedberg, 1912, 1951; Bałuk, 2003), Romania (Hoernes & Auinger, 1891), Slovenia (Mikuž, 2003, 2009), Ukraine (Zelinskaya *et al*., 1968); Proto-Mediterranean (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): Cacela Basin, Portugal (Pereira da Costa, 1867), Seville, southwestern Spain (Cárdenas *et al*., 2019); Proto-Mediterranean (Tortonian): Po Basin, Italy (Bellardi, 1847, 1877; Sacco, 1890d; Montanaro, 1937; Ruggieri & Davoli, 1984; Davoli, 1990). Lower Pliocene: Atlantic, Guadalquivir Basin, S. Spain (González Delgado, 1993; Ruiz Muñoz, 1997; Landau *et al*., 2011); western Mediterranean, NE Spain (Gili & Martinell, 1993), France (Fontannes, 1880; Martinell & Domènech, 1986), Morocco (Lecointre, 1954); central Mediterranean, Italy (Bellardi, 1877; Pelosio, 1967; Bernasconi & Robba, 1984; Chirli, 1997; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez *et al*., 1996, 2002), France (Martinell & Domènech, 1986; Chirli & Richard, 2008); central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Cipolla, 1914; Ruggieri & Curti, 1959; Caretto, 1963; Palla, 1967; Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992, Della Bella & Scarponi, 2007). Lower Pleistocene: central Mediterranean, Italy (Brambilla *et al*., 1990).

Genus *Borsonia* Bellardi, 1839

Type species – *Borsonia prima* Bellardi, 1839, by monotypy, Miocene, Italy.

1839 *Borsonia* Bellardi, p. 30.
1931 *Boettgeria* Peyrot, p. 66. Type species (by original designation): *Borsonia* (*Boettgeria*) *gallica* Peyrot, 1931, Miocene, France. Name attributed by Peyrot to Degrange-Touzin. Junior homonym of *Boettgeria* Boettger, 1863, attributed to Heynemann [Clausiliidae]
1943 *Boettgeriola* Wenz, p. 1424. Type species (by typification of replaced name): *Borsonia* (*Boettgeria*) *gallica* Peyrot, 1931, Miocene, France. *Nom. nov. pro Boettgeria* Peyrot, 1931, *non* Heynemann, 1863 [Clausiliidae].

Note – The presence of this genus in the Pliocene of the Estepona Basin is interesting, as it does not seem to occur in the Pliocene further within the Mediterranean. References to Italian occurrences within the genus in Bellardi (1877) all refer to older Middle Miocene strata. Today the genus is associated with deeper waters and occurs off Europe, Azores, and West Africa (Dautzenberg, 1891; Locard, 1897; Bouchet & Warén, 1980). Therefore, *Borsonia* joins a cohort of taxa that after the Messinian Salinity Crisis only managed to recolonise the Pliocene Mediterranean adjacent to the Strait of Gibraltar but did not manage to extend their range further eastwards.

***Borsonia mediterranea* Vera-Peláez, 2002**
Plate 7, figs 1-4

1996 *Borsonia* (*Borsonia*) sp. 2 – Vera-Peláez, p. 281, pl. 16, fig. 6, pl. 17, figs 1-11.
*2002 *Borsonia* (*Borsonia*) *mediterranea* Vera-Peláez, p. 188, pl. 1, figs R, S, pl. 10, figs A, B.

Material and dimensions – Maximum height 12.8 mm, width 4.8 mm. **VC**: NHMW 2020/0171/0159-0162 (2), NHMW 2020/0171/0163 (26). **VS**: NHMW 2020/0171/0164 (6).

Description – Shell medium sized, broad to moderately broadly turriform, with strongly gradate spire (apical angle 37.7-47.8°). Protoconch paucispiral, dome-shaped, of 1.7 smooth whorls, with large nucleus, last whorl with microsculpture of crowded spiral rows of tiny micropustules, last quarter whorl with sinuous axial riblets (dp = 825 μm, hp = 675 μm, dp/hp = 1.22, dV1 = 635 μm, dn = 370 μm). Teleoconch of up to five sharply angular whorls, with shoulder placed just above mid-whorl forming periphery, subsutural ramp concave, sharply delimited, below shoulder profile straight-sided, tapering inwards to suture, suture superficial, linear. Sculpture on first teleoconch whorl of 10-11 axial ribs, arcuate over subsutural ramp, opisthocline below shoulder, overrun by two cords, adapical stronger, and forming shoulder. On later whorls axials over subsutural ramp weaken and disappear on last two whorls, below shoulder low, rounded, 13-15 on penultimate whorl, rapidly weakening rapidly below, not reaching abapical suture, form-

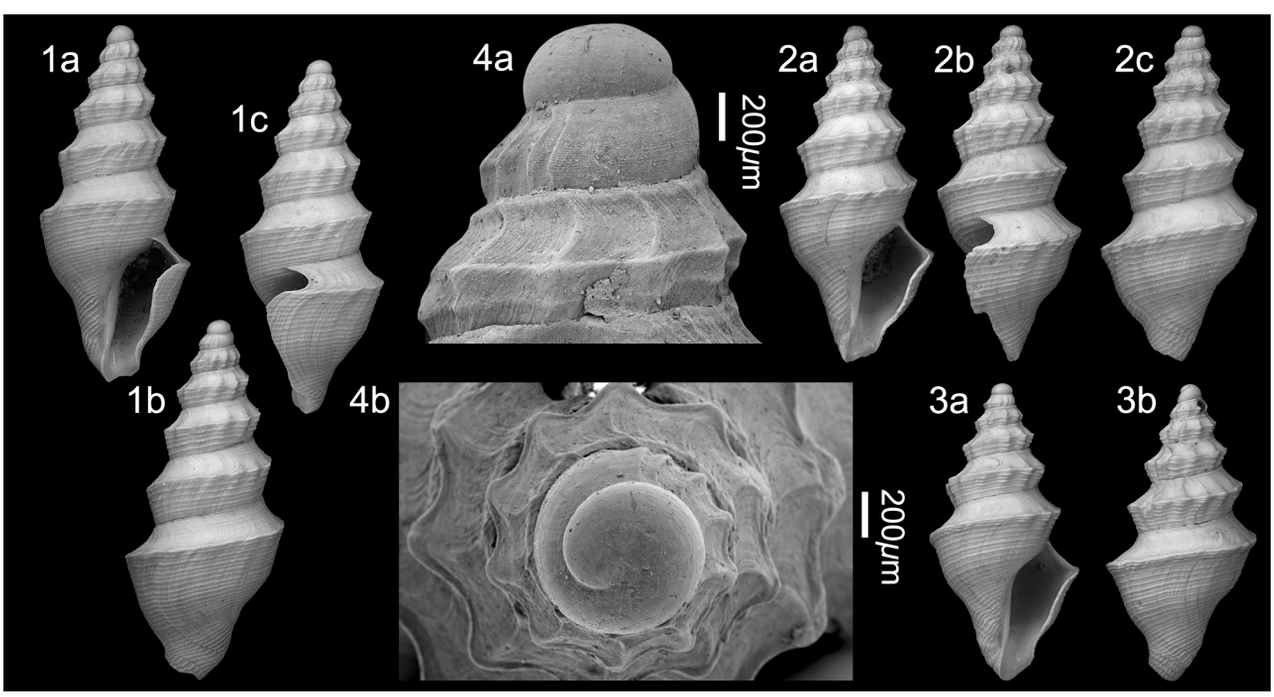

Plate 7. *Borsonia mediterranea* Vera-Peláez, 2002; 1. NHMW 2020/0171/0159, height 10.1 mm, width 4.3 mm; 2. NHMW 2020/0171/0160, height 12.8 mm, width 4.8 mm; 3. NHMW 2020/0171/0161, height 9.2 mm, width 4.4 mm (digital images); 4. NHMW 2020/0171/0162, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ing narrow, horizontally elongated tubercles at shoulder. Spiral sculpture consisting of a very fine threads over subsutural ramp, strengthened shoulder cord, somewhat carinate in gerontic specimens, and fine, close-set cords and threads of roughly alternating strength below shoulder. Last whorl 59-63% of total height, with concave subsutural ramp, sharply angled at shoulder, convex below, strongly constricted at base; fine spirals continuing over base; siphonal fasciole poorly delimited, weakly rounded, bearing slightly stronger spirals. Aperture subquadrate, outer lip sharp, smooth within; anal sinus broadly and symmetrically U-shaped, with apex mid-ramp; siphonal canal short, bent slightly to left, unnotched. Columella smooth, moderately excavated in upper half, straight below, weakly twisted at fasciole. Columellar and parietal callus weakly thickened, sharply delimited, forming narrow callus margin bordered by indented groove.

Discussion – For comparison see under *Borsonia plioalboranensis* Vera-Peláez, 2002.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 1996, 2002).

***Borsonia plioalboranensis* Vera-Peláez, 2002**
Plate 8, figs 1-3

1996 *Borsonia* (*Borsonia*) sp. 1 – Vera-Peláez, p. 277, text-figs 12a-c, m, 13, pl. 16, figs 1-5, 7-9.
*2002 *Borsonia* (*Borsonia*) *plioalboranensis* Vera-Peláez, p. 186, pl. 1, figs T, U, pl. 9, figs M, N.

Material and dimensions – Maximum height 9.7 mm, width 4.6 mm. **CO**: NHMW 2020/0171/0158 (8). **VC**: NHMW 2020/0171/0165-0167 (3), NHMW 2020/0171/0168 (19). **VS**: NHMW 2020/0171/0169 (16).

Description – Shell small, relatively squat, broadly biconic, with regularly conical spire (apical angle 41.2-41.7°). Protoconch paucispiral, dome-shaped, of 1.7-1.9 smooth whorls, with large bulbous nucleus (dp = 885 μm, hp = 860 μm, dp/hp = 1.02, dV1 = 695 μm, dn = 380 μm). Junction with teleoconch marked by beginning of axial sculpture. Teleoconch of 4.5 angular whorls, with shoulder placed mid-whorl, subsutural ramp concave, sharply delimited, below shoulder profile straight-sided, tapering inwards to suture: suture moderately impressed, linear. Sculpture on first teleoconch whorl of about 13 strongly opisthocline, sinuous, rounded axial ribs and tubercular mid-whorl. On second whorl portion of rib on subsutural ramp fades rapidly, ribs forming horizontally elongated tubercles at shoulder, below shoulder low, rounded, 12-16 on penultimate whorl, weakening below, but reaching abapical suture. In some gerontic specimens nodules disappear on last two whorls, replaced by smooth, prominent shoulder carina. Spiral sculpture much reduced; a few flattened cords most evident over base and siphonal fasciole. Last whorl 66-67% of total height, with moderate width, concave subsutural ramp, sharply angled at shoulder, weakly convex below, weakly to moderately constricted at base; siphonal fasciole poorly delimited, weakly rounded. Aperture elongate-subquadrate, 50-53% of total height, outer lip sharp, smooth within; anal sinus narrowly and symmetrically U-shaped, with apex mid-ramp; siphonal canal short, bent slightly to left, un-

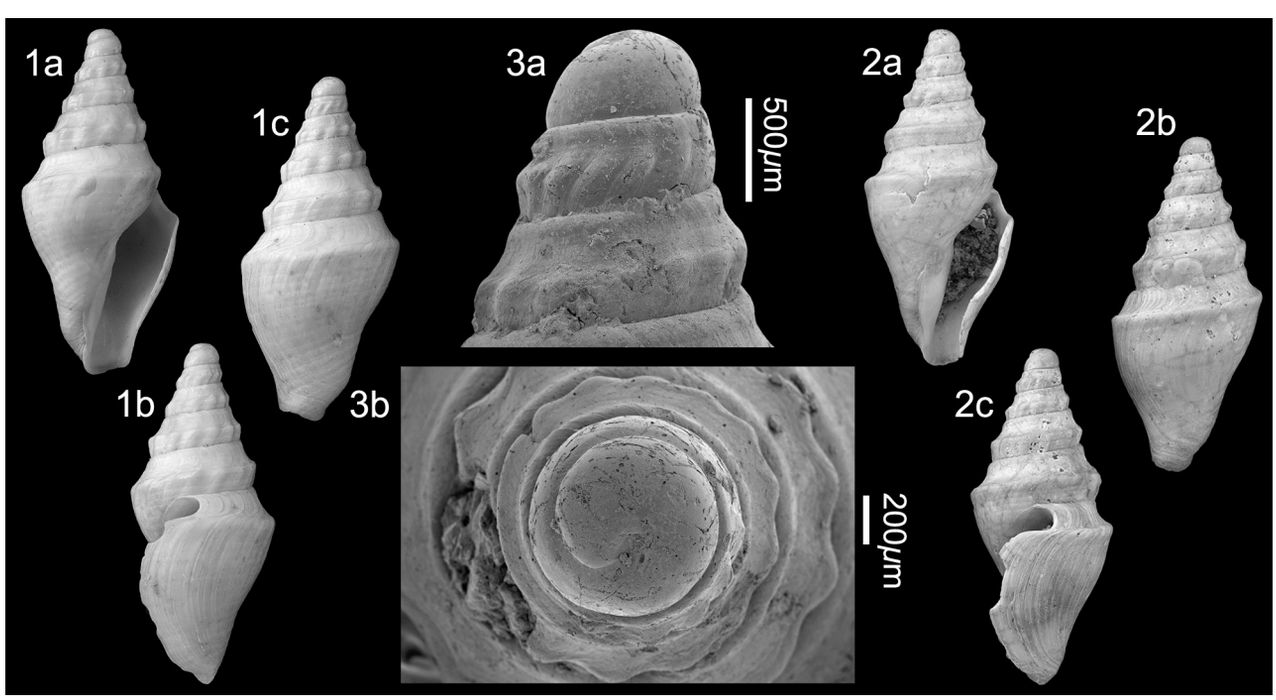

Plate 8. *Borsonia plioalboranensis* Vera-Peláez, 2002; 1. NHMW 2020/0171/0165, height 8.1 mm, width 3.6 mm; 2. NHMW 2020/0171/0166, height 7.5 mm, width 3.2 mm (digital images); 3. NHMW 2020/0171/0167, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

notched. Columella weakly excavated in upper third, straight, with broad, subobsolete fold at its adapical end. Columellar and parietal callus weakly thickened, sharply delimited, forming narrow callus margin bordered by indented groove.

Discussion – *Borsonia plioalboranensis* Vera-Peláez, 2002 is a very characteristic little species. There is quite some intraspecific variability as to broadness and sculpture. In gerontic specimens the shoulder tubercles tend to disappear and are replaced by an elevated shoulder carina and the columellar callus is strongly thickened and slightly detached. *Borsonia mediterranea* Vera-Peláez, 2002, with which it coexists in the Estepona deposits, is larger shelled, more elongated, and has a strongly gradate spire as opposed to the regularly conical spire seen in *B. plioalboranensis*. The only comparable extant eastern Atlantic species is *B. hirondelleae* (Dautzenberg, 1891), which has a slenderer fusiform profile as opposed to biconic. *Borsonia mediterranea* has a more strongly gradate profile than *B. hirondelleae*, with a far sharper and stronger shoulder.
As discussed in the generic note, the genus was widespread in the European Miocene, but never very speciose. The type species from the Middle Miocene of Italy, *B. prima* Bellardi, 1839 (syntype figured by Ferrero Mortara *et al*., 1981, pl. 18, fig. 1) differs from both Spanish species in being tall, slender biconic with a stronger columellar fold. *Borsonia plicata* Beyrich, 1848 from the upper Oligocene of the North Sea Basin has extraordinarily variable sculpture, tubercular at the shoulder to almost completely smooth (see R. Janssen, 1979, pl. 17, figs 61-63), but differs from both Spanish species in being more fusiform, with a taller spire and not biconic. *Borsonia laeviuscula* von Koenen, 1890, also from the Oligocene of the North Sea Basin, is fusiform, almost smooth, with non-shouldered whorls. *Borsonia meridionalis* Lozouet, 2017 from the Atlantic upper Oligocene of the Adour Basin, France is more similar to the Estepona species; it differs from *B. mediterranea* in having less gradate whorls and a much stronger columellar fold, and from *B. plioalboranensis* in being less squat, and again having a much stronger fold.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 1996, 2002).

Genus *Drilliola* Locard, 1897

Type species – *Taranis emendata* Monterosato, 1872, by monotypy, present-day, Mediterranean.

1897 *Drilliola* Locard, p. 214. Name attributed by Locard to Monterosato. Made available by use by Cossmann, 1903, p. 188, and subsequent authors.

Note – Bouchet & Warén (1980) considered *Microdrillia* Casey, 1903 a synonym of *Drilliola* Locard, 1897, as species of both genera have a similar radula and operculum. The protoconch of the type species of *Drilliola* is quite distinct, paucispiral and bicarinate, whereas that of the type species of *Microdrillia* has a multispiral protoconch. However, as seen in an ever increasing number of turrid genera, protoconch type is not a reliable generic character. As pointed out by Lozouet (2017, p. 16), the teleoconch shape and sculpture of *Drilliola*, *Microdrillia*, *Tomopleura* Casey, 1904, and *Paradrilliola* Gatto, 1991 are all very similar. Despite this observation Lozouet (2017, p. 22) continued to use the genus *Microdrillia* for a species from the upper Oligocene of France with the same type of protoconch as *M. crispata* (De Cristofori & Jan, 1832) (*M. aturensis* Lozouet, 2017). The group is not speciose in the Estepona assemblages and represented by the well-known species *Drilliola emendata* (Monterosato, 1872), *Microdrillia crispata* and *M. serratula* (Bellardi, 1877). We adopt the classical generic framework for these species until their relationships are clarified by molecular data.
Lozouet (2017, p. 18 fig. 5) introduced a numerical system for description of the spiral sculpture in *Drilliola*, which has been adopted herein (Plate 9, figs 1-3).

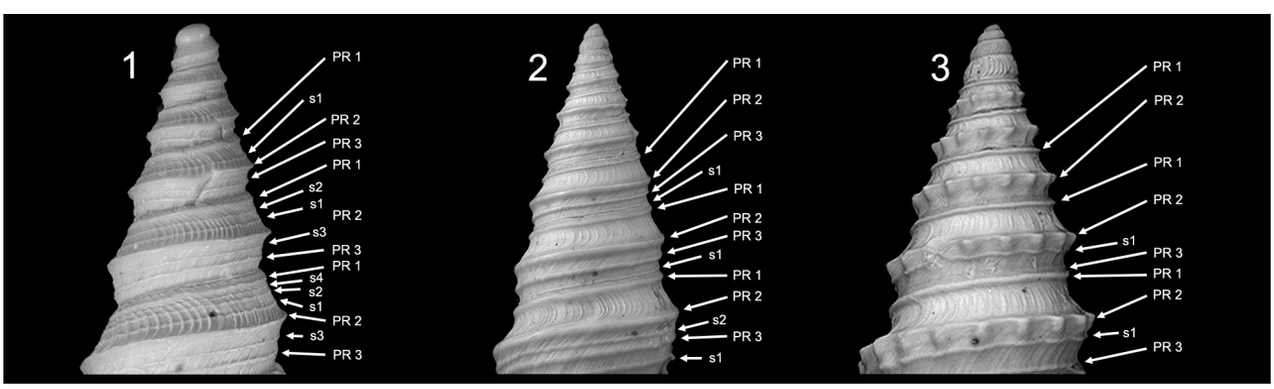

Plate 9. Terminology used for the genera *Drilliola* Locard, 1897 and *Microdrillia* Casey, 1903: 1. *Drilliola emendata* (Monterosato, 1872); NHMW 2020/0171/0188, height 12.8 mm, width 3.3 mm; 2. *Microdrillia crispata* (De Cristofori & Jan, 1832); NHMW 2020/0171/0127, height 12.8 mm, width 4.8 mm; 3. *Microdrillia plioserratula* nov. sp.; **holotype** NHMW 2020/0171/0131, height 9.0 mm, width 3.7 mm (digital images). All: Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene. Adapted from Lozouet (2017, p. 17-18, fig. 5): PR = primary ribs, s = secondary ribs counted in order of appearance.

***Drilliola emendata* (Monterosato, 1872)**
Plate 9, fig. 1; Plate 10, figs 1-4

1844 *Pleurotoma Renieri* Scacchi – Philippi, p. 176, pl. 26, fig. 22 (*non* Scacchi, 1835).
1862 *Pleurotoma crispatum* De Cr. et Jan – Brugnone, p. 14, fig. 7 [*non Microdrillia crispata* (De Cristofori & Jan, 1832)].
*1872 *Taranis emendata* Monterosato, p. 17, 34.
1897 *Pleurotoma emendatum* var. *atlantica* Locard, p. 214, pl. 11, fig. 1.
1944 *Asthenotoma* (*Drilliola*) *emendata* (Monterosato) – Wenz, p. 1414, fig. 3994.
1966 *Drilliola emendata* (Monterosato, 1872) – Powell, p. 94, pl. 13, fig. 14.
1971 *Taranis albatrossi* Nordsieck, p. 189, fig. 3.
1975 *Asthenotoma* (*Drilliola*) *emendata* Monterosato) [*sic*] – Di Geronimo, p. 126, pl. 1, fig. 8.
1977 *Drilliola emendata* (Monterosato, 1870 [*sic*]) – Nordsieck, p. 18, pl. 2, fig. 13.
1977 *Taranis comatotropis albatrosi* [*sic*] Nordsieck – Nordsieck, p. 49, pl. 14, fig. 113.
1980 *Drilliola emendata* (Monterosato, 1872) – Bouchet & Warén, p. 32, figs 29, 83, 207.
1991 *Drilliola emendata* (Monterosato, 1872) – Gatto, p. 237, pl. 5, fig. 4.
1996 *Drilliola emendata* (Monterosato, 1872) – Vera-Peláez, p. 351, text-figs 15a-d, 18h-i, 20g, 23, pl. 23, figs 1-12.
1999 *Drilliola emendata* (Monterosato, 1872) – Ardovini & Cossignani, p. 67, 68, unnumbered fig. bottom row left.
2002 *Drilliola emendata* (Monterosato, 1872) – Vera-Peláez, p. 195, pl. 2, figs P, Q, R, pl. 11, figs A, B.
2014 *Drilliola emendata* (Monterosato, 1872) – Gofas *et al*., p. 542, figs 4R, S.
2016 *Drilliola emendata* (Monterosato, 1872) – Negri & Corselli, p. 65, figs 14n-p.
2022 *Drilliola emendata* (Monterosato, 1872) – Oliver *et al*., p. 369, figs 3, 42A.

Material and dimensions – Maximum height 13.4 mm, width 4.8 mm. **CO**: NHMW 2020/0171/0186 (50+). **VC**: NHMW 2020/0171/0187-0190 (4), NHMW 2020/0171/0191 (50+).

Description – Shell small to medium sized, moderately broadly turriform, with gradate spire (apical angle 32.4-32.7°). Protoconch paucispiral, flattened, of 1.75-2 whorls, with medium sized nucleus, sculptured by two strong elevated spiral cords appearing after the nucleus and microsculpture of tiny scattered micropustules (Estepona specimen: dp = 790 μm, hp = 720 μm, dp/hp = 1.10, dV1 = 550 μm, dn = 240 μm). Junction with teleoconch marked by appearance of axial riblets. Teleoconch of up to 5.5 sharply carinate whorls, with shoulder placed mid-whorl, profile concave above and below shoulder, separated by narrowly impressed, linear suture. Spiral sculpture strongly dominant. On first teleoconch whorl PR1-3 appear simultaneously at the protoconch/teleoconch junction, PR 1 weakest, PR 2 strong, marking shoulder, PR 3 just above suture. Second whorl s1 and s2 appear simultaneously s1 just below mid-subsutural ramp, s2 between PR2 and PR 3. Later whorls PR 2 strongly carinate, fur-

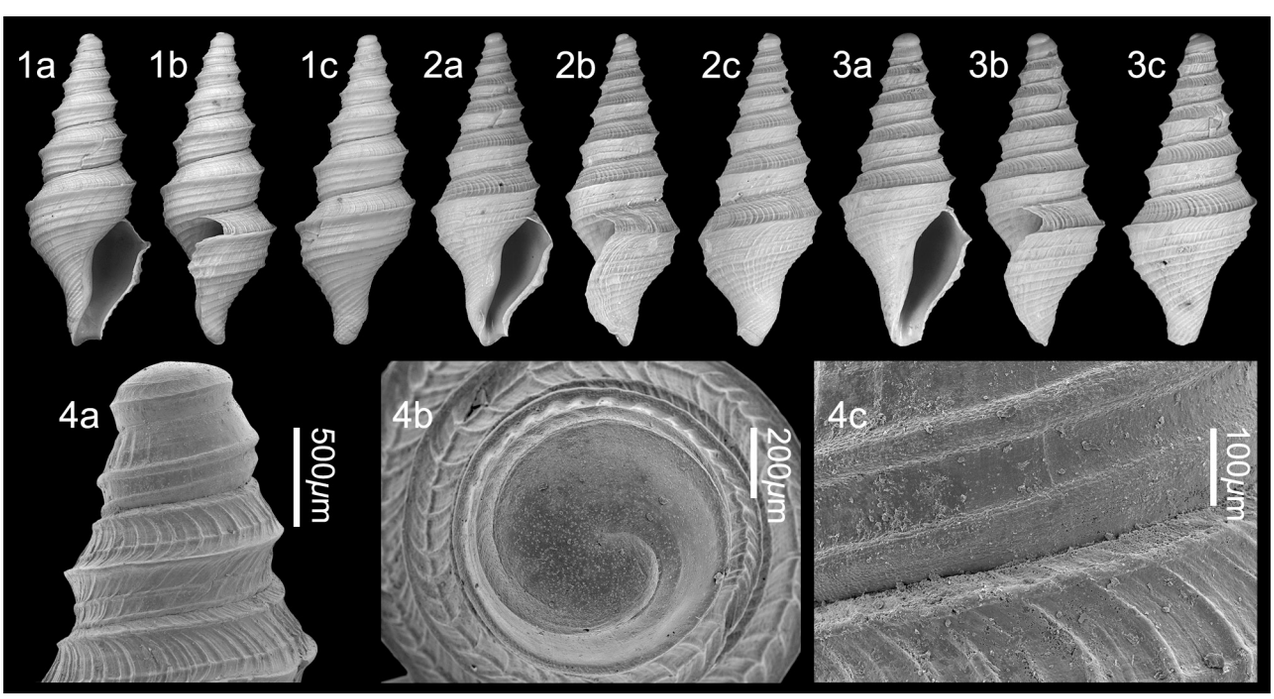

Plate 10. *Drilliola emendata* (Monterosato, 1872); 1. NHMW 2020/0171/0187, height 9.3 mm, width 3.5 mm; 2. NHMW 2020/0171/0188, height 12.8 mm, width 3.3 mm; 3. NHMW 2020/0171/0189, height 7.5 mm, width 3.1 mm (digital image); 4. NHMW 2020/0171/0190, 4a-b, detail of protoconch, 4c, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ther secondary cords become intercalated. Axial sculpture of fine arcuate riblets over subsutural ramp continuing strongly opisthocline in spiral interspaces below shoulder. Last whorl 57-58% of total height, with broad, concave subsutural ramp, sharply angled at PR 2, convex below, strongly constricted at base; subequal spirals continuing over base with single s3 intercalated mid-whorl; base weakly delimited by slightly strengthened spiral; siphonal fasciole not delimited. Aperture 40-43% of total height, subquadrate, outer lip sharp; anal sinus broadly and asymmetrically U-shaped, with apex on abapical half of ramp, close to shoulder carina; siphonal canal moderately short, recurved, shallowly notched. Columella smooth, broadly excavated, strongly twisted at fasciole. Columellar and parietal callus weakly thickened, sharply delimited, forming narrow indented callus margin.

Discussion – *Drilliola emendata* (Monterosato, 1872) is strongly variable in sculpture, both in the number of axial and secondary spiral elements, and in their strength and thickness. Some specimens have an almost reticulated surface sculpture whereas others are almost smooth, except for the peripheral carina (PR 2), which is invariably sharply developed.
Species with similar teleoconch sculpture, such as *Pleurotoma loprestiana* Calcara, 1841, placed by some authors in the genus *Drilliola* Locard, 1897 (*e.g.*, Bouchet & Warén, 1980), differ in having a multispiral protoconch, and are here placed in the genus *Microdrillia* Casey, 1903 (see generic note).
Lozouet (2017) included a number of Atlantic upper Oligocene species from France in the genus *Drilliola*, none of which have a carinate paucispiral protoconch.
Today this species inhabits the bathyal zone of the Mediterranean and the continental slopes of Iberia and West Africa (Bouchet & Warén, 1980, p. 34). In Estepona it is found in both the shallower and deeper water deposits.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 1996, 2002). Lower Pleistocene: Sicily, Italy (Di Geronimo, 1975). Present-day: Atlantic continental slopes of Iberia (Oliver *et al*., 2022) and NW Africa, Mediterranean (Nordsieck, 1977; Bouchet & Warén, 1980), western Mediterranean (Gofas *et al*., 2014), central Mediterranean (Ardovini & Cossignani, 1999; Negri & Corselli, 2016).

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

Type species – *Murex mitriformis* W. Wood, 1828, by original designation, present-day, West Africa.

1853 *Genota* H. Adams & A. Adams, p. 89.
1883b *Genotia* Fischer, p. 589. Unjustified emendation of *Genota*.

***Genota bonnanii* Bellardi, 1877**
Plate 11, figs 1-4

1814 *Murex* (*Pleurotoma*) *reticulatus* Brocchi, p. 435, pl. 9, fig. 12 (*nomen oblitum*).
1847 *Pleurotoma ramosa* Bast. Var. B – Bellardi, p. 23, pl. 1, fig. 3 [*non Genota ramosa* (de Basterot, 1825)].
*1877 *Genota Bonnanii* Bellardi, p. 87, pl. 3, fig. 8.
1976 *Genota* (*G.*) *bonnanii* Bellardi, 1877 – Pavia, p. 151, pl. 9, fig. 17.
1978 *Murex reticulatus* Brocchi, 1814 – Pinna & Spezia, p. 152, pl. 40, fig. 5.
1980 *Genota* (*G.*) *bonnanii* Bellardi, 1877 – Pavia, p. 219, pl. 3, figs 6, 7, 10, 11, 15.
1981 *Genota bonnanii* Bellardi, 1877 – Ferrero Mortara *et al*., p. 66, pl. 10, fig. 12.
1992 *Genota bonnanii* Bellardi, 1877 – Cavallo & Repetto, p. 136, fig. 364.
1993 *Genota* (*Genota*) *bonnanii* Bellardi, 1877 – González Delgado, p. 48, pl. 6, figs 7, 8.
?1996 *Genota bonnanii* Bellardi, 1877 – Vera-Peláez (*partim*), p. 581, pl. 42, figs 10-12 only [not figs 1-4, 9 = *Genota domenechae* Vera-Peláez & Lozano-Francisco, 2001].
1997 *Genota Bonnanii* Bellardi, 1877 – Chirli, p. 101, pl. 29, figs 1, 2.

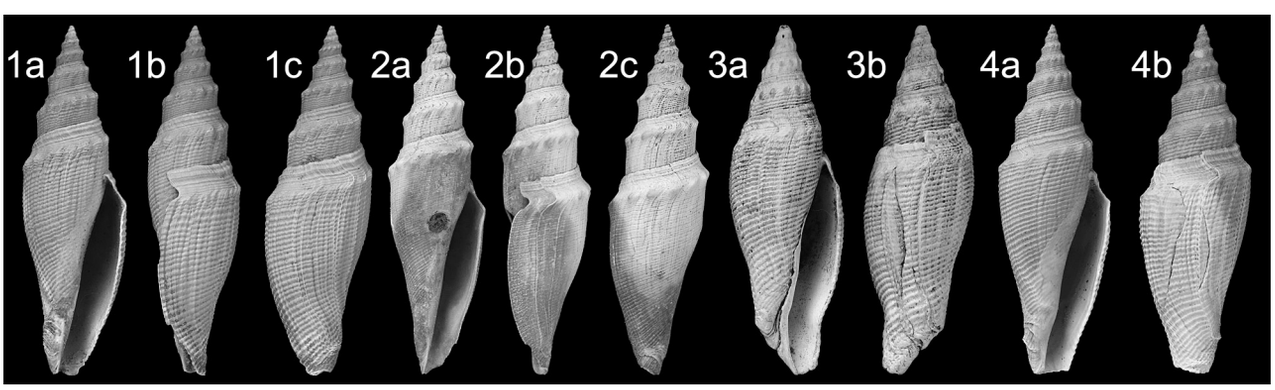

Plate 11. *Genota bonnanii* Bellardi, 1877; 1. NHMW 2020/0171/0584, height 50.2 mm, width 14.8 mm; 2. NHMW 2010/0054/0167, height 55.5 mm, width 15.2 mm; 3. NHMW 2020/0171/0585, height 54.4 mm, width 17.3 mm; 4. NHMW 2010/0054/0166, height 55.5 mm, width 14.8 mm; (digital images). Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, lower Pliocene.

2001b *Genota bonnanii* Bellardi, 1877 – Vera-Peláez & Lozano-Francisco, p. 70, pl. 1, figs 1-5, pl. 3, fig. 8 (?pl. 1, fig. 7, pl. 3, figs 9).
2001b *Genota lusitaniae* Vera-Peláez & Lozano-Francisco, p. 74, pl. 2, figs 1-6, pl. 3, figs 4-6.
?2002 *Genota bonnanii* Bellardi, 1877 – Vera-Peláez, p. 213, pl. 5, figs X, Y.
2007 *Genota bonnanii* Bellardi, 1877 – Della Bella & Scarponi, p. 66, figs 131-134.
2011 *Genota bonnanii* Bellardi, 1877 – Landau *et al*., p. 33, pl. 17, fig. 1.
2011 *Genota lusitaniae* Vera-Peláez & Lozano-Francisco, 2001 – Landau *et al*., p. 33, pl. 17, figs 2-3.

non 1993 *Genota* (*Genota*) *bonnanii* Bellardi, 1877 – González Delgado, p. 48, pl. 6, figs 7, 8 (= *Genota lusitaniae* Vera-Peláez & Lozano-Francisco, 2001b).

Discussion – Vera Peláez (1996, 2002) and Vera-Peláez & Lozano-Francisco (1998, 2001b) separated one specimen from Estepona as *Genota bonnanii* Bellardi, 1877. It was said by those authors to differ from *Genota domenechae* Vera-Peláez & Lozano-Francisco, 2001 in being larger, in having a more fusiform [*sic*] aperture and siphonal canal, and by having stronger, thicker, more sinuous spiral cords that formed tubercles at the intersections (Vera-Peláez, 2002, p. 214). Their specimen is 39 mm in height and no mention is made of the protoconch.
Genota bonnanii was reviewed by Della Bella & Scarponi (2007, p. 66, figs 131-134). The shell is slender fusiform with relatively strong spiral sculpture as described by the Spanish authors, and it was shown to have a planktotrophic type protoconch; multispiral of about three whorls with axial riblets on the last quarter-whorl.
Size cannot separate *G. bonnanii* from *G. domenechae*, as they attain a similar maximum size (see below). The specimen from Velerín (Vera-Peláez & Lozano-Francisco, pl. 1, fig. 7; 2002, pl. 5, figs X, Y) does indeed have stronger spiral sculpture than that seen in *G. domenechae*, but the protoconch is not preserved. The sculpture in *G. domenechae* is rather variable (Plate 12, figs 1-6), and an intact protoconch would be required to confirm this record for the Estepona assemblages.
Genota lusitaniae Vera-Peláez & Lozano-Francisco, 2001 from the Atlantic Lower Pliocene Guadalquivir Basin, was said to differ from *G. bonnanii* in being larger (up to 54 mm in height; *fide* Vera-Peláez & Lozano-Francisco, 2001b, table 4), with a more gradate spire, fewer but stronger axial ribs that are more strongly tuberculose at the shoulder, and more regular spiral sculpture. The protoconch is multispiral composed of about three whorls. It was recorded by those authors to occur together with *G. bonnanii* in the Guadalquivir Basin. Numerous specimens are at hand from those deposits, and it is possible to find intermediate specimens between typical *G. lusitaniae* and *G. bonnanii*. They are highly variable in profile, sculpture and strength of the shoulder (Plate 11, figs 1-4). Moreover, they share the same type of protoconch. We consider *Genota lusitaniae* Vera-Peláez & Lozano-Francisco, 2001 a junior subjective synonym of *G. bonnanii* Bellardi, 1877.

Distribution – Lower Pliocene: Atlantic: Guadalquivir Basin, S. Spain (González Delgado, 1993; Vera-Peláez, 2001b; Landau *et al*., 2011); central Mediterranean, Italy (Bellardi, 1877; Pavia, 1976, 1980; Cavallo & Repetto, 1992; Chirli, 1997; Della Bella & Scarponi, 2007). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002; Vera-Peláez & Lozano-Francisco, 2001b), central Mediterranean, Italy (Bellardi, 1877; Della Bella & Scarponi, 2007).

Genota domenechae **Vera-Peláez & Lozano-Francisco, 2001**
Plate 12, figs 1-6

?1996 *Genota bonnanii* Bellardi, 1877 – Vera-Peláez (*partim*), p. 581, text-figs 51, 52, pl. 42, figs 1-4, 9 only [*non Genota bonnanii* Bellardi, 1877].
?1998 *Genota bonnanii* Bellardi, 1877 – Vera-Peláez & Lozano-Francisco, p. 134, pl. 1, figs 1-4 [*non Genota bonnanii* Bellardi, 1877].
*2001b *Genota domenechae* Vera-Peláez & Lozano-Francisco, p. 38, pl. 3, figs 10-15, pl. 4, figs 12-14, pl. 9, fig. 6.
?2001b *Genota bonnanii* Bellardi, 1877 – Vera-Peláez & Lozano-Francisco (*partim*), p. 70, pl. 1, fig. 7 (?3-5), pl. 3, fig. 9 [?*non Genota bonnanii* Bellardi, 1877].
2002 *Genota domenechae* Vera-Peláez & Lozano-Francisco, 2001 – Vera-Peláez, p. 213, pl. 5, figs A, B, pl. 14, figs C, D.
?2002 *Genota bonnanii* Bellardi, 1877 – Vera-Peláez, p. 213, pl. 5, figs X, Y [*non Genota bonnanii* Bellardi, 1877].

Material and dimensions – Maximum height 38.3 mm, width 12.6 mm. **CO**: NHMW 2020/0171/0250 (1), NHMW 2020/0171/0251 (15), NHMW 2020/0171/0440 (1). **VC**: NHMW 2020/0171/0252-0253 (2), NHMW 2020/0171/0254 (26), NHMW 2020/0171/0438-0439 (2). **VS**: NHMW 2020/0171/0255 (8). **PQ**: NHMW 2020/0171/0320 (1), NHMW 2020/0171/0256 (2), NHMW 2020/0171/0586-0587 (2).

Description – Shell very large, moderately slender fusiform, relatively fragile to moderately thick-shelled, with mid-height gradate spire (apical angle 35.9-47°). Protoconch paucispiral, tall, composed of two convex whorls, with large nucleus, junction marked by sinusigera (dp = 1.1-1.3 mm, hp = 1.13-1.4 mm, dp/hp = ~1.0, dV1 = 850-900 μm, n = 500-700 μm). Teleoconch of up to six weakly angular whorls with moderately broad, weakly concave to weakly convex, subsutural ramp, delimited by obtusely angled, weakly tuberculate shoulder, weakly convex below shoulder. Suture linear, narrowly impressed. Axial ribs represented by about 18 narrow, weak, axially elongated tubercles at shoulder, below opisthocline, weak-

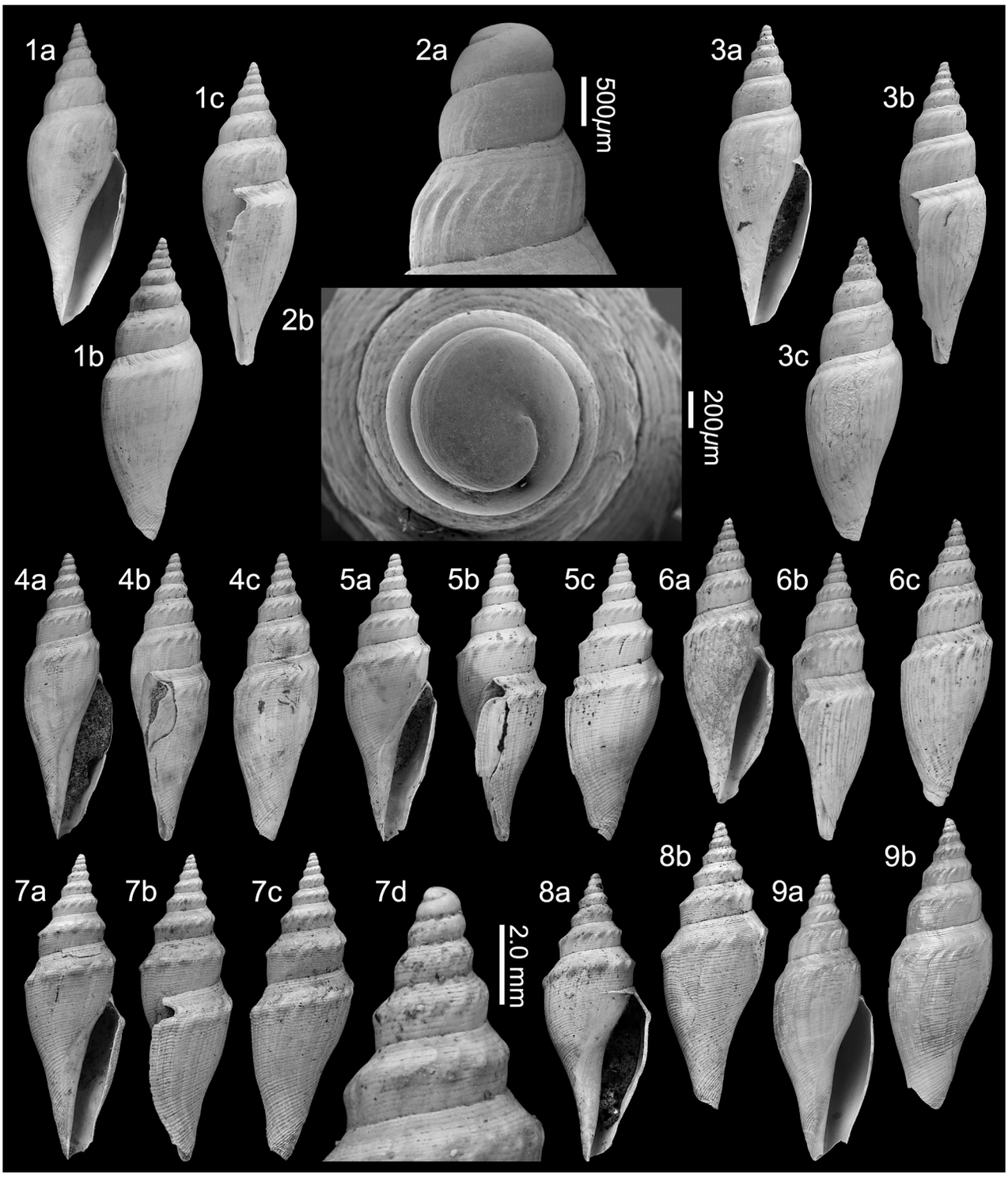

Plate 12. *Genota domenechae* Vera-Peláez & Lozano-Francisco, 2001; 1. NHMW 2020/0171/0252, height 38.3 mm, width 12.6 mm (digital image); 2. NHMW 2020/0171/0253, detail of protoconch (SEM image). Velerín carretera. 3. NHMW 2020/0171/0250, height 37.8 mm, width 11.6 mm. Velerín conglomerates. 4. NHMW 2020/0171/0438, height 34.1 mm, width 10.4 mm; 5. NHMW 2020/0171/0439, height 30.9 mm, width 10.1 mm. Velerín carretera. 6. NHMW 2020/0171/0440, height 35.0 mm, width 11.1 mm (digital images). Velerín conglomerates, Velerín. 7. NHMW 2020/0171/0320, height 42.9 mm, width 13.4 mm; 8. NHMW 2020/0171/0586, height 27.6 mm, width 9.7 mm; 9. NHMW 2020/0171/0587, height 31.5 mm, width 10.8 mm (digital images). Parque Antena Estepona, Lower Piacenzian, Upper Pliocene.

ening towards and not reaching abapical suture. Spiral sculpture of very fine, close-set, flattened, irregular spiral cords separated by narrow grooves over entire surface. Last whorl 70-73% of total height, subsutural ramp weakly concave, shoulder weak, weakly to moderately nodular, whorl weakly convex below, hardly constricted at base. Aperture elongate, 52-56% of total height, outer lip simple; anal sinus broad, relatively deep, symmetrically U-shaped, with apex on abapical half of ramp; siphonal canal relatively long, open, straight, unnotched. Columella almost straight, smooth. Columellar callus reduced to weak callus wash.

Discussion – *Genota domenechae* Vera-Peláez & Lozano-Francisco, 2001 was said to differ from *Genota bonnanii* Bellardi, 1877 in being smaller, thinner shelled, less slender, in having weaker sculpture, a shorter siphonal canal and, above all, in having a paucispiral as opposed to multispiral protoconch. Whilst the above differences tend to be true, there is also a wide range of variability in all teleoconch characters (see Plate 12, figs 1-9). The only reliable character is the protoconch that is paucispiral in all the specimens figured herein from Estepona.
As discussed above, the single record of *G. bonnanii* for the Estepona Pliocene lacks its protoconch and may well represent a coarsely sculptured form of *G. domenechae*. For further discussion see under *G. bonnanii*.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002; Vera-Peláez & Lozano-Francisco 2001b).

Genus *Microdrillia* Casey, 1903

Type species – *Oligotoma meyeri* Cossmann, 1889, by subsequent designation (Cossmann, 1906), Eocene, France.

1903 *Microdrillia* Casey, p. 276.
1925 *Acrobela* Thiele, p. 238. Type species (by original designation): *Bela optima* Thiele, 1925, present-day, East Africa. Junior homonym of *Acrobela* Foerster, 1862 [Hymenoptera].
1977 *Acropota* Nordsieck, p. 18. Type species (by typification of replacment name): *Bela optima* Thiele, 1925, present-day, East Africa. *Nom. nov. pro Acrobela* Thiele, 1925, *non Acrobela* Foerster, 1862 [Hymenoptera].

***Microdrillia crispata crispata* (De Cristofori & Jan, 1832)**
Plate 9, fig. 2; Plate 13, figs 1-2

*1832 *Pleurotoma crispata* De Cristofori & Jan, p. 9.
1847 *Pleurotoma crispata* Cristofori & Jan, 1832 – Bellardi, p. 69, pl. 4, fig. 2.
1877 *Drillia crispata* Jan – Bellardi, p. 131, pl. 4, fig. 21.
1877 *Drillia unifilosa* Bellardi, p. 134, pl. 4, fig. 24.
1915 *Drillia crispata* (Jan) – Harmer, p. 226, pl. 27, figs 22, ?23.
1955 *Drillia crispata* Jan – Malaroda, p. 54, pl. 1, fig. 6.
1937 *Drillia* (*Crassispira*) *bifilosa* Bell. – Montanaro, p. 157 [127], pl. 7 [10], figs 31, 32.
1937 *Drillia* (*Crassispira*) *crispata* (Jan) in Bell. – Montanaro, p. 157 [127], pl. 7 [10], figs 32, 34.
1965 *Microdrillia crispata* (Jan) – Moroni & Torre, p. 35, pl. 1, figs 5, 9.
1968 *Microdrillia crispata* (Jan, 1832) – Robba, p. 595, pl. 45, fig. 8.
1973 *Microdrillia* (*Mircrodrillia*) *crispata* (Cristofori & Jan) 1832 – Caprotti & Vescovi, p. 179, pl. 3, fig. 15.
1974 *Asthenotoma crispata* (Jan, 1832) – Malatesta, p. 418, pl. 31, fig. 1.
1975 *Asthenotoma* (*Drilliola*) *crispata* (De Crist. & Jan) – Di Geronimo, p. 126, pl. 1, fig. 7.
1976 *Microdrillia crispata* (De Crist. & Jan) – Caprotti, p. 48, pl. 17, fig. 15.
1984 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Bernasconi & Robba, p. 268, pl. 1, figs 5, 6.
1986 *Microdrillia crispata* (Cristofori & Jan) – Della Bella & Tabanelli, p. 162, pl. 1, figs 3, 6.
1986 *Microdrillia serratula* (Bellardi) – Della Bella & Tabanelli, p. 164, pl. 1, fig. 4.
1992 *Stenodrillia crispata* (Jan, 1832) – Cavallo & Repetto, p. 134, fig. 354.
1992 *Drillia unifilosa* Bellardi, 1877 – Gatto, p. 486, pl. 1, figs 8-9.
1992 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Gatto, p. 486, pl. 1, fig. 10.
1996 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Vera-Peláez, p. 357, text-fig. 24, pl. 24, figs 1-5, 7, 9, 10.
1997 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Chirli, p. 28, pl. 7, figs 11, 12, pl. 8, figs 1, 2.
2002 *Microdrillia crispata* (Cristofori & Jan, 1832) – Vera-Peláez, p. 194, pl. 2, figs X, Y, Z, pl. 11, figs C, D.
2002 *Microdrillia serratula* (Bellardi, 1877) – Vera-Peláez, p. 194, pl. 2, figs Ñ, O, pl. 11, figs C, D.
2007 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Della Bella & Scarponi, p. 58, figs 111-122.
2008 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Chirli & Richard, p. 62, pl. 12, fig. 6.
2018 *Microdrillia crispata crispata* (Jan, 1832) – Brunetti & Cresti, p. 92, fig. 370.

non 1844 *Pleurotoma crispata* De Cr. et Jan – Philippi, p. 170, pl. 26, fig. 12 [= *Microdrillia loprestiana* (Calcara, 1841)].
non 1854 *Pleurotoma crispata* Jan – Hörnes, p. 367, pl. 39, fig. 13 [= ?*M. teretiaeformis* A.W. Janssen, 1972].
non 1862 *Pleurotoma crispatum* De Cr. et Jan – Brugnone, p. 14, fig. 7 [= *Drilliola emendata* (Monterosato, 1872)].
non 1872 *Pleurotoma crispata* Jan – Wood, p. 35, pl. 6, fig. 13.

non 1891 *Pleurotoma* (q. *Drillia*) *crispata* Jan – Hoernes & Auinger, p. 324, pl. 42, figs 7-10 [= ?*M. teretiaeformis* A.W. Janssen, 1972].

non 1931 *Drillia* (*Crassispira*) *crispata* Jan – Peyrot, p. 163, pl. 7, figs 32, 34.

non 1938 *Drillia crispata* (Jan) – Friedberg, p. 146, text-fig. 47 [= ?*M. teretiaeformis* A.W. Janssen, 1972].

non 1960 *Asthenotoma crispata* Jan – Baldí, p. 85, pl. 3, fig. 7 [= ?*M. teretiaeformis* A.W. Janssen, 1972].

non 1960 *Drillia? crispata* Jan 1832 – Kojumdgieva p. 202, pl. 48, fig. 11 [= ?*M. teretiaeformis* A.W. Janssen, 1972].

non 1964 *Microdrillia crispata* Jan – Anderson, p. 297, pl. 37, fig. 248 [= *M. teretiaeformis* A.W. Janssen, 1972].

non 2003 *Microdrillia crispata* (De Cristofori & Jan, 1832) – Bałuk, p. 52, pl. 17, figs 5-7 [= ?*M. teretiaeformis* A.W. Janssen, 1972].

Material and dimensions – Maximum height 13.4 mm, width 4.8 mm. **CO**: NHMW 2020/0171/0126 (12). **VC**: NHMW 2020/0171/0127-0128 (2), NHMW 2020/0171/0129 (6). **VS**: NHMW 2020/0171/0130 (3).

Description – Shell medium sized, moderately slender turriculate, with a tall, conical spire (apical angle 29.2°). Protoconch tall, conical multispiral, of 3.7-4.0 strongly convex whorls, with small nucleus (Estepona specimen: dp = 1005 μm, hp = 720 μm, dp/hp = 1.40, dV1 = 265 μm, dn = 170 μm), bearing microsculpture: first whorl with irregular spiral cordlets, on second whorl close-set axial riblets become predominant, with irregular, crowded spiral threads in interspaces, forming reticulated pattern, last whorl riblets strengthen, about 34 on last protoconch whorl, and become wider separated, spiral threads weaken. Junction with teleoconch marked by sinusigera and abrupt development of elevated central carina. Teleoconch of up to seven sharply carinate whorls, with shoulder placed mid-whorl, whorl profile concave above and below shoulder, separated by narrowly impressed, linear suture. Spiral sculpture PR 1 and PR 2 appear at protoconch/teleoconch boundary; PR 1 weak, placed just below suture, PR 2 forming elevated shoulder carina. On second whorl PR 3 appears just above suture, weak. Secondary sculpture on spire whorls variably developed and appearing late, on 5th whorl; one or two secondaries between PR2 and PR 3, and PR 3 and suture, not present in all specimens. Fine prominent, arcuate axial riblets over subsutural ramp, continuing below as opisthocline riblets. Last whorl 52-54% of total height; subsutural ramp moderately broad concave, carinate at shoulder, convex below, moderately constricted at base; five primary spirals below carina, with occasional secondary thread intercalated; siphonal fasciole poorly delimited, bearing finer cords. Aperture 39-40% of total height, narrow subquadrate, outer lip sharp; anal sinus broad, very deep symmetrically U-shaped, with apex mid-ramp; siphonal canal moderate length, recurved, shallowly notched. Columella smooth, twisted. Columellar and parietal callus weakly thickened, moderately delimited, forming narrow indented callus margin.

Discussion – The species concept for this taxon used by various authors is unclear and confusing. Traditionally three similar species were recognised. *Microdrillia crispata* (De Cristofori & Jan, 1832) from the Pliocene Mediterranean, *M. serratula* (Bellardi, 1877) from the Middle Miocene of Italy, and the present-day eastern Atlantic and Mediterranean *M. loprestiana* (Calcara, 1841). According to Bernasconi & Robba (1984, p. 269-270), *M. serratula* differed from *M. crispata* in having less dense axial ribbing on the protoconch and a tuberculate shoulder carina. *Microdrillia loprestiana* has a protoconch of at least five whorls (vs. 4-4.75 for *M. crispata*) with coarser and fewer riblets on the protoconch, less convex teleoconch whorls, and a shorter siphonal fasciole.
Della Bella & Tabanelli (1986) recognised a separate form in the Upper Pliocene and Lower Pleistocene of Italy: *M. crispata vatreni* Della Bella & Tabanelli, 1986. This was said to differ from *M. c. crispata* in having a wider apical angle of the protoconch (45-48° vs. 39-43°), larger protoconch, and a tuberculose carina, coalescing on the last whorl to form an irregular shoulder cord. Those authors figured the protoconchs of both subspecies (1986, pl. 1, figs 5a, 6a). Measurements taken from these give: *M. c. crispata*, 3.75 whorls, dp = 745 μm; *M. c. vatreni*, 3.8

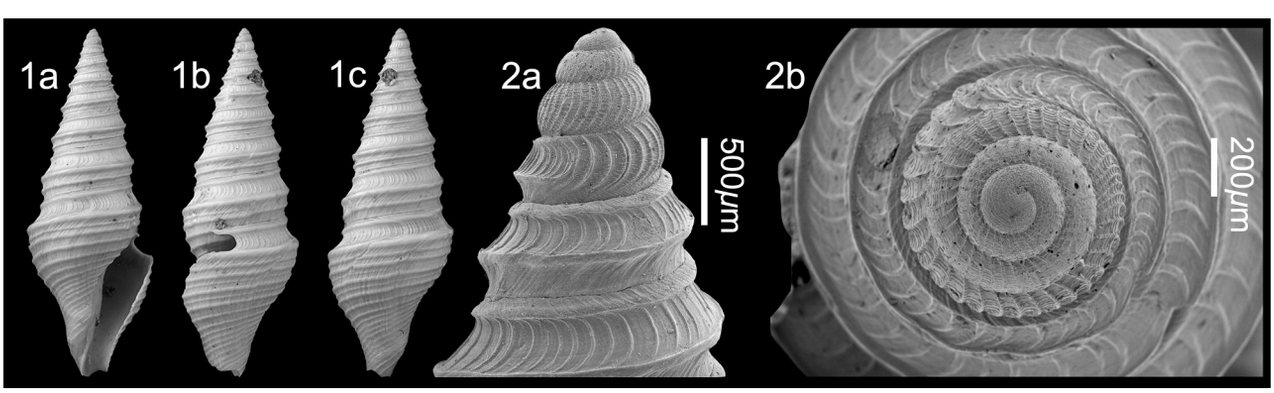

Plate 13. *Microdrillia crispata crispata* (De Cristofori & Jan, 1832); 1. NHMW 2020/0171/0127, height 12.8 mm, width 4.8 mm (digital image); 2. NHMW 2020/0171/0009, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

whorls, dp = 889 μm. *Microdrillia serratula* was said to differ from the Pleistocene subspecies in being larger and having the tubercles on the shoulder carina more strongly developed and continuing sharply delimited onto the last whorl (Della Bella & Tabanelli, 1986, p. 164). Those authors noted that *M. serratula* was a predominantly Miocene species and that their illustrations represented the first Lower Pliocene records (for further discussion see under *M. plioserratula* nov. sp.).

Gatto (1992) and Della Bella & Scarponi (2007, p. 60) argued that there was a gradual transition between *M. crispata* and *M. serratula*. There was a gradual reduction in the number of protoconch whorls. Lower Pliocene specimens usually had more than four protoconch whorls, whereas the 'middle' [*sic*] Pliocene specimens with this number of protoconch whorls was very uncommon. Moreover, Pliocene specimens had a smooth shoulder carina.

Della Bella & Scarponi (2007) noted that *M. crispata vatreni* seemed also to be present, albeit rare, in the Middle Miocene Paratethys (under the name *Pleurotoma adelae* Hoernes & Auinger, 1891). It is unclear what final taxonomic stance those authors took, as the species is named *M. crispata*, not as the subspecies *M. crispata crispata*, and yet the subspecies *M. c. vatreni* is not included in the chresonymy. Furthermore Della Bella & Scarponi finish their discussion with the paragraph "*Per quanto riguarda il morfotipo* serratula *(Bellardi, 1877), da noi mai ritrovato nei depositi studiati, si condivide l'interpretazione di Bernasconi & Robba (1984), nel ritenerlo molto diffuso nel Miocene ed estremamente raro nel Pliocene".* [As far as the *serratula* (Bellardi, 1877) morphotype is concerned, which was not found in the deposits studied, we follow the opinion of Bernasconi & Robba (1984), that it was widespread in the Miocene and extremely rare in the Pliocene.] (2007, p. 60), and yet Bellardi's species is entered in synonymy in their chresonymy.

As far as the Estepona assemblages are concerned, both *M. crispata* and '*M. serratula*' morphotypes are present, although the latter is extremely uncommon. However, they vary in detail from the figures given by the Italian authors discussed above (for further discussion see under *M. plioserratula* nov. sp.). The Spanish specimens of *M. c. crispata* have a protoconch of 3.8-4.0 whorls, which agrees with the whorl count for the post-Lower Pliocene specimens given by Della Bella & Scarponi (2007, p. 60). The apical angle of about 59° and diameter of about 1 mm is far broader than the protoconch angle given by Bernasconi & Robba (1984) and larger than the protoconch figured by for either *M. c. crispata* or *M. c. vatreni* by Della Bella & Tabanelli (1986). The last protoconch whorl has about 34 riblets, which is more than the figure given by Bernasconi & Robba (1984) for *M. crispata* of 21-26 on the last protoconch whorl. The teleoconch characters of the Spanish specimens fit with those given by authors based on Italian specimens.

Two specimens are at hand on the '*serratula*' morphotype. Based on the Spanish material in which the protoconch is slightly abraded and the first protoconch whorl is damaged, the size, number of whorls and sculpture are similar. However, there is a difference in sculpture from the protoconch/teleoconch boundary, PR 1 and PR 2 appear simultaneously, but PR 2 is tubercular and continues strongly so to the aperture, which separates it from *M. c. vatreni*. On the fourth whorl a secondary spiral appears just below the tubercles and PR 3 is mostly obscured by the suture and only becomes fully exposed on the last whorl. There is no further secondary spiral sculpture below the shoulder on the last whorl, the profile is broader (apical angle 49° vs. 32° in *M. c. crispata*), and the last whorl slightly lower and broader. Moreover, there are no intermediate specimens.

Based on the Estepona material it is difficult to consider *M. c. crispata* and '*M. serratula*' a single species, and we therefore separate the two forms at full species rank despite the differences in protoconch shape and sculpture outlined above.

Several other closely related species occur in the European Neogene. According to the original description, *M. teretiaeformis* A.W. Janssen, 1972 from the Middle Miocene North Sea Basin differs from *M. serratula* in having a smaller protoconch with fewer riblets on the last whorl (~13, *fide* A.W. Janssen, 1972, p. 45). However, A.W. Janssen also considered *M. serratula* to occur in the same German deposits at Twistringen and illustrated a specimen (1972, pl. 11, fig. 2). That specimen does indeed have far fewer axial riblets on all whorls and is unlikely to be conspecific with the specimens identified herein as *M. serratula*. This is confirmed for all the other records for *M. serratula* from the North Sean Basin Miocene that are excluded from the synonymy. Apart from the protoconch differences, *M. teretiaeformis* has lirae within the outer lip, absent in *M. c. crispata*, *M. c. vatreni* and *M. serratula*. *Microdrillia aturensis* Lozouet, 2017 from the Atlantic upper Oligocene of France, has a protoconch with far fewer axial riblets, the spire is lower, and has a less prominent shoulder carina.

Landau *et al*. (2013, p. 259) identified specimens from the Middle Miocene eastern Proto-Mediterranean as *M. teretiaeformis* and considered the Middle Miocene Paratethyan specimens illustrated by various authors closer to *M. teretiaeformis* than to *M. crispata*. Kovács & Vicián (2021, p. 141) followed the same position and further commented that the protoconchs of specimens recorded as *M. crispata* from the Paratethys had subangulate whorls with widely-spaced axial riblets while the Pliocene *M. crispata* has rounded protoconch whorls. Moreover, the Paratethyan species has a more pointed protoconch with one whorl more than the Pliocene species. We are not entirely certain that the Paratethyan and North Sea Basin specimens are conspecific, and they may yet represent two distinct species. In any case, neither of these populations represent *M. crispata*.

We have provisionally included Harmer's (1914, pl. 27, fig. 23) record based on a single worn shell. This will require confirmation.

Distribution – Middle Miocene: Proto-Mediterranean, Italy (Bellardi, 1847, 1877). Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1877; Montanaro, 1937; Rob-

ba, 1968; Bernasconi & Robba, 1984). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Moroni & Torre, 1965; Bernasconi & Robba, 1984; Della Bella & Tabanelli, 1986; Cavallo & Repetto, 1992; Chirli, 1997; Brunetti & Cresti, 2018). Upper Pliocene: North Sea Basin: Red Crag, England (Harmer, 1915); western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002), France (Chirli & Richard, 2008); central Mediterranean, Italy (Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976). Lower Pleistocene: central Mediterranean, Italy (Di Geronimo, 1975).

***Microdrillia plioserratula* nov. sp.**
Plate 9, fig. 3; Plate 14, figs 1-2

1986 *Microdrillia serratula* (Bellardi) – Della Bella & Tabanelli, p. 164, pl. 1, fig. 4.
1996 *Microdrillia serratula* (Bellardi, 1877) – Vera-Peláez, p. 365, pl. 24, figs 6, 8, 13, 14.
2002 *Microdrillia serratula* (Bellardi, 1877) – Vera-Peláez, p. 194, pl. 2, figs Ñ, O, pl. 11, figs Ñ, O.

non 1877 *Drillia serratula* Bellardi, p. 133, pl. 4, fig. 22.
non 1981 *Drillia serratula* Bellardi, 1877 – Ferrero Mortara *et al*., p. 72, pl. 13, fig. 6.
non 1891 *Pleurotoma* (r. *Drillia*) *serratula* Bell. – Hoernes & Auinger, p. 325, pl. 42, fig. 1 [? = *Microdrillia adelae* (Hoernes & Auinger, 1891)].
non 1904 *Drillia serratula* var. *pluridenticulata* Sacco, p. 46, pl. 12, fig. 42.
non 1972 *Microdrillia serratula* (Bellardi, 1878 [*sic*]) – A.W. Janssen, p. 45, pl. 11, fig. 2 [= *Microdrillia* sp.].
non 2007 *Microdrillia* aff. *serratula* (Bellardi, 1878 [*sic*]) – Janssen & Wienrich, *in* Wienrich, p. 684, pl. 112, fig. 1, pl. 146, figs 6-7 [= *Microdrillia* sp.].

Type material – Holotype NHMW 2020/0171/0131, height 9.0 mm, width 3.7 mm; paratype 1 NHMW 2020/0171/0132, height 8.2 mm, width 3.6 mm; paratype 2 NHMW 2020/0171/0133 (juvenile)

Other material – Specimen from Lower Pliocene of Rio dè Ronchi (Borgo Rivola, Italy) illustrated by Della Bella & Tabanelli (1986, pl. 1, fig. 4).

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

Type stratum – Lower Piacenzian, Upper Pliocene.

Etymology – name reflecting this Pliocene species' similarity to *Microdrillia serratula* (Bellardi, 1877) from the Middle Miocene of Italy. *Microdrillia* gender feminine.

Diagnosis – *Microdrillia* species of small size, rather squat, with strongly carinate whorls, 14-16 tubercles on carina, strongly constricted at base, short siphonal fasciole.

Description – Shell small, broadly turriculate, rather squat, conical spire (apical angle 37.9-40.2°). Protoconch tall, conical multispiral, of about four strongly convex whorls (dp = 855 μm, hp reconstructed = 1198 μm, dp/hp = 0.71), bearing microsculpture: (nucleus missing, surface early whorls abraded) on second whorl close-set ax-

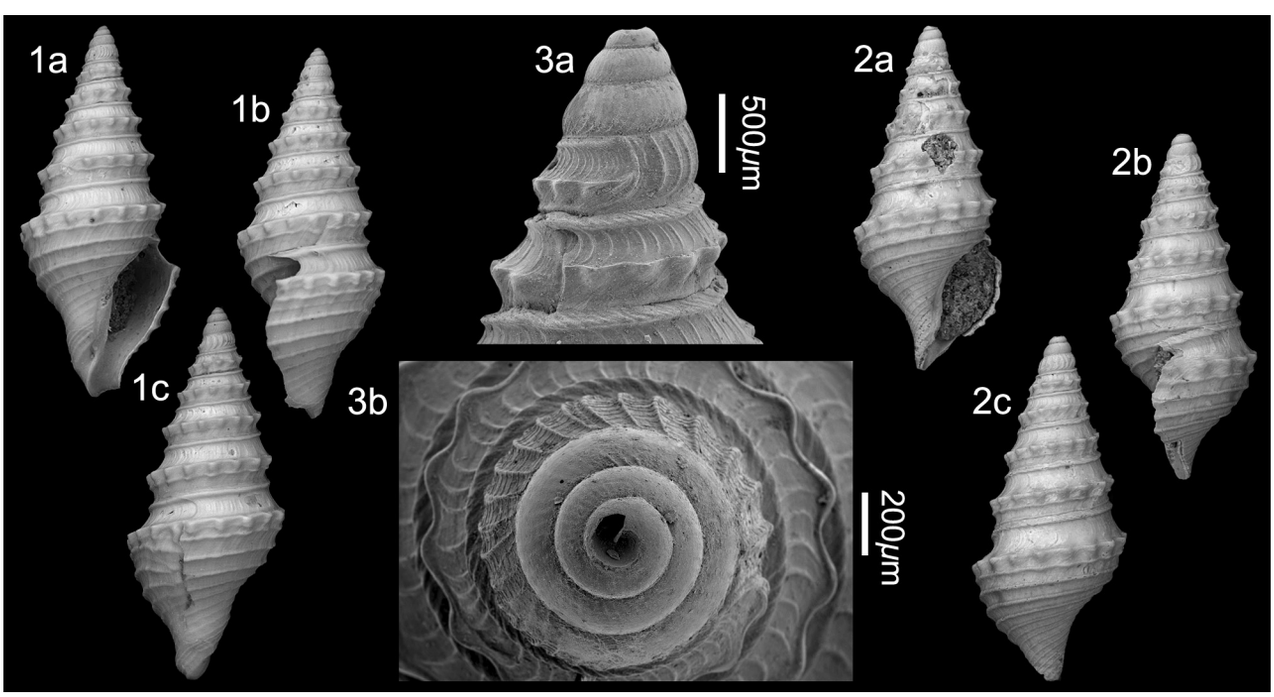

Plate 14. *Microdrillia plioserratula* nov. sp.; 1. **Holotype** NHMW 2020/0171/0131, height 9.0 mm, width 3.7 mm; 2. **Paratype 1** NHMW 2020/0171/0132, height 8.2 mm, width 3.6 mm (digital images); 3. **Paratype 2** NHMW 2020/0171/0133 (juvenile), detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

ial riblets become predominant, with irregular, crowded spiral threads in interspaces, forming reticulated pattern, last whorl riblets strengthen and become wider separated, spiral threads weaken. Junction with teleoconch marked by sinusigera and abrupt development of elevated central carina. Teleoconch of up to five sharply carinate whorls, with shoulder placed mid-whorl, whorl profile concave above and below shoulder, separated by superficial, linear suture. Spiral sculpture PR 1 and PR 2 appear at protoconch/teleoconch boundary; PR 1 moderate strength, placed just below suture, PR 2 forming elevated, strongly tubercular shoulder carina. On second tubercles on carina strengthen, triangular flattened adapical, elongated axially, but not forming ribs. On penultimate whorl single secondary cord develops undulating under tubercles; PR 3 most obscured by abapical suture. Fine arcuate axial riblets over subsutural ramp, weakly developed below carina. Last whorl 57% of total height; subsutural ramp deeply concave, strongly angled at carinate shoulder bearing 14-16 tubercles, convex below, moderately constricted at base; five primary spirals below carina, no secondary sculpture; siphonal fasciole poorly delimited, weakly rounded, bearing finer cords. Aperture 42% of total height, subquadrate, outer lip sharp; anal sinus broad, very deep symmetrically U-shaped, with apex mid-ramp; siphonal canal moderate length, recurved, shallowly notched. Columella smooth, twisted. Columellar and parietal callus weakly thickened, moderately delimited, forming narrow indented callus margin.

Discussion – All authors working with Pliocene assemblages who recognised *Microdrillia serratula* (Bellardi, 1877) as distinct from *M. crispata crispata* (De Cristofori & Jan, 1832) considered the Pliocene specimens conspecific with the Upper Miocene type material (Della Bella & Tabanelli, 1986; Vera-Peláez, 1996, 2002). The syntype illustrated by Ferrero Mortara *et al*. (1981, pl. 13, fig. 6) from the Middle Miocene of the Colli Torinesi seems far more slender, the base is less constricted and the siphonal canal is longer than any of the Pliocene specimens. Furthermore, it has fewer tubercles at the carina (14-16 vs. at least 20 on the last whorl). These differences are also clearly illustrated in the specimen illustrated by Della Bella & Tabanelli (1986, pl. 1, fig. 4) from the Lower Pliocene of Rio dè Ronchi (Borgo Rivola, Italy). We therefore consider these Pliocene forms from Spain and Italy a distinct species: *Microdrillia plioserratula* nov. sp. The Middle Miocene specimen also from the Colli Torinesi described by Sacco (1904, p. 46, pl. 12, fig. 42) as *Drillia serratula* var. *pluridenticulata* is very poorly illustrated. It represents Bellardi's (1877, p. 133) var. A, said to differ from *M. serratula* in having a weaker carina with finer tubercles and is very weakly constricted at the base, further distancing this form from the Pliocene *M. plioserratula*.

The Miocene North Sea Basin specimens illustrated as *M. serratula* by A.W. Janssen (1984, pl. 11, fig. 2) and *M.* aff. *serratula* by Janssen & Wienrich, *in* Wienrich (2007, pl. 112, fig. 1, pl. 146, figs 6-7) represent a further undescribed *Microdrillia* species.

For discussion see under *Microdrillia crispata crispata* (De Cristofori & Jan, 1832).

Distribution – Lower Pliocene: central Mediterranean, Italy (Della Bella & Tabanelli (1986). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002).

Genus *Pseudotoma* Bellardi, 1875

Type species – Murex intortus Brocchi, 1814, by original designation, Pliocene, Italy.

1875 *Pseudotoma* Bellardi, p. 20.

1899 *Acamptogenotia* Rovereto, p. 103. Type species (by typification of replaced name): *Murex intortus* Brocchi, 1814, Pliocene, Italy. Unnecessary substitute name for *Pseudotoma* Bellardi, 1875, by Rovereto, believed to be a junior homonym of "*Pseudotoma* Stephens, 1852", obviously an error for *Pseudotomia* Stephens, 1829 [Lepidoptera].

1924 *Pseudotomina* Finlay, p. 515. Type species (by typification of replaced name): *Murex intortus* Brocchi, 1814, Pliocene, Italy. Unnecessary substitute name for *Pseudotoma* Bellardi, 1875, considered a junior homonym of *Pseudotomus* Cope, 1872 [Mammalia]. Finlay stated the type species to be *P. laevis* Bellardi, 1877, but under Art. 67.8 (ICZN, 1999) the type species of *Pseudotoma* is also the type species of *Pseudotomina*.

Note – Vera-Peláez (2002, p. 214) argued that the valid name should be *Acamptogenotia* Rovereto, 1884 [*sic*] (correct date is 1899). However, as noted above, this is an unnecessary substitute name for *Pseudotoma* Bellardi, 1875, and therefore Bellardi's name has priority.

***Pseudotoma bonellii* (Bellardi, 1847)**
Plate 15, figs 1-2

1839 *Pleurotoma Bonellii* Bellardi, p. 3 (*nomen nudum*).

*1847 *Pleurotoma bracteata* Brocchi (*Murex*) – Bellardi, p. 18, pl. 1, fig. 5.

1874 *Pleurotoma Bonellii* var *elongata* Foresti, p. 359, pl. 1, figs 11-12 [*non Pleurotoma elongata* Deshayes, 1834, *nec* Anton, 1838, *nec* Gray & Sowerby, 1839].

1877 *Pseudotoma Bonellii* Bellardi, p. 218, pl. 7, fig. 13.

1896 *Pseudotoma Bonellii* Bell. – Cossmann, p. 146, pl. 7, figs 11-12.

1904 *Pseudotoma Bonellii* var. *dertolonga* Sacco, p. 113, pl. 24, figs 51, 52.

1904 *Pseudotoma Bonellii* var. *pliocenica* Sacco, p. 113, pl. 24, figs 53, 54.

1904 *Pseudotoma Bonellii* var. *pseudoscalarata* Sacco, p. 113, pl. 24, fig. 55.

1904 *Pseudotoma Bonellii* var. *dertobrevis* Sacco, p. 113, pl. 24, fig. 56.
1904 *Pseudotoma Bonellii* var. *obtusecostata* Sacco, p. 113, pl. 24, fig. 57.
1931 *Genotia* (*Pseudotoma*) *Bonelli* Bellardi – Peyrot, p. 60, pl. 1, figs 2, 3.
1967 *Genota* (*Pseudotoma*) *bonellii* (Bellardi) – Pelosio, p. 167 [67], pl. 46, figs 12-15, 18.
1968 *Genota* (*Pseudotoma*) *bonellii* (Bellardi, 1839 [*sic*]) – Robba, p. 609, pl. 46, fig. 6.
1974 *Genota* (*Pseudotoma*) *bonellii* (Bellardi) 1839 [*sic*] – Caprotti, p. 34, pl. 4, figs 2, 7.
1976 *Genota* (*Pseudotoma*) *bonellii* (Bellardi) – Marasti & Raffi, p. 197, pl. 2, fig. 16.
1978 *Pseudotoma bonellii* Bellardi [*sic*] – Cuscani Politi, p. 37, 38, 43, pl. 4, fig. 13.
1981 *Pseudotoma bonellii* (Bellardi, 1847) – Ferrero Mortara *et al*., p. 82, pl. 16, fig. 8.
1984 *Pseudotoma bonellii* Bellardi, 1877 [*sic*] – Bernasconi & Robba, p. 312, pl. 8, fig. 1.
1992 *Pseudotoma bonellii* Bellardi, 1877 [*sic*] – Cavallo & Repetto, p. 136, fig. 361.
1996 *Pseudotoma bonellii* (Bellardi, 1939 [*sic*]) – Vera-Peláez, p. 595, text-figs 30c, d, 31d, 55, 56, pl. 43, figs 1-4, pl. 44, fig. 4.
1997 *Genota bonellii* (Bellardi, 1939 [*sic*]) – Chirli, p. 100, pl. 28, figs 10-12.
1998 *Pseudotoma bonellii* (Bellardi, 1847) – Vera-Peláez & Lozano-Francisco, p. 145, pl. 2, figs 1-4, 11-13.
2002 *Acamptogenotia bonellii* (Bellardi, 1939 [*sic*]) – Vera-Peláez, p. 214, pl. 5, figs E, F, pl. 14, figs E, F.
2007 *Pseudotoma bonellii* (Bellardi, 1847) – Della Bella & Scarponi, p. 68, figs 135-138.
2008 *Pseudotoma bonellii* (Bellardi, 1847) Bellardi, 1839 (*nomen nudum*) – Chirli & Richard, p. 63, pl. 12, figs 7, 8.
2009 *Pseudotoma bonellii* (Bellardi, 1847) – Zunino & Pavia, p. 359, pl. 2, fig. 4.
2018 *Pseudotoma bonellii* (Bellardi, 1877 [*sic*]) – Brunetti & Cresti, p. 92, fig. 371.

non 1854 *Pleurotoma bracteata* Brocc. – Hörnes, p. 332, pl. 36, fig. 3 [= *Pseudotoma subspinosa* (Boettger, 1902)].
non 1891 *Pseudotoma Bonellii* Bell. vars A and F, G – Hoernes & Auinger, p. 371, pl. 34, figs 5-7, 9, 10 [= *Pseudotoma subspinosa* (Boettger, 1902)].
non 1966 *Acamptogenotia bonellii* Bellardi, 1839 [*sic*] – Strausz, p. 446, pl. 22, figs 3, 4 [= *Pseudotoma subspinosa* (Boettger, 1902)].
non 1994 *Genota* (*Pseudotoma*) *bonellii* (Bellardi, 1839 [*sic*]) – Nikolov, p. 67, pl. 8, figs 1-2 [= *Pseudotoma subspinosa* (Boettger, 1902)].
non 1998 *Genota* (*Pseudotoma*) *bonellii* (Bellardi) – Schultz, p. 76, pl. 31, fig. 9 [= *Pseudotoma subspinosa* (Boettger, 1902)].
non 2003 *Genota* (*Pseudotoma*) *bonellii* (Bellardi, 1939 [*sic*]) – Bałuk, p. 56, pl. 18, fig. 1 [= *Pseudotoma subspinosa* (Boettger, 1902)].

Material and dimensions – Maximum height 23.2 mm, width 11.5 mm. **CO**: NHMW 2020/0171/0272 (1). **PQ**: NHMW 2020/0171/0273 (1), NHMW 2020/0171/0274 (3).

Description – Shell medium sized, broadly biconic, with low, gradate spire (apical angle 58.9-59.1°). Protoconch large, low dome-shaped, multispiral, of 3.5-4 convex whorls, with small nucleus, 2-4 spiral cords on last two protoconch whorls (Estepona specimen: dp = 2080 μm, hp = 1550 μm, dp/hp = 1.34, dV1 = 300 μm, dn = 150 μm). Junction with teleoconch marked by sinusigera. Teleoconch of up to five low, angular whorls, with concave subsutural ramp, sharply angled at shoulder, weakly convex below tapering towards suture, suture deeply impressed undulating. Sculpture on first whorl of weak subsutural cord, stronger shoulder cord, with variable number of secondary cords. Abapically further cords develop of roughly alternate strength, finer over subsutural ramp; spiral sculpture cut by crowded axial growth lines finely beading cords. Axial sculpture of opisthocline ribs, weakly developed over subsutural ramp, stronger below shoulder, overrun by spirals, slightly spinous at intersections. Last whorl tall, 70-71% of total height, with concave subsutural ramp, angled at shoulder, weakly rounded below, moderately constricted at base; base and siphonal fasciole no delimited. Aperture elongate-subquadrate, 52% of total height, outer lip sharp, smooth within; anal sinus broadly and shallowly U-shaped, occupying entire subsutural ramp, with apex mid-ramp; siphonal canal moderate length, slightly recurved and twisted adaxially, unnotched. Columella smooth. Columellar and parietal callus thin, forming broad indented callus margin.

Discussion – Date and authorship of this species were discussed by Tucker & Gatto (1996), who concluded that the *nomen nudum* introduced by Bellardi (1839, p. 3) was made available by Bellardi (1847, p. 18). Tucker & Gatto (1996) selected a lectotype, although a lectotype had already been selected by Bernasconi & Robba (1984, p. 312).
Characteristic, although rather variable species; in some specimens further primary cords below the shoulder may become carinate, with more or less prominent spines produced at the sculptural intersections.
This name has been used for a number of forms ranging from Middle Miocene to Upper Pliocene that we do not consider conspecific. Bernasconi & Robba (1984, p. 312) designated the lectotype as being from the Upper Miocene Tortonian locality of S. Agata Alessandria, Italy (figured by Ferrero-Mortara *et al*., 1981, pl. 16, fig. 8). We have examined specimens from the Tortonian of Italy and can find no difference between these and the Pliocene specimens.
The Paratethyan shells described by numerous authors as *Pseudotoma bonellii* (Bellardi, 1847) differ in having a more elongated shell, the carina is sharper and more elevated resulting in a more strongly biconcave whorl profile. The carina is also placed lower, so that the subsutural ramp is broader with more numerous

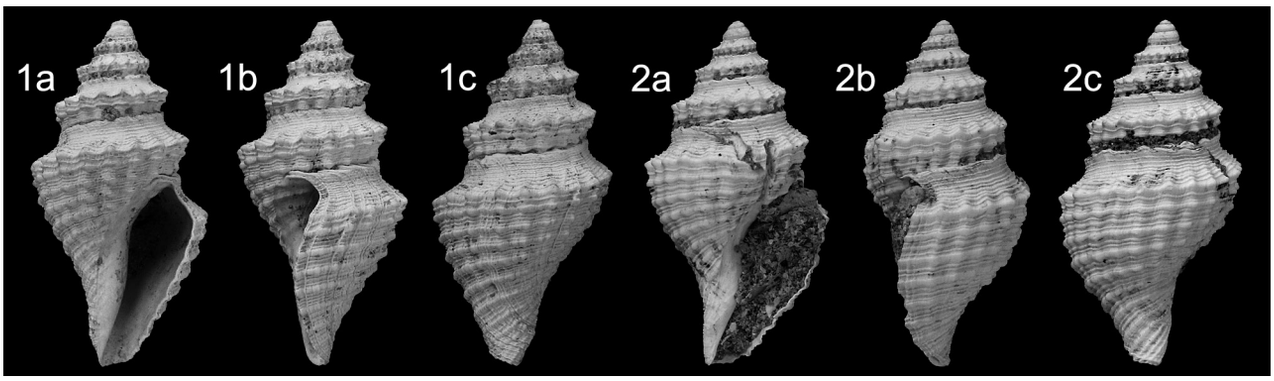

Plate 15. *Pseudotoma bonellii* (Bellardi, 1847); 1. NHMW 2020/0171/0273, height 23.2 mm, width 11.5 mm. Parque Antena. 2. NHMW 2020/0171/0272, height 23.0 mm, width 11.9 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

finely beaded threads and the distance below to the suture reduced. The axial ribs are narrower and form sharper spines over the carina. Below the carina on the last whorl the primary spiral cords are narrower and more clearly divided into cords of primary to tertiary strength. The name *Pseudotoma subspinosa* (Boettger, 1902) is available for this Miocene Paratethyan species. The protoconchs in *P. subspinosa* and *P. bonellii* are the same.

The Paratethyan subspecies *Genota* (*Pseudotoma*) *bonellii botensis* Csepreghy-Meznerics, 1969 was erected for specimens from the Bükk Mountains, Borsodbóta (Hungary). The specimens illustrated by Nikolov (1994, pl. 8, figs 3-5) from the Dacian Basin, Târnene (Bulgaria) seem to be identical to the rest of the Paratethyan specimens considered herein to be *P. subspinosa*.

The Middle and Upper Miocene records of *P. bonellii* from the Atlantic Aquitaine Basin of France (Peyrot, 1931, p. 60, pl. 1, figs 2, 3) seem to be to agree with that species, although we have not seen comparative material from those assemblages.

Pseudotoma bonellii is found in the deeper water deposits in Estepona which coincides with the lower circumlittoral to upper bathyal habitat given by Della Bella & Scarponi (2007, p. 69).

Distribution – Middle Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1931); Proto-Mediterranean, Italy (Bellardi, 1877; Zunino & Pavia, 2009). Upper Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1931); Proto-Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Robba, 1968; Bernasconi & Robba, 1984). Lower Pliocene: central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Pelosio, 1967; Caprotti, 1974; Chirli, 1997; Della Bella & Scarponi, 2007; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996; Vera-Peláez & Lozano-Francisco, 1998, 2002), France (Chirli & Richard, 2008); central Mediterranean, Italy (Marasti & Raffi, 1976; Cavallo & Repetto, 1992).

***Pseudotoma intorta* (Brocchi, 1814)**
Plate 16, figs 1-3

*1814	*Murex intortus* Brocchi, p. 427, pl. 8, fig. 17.
1847	*Pleurotoma intorta* Brocchi (*Murex*) – Bellardi, p. 544, pl. 1, fig. 13.
1877	*Pseudotoma intorta* (Brocch.) – Bellardi, p. 214, pl. 7, fig. 10.
1880	*Pseudotoma intorta* (Brocchi) – Fontannes, p. 258, pl. 12, fig. 31.
1896	*Pleurotoma intorta* Br. – Cossmann, p. 146, pl. 8, fig. 11.
1904	*Pseudotoma intorta* var. *muticocarinata* Sacco, p. 113, pl. 24, fig. 47.
1907	*Pleurotoma intorta* Brocchi – Ravn, p. 355, pl. 7, fig. 4.
1915	*Pseudotoma intorta* (Brocchi) – Harmer, p. 212, pl. 26, fig. 13 (only), ?14 [figs 11-12 = *Pseudotoma intorta nysti* (Glibert, 1954)].
1944	*Genotia* (*Pseudotoma*) *intorta* (Brocchi) – Wenz, p. 1462, fig. 4137.
1955	*Genotia* (*Pseudotoma*) *intorta* (Brocchi 1814) – Rossi Ronchetti, p. 298, fig. 159.
1956	*Acamptogenotia intorta* (Brocchi, 1814) – Rassmussen, p. 96, pl. 10, fig. 1.
1958	*Acamptogenotia intorta* (Brocchi, 1814) – Rassmussen, p. 190, pl. 23, fig. 8.
1966	*Acamptogenotia intorta* (Brocchi, 1814) – Powell, p. 37, pl. 4, fig. 1.
1973	*Genotia* (*Pseudotoma*) *intorta* (Brocchi) 1814 – Caprotti & Vescovi, p. 181, pl. 3, fig. 18.
1974	*Acamptogenotia intorta* (Brocchi, 1814) – Malatesta, p. 411, pl. 31, fig. 22.
1976	*Genota intorta* (Brocchi) – Caprotti, p. 48, pl. 17, fig. 18.
1976	*Genotia* (*Acamptogenotia*) *intorta* (Brocchi, 1814) – Pavia, p. 151, pl. 9, figs 18, 19.
1978	*Murex intortus* Brocchi, 1814 – Pinna & Spezia, p. 150, pl. 37, fig. 5.
1982	*Genotia* (*Acamptogenotia*) *intorta* (Brocchi, 1814) – Martinell, p. 111, pl. 1, figs 21, 22.
1984	*Genotia* (*Acamptogenotia*) *intorta* (Brocchi) –

Martinell *et al*., p. 13, pl. 1, fig. 6.

1984 *Pseudotoma intorta* (Brocchi, 1814) – Bernasconi & Robba, p. 313, pl. 8, fig. 2.

1992 *Pseudotoma intorta* (Brocchi, 1814) – Cavallo & Repetto, p. 136, fig. 363.

1996 *Pseudotoma intorta* (Brocchi, 1814) – Vera-Peláez, p. 587, text-figs 30a, b, 31c, 53, 54, pl. 43, figs 5-10, pl. 44, fig. 3.

1998 *Pseudotoma intorta* (Brocchi, 1814) – Vera-Peláez & Lozano-Francisco, p. 139, pl. 2, figs 5-10.

1997 *Genota intorta* (Brocchi, 1814) – Chirli, p. 102, pl. 29, figs 5-7.

2002 *Acamptogenotia intorta* (Brocchi, 1814) – Vera-Peláez, p. 214, pl. 5, figs C. D.

2005 *Acamptogenotia intorta* (Brocchi, 1814) – Schnetler, p. 109, pl. 7, fig. 13.

2007 *Pseudotoma intorta* (Brocchi, 1814) – Della Bella & Scarponi, p. 70, figs 139-142.

2008 *Pseudotoma intorta* (Brocchi, 1814) – Chirli & Richard, p. 64, pl. 12, fig. 10.

2010 *Pseudotoma intorta* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 46, unnumbered fig. p. 62 middle row centre.

2018 *Pseudotoma intorta* (Brocchi, 1814) – Brunetti & Cresti, p. 92, fig. 373.

non 1845 *Pleurotoma intorta* Brocc. – Nyst, p. 509, pl. 41, fig. 2 [= *Pseudotoma intorta nysti* (Glibert, 1954)].

non 1847 *Pleurotoma intorta* Brocc. – Grateloup, pl. 11, fig. 40 [= *Pseudotoma subintorta* (d'Orbigny, 1852)].

non 1848 *Pleurotoma intorta* Broc. – Wood, p. 53, pl. 6, fig. 4 [= *Pseudotoma intorta nysti* (Glibert, 1954)].

non 1854 *Pleurotoma intorta* Brocc. – Hörnes, p. 331, pl. 36, fig. 1 [*Pseudotoma theresiae* (Hoernes & Auinger, 1891)].

non 1854 *Pleurotoma intorta* Brocc. – Hörnes, p. 331, pl. 36, fig. 2 [*Pseudotoma* sp.].

non 1872 *Pleurotoma intorta* Broc. – von Koenen, p. 233 [= *Pseudotoma escheri* (Mayer, 1861)].

non 1878 *Pleurotoma intorta* Brocc. – Nyst, pl. 3, fig. 11 [= *Pseudotoma intorta nysti* (Glibert, 1954)].

non 1882 *Pleurotoma intorta* Brocc. – Nyst, p. 47 [= *Pseudotoma intorta nysti* (Glibert, 1954)].

non 1915 *Pseudotoma intorta* var. *Morreni* (S.V. Wood non de Koninck) – Harmer, p. 213, pl. 26, figs 15, 16 [= *Pseudotoma intorta nysti* (Glibert, 1954)].

non 1931 *Genotia* (*Pseudotoma*) *intorta* Brocchi – Peyrot, p. 56, pl. 1, figs 23, 27 [= *Pseudotoma praecedens* Bellardi, 1877].

non 1966 *Acamptogenotia intorta* Brocchi, 1814 – Strausz, p. 445, pl. 21, figs 21-24 [= *Acamptogenotia florae* (Hoernes & Auinger, 1891)].

Material and dimensions – Maximum height 54.8 mm, width 19.9 mm. **CO**: NHMW 2020/0171/0441-0443 (3), NHMW 2020/0171/0444 (3). **EL**: NHMW 2020/0171/0445 (1).

Description – Shell very large, solid, moderately broad biconic, with gradate spire (apical angle 40.4-43.8°). Protoconch large, dome-shaped, multispiral, of 3.5 strongly convex whorls, with small nucleus, up to five spiral cords on last two protoconch whorls (*fide* Della Bella & Scarponi, 2007, fig. 139; not preserved in Estepona material). Teleoconch of up to six angular whorls, with concave subsutural ramp, angled at shoulder, weakly convex below, weakly constricted at base, suture superficial, linear. Sculpture of fine spiral cords of alternate strength cover entire whorl surface. Axials reduced to small, rounded tubercles at shoulder, 12 on penultimate whorl. Last whorl tall, 66-70% of total height, with concave subsutural ramp, roundly angled at shoulder, weakly rounded below, weakly constricted at base; siphonal fasciole moderately developed, rounded. Aperture elongate-subquadrate, anal sinus broad, shallow U-shaped, occupying entire subsutural ramp, with apex just below mid-ramp; siphonal canal moderately short, shallowly notched. Columella weakly excavated, smooth. Columellar and parietal forming thin but broad callus rim extending over medial side of venter, forming broad callus rim bordering aperture with indented edge.

Discussion – *Pseudotoma intorta* (Brocchi, 1814) is one of the largest and most solid turrids in the Mediterranean Pliocene, attaining a height of almost 55 mm in the Estepona deposits. It is immediately separated from *Pseu-*

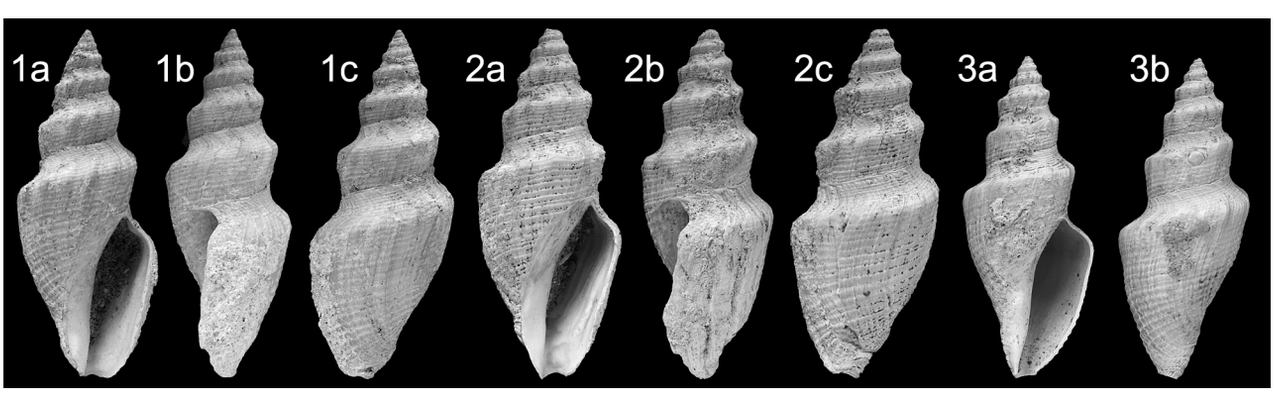

Plate 16. *Pseudotoma intorta* (Brocchi, 1814); 1. NHMW 2020/0171/0441, height 53.2 mm, width 20.9 mm; 2. NHMW 2020/0171/0442, height 53.6 mm, width 21.7 mm; 3. NHMW 2020/0171/0443, height 47.0 mm, width 17.7 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

dotoma bonellii (Bellardi, 1847) by its much larger size, more solid shell, and much weaker sculpture, the axials almost absent, except at the shoulder.
This group is widely distributed in the European Oligocene to Upper Pliocene and undoubtedly represents a species complex rather than a single taxon.
In the Lower Miocene Atlantic of the Aquitaine Basin, France *Pseudotoma girundica* (Peyrot, 1931) is more evenly fusiform with a rounded shoulder and no axial sculpture.
Pseudotoma subintorta (d'Orbigny, 1852) (*nom. nov. pro Pleurotoma intorta* Brocchi *non* Grateloup, 1847) from the Langhian Middle Miocene of Saubrigues, France (Peyrot, 1931, p. 5) differs from *P. intorta* in being squatter, with a less oblique suture and the axial sculpture is very weak but spinous at the shoulder.
In the Middle Miocene Proto-Mediterranean of Italy *Pseudotoma praecedens* Bellardi, 1877 has a squatter profile than *P. intorta*, resulting in a less oblique suture and the shoulder tubercles are rounder and more numerous. *Pseudotoma genei* Bellardi, 1877, *P. orbignyi* Bellardi, 1877 and *P. striolata* Bellardi, 1877 are all almost smooth and and evenly fusiform, unshouldered, and belong to a different group (see Ferrero Mortara *et al*., 1981, pl. 15, fig. 7, pl. 16, figs 1, 2 for syntypes of all three).
In the North Sea Basin Miocene of Belgium *Pseudotoma escheri* (Mayer, 1861) is immediately separated by its paucispiral protoconch and more slender fusiform profile, only weakly shouldered. *Pseudotoma straeleni* (Glibert, 1954) from the same Belgian deposits is a tall-spired species with a relatively short last whorl, the shoulder is more rounded and the axials weaker.
The North Sea Basin Pliocene specimens represent a distinct species/subspecies: *Pseudotoma intorta nysti* (Glibert, 1954) that differs in being larger, higher spired, the shoulder is weaker bearing weaker tubercles, the spiral sculpture is finer, and the last whorl is broader and more strongly constricted at the base.
Therefore, we do not consider *P. intorta* as widely distributed stratigraphically or geographically as described by Della Bella & Scarponi (2007, p. 71), and consider it a member of a species complex rather than a single long-lived and widely distributed species. The Estepona specimens are conspecific with those of the Italian Pliocene and as interpreted herein, *P. intorta* is restricted to the Pliocene Mediterranean.
In Estepona it has only been found in the shallow-water deposits, which coincides with the lower circumlittoral habitat recorded by Della Bella & Scarponi (2007, p. 71).

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Martinell, 1982; Martinell *et al*., 1984; Gili & Martinell, 1993), France (Fontannes, 1880; Cossmann, 1896); central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Pavia, 1976; Bernasconi & Robba, 1984; Cavallo & Repetto, 1992; Chirli, 1997; Della Bella & Scarponi, 2007; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996; Vera-Peláez & Lozano-Francisco 1998, 2002), France (Chirli & Richard, 2008); central Mediterranean (Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Della Bella & Scarponi, 2007).

Family Clathurellidae H. Adams & A. Adams, 1858

For clathurellids the shells are caracterised as small (<10 mm), medium (10-20 mm) large (>20 mm), breadth is described as very broad (SL/MD <2.0), broad (SL/MD 2.0-2.5), moderately broad, (SL/MD = 2.5-2.7), moderately slender (SL/MD = >2.7-3.3), slender (SL/MD >3.3).

Genus *Pleurotomoides* Bronn, 1831

Type species – *Defrancia pagoda* Millet, 1827, by typification of replaced name, Miocene, France.

1827 *Defrancia* Millet, p. 437. Type species (by subsequent designation, Dall, 1908): *Defrancia pagoda* Millet, 1827, Miocene, France. Junior homonym of *Defrancia* Bronn, 1825 [Bryozoa].
1831 *Pleurotomoides* Bronn, p. 555. Type species (by typification of replaced name): *Defrancia pagoda* Millet, 1827, Miocene, France. *Nom. nov. pro Defrancia* Millet, 1827, *non* Bronn, 1825 [Bryozoa].
1848 *Lora* Gistel, 1848, p. ix. Type species (by typification of replaced name): *Defrancia pagoda* Millet, 1827, Miocene, France. *Nom. nov. pro Defrancia* Millet, 1827, *non* Bronn, 1825 [Bryozoa].
1883 *Bellardia* Bucquoy, Dautzenberg & Dollfus, 1883, p. 85, 88. Type species (by typification of replaced name): *Murex gracilis* Montagu, 1803, present-day, British Isles. Junior homonym of *Bellardia* Robineau-Desvoidy, 1863 [Diptera] and *Bellardia* Mayer, 1870.
1883 *Bellardiella* Fischer, p. 593. Type species (by typification of replaced name): *Murex gracilis* Montagu, 1803, present-day, British Isles. *Nom. nov. pro Bellardia* Bucquoy, Dautzenberg & Dollfus, 1882, *non Bellardia* Robineau Desvoidy, 1863 [Diptera]. Junior homonym of *Bellardiella* Tapparone Canefri, 1883 [Pupinidae/Cyclophoridae].
1884 *Comarmondia* Monterosato, p. 135. Type species (by typification of replaced name): *Murex gracilis* Montagu, 1803, by typification of replaced name, present-day, British Isles. *Nom. nov. pro Bellardia* Bucquoy, Dautzenberg & Dollfus, 1883, *non Bellardia* Robineau-Desvoidy, 1863 [Diptera].
1928 *Bellatula* Strand, p. 39. Type species (by typification of replaced name): *Murex gracilis* Montagu, 1803, present-day, British Isles. *Nom. nov. pro Bellardiella* Fischer, 1883 [20 December], *non* Tapparone Canefri, 1883. Junior objective synonym of *Comarmondia* Monterosato, 1884.

Note – Della Bella & Scarponi (2007) used the genus *Clathurella* Carpenter, 1857 (type species *Clavatula rava*

Hinds, 1843, tropical western America) for a group of species very much like those discussed here under *Pleurotomoides* Bronn, 1831. Powell (1966) considered the most important characters in *Clathurella* [in comparison with *Glyphostoma* Gabb, 1873] to be the short siphonal canal, weaker apertural dentition and less impressed anal sinus. Whilst *Clathurella ringens* (Bellardi, 1847) might fit this generic description, all the other species included in that genus by Della Bella & Scarponi (2007) have a long siphonal canal and are probably better placed in *Pleurotomoides*. Landau *et al*. (2013) followed Powell (1966) in placing species within this group with a multispiral protoconch in the genus *Clathurella* and those with a paucispiral protoconch in the genus *Pleurotomoides*. However, in their review of the Upper Miocene Tortonian species of NW France, Landau *et al*. (2020) showed that species with both types of protoconch were included by Millet (1827) in the genus *Defrancia* Millet, 1827 (= *Pleurotomoides*). Therefore, we include all these European Neogene species within the genus *Pleurotomoides*. We note that all the Italian Pliocene species illustrated by Della Bella & Scarponi (2007) have a multispiral protoconch with the last whorls carinate and axial riblets below the carina. This protoconch type is not seen in the Upper Miocene Tortonian species from NW France. However, in an ever increasing group of turrids protoconch type and sculpture is not a constant generic character.

Della Bella & Scarponi (2007) considered *Comarmondia* Monterosato, 1884 a junior subjective synonym of *Clathurella* Carpenter, 1857, however this opinion was not supported by molecular studies (Bouchet *et al*., 2011). *Clathurella* has *Clavatula rava* Hinds, 1843 from tropical West America as type species. As discussed above, the European species included by Della Bella & Scarponi in *Clathurella* are here placed in *Pleurotomoides* Millet, 1827. *Comarmondia gracilis* (Montagu, 1803), the type species for the genus, is extremely similar in teleoconch characters to *Pleurotomoides suturalis* (Millet, 1827) (see Landau *et al*., 2020, p. 19, pl. 15, figs 1-3), which differs in having a paucispiral protoconch. If, as argued above, the protoconch cannot be used as a generic character in this group, *Comarmondia* becomes a synonym of *Pleurotomoides*.

***Pleurotomoides gracilis* (Montagu, 1803)**
Plate 17, figs 1-5

*1803 *Murex gracilis* Montagu, p. 267, pl. 15, fig. 5.
1804 *Murex emarginatus* Donovan, pl. 169, fig. 2.
1814 *Murex oblongus* Renieri var. *exquisite transversim striata* – Brocchi, p. 430, pl. 9, fig. 19.
1829 *Pleurotoma Comarmondi* Michaud, p. 263, unnumbered plate, fig. 6.
1851 *Mangelia gracilis* Montagu – Forbes & Hanley, p. 473, pl. 114, fig. 4, pl. RR, fig. 8.
1867 *Defrancia gracilis* Montagu – Jeffreys, p. 363, pl. 88, fig. 6.
1879 *Clathurella Malenae* De Stefani & Pantanelli, p. 126.
1882 *Pleurotoma gracile* (Mtg.) – Bucquoy *et al*., p. 88, pl. 14, figs 1, 2.
1888 *Clathurella luisae* var. *Malenae* De St. e Pant. – De Stefani, p. 217, pl. 11, fig. 32.
1904 *Bellardiella gracilis* (Mont.) – Sacco, p. 53, pl. 14, figs 2, 3.
1904 *Bellardiella gracilis* var. *obsoletecostata* Sacco, p. 53, pl. 14, fig. 4.
1910 *Daphnella* (*Bellardiella*) *gracilis* Mtg. – Cerulli-Irelli, p. 61 [253], pl. 5 [36], figs 50-53.
1914 *Daphnella* (*Bellardiella*) *gracilis* Montagu – Cipolla, p. 153 [49], pl. 13 [2], figs 26-28.
1915 *Bellardiella gracilis* (Montagu) – Harmer, p. 241, pl. 28, figs 34, 35.
1943 *Comarmondia gracilis* (Montagu) – Wenz, p. 1451, fig. 4107.
1955 *Philbertia* (*Comarmondia*) *gracilis* (Mont.) – Moroni, p. 120, pl. 6, fig. 34.
1960 *Comarmondia gracilis* Montagu, 1803 – Glibert, p. 17, pl. 4, fig. 17, pl. 5, fig. 5.
1963 *Comarmondia gracilis* (Montagu) – Venzo & Pelosio, p. 131, pl. 41, fig. 35.
1966 *Comarmondia gracilis* (Montagu, 1803) – Powell, p. 135, pl. 22, figs 4, 5.
1968 *Comarmondia gracilis* (Montagu) – Nordsieck, p. 174, pl. 29, fig. 94.00.
1970 *Comarmondia gracilis* (Montagu) – Parenzan, p. 207, pl. 44, fig. 840.
1973 *Comarmondia* (*Comarmondia*) *gracilis* (Montagu) – Caprotti & Vescovi, p. 180, pl. 3, fig. 22.
1974 *Comarmondia gracilis* (Montagu, 1803) – Malatesta, p. 436, pl. 31, fig. 11.
1976 *Comarmondia gracilis* (Montagu) – Caprotti, p. 48, pl. 17, fig. 22.
1977 *Comarmondia gracilis* (Montagu, 1803) – Nordsieck, p. 49, pl. 15, fig. 117.
1980 *Comarmondia gracilis* (Montagu, 1803) – Bogi *et al*., p. 16, fig. 14.
1984 *Comarmondia gracilis* (Montagu, 1803) – Bernasconi & Robba, p. 326, pl. 10, figs 3-5.
1985 *Comarmondia gracilis* (Montagu, 1803) – Fretter & Graham, p. 532, fig. 367.
1992 *Comarmondia gracilis* (Montagu, 1803) – Cavallo & Repetto, p. 147, fig. 406.
1996 *Comarmondia gracilis* (Montagu, 1803) – Vera-Peláez, p. 462, text-figs 23h-l, 24c, d, 36, pl. 31, figs 1-13.
1997 *Comarmondia gracilis* (Montagu, 1803) – Chirli, p. 90, pl. 26, figs 1-4.
1999 *Comarmondia gracilis* (Montagu, 1803) – Ardovini & Cossignani, p. 67, 68, unnumbered fig top row middle.
2002 *Comarmondia gracilis* (Montagu, 1803) – Vera-Peláez, p. 204, pl. 3, figs C', D', pl. 12, figs G, H.
2007 *Clathurella gracilis* (Montagu, 1803) – Della Bella & Scarponi, p. 23, figs 29-40.
2010 *Clathurella gracilis* (Montagu, 1803) – Sosso & Dell'Angelo, p. 46, unnumbered fig. p. 62 top row left.
2011 *Clathurella gracilis* (Montagu, 1803) – Chirli & Linse, p. 168, pl. 57, fig. 3.

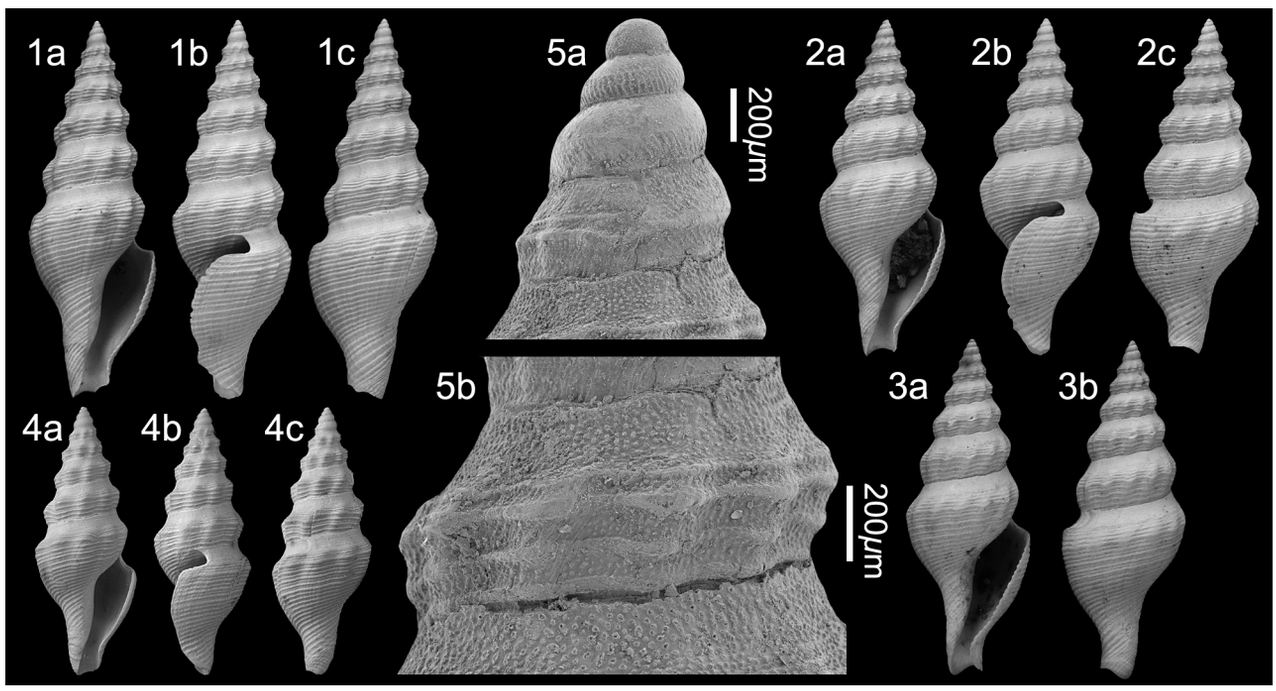

Plate 17. *Pleurotomoides gracilis* (Montagu, 1803); 1. NHMW 2020/0171/0404, height 14.8 mm, width 5.0 mm; 2. NHMW 2020/0171/0405, height 12.4 mm, width 4.5 mm; 3. NHMW 2020/0171/0406, height 12.3 mm, width 4.4 mm; 4. NHMW 2020/0171/0590, height 9.7 mm, width 3.5 mm (digital images); 4. NHMW 2020/0171/0407, 4a, detail of protoconch, 4b, detail of teleoconch microsculpture (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2018 *Clathurella gracilis* (Montagu, 1803) – Brunetti & Cresti, p. 90, fig. 362.
2021 *Comarmondia gracilis* (Montagu, 1803) – Avrithis & Fischer, p. 93, fig. 13.
2022 *Comarmondia gracilis* (Montagu, 1803) – Oliver *et al*., p. 376, figs 7, 42A.

non 1814 *Murex gracilis* Brocchi, p. 437, pl. 9, fig. 16 (= turrid spire fragment, unidentifiable).

Material and dimensions – Maximum height 15.1 mm, width 5.7 mm. **CO**: NHMW 2020/0171/0403 (5). **VC**: NHMW 2020/0171/0404-0407 (4), NHMW 2020/0171/0408 (5), NHMW 2020/0171/0590 (10). **EL**: NHMW 2020/0171/0409 (1).

Description – Shell medium sized, moderately broad fusiform, with tall gradate spire. Protoconch tall, conical, multispiral, consisting of 3.5-4 convex whorls; surface covered in micropustules, last two whorls sharply carinate mid-whorl, with micropustules arranged in prosocline rows (Estepona specimens: dp = 660-820 μm, hp = 940-1090 μm, dp/hp = 0.70, dV1 = 255 μm, dn = 135 μm). Junction with teleoconch marked by sinusigera. Teleoconch of six roundly shouldered whorls with moderate width, concave, subsutural ramp, delimited by rounded shoulder, convex below. Suture shallow, weakly undulating. Sculpture of broad, rounded, orthocline axial ribs (T2 = 8-9, TP = 10-12), slightly narrower than their interspaces, commencing at shoulder, merging abapically with suture, overrun by narrow spiral cords, three on first teleoconch whorl, about eight primary cords on penultimate whorl, with secondaries intercalated; shoulder cord slightly strengthened. Entire surface covered in micropustules. Last whorl 57-60% of total height, with concave subsutural ramp; adapical half of ramp with very faint spiral threads and crowded micropustules, abapical half with 3-4 narrow cords, shoulder delimited by slightly stronger cord, profile convex below, moderately constricted at base; axials weakening below shoulder, subobsolete over base, spirals narrow with secondaries intercalated in some interspaces, strengthening slightly over siphonal fasciole; siphonal fasciole not delimited. Aperture 41-46% of total height, elongate-subquadrate, narrow; anal sinus broad, deeply and asymmetrically U-shaped, with apex on lower half of ramp; outer lip sharp, weakly thickened by varix, smooth within; siphonal canal moderately long, recurved and bent abaxially, notched at tip. Columella weakly excavated, twisted. Columellar and parietal callus hardly thickened, forming narrow callus rim with spiral sculpture over venter showing through; no parietal tubercle developed.

Discussion – The most similar species in teleoconch characters is *Pleurotomoides suturalis* (Millet, 1827) from the Tortonian Upper Miocene of NW France that is immediately separated by its paucispiral protoconch. Apart from the protoconch characters, the French fossil species has weaker axial sculpture than any specimen of *Pleurotomoides gracilis* (Montagu, 1803) we have seen, and the ribs are narrower. *Pleurotomoides vanderdoncki* Landau, Van Dingenen & Ceulemans, 2020, also from

the Tortonian of France, differs in being smaller, with a narrower, more horizontal subsutural ramp, sharper shoulder and stronger axial sculpture, as well as having a protoconch of only two whorls.
Today this species is found at depths of 7-150 m (Fretter & Graham, 1985), although Della Bella & Scarponi (2007, p. 24) noted that Mediterranean specimens did not occur at less than 50 m depth and considered it a circalittoral and upper bathyal species. This latter view is supported by the Estepona distribution, where the species is far more abundant in the deeper water deposits.

Distribution – Upper Miocene, Proto-Mediterranean, Italy (Moroni, 1955; Venzo & Pelosio, 1963). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1915); central Mediterranean, Italy (Sacco, 1904; Bernasconi & Robba, 1984; Cavallo & Repetto, 1992; Chirli, 1997; Della Bella & Scarponi, 2007; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: North Sea Basin, Belgium (Glibert, 1960); western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002); central Mediterranean, Italy (Cipolla, 1914; Caprotti & Vescovi, 1973; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910; Della Bella & Scarponi, 2007); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011), Kos, Greece (Avrithis & Fischer, 2021). Present-day: Atlantic, British Isles (Montagu, 1803; Forbes & Hanley, 1851; Jeffreys, 1867; Fretter & Graham, 1985), continental shelf of Galicia, Spain (Oliver *et al*., , 2022), central Mediterranean (Nordsieck, 1977; Bogi *et al*., 1980; Ardovini & Cossignani, 1999).

***Pleurotomoides littoralis* Vera-Peláez, 2002**
Plate 18, figs 1-3

*2002 *Pleurotomoides littoralis* Vera-Peláez, p. 203, pl. 3, figs T, U, V, W, X, pl. 17, figs M, N.

Material and dimensions – Maximum height 15.1 mm, width 5.5 mm. **CO**: NHMW 2020/0171/0257-0259 (3), NHMW 2020/0171/0260 (1).

Description – Shell medium sized, moderately slender fusiform, with strongly gradate spire. Protoconch tall, conical, multispiral, consisting of 3.5-3.75 convex whorls; surface covered with micropustules, last two whorls sharply carinate mid-whorl, with micropustules arranged in prosocline rows (dp = 790 μm, hp = 925 μm, dp/hp = 0.85, dV1 = 250 μm, dn = 150 μm). Junction with teleoconch marked by sinusigera. Teleoconch of up to 6.5 strongly shouldered whorls with moderately broad, concave subsutural ramp, delimited by roundly angled shoulder, convex below. Suture shallow, weakly undulating. Axial sculpture of rounded, weakly opisthocline ribs (T2 = 8-9, TL = 15-18), slightly narrower than their interspaces, narrowed over subsutural ramp. Ribs persisting to adapical suture, stronger from shoulder to abapical suture, overrun by prominent narrow spiral cords, two on first teleoconch whorl, a third appearing over subsutural ramp on second whorl, abapically with secondaries intercalated in interspaces; secondaries rapidly strengthening to become equal in strength to primaries, cords slightly swollen over intersections. Secondary cords finer, closer-spaced over subsutural ramp. Last whorl 56-59% of total height, with relatively broad, concave subsutural ramp, roundly angled at shoulder, weakly convex below, moderately constricted at base; axials extending narrowed over base, beading cords; siphonal fasciole poorly delimited, with cords only. Aperture 39-42% of total height, ovate; outer lip sharp, with crenulated edge, thickened by strong varix, bearing strong adapical tubercle within delimiting lateral border of anal sinus and weaker abapical tubercle delimiting lateral border of siphonal canal, plus a few short, weak lirae between; anal sinus broad, deeply and asymmetrically U-shaped, with apex on adapical half of ramp; siphonal canal moderately long, straight, slightly recurved shallowly notched. Columella excavated in adapical third, straight below, bearing irregular tubercles along entire length. Columellar callus moderately thickened, parietal callus thin, sharply delimited, forming narrow callus rim; strong bifid parietal tubercle.

Discussion – *Pleurotomoides littoralis* Vera-Peláez, 2002 differs from *Pleurotomoides serventii* Pelosio, 1967 in being slightly broader, having more strongly shouldered

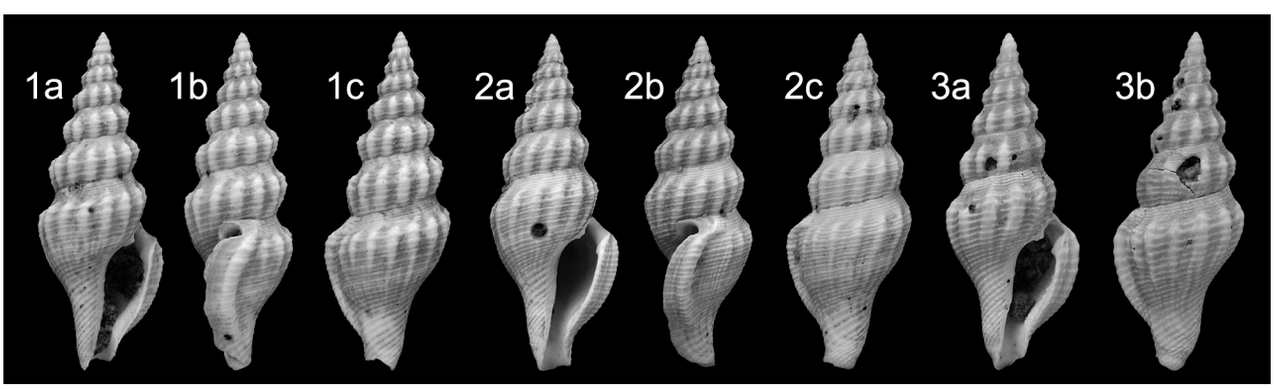

Plate 18. *Pleurotomoides littoralis* Vera-Peláez, 2002; 1. NHMW 2020/0171/0257, height 15.1 mm, width 5.5 mm; 2. NHMW 2020/0171/0258, height 14.8 mm, width 5.2 mm; 3. NHMW 2020/0171/0259, height 14.2 mm, width 5.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

whorls, the spiral sculpture is coarser, the axial ribs are narrowed over the subsutural ramp, but present along the entire spire height, whereas in *P. serventii* they disappear over on the ramp of at least the last two whorls and in *P. littoralis* they continue strongly developed below the shoulder to the abapical suture, whereas in *P. serventii* they weaken on the lower half of the whorl and do not reach the suture. Moreover, the ribs persist over the base, whereas in *P. serventii* they do not. Lastly, the labial varix and apertural dentition are more strongly developed in *P. littoralis*. *Pleurotomoides robbai* (Della Bella & Scarponi, 2007) from the Pliocene of Italy differs in being slightly slenderer elongate and having the siphonal canal longer, more recurved and twisted abaxially.
Pleurotomoides ringens (Bellardi, 1847) from the Pliocene Mediterranean (see below) is smaller, squatter, with fewer broader ribs, and has even stronger apertural armature. Landau *et al*. (2013, p. 260-262) described several species under the genus *Clathurella* Carpenter, 1857 from the Middle Miocene eastern Proto-Mediterranean of the Karaman Basin, Turkey, which we now consider should be placed in *Pleurotomoides* Bronn, 1831. Of these, *Pleurotomoides* sp. (as *Clathurella* sp. pl. 43, fig. 9) is similar in profile to *P. littoralis*, but has fewer, stronger axial ribs. In the Middle Miocene Paratethys, the most similar species in profile and sculpture is *P. densestriata* (Boettger, 1906) from Kostej (Coşteiu de Sus, Romania), but that species differs in having fewer axial ribs and denser spiral sculpture.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 2002).

***Pleurotomoides ringens* (Bellardi, 1847)**
Plate 19, figs 1-5

*1847	*Raphitoma ringens* Bellardi, p. 104, pl. 4, fig. 24.
1877	*Clathurella ringens* Bell. – Bellardi, p. 257, pl. 8, fig. 14.
1877	*Clathurella spreafici* Bellardi, p. 258, pl. 8, fig. 15.
1877	*Clathurella albigonensis* Bellardi, p. 258, pl. 8, fig. 16.
1981	*Clathurella ringens* (Bellardi, 1847) – Ferrero Mortara *et al*., p. 86, pl. 16, fig. 9.
1981	*Clathurella spreafici* Bellardi, 1877 – Ferrero Mortara *et al*., p. 86, pl. 16, fig. 11.
1981	*Clathurella albigonensis* Bellardi, 1877 – Ferrero Mortara *et al*., p. 86, pl. 16, fig. 12.
1984	*Clathurella spreafici* Bellardi, 1877 – Bernasconi & Robba, p. 320, pl. 8, fig. 6, pl. 9, fig. 1.
1997	*Clathurella ringens* (Bellardi, 1847) – Chirli, p. 47, pl. 13, figs 4?, 5?
1997	*Clathurella spreafici* Bellardi, 1877 – Chirli, p. 49, pl. 13, fig. 10.
2007	*Clathurella ringens* (Bellardi, 1847) – Della Bella & Scarponi, p. 26, figs 41-44.

Material and dimensions – Maximum height 9.5 mm, width 4.7 mm. **CO**: NHMW 2020/0171/0468-0471 (4), NHMW 2020/0171/0590 (1).

Description – Shell small, squat broadly fusiform, spire gradate, with relatively wide apical angle (~47°). Protoconch multispiral, last two whorls carinate (apex missing in all specimens; illustrated by Bernasconi & Robba, 1984, pl. 8, fig. 6). Teleoconch of five whorls with narrow, concave subsutural ramp, delimited by rounded, high-placed shoulder, convex below, separated by narrowly impressed, undulating suture. Axial sculpture of broad, weakly prosocline, rounded ribs, nine on last whorl, slightly narrower than their interspaces, subobsolete over subsutural ramp, strengthening from shoulder to abapical suture. Spiral sculpture of prominent, narrow spiral cords, three weaker cords over subsutural ramp, two primary cords of first whorl, adapical forming slightly strengthened shoulder cord; on second whorl third primary develops between existing primaries, rapidly becoming equal in strength; cords slightly swollen over axial ribs. Last whorl broad, with profile and sculpture as described above, roundly angled at shoulder, convex below, moderately constricted at base; axials extending narrowed over base, beading cords; siphonal fasciole moderately delimited, slightly swollen, with cords only. Aperture small, subquadrate; outer lip sharp, with crenulated edge, strongly thickened by varix, bearing adapical tubercle within delimiting lateral border of anal sinus, abapical tubercle delimiting lateral border of siphonal canal, plus a couple of denticles between, denticulation variably developed; anal sinus broad, deeply and symmetrically U-shaped, with apex mid-ramp; siphonal canal moderately short, recurved and bent abaxially, shallowly notched. Columella strongly excavated in adapical third, straight below, bearing 2-3 broad, poorly delimited folds mid-aperture. Columellar and parietal callus poorly developed and delimited, forming narrow indented callus rim; strong parietal tubercle.

Discussion – Bernasconi & Robba (1984, p. 320) considered *C. albigonensis* Bellardi, 1877 (holotype figured by Ferrero Mortara *et al*., 1981, pl. 16, fig. 12) a junior subjective synonym of *Clathurella spreafici* Bellardi, 1877 (holotype figured by Ferrero Mortara *et al*., 1981, pl. 16, fig. 11). Based on a re-examination of type material, Della Bella & Scarponi (2007, p. 26) concluded that there were no significant differences between *C. spreafici* and *C. ringens* (syntype figured by Ferrero Mortara *et al*., 1981, pl. 16, fig. 9); *C. ringens* was squatter, with a wider apical angle and a more squared shoulder, due to a strengthened shoulder cord, and stronger apertural armature. However, they hesitated in formally synonymising the two, as *C. spreafici* was based on a single specimen.
Pleurotomoides ringens (Bellardi, 1847) seems to be uncommon in all deposits. Five specimens are at hand from Estepona that agree with the specimen figured by Della Bella & Scarponi (2007, figs 41-44) from the Pliocene of Italy. The shoulder cord is only slightly strengthened and the apertural armature is variable; strongly developed in most specimens, weak in one (Plate 19, fig. 3), which would support the synonymy proposed by Bernasconi & Robba (1984). In our opinion, *Clathurella spreafici* and

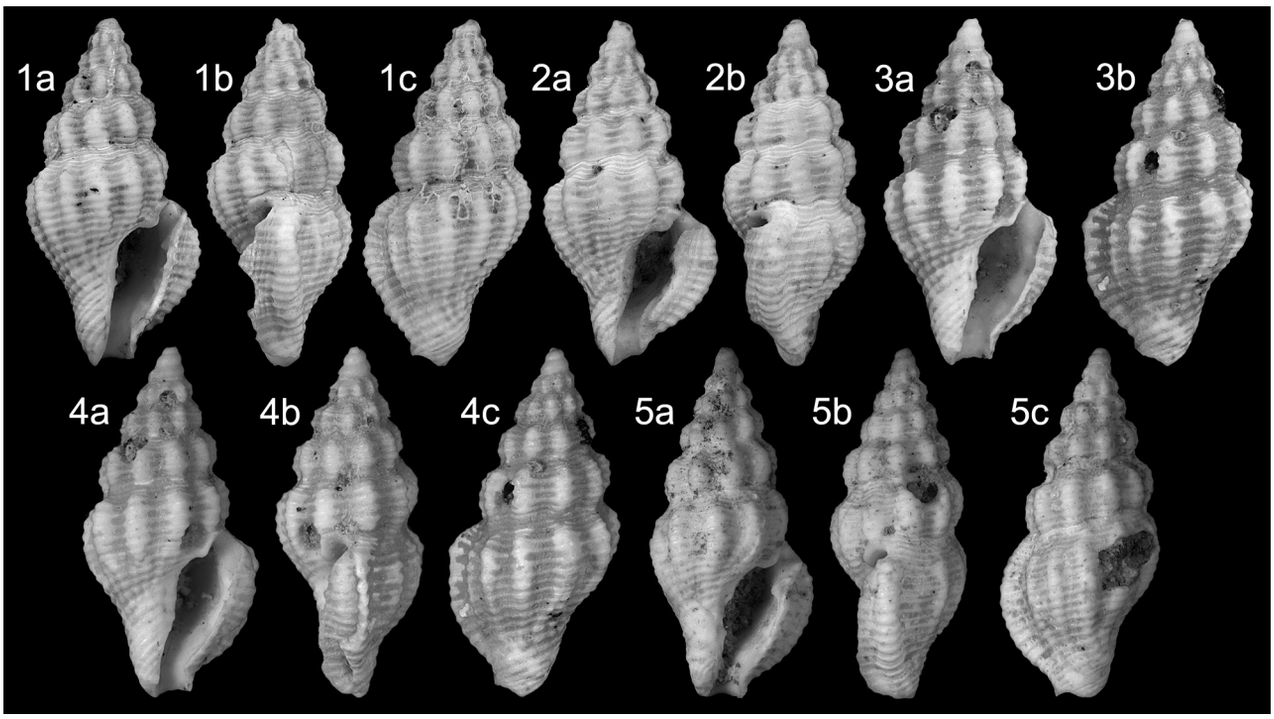

Plate 19. *Pleurotomoides ringens* (Bellardi, 1847); 1. NHMW 2020/0171/0468, height 9.5 mm, width 4.7 mm; 2. NHMW 2020/0171/0469, height 6.7 mm, width 3.2 mm; 3. NHMW 2020/0171/0470, height 7.0 mm, width 3.6 mm; 4. NHMW 2020/0171/0471, height 7.1 mm, width 3.6 mm; 5. NHMW 2020/0171/0590, height 9.0 mm, width 4.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

C. albigonensis are both junior subjective synonyms of *Pleurotomoides ringens*.

It is separated from its congeners by its small size and stockier profile. In the Estepona assemblage it is most like *Pleurotomoides littoralis* Vera-Peláez, 2002, but apart from being smaller and stockier, it has fewer, broader ribs and even stronger apertural armature.

Della Bella & Scarponi (2007, p. 26) noted that in the Italian assemblages *P. ringens* was an infralittoral and circalittoral species, and in Estepona it is found in Velerín conglomerates assemblage, but not the deeper-water deposits, also suggesting a relatively shallow-water habitat.

Pleurotomoides casilorica (Boettger, 1906) from the Middle Miocene Paratethys, but also found in the Middle Miocene eastern Proto-Mediterranean of the Karaman Basin, Turkey (Landau *et al*., 2013, p. 260, pl. 43, figs 4, 5, pl. 70, fig. 5) shares the squat form and short siphonal canal seen in *P. ringens* but differs in having broader ribs and the spiral sculpture is much finer. *Pleurotomoides lienardioides* Lozouet 1999, from the Atlantic upper Oligocene of France, is a squat congener, but is separated by its widely spaced spiral cords.

Distribution – Lower Pliocene: western Mediterranean, NE Spain (Gili & Martinell, 1993); central Mediterranean, Italy (Bernasconi & Robba, 1984; Chirli, 1997; Della Bella & Scarponi, 2007). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper); central Mediterranean, Italy (Bellardi, 1847, 1877).

***Pleurotomoides scalaria* (De Cristofori & Jan, 1832)**
Plate 20, figs 1-4

*1832	*Pleurotoma scalaria* De Cristofori & Jan, p. 9.
1847	*Raphitoma scalaria* Jan (*Murex*) – Bellardi, p. 106, pl. 4, fig. 26.
1877	*Clathurella scalaria* (Jan) – Bellardi, p. 248, pl. 8, fig. 1.
1877	*Clathurella laxecostulata* Bellardi, p. 250.
1904	*Clathurella scalaria* var. *ligustica* Sacco, p. 51, pl. 13, figs 28, 29.
1904	*Clathurella laxecostulata* Bell. – Sacco, p. 51, pl. 13, fig. 30.
1967	*Pleurotomoides* (*Pleurotomoides*) *scalarium* (Jan) – Pelosio, p. 165 [65], pl. 46, fig. 11.
1971	*Pleurotomoides* (*Pleurotomoides*) *scalarium* (De Cr. e Jan, 1832) – Pinna, p. 429, pl. 77, fig. 8.
1978	*Pleurotoma scalaria* De Cristofori & Jan, 1832 – Pinna & Spezia, p. 158, pl. 44, fig. 4.
1984	*Clathurella scalaria* (De Cristofori & Jan, 1832) – Bernasconi & Robba, p. 322, pl. 9, figs 2-4.
1992	*Pleurotomoides scalaria* (De Cristofori & Jan, 1832) – Cavallo & Repetto, p. 136, fig. 365.
1995	*Clathurella scalaria* (De Cr. & Jan) – Tabanelli & Segurini, p. 11, pl. 2, fig. 10.
1996	*Pleurotomoides scalaria* (De Cristofori & Jan, 1832) – Vera-Peláez, p. 447, pl. 32, figs 1-9.
1997	*Clathurella scalaria* (De Cristofori & Jan, 1832) – Chirli, p. 47, pl. 13, figs 6, 7.
1999	*Pleurotomoides scalaria* – Vera-Peláez *et al*., p. 7,

fig. 6.

2002 *Pleurotomoides scalaria* (Cristofori & Jan, 1832) – Vera-Peláez, p. 202, pl. 3, figs Y, Z, pl. 12, figs I, J.

2007 *Clathurella scalaria* (De Cristofori & Jan, 1832) – Della Bella & Scarponi, p. 29, figs 45-48.

2010 *Clathurella scalaria* (De Cristofori & Jan, 1832) – Sosso & Dell'Angelo, p. 46, unnumbered fig. p. 62 top row right.

2018 *Clathurella scalaria* (Cristofori & Jan, 1832) – Brunetti & Cresti, p. 90, fig. 364.

non 1841 *Pleurotoma scalaris* Bellardi & Michelotti, p. 6, pl. 1, fig. 5.

Material and dimensions – Maximum height 18.1 mm, width 7.5 mm. **VC**: NHMW 2020/0171/0337-0338 (2), NHMW 2020/0171/0339 (4), NHMW 2020/0171/0410 (1). **VS**: NHMW 2020/0171/0588 (4). **PQ**: NHMW 2020/0171/0340 (4). **EL**: NHMW 2020/0171/0336 (1).

Description – Shell medium sized, broadly fusiform, with strongly gradate pagodiform spire. Protoconch tall, conical, multispiral, consisting of 3.5-3.75 convex whorls; surface covered with micropustules, last two whorls sharply carinate mid-whorl, with micropustules arranged in close-set, irregular prosocline rows (Estepona specimens: dp = 675 μm, hp = 1000-1030 μm, dp/hp = 0.70, dV1 = 290 μm, dn = 185 μm). Teleoconch of six sharply angular whorls with broad, concave, subsutural ramp, delimited by sharp, acutely-angled and elevated shoulder carina, weakly convex below, tapering in towards suture, suture superficial, linear. Sculpture of narrow, rounded, orthocline axial ribs (T2 = 8-9, TL = 9-17), half to one-third width of their interspaces, commencing at shoulder, weakening rapidly abapically, not reaching suture, overrun by narrow spiral cords, three on spire whorl whorls, with 1-2 weaker cords at periphery of subsutural ramp, no secondaries intercalated on spire whorls; shoulder cord slightly strengthened, sharp. Entire surface covered with micropustules roughly arranged in spiral rows. Last whorl 60-63% of total height, with broad, shallow, concave subsutural ramp, smooth, except for a few weak cords at the periphery, shoulder strongly elevated, sharply carinate, profile weakly convex below, moderately constricted at base; axials obsolete to weak over last whorl, not extending over base, spirals narrow with secondaries in some interspaces, spirals extending over siphonal fasciole that is not developed. Aperture ovate, 45-49% of total height; outer lip sharp, thickened by strong varix, bearing weak adapical tubercle within delimiting lateral border of anal sinus and even weaker abapical tubercle delimiting lateral border of siphonal canal, plus a few short, additional weak lirae on the abapical portion in some specimens; anal sinus moderate width, deeply and asymmetrically U-shaped, with apex on upper half of ramp; siphonal canal long, straight, unnotched. Columella strongly excavated in adapical third, straight below. Columellar and parietal callus hardly thickened, forming narrow callus rim with spiral sculpture over venter showing through; small parietal tubercle.

Discussion – *Pleurotomoides scalaria* (De Cristofori & Jan, 1832) is a very characteristic species with its

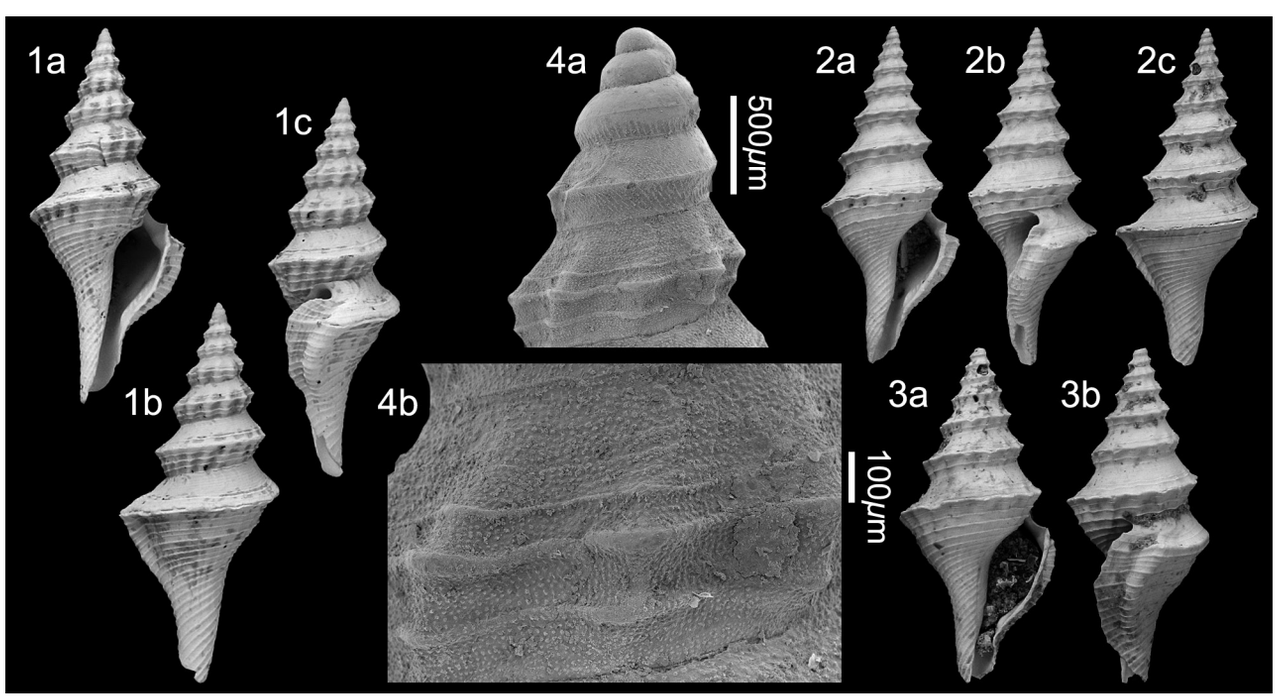

Plate 20. *Pleurotomoides scalaria* (De Cristofori & Jan, 1832); 1. **NHMW 2020/0171/0336, height 15.8 mm, width 6.7 mm.** El Lobillo. 2. NHMW 2020/0171/0337, height 16.7 mm, width 6.8 mm; 3. NHMW 2020/0171/0334, height 16.1 mm, width 7.5 mm (digital images). 4. NHMW 2020/0171/0410, 4a, detail of protoconch, 4b, detail of teleoconch microsculpture (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

strongly elevated shoulder carina and cannot be confused with any of its congeners. In the Upper Miocene Tortonian of north-western France *P. pagoda* (Millet, 1827) is also sharply carinate, but differs in its stouter profile and stronger axial sculpture.
Habitat of this species is considered lower circumlittoral to upper bathyal (Della Bella & Scarponi, 2007, p. 29). In Estepona it is found most commonly in the deeper-water deposits.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1877; Sacco, 1904). Lower Pliocene: western Mediterranean, NE Spain (Gili & Martinell, 1993); central Mediterranean, Italy (Bellardi, 1877; Sacco, 1904; Pelosio, 1967; Pinna, 1971; Bernasconi & Robba, 1984; Cavallo & Repetto, 1992; Chirli, 1997; Della Bella & Scarponi, 2007; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002; Vera-Peláez *et al*., 1999); central Mediterranean, Italy (Tabanelli & Segurini, 1995).

***Pleurotomoides serventii* Pelosio, 1967**
Plate 21, figs 1-4

*1967	*Pleurotomoides* (*Pleurotomoides*) *serventii*	Pelosio, p. 166 [66], pl. 46, figs 9-10.
1992	*Pleurotomoides serventii*	Pelosio, 1967 – Cavallo & Repetto, p. 136, fig. 366.
1996	*Pleurotomoides serventii*	Pelosio, 1966 [*sic*] – Vera-Peláez, p. 455, pl. 33, figs 1-10.
2002	*Pleurotomoides serventii*	Pelosio, 1966 [*sic*] – Vera-Peláez, p. 203, pl. 3, figs A', B', pl. 12, figs K, L.
2007	*Pleurotomoides serventii*	Pelosio, 1967 – Della Bella & Scarponi, p. 31, figs 49-52.

Material and dimensions – Maximum height 19.3 mm, width 7.2 mm. **CO**: NHMW 2020/0171/0589 (1). **VC**: NHMW 2020/0171/0411-0414 (4), NHMW 2020/0171/0415 (21). **VS**: NHMW 2020/0171/0416 (4).

Description – Shell medium sized, moderately broadly fusiform, strongly gradate spire. Protoconch tall, conical, multispiral, consisting of 3.5-3.75 convex whorls; surface covered with micropustules, last two whorls sharply carinate mid-whorl, with micropustules arranged in close-set, irregular prosocline rows (Estepona specimens: dp = 760-800 μm, hp = 1020-1060 μm, dp/hp = 0.75, dV1 = 255 μm, dn = 120 μm). Teleoconch of six roundly shouldered whorls with moderately broad, concave, subsutural ramp, delimited by rounded shoulder, convex below, suture shallow, weakly undulating. Axial sculpture of narrow, rounded, orthocline to weakly opisthocline axial ribs (T2 = 8-9, TL = 12-14), half width of their interspaces, narrow over subsutural ramp, stronger at periphery, weakening again towards abapical suture, overrun by narrow spiral cords, two on first teleoconch whorl, a third appearing over subsutural ramp on second whorl, abapically secondaries intercalated in interspaces; small horizontally elongated tubercles developed on primary cords at intersections. Secondary sculpture on subsutural ramp of fine, close-

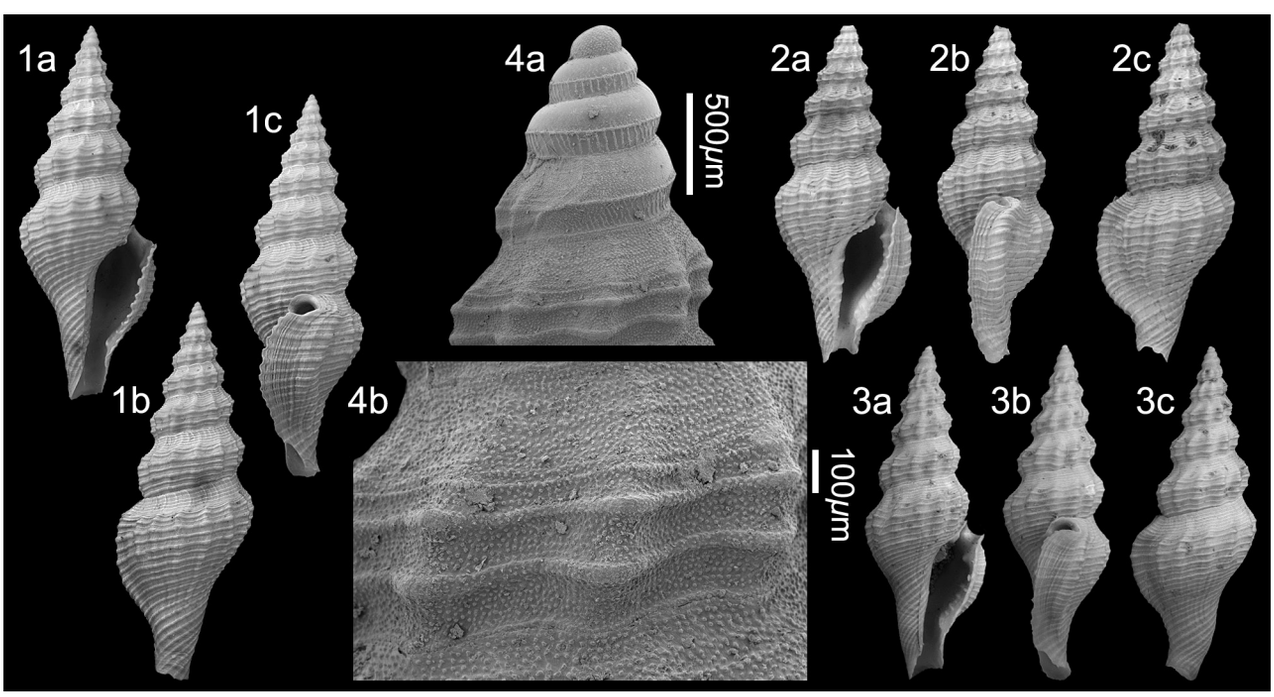

Plate 21. *Pleurotomoides serventii* Pelosio, 1967); 1. NHMW 2020/0171/0411, height 19.3 mm, width 7.2 mm; 2. NHMW 2020/0171/0412, height 16.2 mm, width 6.4 mm; 3. NHMW 2020/0171/0413, height 15.8 mm, width 5.4 mm (digital images). 4. NHMW 2020/0171/0410, 4a, detail of protoconch, 4b, detail of teleoconch microsculpture (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

set spirals, strengthening towards periphery, crossed by arcuate axial riblets forming reticulated pattern; primary axial subobsolete over ramp on last two whorls. Entire surface covered in micropustules roughly arranged in spiral rows. Last whorl 59-60% of total height, with relatively broad, concave subsutural ramp, rounded at shoulder, convex below, moderately constricted at base; axials weakening over base, beading cords; siphonal fasciole not delimited, bearing only cords. Aperture elongate-ovate, 41-42% of total height; outer lip sharp, with crenulated edge, thickened by moderately strong varix, bearing strong adapical tubercle within delimiting lateral border of anal sinus and weaker abapical tubercle delimiting lateral border of siphonal canal, plus a few short, weak lirae between; anal sinus broad occupying entire ramp, deeply and symmetrically U-shaped, with apex mid-ramp; siphonal canal long, straight, unnotched. Columella strongly excavated in adapical third, straight below. Columellar and parietal callus hardly thickened, forming narrow callus rim with spiral sculpture over venter showing through; small parietal tubercle.

Discussion – *Pleurotomoides serventii* Pelosio, 1967 is very similar to *P. robbai* Della Bella & Scarponi, 2007, also from the Italian Pliocene, which differs most importantly in protoconch microsculpture. In *P. serventii* the prosocline riblets seen on the last two protoconch whorls are irregular and close-set axial, whereas in *P. robbai* they are stronger and wider spaced. The two cannot be separated based on teleoconch characters.
Habitat of this species is considered lower circumlittoral to upper bathyal (Della Bella & Scarponi, 2007, p. 31). *Pleurotomoides luisae* (von Koenen, 1872) from the North Sea Basin Miocene of Germany differs from *P. serventii* in having a lower spire, having more convex whorls, broader and rounder ribs, and coarser spiral sculpture, although the series of specimens illustrated by R. Janssen & Wienrich, *in* Wienrich (2007, pl. 149, figs 1-5) show an important degree of intraspecific variability. *Pleurotomoides simplex* (Sorgenfrei, 1958), also from the North Sea Basin Miocene, has weaker sculpture than either *P. luisae* or *P. serventii*. *Pleurotomoides milleti* (Millet, 1827) from the Upper Miocene of north-western France differs from *P. serventii* in having a weak shoulder, more convex whorls, and far more numerous axial ribs. *Pleurotomoides variabilis* (Millet, 1827), also from the Upper Miocene of north-western France, differs in being lower spired, with a broader last whorl, and having weak apertural dentition with no folds on the columella.

Distribution – Lower Pliocene: central Mediterranean, Italy (Pelosio, 1967; Cavallo & Repetto, 1992; Della Bella & Scarponi, 2007). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996, 2002).

Family Mitromorphidae Casey, 1904
(= Diptychomitrinae Bellardi, 1888 = Mitrolumnidae Sacco, 1904)

For mitromorphids the shells are categorised as small (<7.0 mm), medium (7-9 mm), large (>9.0 mm), SL/MD ratio for breadth overlap too much between species to give useful descriptive terms.

Genus and subgenus *Mitromorpha* Carpenter, 1865

Type species – *Daphnella filosa* Carpenter, 1864, *non* Dujardin, 1837 (= *Mitromorpha carpenteri* Glibert, 1954), by monotypy, present-day, California.

1865 *Mitromorpha* Carpenter, p. 182.
1888 *Clinomitra* Bellardi, p. 10. Type species (by monotypy): *Clinomitra rovasendae* Bellardi, 1888, Miocene, Italy.
1937 *Cymakra* Gardner, p. 421. Type species (by original designation): *Cymakra poncei* Gardner, 1937, Miocene, Florida, USA.
1904 *Helenella* Casey, p. 167. Type species (by subsequent designation, Cossmann, 1906): *Pleurotoma multigranosa* E.A. Smith, 1890, present-day, St. Helena.
1922 *Mitrithara* Hedley, p. 233. Type species (by original designation): *Columbella alba* Petterd, 1879, present-day, Tasmania, Australia.

Subgenus *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883

Type species – *Mitra columbellaria* Scacchi, 1836 [*Mitra olivoidea sensu* Bucquoy, Dautzenberg & Dollfus, 1883, *non* Cantraine, 1835], present-day, Mediterranean.

1883 *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, p. 115, 121.

Note – Species in the subgenus *Mitromorpha* Carpenter, 1865 lack well defined columella folds, whereas species in *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883 have two columellar folds, although in Mediterranean species these only develop in fully adult specimens (Amati *et al*., 2015, *inter alia*). *Mitrolumna* was relegated to subgenus rank by Kilburn (1986) and Drivas & Jay (1986) based on having similar radular formulae.

***Mitromorpha* (*Mitrolumna*) *bogii* Amati, Smriglio & Oliverio, 2015**
Plate 22, figs 1-3

?1996 *Mitrolumna olivoidea* (Cantraine, 1835) – Vera-Peláez, p. 311, pl. 19, figs 7, 8, pl. 10, figs 1-12 [*non Mitromorpha* (*Mitrolumna*) *olivoidea* (Cantraine, 1835)].

?2002 *Mitrolumna olivoidea* (Cantraine, 1835) – Vera-Peláez, p. 195, pl. 2, fig. V, pl. 11, figs G, H [*non Mitromorpha* (*Mitrolumna*) *olivoidea* (Cantraine, 1835)].

*2015 *Mitromorpha* (*Mitrolumna*) *bogii* Amati, Smriglio & Oliverio, p. 174, figs 19A-L, 20, 27N, 28G.

Material and dimensions – Maximum height 8.6 mm, width 3.7 mm. **CO**: NHMW 2020/0171/0613 (2). **VC**: NHMW 2020/0171/0117-0119 (3), NHMW 2020/0171/0120 (35). **VS**: NHMW 2020/0171/0121 (4).

Description – Shell small to medium sized for genus, solid, slender biconic. Protoconch paucispiral, of 1.75 convex whorls, with medium-sized nucleus; microsculpture of scattered pustules (dp = 600 μm, hp = 450 μm, dp/hp = 1.33, dV1 = 490 μm, dn = 230 μm). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of 4.5-5 weakly convex whorls, with periphery at abapical suture, separated by narrowly impressed, linear suture. Axial sculpture of narrow, opisthocline ribs, about 13-14 on first teleoconch whorl, widening towards abapical suture. Ribs fade on third whorl, absent from second half penultimate whorl. Spiral sculpture of narrow spiral cords, slightly narrower than their interspaces, 4-5 on first whorl, 7-9 on penultimate whorl, not swollen or forming tubercles at intersections. Last whorl moderately inflated, 71-73% of total height, evenly convex, weakly constricted at base, bearing 26-32 cords, 9-10 above aperture, weakened or obsolete mid-whorl in some specimens, slightly stronger and wider spaced over siphonal fasciole. Aperture elongate, narrow, 49-51% of total height; outer lip not thickened, sharp edged, bearing 7-8 irregular denticles within, two adapical denticles closer spaced and stronger in most fully grown specimens; anal sinus very shallow U-shaped; siphonal canal short, wide, straight. Columella straight, bearing two stout folds deep within, placed mid-aperture. Columellar and parietal callus sharply delimited forming very narrow callus margin.

Discussion – These specimens from Estepona probably fit within the range of variability for *Mitromorpha* (*Mitrolumna*) *bogii* Amati, Smriglio & Oliverio, 2015. Certainly, the shell profile, protoconch dimensions and sculpture, teleoconch sculpture and apertural dentition agree with the Estepona specimens (note: Amati *et al*. do not count the nucleus as the first half protoconch whorl as is done in this paper) (see Table 1). There are a few minor differences: the shells are larger than present-day *M.* (*M.*) *bogii* (maximum height 8.6 mm vs. 7.5 mm), the ribs are more strongly developed than in most specimens of *M.* (*M.*) *bogii* (although one of the specimens illustrated by Amati *et al*., 2015, fig. 19I also has similarly developed ribs), and the early whorls are slightly more swollen just above the suture than in *M.* (*M.*) *bogii*.

Mitromorpha (*M.*) *olivoidea* (Cantraine, 1835) differs from *M.* (*M.*) *bogii* in its colour pattern.

A hazel-tawny background with a row of subsutural blotches more evident on the last whorl in *M.* (*M.*) *olivoidea*, whereas *M.* (*M.*) *bogii* has no colour pattern. Colour preservation in fossil shells is variable, but none of the specimens identified herein as *M.* (*M.*) *bogii* have any colour pattern whereas other congeners in the Estepona deposits do (see below). They also differ in the number of spiral cords (34-39 vs. 25-32 in *M.* (*M.*) *bogii*).

This species is found predominantly in the deeper-water

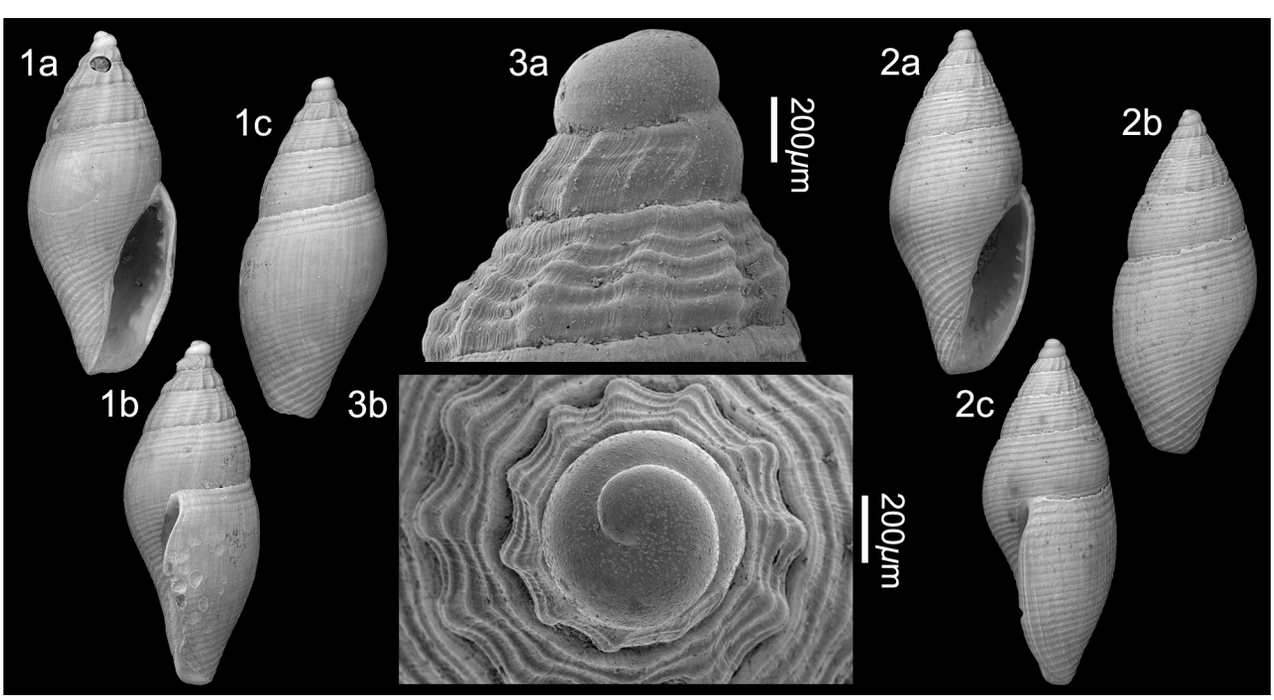

Plate 22. *Mitromorpha* (*Mitrolumna*) *bogii* Amati, Smriglio & Oliverio, 2015; 1. NHMW 2020/0171/0117, height 8.6 mm, width 3.7 mm; 2. NHMW 2020/0171/0118, height 8.6 mm, width 3.5 mm (digital images); 3. NHMW 2020/0171/0119, detail of protoconch (SEM image). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

deposits of Velerín carretera. Amati *et al*., (2015, p. 174) noted that *M.* (*M.*) *bogii* was known only from empty shell found in the Tyrrhenian and Jonian seas at depths of 200-450 m, whereas *M.* (*M.*) *olivoidea* tends to be a shallower-water species (70-160 m depth). However, they also noted that several of the Mediterranean extant species, including *M.* (*M.*) *bogii*, were sympatric (2015, p. 163). This does not seem to be the case in the Estepona deposits where all the deeper-water specimens are this species.
Vera-Peláez (1996, 2002) illustrated a juvenile specimen from the deeper water assemblage of Parque Antena as *Mitrolumna olivoidea*. It is difficult to be certain, but it probably represents this species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper). Present-day: central Mediterranean (Amati *et al*., 2015)

***Mitromorpha* (*Mitrolumna*) *velerinensis* nov. sp.**
Plate 23, figs 1-3

?2010 *Mitromorpha* aff. *tognettii* Della Bella & Scarponi, 2007 – Sosso & Dell' Angelo, p. 46, unnumbered fig. mid row left p. 62.

Type material – Holotype NHMW 2020/0171/0113, height 9.4 mm, width 4.2 mm; paratype 1 NHMW 2020/0171/0114, height 8.1 mm, width 3.6 mm; paratype 2 NHMW 2020/0171/0115 (juvenile); paratype 3 NHMW 2020/0171/0611, height 8.2 mm, width 3.5 mm; paratype 4 NHMW 2020/0171/0612, height 8.3 mm, width 3.5 mm.

Other material – **CO**: NHMW 2020/0171/0116 (36).

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

Type stratum – Lower Piacenzian, Upper Pliocene.

Etymology – Named after the type locality of Velerín, Estepona, Spain. *Mitromorpha* gender feminine.

Diagnosis – *Mitromorpha* (*Mitrolumna*) species with smooth paucispiral protoconch, 5-5.5 teleoconch whorls, axial sculpture of 13-15 ribs restricted to first two teleoconch whorls, spiral sculpture of three cords on first whorl, on later spire whorls cords fade towards lower suture, last whorl with three subsutural cords, mid portion smooth, cords over base and fasciole, 4-6 irregular labial denticles.

Material and dimensions – Maximum height 9.4 mm, width 4.2 mm. **CO**: NHMW 2020/0171/0113-0115 (3), NHMW 2020/0171/0116 (8).

Description – Shell medium to large for genus, solid, moderately slender biconic. Protoconch paucispiral, of 1.75 convex whorls, with medium-sized nucleus; no microsculpture (dp = 560 μm, hp = 500 μm, dp/hp = 1.12, dV1 = 420 μm, dn = 195 μm). Junction with teleoconch sharply delimited by sinusigera. Teleoconch of 5.0-5.5 weakly convex whorls, with periphery at abapical suture, separated by narrowly impressed, linear suture. Axial sculpture of narrow, opisthocline ribs, about 13-15 on first teleoconch whorl, widening towards abapical suture. Ribs fade on second whorl, absent on last 3.0-3.5 whorls. Spiral sculpture

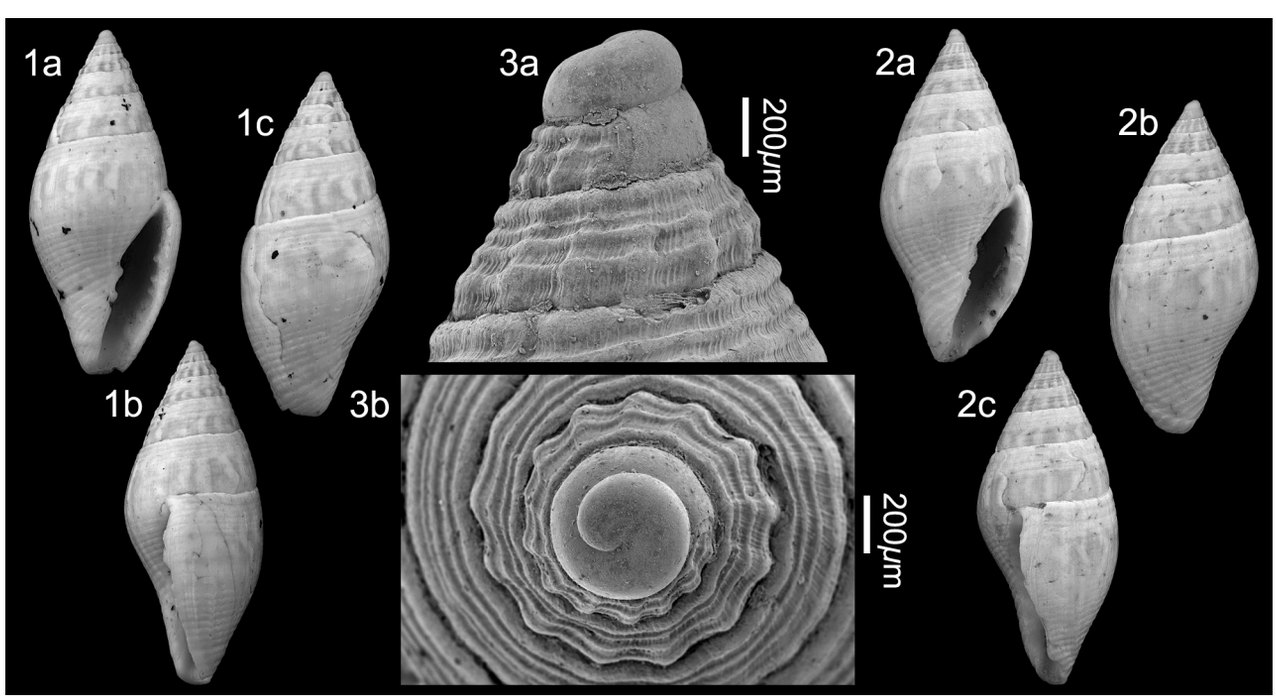

Plate 23. *Mitromorpha* (*Mitrolumna*) *velerinensis* nov. sp.; 1. **Holotype** NHMW 2020/0171/0113, height 9.4 mm, width 4.2 mm; 2. **Paratype 1** NHMW 2020/0171/0114, height 8.1 mm, width 3.6 mm (digital images); 3. **Paratype 2** NHMW 2020/0171/0115 (juvenile), detail of protoconch (SEM image). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

of narrow spiral cords, slightly narrower than their interspaces, three on first whorl, on second whorl further cord intercalated between the upper two cords, fourth cord appears just above suture, 5-7 on penultimate whorl, fading towards abapical suture. Last whorl moderately inflated, 69-70% of total height, evenly convex, weakly constricted at base, bearing 15-17 cords, three strongly developed cords just below suture, surface smooth mid-whorl, cords reappear on the base and siphonal fasciole, slightly stronger and wider spaced over fasciole. Aperture elongate, narrow, 47-48% of total height; outer lip not thickened, sharp edged, bearing 4-6 irregular denticles within, adapical denticle stronger in most fully grown specimens; anal sinus very shallow U-shaped; siphonal canal short, wide, straight. Columella straight, bearing two stout folds deep within, placed mid-aperture. Columellar and parietal callus sharply delimited forming very narrow callus margin. Colour pattern preserved of vertical white flammules over orange background on spire whorls below subsutural ramp and above aperture on last whorl.

Discussion – In its colour pattern, *Mitromorpha* (*Mitrolumna*) *velerinensis* nov. sp. is reminiscent of *M.* (*M.*) *karpathoensis* (Nordsieck, 1969), but differs in being larger, having the axial ribs fading earlier; in *M.* (*M.*) *karpathoensis* ribs are usually present on the penultimate whorl, the outer lip is not 'pinched' mid-whorl as it is in *M.* (*M.*) *karpathoensis*, and it has fewer labial denticles (see Table 1). Moreover, the light blotches below the suture are broader and wider spaced in *M.* (*M.*) *karpathoensis. Mitromorpha* (*M.*) *olivoidea* (Cantraine, 1835) is similar in size and number of teleoconch whorls but differs from *M.* (*M.*) *velerinensis* in having far more numerous cords on the last whorl and usually more numerous labial denticles (see Table 1).
The specimen from the Lower Pliocene of Rio Torsero (Italy) illustrated by Sosso & Dell'Angelo (2010, p. 62) as *Mitromorpha* aff. *Tognettii* Della Bella & Scarponi, 2007 may well represent this species. *Mitromorpha* (*M.*) *tognettii* described from the Lower Pliocene of Villa Filicaia (Italy) is similar to *M.* (*M.*) *velerinensis* in having the spiral cords on the last whorl developed just below the suture and on the base, with a smooth mid-whorl, but differs in being smaller, lower H/W ratio, having fewer, broader axial ribs that persist longer even onto the penultimate whorl on one of the paratypes (Della Bella & Scarponi, 2007, fig. 107), and fewer cords on the last whorl (see Table 1). The Italian Pliocene specimen from Bologna (Italy) figured by Della Bella & Scarponi (2007, figs 92-94 as *M.* (*M.*) cf. *karpathoensis* is also similar but has coarser spiral sculpture. Comparing the spiral sculpture on the second teleoconch whorl, in the Estepona specimen a narrower secondary is intercalated between the two adapical cords and a further broad cord appears just above the suture, whereas in the Italian specimen no further cords are intercalated until the penultimate whorl (Della Bella & Scarponi, 2007, figs 92, 94).

Distribution – ?Lower Pliocene: central Mediterranean, Italy (Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

Species removed from Mitromorphidae

***Fedosovia multigranosa* (Vera-Peláez, 2002)**
Plate 24, fig. 1

*2002 *Anarithma*? *Multigranosa* Vera-Peláez, p. 196, figs 2S-U.

Material and dimensions – Height 6.3 mm, width 2.9 mm. **VC**: NHMW 2020/0171/0002 (1).

Species	H	W	H/W	Nw	Nrfw	Nrpw	Nslw (aa)	Nd	Sts
M. (M.) bogii (extant)	6.20-7.50	2.90-3.45	1.956-2.407	4.2-4.5	14-15	absent	25-34 (7-10)	6-11	4-5
M. (M.) bogii (Estepona)	6.45-8.58	2.97-3.60	2.245-2.457	4.5-4.8	13-14	absent	26-32 (9-10)	7-8	4-5
M. (M.) karpathoensis (extant)	6.00-7.90	2.70-2.90	1.910-2.272	4.5-5.2	11-13	20	18-25 (3-4)	10-11	3
M. olivoidea (extant)	8.30-9.50	4.10-4.55	2.021-2.306	5.2-5.5	10-14	absent	34-39 (8-11)	6-9	3-4
M. (M.) velerinensis (Estepona)	7.88-9.37	3.64-4.18	2.214-2.416	5.0-5.5	13-15	absent	15-17 (2-3)	4-6	3
M. (M.) tognettii (Pliocene Italy)	3.9-4.8	1.9-2.5	1.833-2.052	4.0	9-10	present or absent	9-12 (2)	5	2-3

Table 1. Ranges of morphometric characters for *Mitromorpha* (*Mitrolumna*) sp., compared to congeners. Measurements in mm. H: height; W: width; H/W; ratio height/width; Nw: number of whorls; Nrfw: number axial ribs on the first whorl; Nrpw: number axial ribs on the penultimate whorl; Nslw (aa): number of spirals on the last whorl (above the aperture); Nd: number of denticles; Sts: starting number of spiral cordlets (adapted from Amati *et al*., 2015, p. 185, table 1).

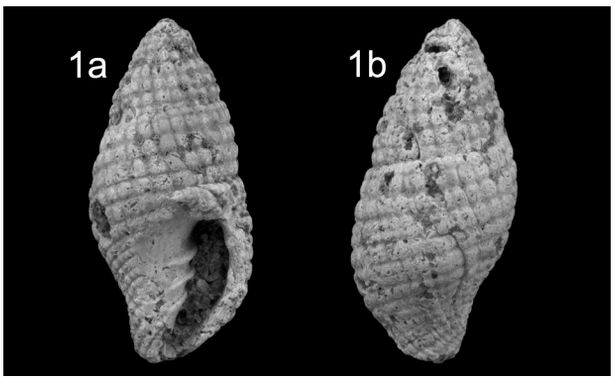

Plate 24. *Fedosovia multigranosa* (Vera-Peláez, 2002); l. NHMW 2020/0171/0002, height 6.3 mm, width 2.9 mm. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Discussion – This species was described within the genus *Anarithma* Iredale, 1916, now placed in the family Mitromorphidae Casey, 1904. Whilst mitromorphid turrids do have columellar folds, they are not as strong or as sharp as those seen in this species. Moreover, the teleoconch sculpture seen in the Estepona species of rows of squarish tubercles is different from that seen in some species of *Anarithma*, in which small tubercles are developed at the sculptural intersections. In our opinion, the Estepona shell should be placed in the family Costellariidae MacDonald, 1860. It is highly reminiscent in sculpture to members of the genus *Fedosovia* Harzhauser & Landau, 2021, although smaller shelled than the Miocene Paratethyan *F. fuchsi* (Hoernes & Auinger, 1880). The protoconch was illustrated by Vera-Peláez, (2002, fig. 2U) and is paucispiral, similar to that of the Paratethyan species (see Harzhauser & Landau, 2021, fig. 4G). *Fedosovia multigranosa* seems to be exceedingly uncommon in the Estepona assemblage, as only the holotype and this specimen are known, both are incomplete.

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

Family Pseudomelatomidae Morrison, 1965
(= Crassispirinae McLean, 1971, Strictispirinae, Strictispiridae McLean, 1971, Zonulispirinae McLean, 1971)

For pseudomelatomids the shells are categorised as small (<15 mm), medium (15-30 mm), large (>35 mm), breadth is described as broad (SL/MD <3), moderately slender (SL/MD = 3-3.2), slender (SL/MD >3.2).

Genus *Crassispira* Swainson, 1840

Type species – *Pleurotoma bottae* (Valenciennes *in* Kiener, 1839), by subsequent designation (ICZN Opinion 754, 1965), present-day, tropical East Pacific.

1840 *Crassispira* Swainson, p. 153, 313.

Note – Vera-Peláez (2002) recognised four *Crassispira* species in the Estepona assemblages, three of which were described as new. The specimens identified by that author as *Crassipira brocchii* (Bellardi & Michelotti, 1841) represent two species: *C. geslini* (Desmoulins, 1842) and *C. leonardiana* Ceregato & Della Bella, 2003. Both of these are large shelled and easily separable from the other three that are small to medium sized. *Crassispira octoacutangula* Vera-Peláez, 2002 with its squat profile, broad ribs starting abruptly at the shoulder and much reduced spiral sculpture only present below the shoulder on the last whorl is also easily characterised.
The other two, *C. plioparvula* Vera-Peláez, 2002 and *C. velerinensis* Vera-Peláez, 2002 are problematic. According to the original descriptions, both are small sized, relatively slender, have the same number of axial ribs, fine spiral sculpture in which the number of spirals stated overlap between the two species, a shallow U-shaped anal sinus, and a short siphonal canal. The illustrations (Vera-Peláez, 2002, P, Q and R, S) are of little help. Both holotypes are based on worn shells whilst, although magnified, all images are out of focus, with areas over and under-exposed, and little detail clearly visible. Unfortunately, neither of these taxa were recognised in his thesis (Vera-Peláez, 1996), which is slightly better illustrated. Moreover, the holotype of *C. plioparvula* shows extensive signs of predation and repair, distorting the sculpture and *C. velerinensis*, based on a single specimen, is abraded and missing its apex. The discussion is also not helpful. *Crassispira plioparvula* is only compared to *C. octoacutangula* which, as stated above, is easily separated, and *C. velerinensis* is not explicitly compared with any of its congeners. Two of the three specimens comprising the type series of *C. plioparvula* are from a locality called 'Finca de Franco', the third is from Velerín [conglomerates suggested by preservation]. 'Finca de Franco' is another name for what is called by our team the El Lobillo locality, again adding to the probability that the material herein (which is all from El Lobillo) is atrributable to that species. *Crassispira velerinensis* is based on a single shell from Velerín [conglomerates suggested by preservation]. All our specimens of *C. velerinensis* are from the Velerín conglomerates.

***Crassispira geslini* (Desmoulins, 1842)**
Plate 25, figs 1-4

*1842 *Pleurotoma Geslini* Desmoulins, p. 178.
1877 *Drillia Geslini* (Desm.) – Bellardi, p. 104, pl. 3, fig. 30.
1914 *Drillia* (*Crassispira*) *Geslini* Desmoulins – Cipolla, p. 119 [15], pl. 12 [1], fig. 7.
1996 *Crassispira* (*Crassispira*) *brocchii* (Bellardi, 1847) [*sic*] – Vera-Peláez (*partim*), p. 429, pl. 29, figs 5-8 (only) (not pl. 29, figs 1-4 = *Crassispira leonardiana* Ceregato & Della Bella, *in* Scarponi & Della Bella, 2003; not 9-11).
1997 *Crassispira seiuncta* (Bellardi, 1877) – Chirli (*partim*), p. 10, fig. 4 (only).

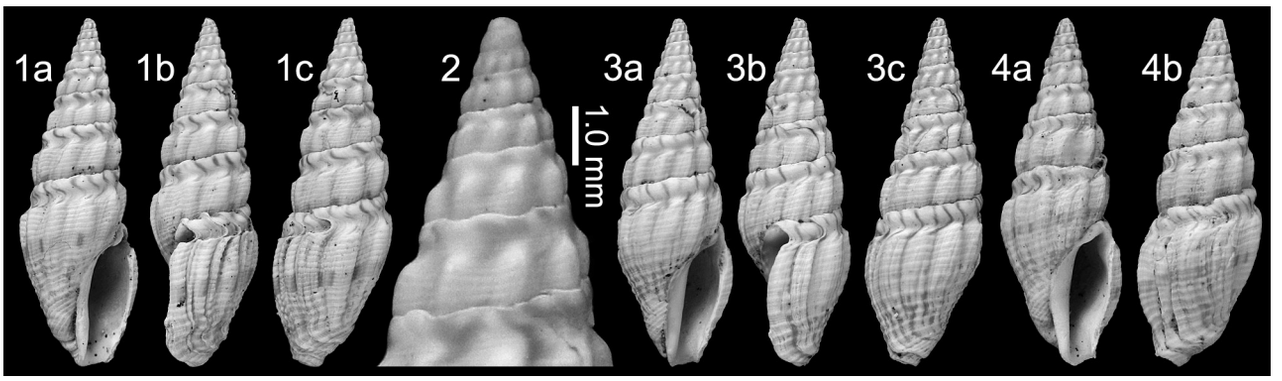

Plate 25. *Crassispira geslini* (Desmoulins, 1842); 1. NHMW 2020/0171/0326, height 35.8 mm, width 11.3 mm; 2. NHMW 2020/0171/0327, height 22.5 mm (juvenile), detail of protoconch and early teleoconch whorls; 3. NHMW 2020/0171/0328, height 32.6 mm, width 11.2 mm; 4. NHMW 2020/0171/0329, height 29.7 mm, width 10.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

2002 *Crassispira* (*Crassispira*) *brocchii* (Bellardi, 1847) [*sic*] – Vera-Peláez (*partim*), p. 198, pl. 3, figs ?L, M (not pl. 12, figs C, D = *Crassispira leonardiana* Ceregato & Della Bella, *in* Scarponi & Della Bella, 2003).

2003 *Crassispira geslini* (Des Moulins, 1842) – Scarponi & Della Bella, p. 49, figs 61, 62, 76.

Material and dimensions – Maximum height 37.8 mm, width 10.9 mm. **CO**: NHMW 2020/0171/0326-0329 (4), NHMW 2020/0171/0330 (32).

Description – Shell medium to large sized, very solid, moderately slender turriform, with tall conical spire (apical angle 31.7-33°). Protoconch paucispiral, of 1.5 convex whorls with medium sized nucleus (Estepona specimen: dp = 440 μm, hp = 440 μm, dp/hp = 1, dV1 = 310 μm, dn = 140 μm). Junction with teleoconch marked by sinusigera. Teleoconch of up to nine whorls, with periphery at abapical suture, separated by narrowly impressed weakly undulating suture. Spire whorls with moderately well developed, weakly nodular subsutural collar, adapically delimiting narrow, deeply concave subsutural ramp, rounded to weakly angled at shoulder placed at about two-thirds whorl height, weakly convex below. Axial sculpture of broad, low, opisthocline ribs develop abruptly at shoulder, second teleoconch whorl eight ribs, penultimate whorl 9-10, equal in width to slightly narrower than their interspaces. Spiral sculpture obsolete or almost so over subsutural collar and ramp, cords of alternate strength below shoulder. Last whorl 55-58% total height, profile and sculpture as described above, shoulder sharp, convex below, weakly constricted at base; axials broadening and strongly varicose towards aperture, subregular cords of primary to tertiary strength over base; siphonal fasciole moderately delimited, weakly rounded, bearing spiral cords. Aperture 38-39% total height, narrow, subquadrate; outer lip weakly thickened by varix, sharp edged, smooth within; anal sinus, moderately wide and deep, symmetrically U-shaped, occupying entire ramp, apex on lower half ramp; siphonal canal short, unnotched. Columella straight, smooth. Columellar and parietal callus thickened, sharply delimited, forming well-developed callus rim; robust parietal tubercle developed adapically. Colour patter preserved consisting of orange comma-shaped flammules on subsutural ramp and two orange bands, upper mid-whorl on last whorl, lower mid-base.

Discussion – *Crassispira geslini* (Desmoulins, 1842) differs from *C. brocchii* (Bellardi & Michelotti, 1841) in being smaller, with a wider apical angle and a relatively taller last whorl, in having a more strongly developed subsutural collar, narrower and more deeply concave subsutural ramp, both of which are devoid of spiral sculpture, or almost so, a sharper shoulder, coarser spiral sculpture below the shoulder and on the base, and a shorter siphonal canal. *Crassispira seiuncta* (Bellardi, 1877) from the Italian Miocene and Pliocene is also closely similar to *C. geslini* but differs in having a slenderer shell with a more acute spire and a narrower columellar callus.
Scarponi & Della Bella (2003) reported this as being the most common *Crassispira* species in the Italian Pliocene assemblages, although often confused with *C. brocchii* and rarely reported. In Estepona it is also the most abundant *Crassipira* where it is found only in the shallower water assemblages, supporting an infra- and circalittoral habitat (Scarponi & Della Bella, 2003).

Distribution – Middle Miocene: central Proto-Mediterranean, Italy (Bellardi, 1877). Lower Pliocene: central Mediterranean, Italy (Chirli, 1997; Scarponi & Della Bella, 2003). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Cipolla, 1914; Scarponi & Della Bella, 2003).

Crassispira leonardiana **Ceregato & Della Bella, 2003**
Plate 26, figs 1-4

1988 *Crassispira sejuncta* [*sic*] (Bellardi, 1877) – Chirli, p. 24, pl. 11, fig. 15 [*non Crassispira seiuncta* (Bellardi, 1877)].

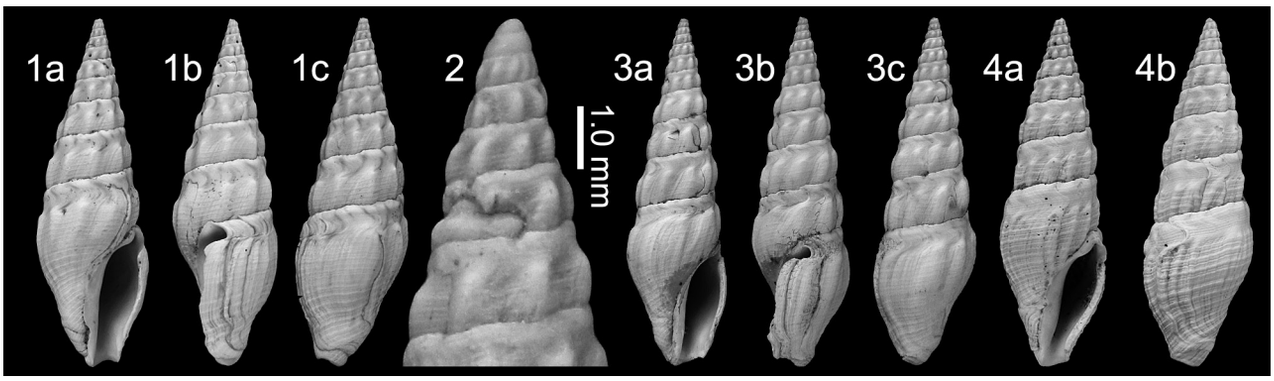

Plate 26. *Crassispira leonardiana* Ceregato & Della Bella, 2003; 1. NHMW 2020/0171/0321, height 32.2 mm, width 10.1 mm; 2. NHMW 2020/0171/0322, height 20.8 mm (juvenile), detail of protoconch and early teleoconch whorls; 3. NHMW 2020/0171/0323, height 30.7 mm, width 8.8 mm; 4. NHMW 2020/0171/0324, height 33.5 mm, width 10.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

1996 *Crassispira* (*Crassispira*) *brocchii* (Bellardi & Michelotti, 1840 [*sic*]) – Vera-Peláez & Batllori Aguilà (*partim*), p. 38, pl. 1, fig. 11, pl. 2, figs 5, 6.

1996 *Crassispira* (*Crassispira*) *brocchii* (Bellardi, 1847) [*sic*] – Vera-Peláez (*partim*), p. 429, pl. 29, figs 1-4 (only) [not figs 5-8 = *Crassispira geslini* (Desmoulins, 1842); not 9-11].

1997 *Crassispira seiuncta* (Bellardi, 1877) – Chirli (*partim*), p. 35, pl. 10, figs 1-3 [*non Crassispira seiuncta* (Bellardi, 1877)] [not fig. 4 = *C. geslini* (Des Moulins, 1842)].

2002 *Crassispira* (*Crassispira*) *brocchii* (Bellardi, 1847) [*sic*] – Vera-Peláez (*partim*), p. 198, pl. 3, figs ?L, ?M, pl. 12, figs C, D [*non Crassispira brocchii* (Bellardi & Michelotti, 1841)].

*2003 *Crassispira leonardiana* Ceregato & Della Bella, *in* Scarponi & Della Bella, p. 50, figs 63-66, 77.

Material and dimensions – Maximum height 33.5 mm, width 10.2 mm. **CO**: NHMW 2020/0171/0321-0324 (4), NHMW 2020/0171/0325 (4).

Description – Shell medium to large sized, very solid, moderately slender turriform, with tall slender conical spire (apical angle 26.8-32.6°). Protoconch multispiral, of 2.5 smooth convex whorls with small nucleus (Estepona specimen: dp = 480 μm, hp = 540 μm, dp/hp = 0.89, dV1 = 260 μm, dn = 170 μm). Junction with teleoconch marked by sinusigera. Teleoconch of up to eight whorls, with periphery at abapical suture, separated by narrowly impressed weakly undulating suture. Spire whorls with broad, subobsoletely nodular, poorly delimited subsutural collar, adapically delimiting moderate-width, weakly concave subsutural ramp, rounded at shoulder placed at about two-thirds whorl height, weakly convex below. Axial sculpture of broad, low, opisthocline ribs develop abruptly at shoulder, 7-8 on second whorl, 10-11 on penultimate, equal in width to slightly narrower than their interspaces. Spiral sculpture of weak, narrow cords over subsutural collar and ramp, slightly stronger and of alternate strength below shoulder. Last whorl 48-54% total height, profile and sculpture as described above, shoulder weakening abapically, convex below, weakly constricted at base; axials weaker, more numerous, and closer-spaced towards aperture, irregular cords of primary to tertiary strength over base; siphonal fasciole moderately delimited, weakly rounded, bearing spiral cords. Aperture 33-38% total height, narrow, subquadrate; outer lip incomplete, smooth within; anal sinus, moderately wide and deep, symmetrically U-shaped, occupying entire ramp, apex on lower half ramp; siphonal canal moderately short, recurved at tip, unnotched. Columella straight, smooth. Columellar and parietal callus thickened, sharply delimited, forming well-developed callus rim; robust parietal tubercle developed adapically. Colour patter preserved in one juvenile consisting of orange comma-shaped flammules on subsutural ramp and narrow orange band midwhorl on last whorl.

Discussion – *Crassispira leonardiana* Ceregato & Della Bella, 2003 is the only Pliocene Mediterranean *Crassispira* species with a multispiral protoconch of about 2.5 whorls with a small nucleus, suggesting planktotrophic development. All other species described from the Italian Pliocene (Scarponi & Della Bella, 2003) and from the Spanish Pliocene (herein) have a paucispiral protoconch of 1.5-2 whorls with a medium to large sized nucleus, suggesting direct development.

In the Estepona Velerín conglomerates material there are two extremely similar species *C. geslini* (Desmoulins, 1842) and *C. leonardiana*. They can easily be separated based on protoconch characters, as *C. geslini* has a paucispiral protoconch. However, the Estepona material presents a problem; almost all the large adult *Crassispira* specimens are without protoconch.

Separation based on teleoconch characters is more difficult; *C. geslini* has a broader subsutural collar, narrower, more deeply concave ramp, the spiral sculpture above the shoulder is weaker to subobsolete, the shoulder, especially on the last whorl is more strongly developed, and the ribs on the last whorl tend to become broad and strongly varicose. In the Velerín conglomerates *C. geslini* seems

to be far more abundant than *C. leonardiana*.
Vera-Peláez & Batllori Aguilá (1996) and Vera-Peláez (2002) mixed these two species in the Iberian Pliocene and identified them as *C.* (*C.*) *brocchii* with the author misquoted as (Bellardi & Michelotti, 1840 [*sic*]) and (Bellardi, 1847) [*sic*] respectively. *Crassispira brocchii* (Bellardi & Michelotti, 1841) is a larger, more slender species, with a paucispiral protoconch, relatively strong spiral sculpture on the subsutural ramp, and a relatively shorter last whorl. We have not identified *C. brocchii* in the Estepona deposits. The illustrations in Vera-Peláez (2002) are extremely poor, but probably represent *C. geslini* (2002, pl. 3, figs L, M) and *C. leonardiana* (2002, pl. 12, figs C, D).
Scarponi & Della Bella (2003, p. 51) suggested an infralittoral habitat, possibly associated with brackish environments. In Estepona *C. leonardiana* is found only in the fully marine shallow water deposits, however, its rarity might suggest suboptimal conditions for the species.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 1988, 1997; Scarponi & Della Bella, 2003). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez & Batllori Aguilà, 1996; Vera-Peláez, 1996, 2002).

***Crassispira octoacutangula* Vera-Peláez, 2002**
Plate 27, figs 1-4

1996	*Crassispira* (*Crassispira*) *fratercula* (Bellardi, 1877) – Vera-Peláez & Batllori Aguilà (*partim*), p. 38, pl. 1, figs 8, 9, pl. 2, figs 7, 8 [*non Crassispira fratercula* (Bellardi, 1877)].
1996	*Crassispira* (*Crassispira*) *fratercula* (Bellardi, 1877) – Vera-Peláez, p. 435, pl. 30, figs 1-12 [*non Crassispira fratercula* (Bellardi, 1877)].
*2002	*Crassispira* (*Crassispira*) *octoacutangula* Vera-Peláez, p. 199, pl. 3, figs N, Ñ, O, pl. 12, figs E, F.
non 2021	*Crassispira octoangula* [*sic*] Vera-Pelaez [*sic*], 2002 – Brunetti & Forli, p. 185, figs 3A, B [= *Crassispira plioparvula* Vera-Peláez, 2002].

Material and dimensions – Maximum height 18.7 mm, width 6.4 mm. **CO**: NHMW 2020/0171/0331-0334 (4), NHMW 2020/0171/0335 (15).

Description – Shell small to medium sized, very solid, broadly turriform, with broad conical spire (apical angle 36.7-41.4°). Protoconch paucispiral, small, 1.75 smooth convex whorls with large nucleus (dp = 400 μm, hp = 440 μm, dp/hp = 0.91, dV1 = 300 μm, dn = 200 μm). Teleoconch of up to seven weakly convex whorls, with periphery at abapical suture, separated by narrowly impressed undulating suture. Spire whorls with broad subsutural band, adapically delimiting narrow, concave subsutural ramp, rounded at high-placed shoulder, weakly convex below. Axial sculpture of very broad, opisthocline ribs develop abruptly at shoulder, 8-10 (eight in most specimens) on last whorl, equal in width to their interspaces. No spiral sculpture on spire whorls. Last whorl 57-60% of total height, profile and sculpture as described above, convex below shoulder, hardly constricted at base; axials weaken over base, weak, flattened spiral cords separated by shallow grooves develop over base, strengthening slightly towards siphonal fasciole. Aperture small, subquadrate, 38% of total height; outer lip thickened by rounded labial varix, sharp edged, smooth within; anal sinus, moderately wide, shallow U-shaped, occupying entire ramp, apex mid-ramp; siphonal canal very short, recurved at tip, not notched. Columella straight, smooth. Columellar callus thickened, and parietal callus weakly thickened, sharply delimited, forming narrow callus rim indented adapically; robust parietal tubercle developed adapically in some specimens.

Discussion – *Crassispira octoacutangula* Vera-Peláez, 2002 differs from all its Italian congeners illustrated by Scarponi & Della Bella (2003) in having a smaller squatter shell, with the axials starting more abruptly at the shoulder, and has much weaker spiral sculpture than any of the Italian species. Indeed, except for the subsutural cord, the spire whorls are devoid of spirals. All the Italian species; *C. brocchii* (Bellardi & Michelotti, 1841), *C. calurii* (De Stefani & Pantanelli, 1878),

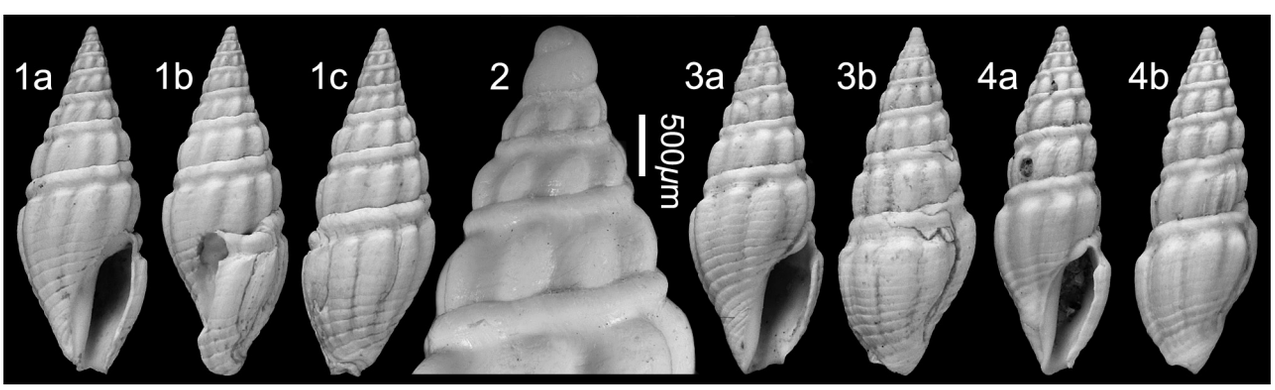

Plate 27. *Crassispira octoacutangula* Vera-Peláez, 2002; 1. NHMW 2020/0171/0331, height 16.0 mm, width 6.0 mm; 2. NHMW 2020/0171/0332 (juvenile), detail of protoconch and early teleoconch whorls; 3. NHMW 2020/0171/0333, height 14.1 mm, width 5.5 mm; 4. NHMW 2020/0171/0334, height 15.2 mm, width 5.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

C. geslini (Desmoulins, 1842), *C. leonardiana* Ceregato & Della Bella *in* Scarponi & Della Bella, 2003, *C. pseudosigma* (Brugnone, 1876), and *C. pustulata* (Brocchi, 1814) have some spiral sculpture on the spire whorls below the shoulder. *Crassispira fratercula* (Bellardi, 1877), with which it was initially confused by Vera-Peláez & Batllori Aguilà (1996) and Vera-Peláez (1996) is an Italian Middle Miocene species from the Colli Torinesi (syntype illustrated by Ferrero Mortara *et al*., 1981, pl. 11, fig. 3), with a taller, slenderer spire giving it a less squat appearance, and spiral sculpture is evident on the spire whorls.

Brunetti & Forli (2021) misinterpreted this species and illustrated a specimen of *Crassispira plioparvula* Vera-Peláez, 2002 as *Crassispira octoangula* [*sic*] (note spelling *lapsus*). This is understandable bearing in mind the very poor quality images in Vera-Peláez (2002). However the specimen illustrated as *Crassispira fratercula* (Bellardi, 1877) by Vera-Peláez & Batllori Aguilà (1996, pl. 1, figs 8, 9, pl. 2, figs 7, 8) is rather better illustrated. It is the same specimen as that figured by Vera-Peláez (1996, pl. 30, figs 5-7) and that reference was included by Vera-Peláez (2002, p. 199) in his chresonymy of *C. octoacutangula*.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez & Batllori Aguilà, 1996; Vera-Peláez, 1996, 2002).

***Crassispira plioparvula* Vera-Peláez, 2002**
Plate 28, figs 1-3

*2002	*Crassispira* (*Crassispira*) *plioparvula* Vera-Peláez, p. 200, pl. 3, figs P, Q, pl. 17, figs I, J.
2021	*Crassispira octoangula* [*sic*] Vera-Pelaez [*sic*], 2002 – Brunetti & Forli, p. 185, figs 3A, B [*non Crassispira octoacutangula* Vera-Peláez, 2002].

Material and dimensions – Maximum height 14.2 mm, width 4.5 mm. **EL**: NHMW 2020/0171/0474-0476 (4), NHMW 2020/0171/0477 (1).

Description – Shell small sized, solid, slender to moderately slender turriform, with tall conical spire (apical angle 29.6-35.8°). Protoconch paucispiral, two smooth, convex whorls with large bulbous nucleus (dp = 480 μm, hp = 380 μm, dp/hp = 1.26, dV1 = 360 μm, dn = 270 μm). Teleoconch of up to six weakly convex whorls, with periphery at shoulder, separated by narrowly impressed undulating suture. Spire whorls with broad, vertical, concave subsutural ramp, rounded at shoulder, weakly convex below. Axial sculpture of very broad, low, opisthocline ribs develop at shoulder and weakening towards abapical suture, 8-10 on last whorl, equal in width to their interspaces. Very fine, flattened, subobsolete spiral cords separated by narrow, superficial grooves cover entire whorl surface. Last whorl 53-58% of total height, with broad, deeply concave subsutural ramp, rounded at tubercular shoulder, convex below, hardly constricted at base; axials reduced to poorly delimited broad tubercles at shoulder, hardly extending abapically, weak spirals over base and siphonal fasciole. Aperture subquadrate, 35-37% of total height; outer lip not thickened by labial varix, sharp edged, smooth within; anal sinus, moderately narrow and deep U-shaped, occupying entire ramp, apex mid-ramp; siphonal canal very short, straight, shallowly notched at tip. Columella straight, smooth. Columellar callus thickened, and parietal callus weakly thickened, sharply delimited, forming narrow callus rim indented adapically, small parietal tubercle.

Discussion – In the material at hand from the shallow water assemblages in Estepona we recognise two smaller *Crassispira* species and have interpreted them as *C. plioparvula* and *C. velerinensis*. Following the interpretation given herein, *C. plioparvula* is slightly larger-shelled, slenderer, with a slightly wider subsutural ramp, on spire whorls the axials are less elevated more rounded at the shoulder and, most importantly, on the last whorl the axials are reduced to broad, poorly defined tubercles at the shoulder that hardly extend abapically, so that there is no axial sculpture below the level of the insertion of the outer lip. There is no appreciable difference in spiral

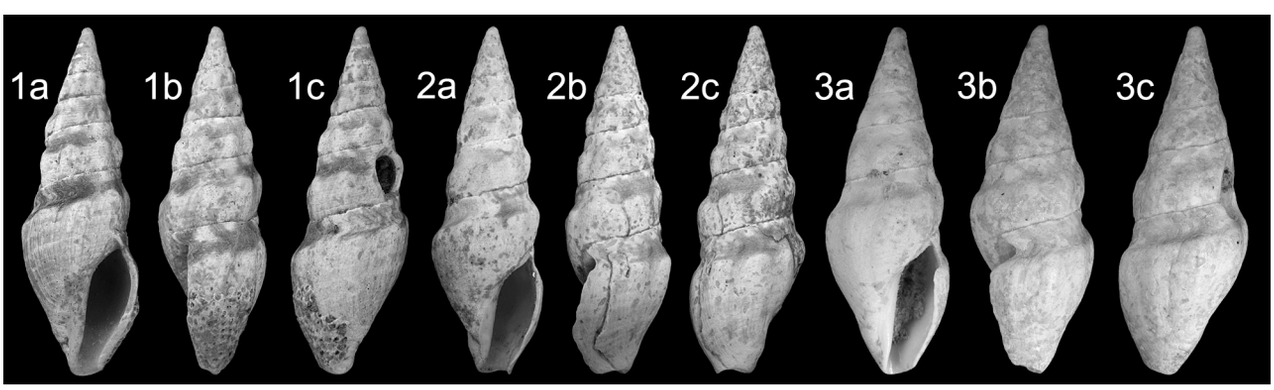

Plate 28. *Crassispira plioparvula* Vera-Peláez, 2002; 1. NHMW 2020/0171/0474, height 13.9 mm, width 4.6 mm; 2. NHMW 2020/0171/0475, height 14.2 mm, width 4.5 mm; 3. NHMW 2020/0171/0476, height 11.4 mm, width 4.1 mm (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

sculpture between the two. All specimens of *C. plioparvula* at hand are worn, but the protoconch is paucispiral, as is typical for the genus. Although they both have a non-planktotrophic type protoconch of roughly similar size, in *C. velerinensis* it is more raised (dp/hp = 1.0 vs. 1.26) and the nucleus is even larger (dn = 300 μm vs. dn = 270 μm).

Crassispira plioparvula is similar also to *C. plioibericostricta* Brunetti & Forli, 2021 from the Atlantic Lower Pliocene 'grey sands' of the Arenas de Huelva Formation, Guadalquivir Basin [= *Crassispira calurii* (De Stefani & Pantanelli, 1878 in Landau *et al*., 2013; *non* De Stefani & Pantanelli, 1878], however, that species is slightly larger and the axial sculpture fades on the first half of the penultimate whorl so that the last whorl is strongly shouldered, but without axials. *Crassispira plioibericostricta* is described as having a multispiral protoconch (Brunetti & Forli, 2021, figs 2F, G). We cannot confirm this as none of the many specimens at hand from the type locality have their protoconch preserved. However, the protoconch illustrated belongs to paratype 4 and we are not convinced that specimen (2021, figs 2K, L) represents the same species.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

***Crassispira velerinensis* Vera-Peláez, 2002**
Plate 29, figs 1-3

*2002 *Crassispira velerinensis* Vera-Peláez, p. 201, pl. 3, figs R, S.

Material and dimensions – Maximum height 12.9 mm, width 4.1 mm. **CO**: NHMW 2020/0171/0478-0480 (4), NHMW 2020/0171/0481 (5).

Description – Shell small sized, solid, broad to moderately slender turriform, with tall conical spire (apical angle 33.1-38.0°). Protoconch paucispiral, two tall, smooth, convex whorls with large bulbous nucleus (dp = 480 μm, hp = 480 μm, dp/hp = 1, dV1 = 360 μm, dn = 300 μm). Teleoconch of up to six weakly convex whorls, with periphery at abapical suture, separated by narrowly impressed undulating suture. Spire whorls with moderately broad, almost vertical, concave subsutural ramp, rounded at shoulder, weakly convex below. Axial sculpture of very broad, opisthocline ribs develop at shoulder, eight on last whorl, slightly narrower than their interspaces. Very fine, flattened, subobsolete spiral cords separated by narrow, superficial grooves cover entire whorl surface. Last whorl 54-55% of total height, profile and sculpture as described above, weakly convex below shoulder, hardly constricted at base; axials subobsolete over base, spirals slightly boader over base, numerous narrow cords over siphonal fasciole. Aperture small, subquadrate, 36-37% of total height; outer lip weakly thickened by labial varix, sharp edged, smooth within; anal sinus, moderately narrow and deep U-shaped, occupying entire ramp, apex mid-ramp; siphonal canal very short, straight, not notched. Columella straight, smooth. Columellar callus thickened, and parietal callus weakly thickened, sharply delimited, forming narrow callus rim indented adapically, no parietal tubercle.

Discussion – The original discussion is short and does not compare this species with any of its congeners. "Crassispira velerinensis *nueva sp. se caracteriza por su pequeñísima talla, su extrema delgadez, por presentar last costulitas axiales muy finas y próximas entre sí y un canal sifonal brevíssimo* [*Crassispira velerinensis* new sp. is characterised by its very small size, extreme slenderness, in having the axial riblets very fine and close spaced and having an extremely short siphonal canal]" (Vera-Peláez, 2002, p. 201). The type is indeed small and the siphonal canal is short, however, the ribs are low and rather broad and not particularly crowded. The shells illustrated herein (Plate 29, figs 1-3) represent better preserved specimens. For further discussion, see under *C. plioparvula* Vera-Peláez, 2002.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez, 2002).

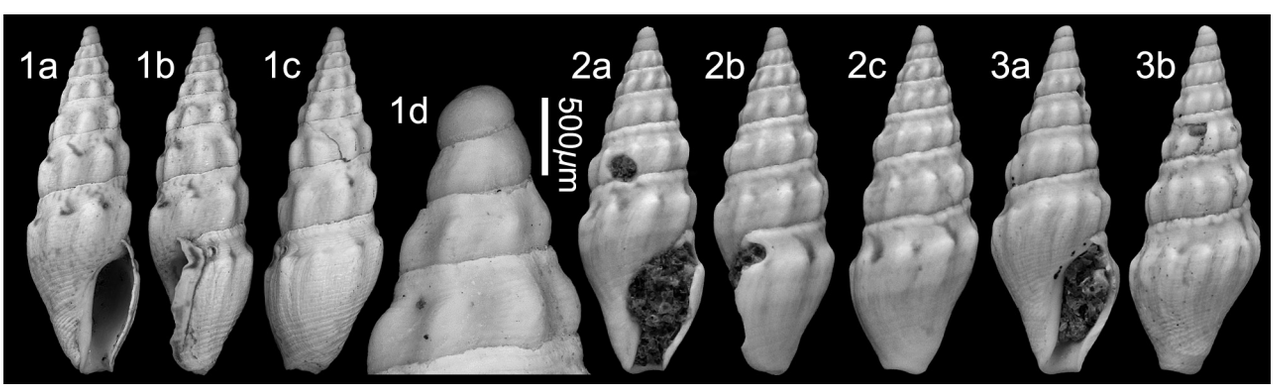

Plate 29. *Crassispira velerinensis* Vera-Peláez, 2002; 1. NHMW 2020/0171/0478, height 12.9 mm, width 4.1 mm, 1d, detail of protoconch; 2. NHMW 2020/0171/0479, height 9.0 mm, width 3.2 mm; 3. NHMW 2020/0171/0480, height 10.7 mm, width 3.8 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Conclusions

In this paper we review the Borsoniidae, Clathurellidae, Mitromorphidae, and Pseudomelatomidae of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. 15 species of Borsoniidae are recorded, of which two are left in open nomenclature. One species is described as new: *Microdrillia plioserratula* nov. sp. Five species of Clathurellidae are recorded. Two Mitromorphidae are recorded, one is described as new: *Mitromorpha* (*Mitrolumna*) *velerinensis* nov. sp. Five species of Pseudomelatomidae Morrison, 1965 are recorded.

This is a slightly greater diversity than recorded by Vera-Peláez (2002). All of his records are either confirmed or reattributed to different species herein, except for *Genota bonnanii* Bellardi, 1877, the presence of which could not be confirmed in the Estepona assemblages.

The assemblage shows a relatively high level of endemism (9 species: 33%). Both shallow and deeper-water taxa are represented.

From a stratigraphic standpoint, most of the species are relatively short-lived (Fig. 2). Only three (11%) occur today and five (18.5%) appeared already during the late Miocene. At species level, there is little association between the Estepona species and any of the upper to Middle Miocene assemblages of the European Atlantic Frontage, Paratethys or Proto-Mediterranean. *Bathytoma cataphracta* (Brocchi, 1814) is the only species with a wide distribution and unusual longevity amongst turrids, present along the Lower and Middle Miocene European Atlantic Frontage, Proto-Mediterranean and Paratethys.

Acknowledgements

Our thanks to Carlos Marques da Silva of the University of Lisbon, Portugal, for his advice and help with graphics. Thanks also to Zoltán Kovács of the Franz Liszt Academy of Music, Budapest, Hungary and Riccardo Giannuzzi-Savelli of Palermo, Italy, for their excellent reviews.

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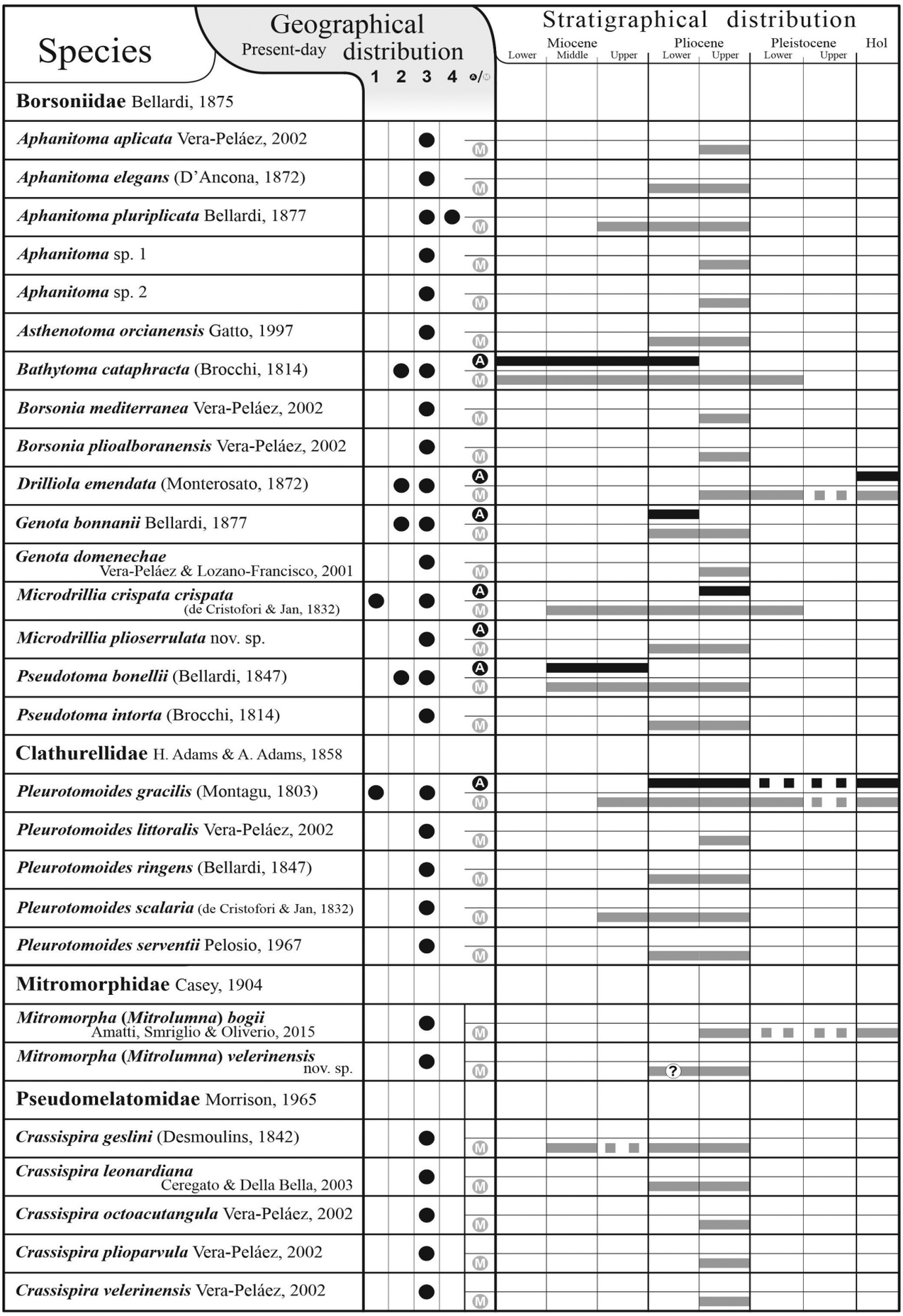
Species
Geographical distribution
Present-day
1 2 3 4 ♂/♀
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower
Middle
Upper
Lower
Upper
Lower
Upper
Borsoniidae Bellardi, 1875
Aphanitoma aplicata Vera-Peláez, 2002
Aphanitoma elegans (D'Ancona, 1872)
Aphanitoma pluriplicata Bellardi, 1877
Aphanitoma sp. 1
Aphanitoma sp. 2
Asthenotoma orcianensis Gatto, 1997
Bathytoma cataphracta (Brocchi, 1814)
Borsonia mediterranea Vera-Peláez, 2002
Borsonia plioalboranensis Vera-Peláez, 2002
Drilliola emendata (Monterosato, 1872)
Genota bonnanii Bellardi, 1877
Genota domenechae Vera-Peláez & Lozano-Francisco, 2001
Microdrillia crispata crispata (de Cristofori & Jan, 1832)
Microdrillia plioserrulata nov. sp.
Pseudotoma bonellii (Bellardi, 1847)
Pseudotoma intorta (Brocchi, 1814)
Clathurellidae H. Adams & A. Adams, 1858
Pleurotomoides gracilis (Montagu, 1803)
Pleurotomoides littoralis Vera-Peláez, 2002
Pleurotomoides ringens (Bellardi, 1847)
Pleurotomoides scalaria (de Cristofori & Jan, 1832)
Pleurotomoides serventii Pelosio, 1967
Mitromorphidae Casey, 1904
Mitromorpha (Mitrolumna) bogii Amatti, Smriglio & Oliverio, 2015
Mitromorpha (Mitrolumna) velerinensis nov. sp.
Pseudomelatomidae Morrison, 1965
Crassispira geslini (Desmoulins, 1842)
Crassispira leonardiana Ceregato & Della Bella, 2003
Crassispira octoacutangula Vera-Peláez, 2002
Crassispira plioparvula Vera-Peláez, 2002
Crassispira velerinensis Vera-Peláez, 2002
A
M
?

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

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