

The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 20: Columbelloidea (Buccinoidea)

Bernard Landau^{1*}, Mathias Harzhauser² & Kevin Monsecour³

¹ Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands; Instituto Dom Luiz da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal; and International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal; email: bernardmlandau@gmail.com

² Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria; email: mathias.harzhauser@nhm-wien.ac.at

³ Research Associate, Institute of Systematics, Evolution, Biodiversity (ISYEB), National Museum of Natural History (MNHN), CNRS, SU, EPHE, UA, CP 51, 57 rue Cuvier, 75005 Paris, France, email: kevin.monsecour@telenet.be

* Corresponding author

ZooBank registration – urn:lsid:zoobank.org:pub:8B7A63A9-F9BE-45DA-98ED-D927BC4C1772

Received 19 September 2023, revised version accepted 27 October 2023.

In this paper we review the Columbelloidea of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain. Twenty species are recorded within six genera, of which four are described as new: *Costoanachis malaquasi* nov. sp., *Mitrella avilai* nov. sp., *Mitrella pagodiformis* nov. sp. and *Mitrella velerinensis* nov. sp.

Relationships at generic level are difficult to interpret at present due to the polyphyletic nature of genera such as *Mitrella*. At species level the assemblage is closely related to that seen in the rest of the Pliocene Mediterranean.

The group is relatively thermophilic, with columbellid diversity drastically reduced in the cooler subtropical Pliocene French-Iberian province to the North, and although columbellid diversity in the present-day subtropical Mediterranean-Moroccan biogeographical province is relatively high, only 4 (20%) of the species found in Estepona survive there today.

KEY WORDS: southern Spain, Upper Pliocene, Gastropoda, Columbelloidea, Buccinoidea, new species

Introduction

In this paper we continue to revise the gastropods found in the Pliocene assemblage of Estepona in southwestern Spain, this part describing and discussing the Columbelloidea Swainson, 1840.

Despite being well represented in the Pliocene Mediterranean, the last work specifically describing this group in the Neogene Mediterranean was that of Sacco (1890b). Although some columbellids are included in almost every subsequent work describing Pliocene Mediterranean assemblages (e.g., Cavallo & Repetto, 1992; Chirli, 2002; Chirli & Richard, 2008; Brunetti & Cresti, 2018; *inter alia*), none can be considered detailed or critical revisions of the group.

Pliocene columbellid diversity in the westernmost Spanish Mediterranean is less well documented. Martinell (1982) recorded one species in the Catalan Pliocene. González Delgado (1989) also one species for the Atlantic Lower Pliocene Guadalquivir Basin of southeastern Spain, later increased to four species in the same assemblages by Landau *et al.* (2011). As with the Italian

literature, columbellids are included as part of a general description of the faunas. Therefore, this contribution is an important contribution to our knowledge of the group in the Pliocene western Mediterranean.

Revision of this group in the fossil faunas has been further hampered by the strong reliance of phylogenies on soft tissue characteristics, obviously lacking in fossil material, and the lack of a comprehensive molecular phylogeny of the group until very recently. Even with the benefit of the molecular phylogeny presented by deMaintenon & Strong (2022), some of the most diverse nominal genera such as *Mitrella* Risso, 1826 and *Anachis* H. Adams & A. Adams, 1953 remain highly polyphyletic. Therefore, our generic concept relies on conchological features and follows the methods used in the revision of the Columbelloidea from the Miocene Paratethys by Harzhauser & Landau (2021).

Age of the deposits

Prior to 2013 the age of the deposits was stated as Late Zanclean (late Early Pliocene) (for list of papers giving

Zanclean age see Landau & Micali, 2021, p. 160) following Guerra Merchán *et al.* (2002). In our later works we have dated the assemblages as earliest Piacenzian, early Late Pliocene, an age corroborated by the assemblage of Euthecosomata (Janssen, 2004). Either way, they form part of the Mediterranean ecostratigraphic unit MPPMU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al.*, 2011, text-fig. 9).

Materials and methods

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

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

The protoconch whorls have been counted using the method described by Jung (1986: p. 9, text-fig. 5). Internal labial denticles are numbered, D1 being the most adapical. Columbelloids grow without denticles within the outer lip until they reach full adult size, at which time the outer lip thickens and denticles are formed. Comments in the description and discussion relating to specimens without denticles probably refer to specimens that are not fully adult.

For descriptions of shell morphology, we provide shell length (SL), maximum diameter (MD) and apical angle (AA) (see Harzhauser & Landau, 2021, fig. 2). In the descriptions we categorise the shells as: small (SL ≤ 7.9 mm), moderately small (8.0-14.9 mm), medium-sized (15.0-19.9 mm), and large (SL ≥ 20.0 mm). The SL/MD ratio is an expression of slenderness of the shell. To be objective in the descriptions we define shell shapes of Estepona Columbelloidea as follows: broad (SL/MD < 2.2), moderately broad (SL/MD = 2.2-2.9), slender (SL/MD ≥ 3.0). The relative width of the aperture is calculated as aperture length (AL) versus aperture width (AW). Apertures are described as narrow (AL/AW > 4.0), moderately narrow (AL/AW = 4.0-3.49), moderately wide (AL/AW = 3.5-3.0) and wide (AL/AW < 3.0).

Abbreviations:

CO: Velerín conglomerates; **PA:** Rio del Padrón;
VC: Velerín Carretera; **VA:** Velerín Antena;
PQ: Parque Antena; **EL:** El Lobillo; see Landau *et al.* (2003, p. 4, text-fig. 1).
NHMW: Natural History Museum Vienna (Austria)
RGM: Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

Systematic palaeontology

Systematics has been updated following Bouchet *et al.* (2017). We have not used subfamilies as arrangement in these at present is not monophyletic. A molecular phylogeny of the family was recently completed by deMaintenon & Strong (2022).

Superfamily Buccinoidea Rafinesque, 1815
 Family Columbelloidea Swainson, 1840
 Genus *Amphissa* H. Adams & A. Adams, 1853

Type species (by subsequent designation, Dall, 1871) – *Buccinum corrugatum* Reeve, 1847 [*non* Brocchi, 1814; = *Amphissa columbiana* Dall, 1916], present-day.

1853 *Amphissa* H. Adams & A. Adams, p. 111.

Amphissa acutecostata (Philippi, 1844)

Plate 1, figs 1-5

- 1835 *Fusus costulatus* Cantraine, p. 393 (*non* Lamarck, 1822).
 *1844 *Buccinum acute-costatum* Philippi, 92, pl. 27 fig. 14.
 1867 *Columbella haliaeeti* Jeffreys, p. 356, pl. 88, fig. 3.
 1889 *Bela Grimaldii* Dautzenberg, p. 26, pl. 2, fig. 2.
 1896 *Bela simplicata* Locard, 140, pl. 5, fig. 2.
 1896 *Bela limatula* Locard, 141, pl. 5, fig. 3.
 1897 *Anachis costulata* var. *elongata* Locard, p. 145.
 1897 *Anachis Haliaeeti* var. *attenuata*, *costulatissima*, *curta* and *major* Locard, p. 149.
 1974 *Anachis (Zafrona) nicolayi* Nordsieck, p. 12, fig. 14.
 1985 *Amphissa acutecostata* (Philippi, 1844) – Bouchet & Warén, p. 165, figs 392, 395-398.
 1997 *Amphissa acutecostata* (Philippi, 1844) – Di Geronimo & La Perna, p. 393, pl. 3, figs 4, 5.
 2003 *Amphissa acutecostata* [*sic*] (Philippi, 1844) – Giannuzzi-Savelli *et al.*, p. 18, 242, figs 560a-c.
 2018 *Amphissa acutecostata* (Philippi, 1844) – Brunetti & Cresti, p. 80, fig. 308.
 2019 *Amphissa acutecostata* (Philippi, 1844) – Gofas *et al.*, p. 147, figs 1-2.

Materials and dimensions – Maximum height 8.5 mm, width 3.4 mm. **CO:** NHMW 2022/0201/0063 (32). **VC:** NHMW 2022/0201/0042-0043 (2), NHMW 2022/0201/0044 (50+), NHMW 2022/0201/0092-0094 (3), RGM. 1404331 (10). **EL:** NHMW 2022/0201/0064 (4). **PQ:** NHMW 2022/0201/0086 (8).

Description – Shell moderately small, moderately broad fusiform, with conical spire (AA = 43-49°). Protoconch tall conical of four convex whorls with small nucleus; first 1.5 whorls covered in dense spiral threads, later whorls with zig-zag spirals on adapical half, axial riblets below and one spiral thread a short distance above the

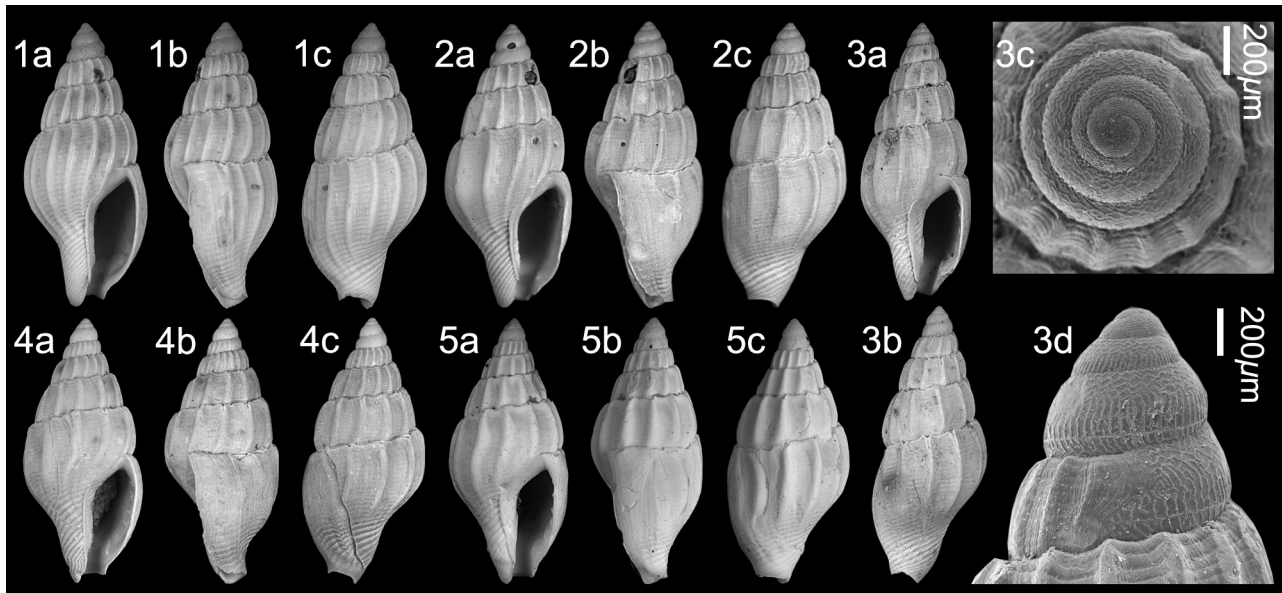


Plate 1. *Amphissa acutecostata* (Philippi, 1844). 1. NHMW 2022/0201/0092, height 6.9 mm, width 3.0 mm; 2. NHMW 2022/0201/0093, height 6.8 mm, width 3.1 mm; 3. NHMW 2022/0201/0042, height 8.5 mm, width 3.3 mm, 3c-d, detail of protoconch (SEM images); 4. NHMW 2022/0201/0043, height 7.1 mm, width 3.2 mm; 5. NHMW 2022/0201/0094, height 6.7 mm, width 3.0 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

suture on last two protoconch whorls ($dp = 840 \mu\text{m}$, $hp = 1005 \mu\text{m}$, $dp/hp = 0.83$, $dn = 155 \mu\text{m}$, $dpl = 235 \mu\text{m}$). Teleoconch junction marked by sinusigera. Teleoconch of up to five convex whorls, with periphery just above abapical suture, separated by moderately impressed linear suture, weakly undulating on later whorls. Sculpture of sharp, slightly opisthoclinal to slightly prosoclinal axial ribs extending between sutures, 10-12 on penultimate whorl. Spiral sculpture of very fine spiral cords covers entire whorl surface, subobsolete in some specimens, especially on the adapical half of the last whorl. Last whorl 63-67% of total height, broadly rounded at periphery placed about mid-whorl, moderately strongly constricted at base; axials weakening over base. Siphonal fasciole medium length, bearing slightly stronger cords. Aperture moderately wide, 41-44% of total height. Outer lip weakly swollen by varix, no palatal swelling, row of about six small denticles within. Anal canal broad V-shaped notch. Siphonal canal moderate length, narrow, open, weakly recurved, notched at tip. Columellar callus slightly thickened, edge erect, with row of small tubercles on outer edge in some specimens and fold delimiting siphonal canal deep within columella; continuous with thinner, moderately expanded parietal callus.

Discussion – *Buccinum acutecostatum* Philippi, 1844 was placed in the genus *Amphissa* H. Adams & A. Adams, 1853 by Bouchet & Warén, 1985, a position followed by all subsequent authors. The Eastern Pacific type species *Buccinum corrugatum* Reeve, 1847 [*non* Brocchi, 1814; = *Amphissa columbiana* Dall, 1916] is somewhat different, with a greater number of axial ribs and a more inflated last whorl. There are some similarities between *Amphissa acutecostata* (Philippi, 1844) and what is placed herein

in *Zafrona* Iredale, 1916, especially in protoconch morphology. However, Philippi's species is unlikely to be a *Zafrona*, due to its weaker spiral sculpture, less thickened outer lip, and much weaker denticles resulting in a more 'open' aperture.

Buccinum acutecostatum Philippi, 1844 was based on Lower Pleistocene fossil material from Italy. Bouchet & Warén (1985) discussed the synonymy of this species and their inability to separate the fossil specimens from Italy from extant specimens. Those authors stressed the variability in sculpture seen in present-day specimens, even within the same population. In Estepona this species is common in the deeper water assemblage of Velerín carretera but displays less variability than suggested by the illustrations given by Bouchet & Warén (1984, figs 392, 395-396). The Estepona specimens are all strongly costate, the spiral sculpture varies from weak to subobsolete, but none of the specimens are almost smooth, as figured by Bouchet & Warén. The protoconch in the Estepona specimens (Pl. 1, figs 3c, d), multispiral with elaborate sculpture, is identical to that figured by Bouchet & Warén (1984, figs 392, 397-398).

Although present in both the shallower and deeper water assemblages in Estepona, it is predominant in the deeper water assemblages. The Velerín conglomerates shallower water deposits of Estepona are storm deposits and some deeper water species occur within it. Di Geronimo & La Perna (1997) also recorded the species from bathyal Pleistocene assemblages in southern Italy.

Distribution – Lower Pliocene: central Mediterranean, Italy (Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper). Lower Pleistocene, central Mediterranean, Italy (Philippi, 1844;

Di Geronimo & La Perna, 1997). Present-day: western Atlantic, northern North America to North Carolina, eastern Atlantic Norway, Bay of Biscay, Azores (Bouchet & Warén, 1985), Alboran Sea (Gofas *et al.*, 2019), bathyal Mediterranean (Giannuzzi-Savelli *et al.*, 2003). Abundant on muddy soil in NE Atlantic upper bathyal depth range (Gofas *et al.*, 2019).

Genus *Costoanachis* Sacco, 1890

Type species (by subsequent designation, Pace, 1902) – *Columbella (Anachis) turrita* Sacco, 1890, Miocene, Italy, a junior homonym of *Columbella turrita* G.B. Sowerby I, 1832, currently accepted as *Costoanachis saccostata* Radwin, 1977b.

1890b *Costoanachis* Sacco, p. 57.

1890b *Ecostoanachis* Sacco, p. 57. *Type species* (by subsequent designation, Pace, 1902): *Columbella cythera* Doderlein, 1863, Middle Miocene, Italy.

Note – As used in the historical literature (Olsson & Harbison, 1953; Keen, 1971; Radwin, 1977b), this genus is likely polyphyletic. Harzhauser & Landau (2021, p. 13) restrict *Costoanachis* to species without spiral sculpture on spire whorls, as also seen in the species ascribed to the genus herein. However, Harzhauser & Landau (2021) also considered a large, low conical, multispiral protoconch typical for the genus. Here we describe a species with a paucispiral protoconch. As with so many other gastropod genera, protoconch type results not to be genus specific.

***Costoanachis semicostata* (Sacco, 1890)**

Plate 2, figs 1-2

*1890b *Columbella (Anachis) semicostata* Sacco, p. 60, pl. 2, fig. 86.

1974 *Anachis (Ecostoanachis) semicostata* (Sacco, 1890) – Malatesta, p. 318, pl. 25, fig. 8.

1981 *Columbella (Anachis) semicostata* Sacco in Bel-

lardi, 1890 – Ferrero Mortara *et al.*, p. 186, pl. 58, fig. 11.

2002 *Anachis semicostata* (Sacco in Bellardi, 1890) – Chirli, p. 5, pl. 1, figs 5-12, pl. 2, figs 1-12.

2010 *Anachis semicostata* (Sacco in Bellardi, 1890) – Sosso & Dell'Angelo, p. 41, 58 unnumbered fig. bottom centre.

2018 *Anachis semicostata* (Sacco in Bellardi, 1890) – Brunetti & Cresti, p. 80, fig. 306.

2022 *Columbella (Anachis) semicostata* Sacco in Bellardi – Kolokotronis, p. 5, figs 1, 2.

2023 *Costoanachis semicostata* (Sacco, 1890) – Sacchetti *et al.*, p. 67, pl. 4, figs I₁-I₂.

Materials and dimensions – Maximum height 8.8 mm, width 3.7 mm. **CO:** NHMW 2022/0201/0045-0046 (2), NHMW 2022/0201/0047 (50+), RGM.1404328 (4). **EL:** NHMW 2022/0201/0048 (32).

Description – Shell small to moderately small, moderately broad fusiform (AA 41-43°). Protoconch multispiral, conical, composed of 3.5 smooth convex whorls, with small nucleus. Junction with teleoconch marked by change in lustre and beginning of adult sculpture. Teleoconch of five weakly convex whorls with periphery at abapical suture, separated by moderately impressed linear suture. Axial sculpture on first teleoconch whorl of about 12 opisthocline ribs extending between sutures, slightly narrower than their interspaces. Abapically, axials fade abruptly after between 1-2 whorls, occasionally persisting onto penultimate whorl. Spiral sculpture absent, except over base and siphonal fasciole. Last whorl 59-64% of total height, moderately inflated, rounded at periphery placed mid-whorl, moderately constricted at base; base bearing narrow spiral cords strengthening towards siphonal fasciole. Siphonal fasciole moderately well delimited, bearing stronger spiral cords. Aperture moderately narrow, 37-43% of total height. Outer lip moderately thickened by varix, almost straight adapically and mid-lip, palatal swelling moderately developed, six denticles within, D1 or D2 strongest. Anal canal U-shaped. Siphonal canal mid-length, open, posteriorly recurved, deeply notched at tip. Columella moderately excavated,

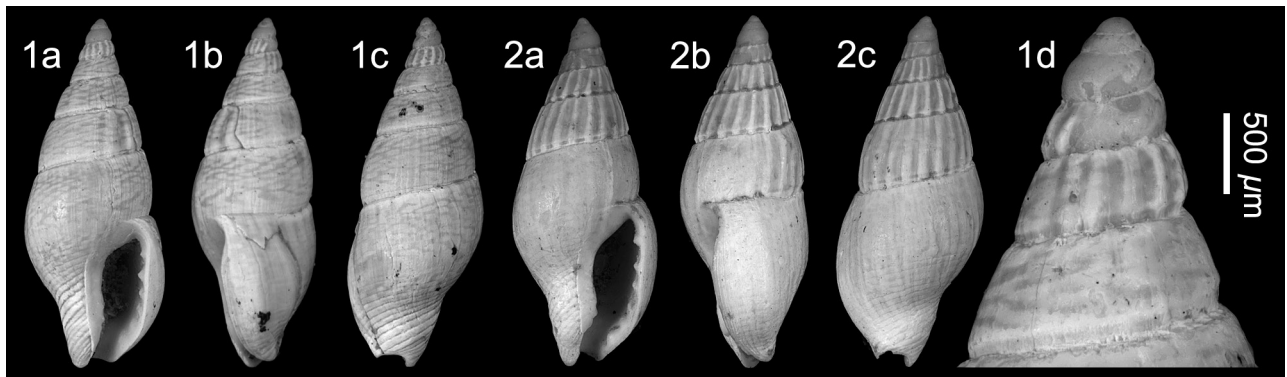


Plate 2. *Costoanachis semicostata* (Sacco, 1890). 1. NHMW 2022/0201/0045, height 7.5 mm, width 3.2 mm, 1d, detail of protoconch; 2. NHMW 2022/0201/0046, height 8.5 mm, width 3.4 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

bearing row of 4-5 denticles. Columellar callus narrow, thickened, sharply delimited, continuous with thinner parietal callus. Colour pattern preserved (Pl. 2, fig. 1): irregular, horizontally elongated white dots and blotches over orange/brown background.

Discussion – In the original description this species was placed in section (subgenus) *Ecostoanachis* Sacco, 1890 (type species *Columbella cythara* Doderlein in Sacco, 1890b; by subsequent designation, Pace, 1902). Harzhauser & Landau (2021, p. 13) placed that genus in synonymy with *Costoanachis* Sacco, 1890.

Costoanachis semicostata (Sacco, 1890) is highly variable in slenderness, in the height of the last whorl, but above all the extent of the axial sculpture. Two specimens are illustrated showing the extremes: disappearing after only one teleoconch whorl (Pl. 2, fig. 1) to persisting onto almost the whole of the penultimate whorl (Pl. 2, fig. 2). In most specimens the axials fade on the second or third whorl.

Costoanachis semiplicata (Sacco, 1890) from the Upper Miocene of Italy is closely similar. The syntype illustrated by Ferrero Mortara *et al.* (1981, pl. 58, fig. 10) seems to have broader ribs that persist onto the penultimate whorl and the base is slightly less constricted. *Costoanachis procorrugata* (Sacco, 1890) (syntype illustrated by Ferrero Mortara *et al.* 1981, pl. 58, fig. 9) from the Middle Miocene Colli Torinesi of Italy and *Costoanachis recticostata* (Sacco, 1890) (syntype illustrated by Ferrero Mortara *et al.* 1981, pl. 58, fig. 3) both differ in having broader ribs that persist onto the last whorl. *Costoanachis semicostata* has often been recorded in Italian Pliocene. It was recently reported from the eastern Mediterranean Pliocene (Kolokotronis, 2022), and herein from the western Mediterranean Estepona Basin. Sacchetti *et al.* (2023) extended its Lower Pliocene distribution to include the mid-Atlantic Azores Archipelago. Interestingly, the colour pattern preserved in the Estepona material of irregular, horizontally elongated white dots and blotches over orange/brown background does not coincide with any of the five colour variations described by Kolokotronis (2022, fig. 2) for specimens from the eastern Mediterranean Pliocene. However, within Columbellidae species colour patterns can be extremely variable.

In Estepona *C. semicostata* is found only in the shallow water deposits of Velerín conglomerates and El Lobillo, where it is relatively abundant.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1890b). Lower Pliocene: Atlantic, Santa Maria Island, Azores (Sacchetti *et al.*, 2023); western Mediterranean, NE Spain (NHMW coll.); central Mediterranean, Italy (Sacco, 1890b; Ferrero Mortara *et al.*, 1981; Chirli, 2002; Sosso & Dell'Angelo, 2010; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1890b; Malatesta, 1974). Pliocene (indeterminate): eastern Mediterranean, Cyprus (Kolokotronis, 2022).

***Costoanachis malaquiasii* sp. nov.**

Plate 3, figs 1-2

ZooBank registration – urn:lsid:zoobank.org:act:98EA99CD-F385-4C68-9BFF-8F9DE04DF85E

Type material – **Holotype** NHMW 2022/0201/0065, height 6.4 mm, width 3.1 mm; **paratype 1** NHMW 2022/0201/0066, height 6.6 mm, width 3.2 mm; **paratype 2** NHMW 2022/0201/0067, height 6.6 mm, width 3.2 mm; **paratype 3** NHMW 2022/0201/0068, height 6.6 mm, width 3.2 mm; **paratype 4** RGM.1404335, height 6.6 mm, width 3.2 mm.

Other material – Maximum height 6.7 mm, width 3.1 mm. **CO:** NHMW 2022/0201/0070 (2). **EL:** NHMW 2022/0201/0071 (2).

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

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

Etymology – Name after Manuel Malaquias, University of Bergen, Norway, in recognition of his help with the Opisthobranch section of this series. *Costoanachis* gender feminine.

Diagnosis – *Costoanachis* species with broad shell, paucispiral protoconch, first 1.5-2.0 teleoconch whorls smooth, later whorls with ten widely spaced opisthocline axial ribs, spirals restricted to siphonal fasciole, five labial denticles.

Description – Shell small, broad fusiform (AA 51-55°). Protoconch paucispiral, composed of about 1.5 smooth convex whorls, with large nucleus. Junction with teleoconch marked by change in luster. Teleoconch of 4.5 weakly convex whorls with periphery at abapical suture, separated by weakly impressed undulating suture. First 1.5-2.0 teleoconch whorls without sculpture. Abapically, narrow, widely spaced, opisthocline axials extending between sutures appear abruptly, ten on penultimate whorl, about one-third width of their interspaces. Spiral sculpture absent, except over siphonal fasciole. Last whorl 65-68% of total height, inflated, rounded at periphery placed mid-whorl, moderately strongly constricted at base; siphonal fasciole relatively short, bearing narrow spiral cords. Aperture narrow, 39-42% of total height. Outer lip moderately thickened by varix, weakly convex, palatal swelling weak, five denticles within, variably developed. Anal canal U-shaped. Siphonal canal relatively short, open, slightly recurved, deeply notched at tip. Columellar and parietal callus hardly developed, poorly delimited, weakly thickened, forming narrow rim.

Discussion – *Costoanachis procorrugata* (Sacco, 1890) from the Middle Miocene Langhian Colli Torinesi of Italy is most similar in sculpture with the same number

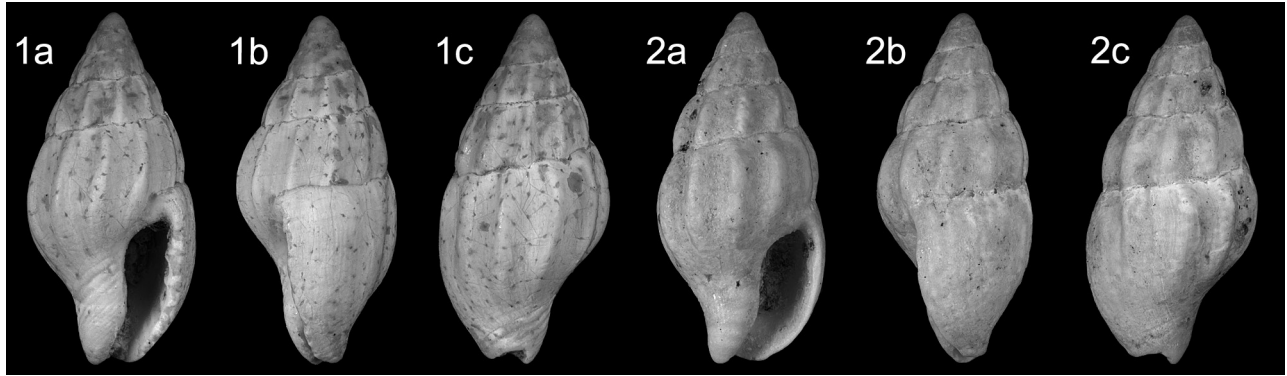


Plate 3. *Costoanachis malaquiasi* sp. nov. 1. **Holotype** NHMW 2022/0201/0065, height 6.4 mm, width 3.1 mm; 2. **Paratype 1** NHMW 2022/0201/0066, height 6.6 mm, width 3.2 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

of ribs and spirals restricted to the siphonal fasciole, but differs in being slenderer, less squat, with the ribs less opisthocline. In the Middle Miocene Paratethys *Costoanachis guembeli* (Hoernes & Auinger, 1880) is slenderer with more numerous ribs, although it must be noted that it is extraordinarily variable in profile and especially the number of axial ribs (see Harzhauser & Landau, 2021, figs 5A-E, 6A), and differs from the Estepona species in having stronger apertural teeth resulting in a narrower aperture. *Costoanachis latecostata* (Boettger, 1902) (lectotype illustrated in Harzhauser & Landau, 2021, figs 6 D₁–D₂) has a similar squat profile, but differs in having flat-sided whorls, and the ribs are straight and almost orthocline as opposed to opisthocline and slightly sinuous. Moreover, both Paratethyan species differ in having a multispiral protoconch.

The new species is also superficially similar to *Amphissa acutecostata* (Philippi, 1844) (see above). However, the shell of *Costoanachis malaquiasi* sp. nov. is far more solid, broader, the siphonal fasciole is much broader, and lacks any spiral sculpture, except over the fasciole. Moreover, they seem to have filled different ecological niches; *A. acutecostata* is found predominantly in the deeper water deposits, whereas *C. malaquiasi* is found exclusively in the shallow water assemblages.

This new species is also superficially similar to some members of the genus *Parvanachis* Radwin, 1968. The Caribbean type species, *P. obesa* (C.B. Adams, 1845), was reported also in the tropical eastern Atlantic from the Canary Islands (Hernández & Boyer, 2005, p. 88, figs 52-54; Hernández *et al.*, 2011, p. 214, figs 68I-K), but *Parvanachis* species differ in being more evenly globose fusiform, with flat-sided spire whorls separated by shallowly incised suture, and in having spiral sculpture. Moreover, the anal canal is deeper and roundly U-shaped.

Costoanachis malaquiasi sp. nov. is uncommon in the Estepona assemblages and found only in the shallower water deposits of Velerín conglomerates and El Lobillo.

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

Genus *Mitrella* Risso, 1826

Type species (by subsequent designation, Cox, 1927) – *Mitrella flaminea* Risso, 1826 (= *Murex scriptus* Linnaeus, 1758), present-day, Mediterranean.

1826 *Mitrella* Risso, p. 247.

Note – The genus *Mitrella* Risso, 1826, as used here, is interpreted rather widely. Molecular results indicate the genus, as presently used, is highly polyphyletic (deMaintenon and Strong, 2022).

Mitrella astensis (Bellardi, 1890)

Plate 4, figs 1-2

- *1890b *Columbella* (*Tetrastomella*) *astensis* Bellardi in Sacco, p. 43, pl. 2, fig. 48.
- 1976 *Mitrella* (*Columbellopsis*) *astensis* (Bellardi, 1890) – Pavia, p. 141, pl. 6, figs 7-10.
- 1981 *Columbella* (*Tetrastomella*) *astensis* Bellardi, 1890 – Ferrero Mortara *et al.*, p. 182, pl. 57, fig. 3.
- 1989 *Mitrella* (*Columbellopsis*) cf. *minor* (Scacchi, 1836) – González Delgado, p. 279, pl. 2, figs 1, 2.
- 1992 *Columbellopsis astensis* (Bellardi, 1890) – Cavallo & Repetto, p. 116, fig. 291.
- 2002 *Mitrella astensis* (Sacco in Bellardi, 1890) – Chirli, p. 6, pl. 3, figs 8-12.
- 2013 *Mitrella astensis* (Sacco in Bellardi, 1890) – Landau *et al.*, p. 27, pl. 13, fig. 18.
- 2022 *Mitrella astensis* Sacco in Bellardi, 1890 [*sic*] – Brunetti, p. 52, fig. 81.

Materials and dimensions – Maximum height 15.1 mm, width 5.4 mm. **VC:** NHMW 2022/0201/0060-0061 (2), NHMW 2022/0201/0062 (21).

Description – Shell moderately small, moderately broad fusiform (AA = 34-37°). Protoconch paucispiral, 1.5 smooth whorls with large nucleus. Teleoconch junction marked by scar and change in lustre. Teleoconch of six al-

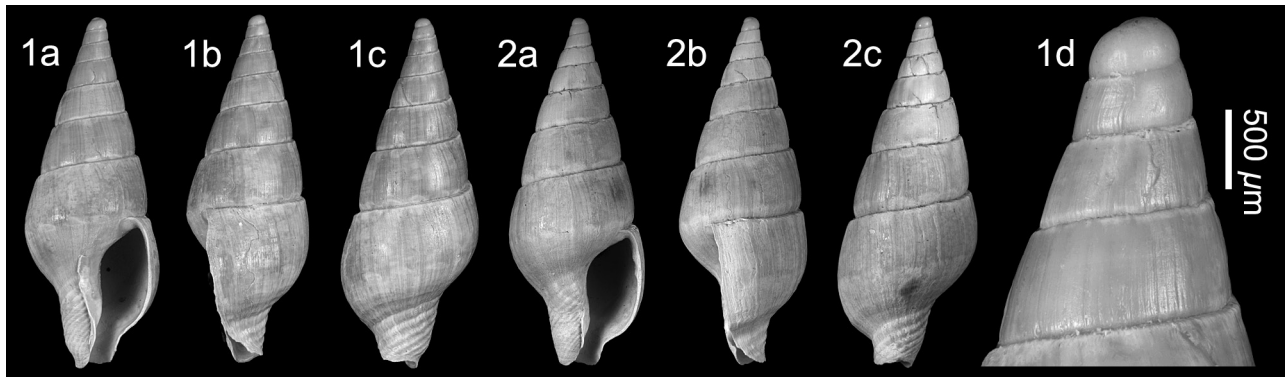


Plate 4. *Mitrella astensis* (Bellardi, 1890). 1. NHMW 2022/0201/0060, height 11.0 mm, width 4.1 mm, 1d, detail of protoconch; 2. NHMW 2022/0201/0061, height 12.1 mm, width 4.6 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

most flat-sided whorls, with periphery at abapical suture, separated by deeply impressed linear suture. Surface smooth, except over siphonal fasciole and base in some specimens. Last whorl 55-59% of total height, roundly angled at periphery placed about mid-whorl, strongly constricted at base; base bearing 2-3 subobsolete cords towards the fasciole in some specimens. Siphonal fasciole medium length, bearing about six well-developed cords. Aperture wide, 37-39% of total height, ovate. Outer lip weakly thickened by broad varix, no palatal swelling, with row of about six denticles within; weakly developed to absent in some specimens. Anal canal broadly V-shaped notch. Siphonal canal moderate length, open, weakly recurved, notched at tip. Columella almost straight, smooth. Columellar callus thin, sharply delimited, erect abapically, continuous with thinner, weakly expanded parietal callus. Colour pattern preserved (Pl. 4, figs 1c, 2c): darker background, row of white blotches adjacent to sutures on spire whorls, on last whorl dark background predominates above periphery, white blotches below.

Discussion – Compared with specimens of *Mitrella astensis* (Bellardi, 1890) from San Gimignano (Siena, Italy), the Estepona specimens have a slightly larger paucispiral protoconch (about 25% larger). However, the protoconch and teleoconch characters are the same. A similar colour pattern is also preserved in some specimens from San Gimignano.

Mitrella condei Rolán, 2005 from present-day Angola is closely similar in shell profile and shares a paucispiral protoconch (possibly one whorl, $dp \sim 700 \mu\text{m}$, P/T boundary not clearly seen; Rolán, 2005, p. 148). However, that species differs in the shape of the aperture that is narrower and more sharply excavated at the upper end of the columella, whereas in the Spanish species the inner lip is more roundly excavated.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (González Delgado, 1989; Landau *et al.*, 2013; Brunetti, 2022); central Mediterranean, Italy (Pavia, 1976; Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central

Mediterranean, Italy (Sacco, 1890b; Ferrero Mortara *et al.*, 1981; Cavallo & Repetto, 1992).

***Mitrella avilai* nov. sp.**

Plate 5, fig. 1

ZooBank registration – urn:lsid:zoobank.org:act:75C1F818-8A30-4CA2-AB37-DAEE3625CC25

Type material – **Holotype** NHMW 2022/0201/0088, height 10.9 mm, width 4.5 mm, **Velerín conglomerates**. **Paratype 1** NHMW 2022/0201/0097, height 10.6 mm, width 4.5 mm, **El Lobillo**.

Other material – Known from type series only.

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

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

Etymology – Name after Sérgio Paulo Ávila Campos Marques, Departamento de Biologia, Universidade dos Açores, in recognition of his contributions to Azorean molluscan palaeontology. *Mitrella* gender feminine.

Diagnosis – *Mitrella* species with ovate shell, cyrtocoid spire, subcylindrical last whorl, elongated aperture bearing six labial denticles, D1 and D2 stronger, and three weak columellar tubercles, columellar and parietal callus continuous forming moderately broad callus rim. Colour pattern of vertical flammules.

Description – Shell moderately small, solid, moderately broad fusiform, with cyrtocoid spire ($AA = 51^\circ$). Protoconch not preserved. Teleoconch of five weakly convex whorls, with periphery at abapical suture, separated by shallow linear suture. Surface smooth, except over lower half of base and siphonal fasciole. Last whorl 64% of total height, barrel-shaped, weakly rounded at periphery

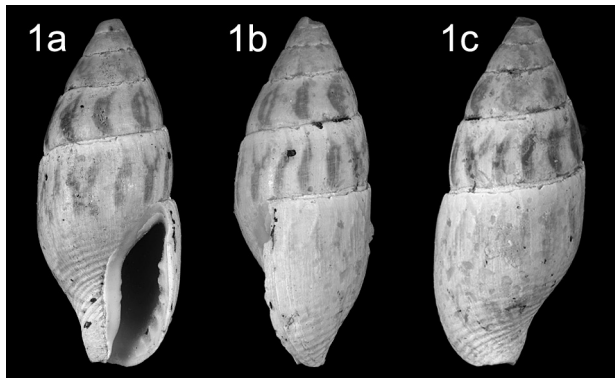


Plate 5. *Mitrella avilai* nov. sp. **Holotype** NHMW 2022/0201/0088, height 10.9 mm, width 4.5 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

placed about mid-whorl, weakly constricted at base; about 16 weak cords over lower half of base and short siphonal fasciole. Aperture narrow, 41% of total height, elongate. Outer lip weakly thickened by varix, moderate palatal swelling, with row of six relatively strong denticles within; D1-D2 over palatal swelling slightly stronger. Anal canal narrow U-shaped notch. Siphonal canal short, open, shallowly notched at tip. Columella straight, bearing three weak tubercles/denticles. Columellar callus thickened, appressed, sharply delimited, continuous with thinner parietal callus, both forming moderately broad callus rim. Colour pattern preserved (Pl. 5, fig. 1): vertically elongated orange/brown flammules extending between sutures on spire whorls, from suture to mid-whorl on last whorl.

Discussion – This species is placed in the genus *Mitrella* Risso, 1826 used in its widest sense.

Harzhauser & Landau (2021) placed a group of European Early and Middle Miocene columbellid species in the genus *Graphicomassa* Iredale, 1929. These species share a subcylindrical last whorl, presence of a subsutural concavity, giving the adapical portion of the last whorl a slightly pinched aspect, slightly gradate spires, and absence of prominent axial sculpture. Extant *Graphicomassa* species are said not to decollate their apex. However, the apex is easily broken if not decollate in many specimens (see deMaintenon, 2016, figs 1B, C-F, I-J). For the Paratethyan Miocene species Harzhauser & Landau (2021) noted that a common feature was a decollate early spire and the development of a low, spirally formed plug. We do not think that presence/absence of a decollate apex is a genus specific character for *Graphicomassa*. However, the Estepona species does not have the gradate spire nor the subsutural concavity on the last whorl typical for the genus. Similarities may be convergent.

The absence of an internal row of columellar denticles allows a separation from *Columbella* Lamarck, 1799. Those authors noted that a decollate apex was also a character of this group.

Although represented by only two specimens, *Mitrella*

avilai nov. sp. is so different from any other European Pliocene to present-day columbellid, that it warrants formal description. It is closest to two Early Miocene Italian species: *G. scalarata* (Sacco, 1890) and *G. inflata* (Bellardi, 1890), which both have subcylindrical last whorls, not concave in the adapical half, but differs in that both the Italian species have gradate spires; characters of the genus *Graphicomassa*. *Mitrella castoris* (Lozano-Francisco & Vera-Peláez, 2006) is vaguely similar in being ovate, but that species is much larger, with a more globose last whorl and a different colour pattern.

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

***Mitrella castoris* (Lozano-Francisco & Vera-Peláez, 2006)**

Plate 6, figs 1-4

- 2006 *Columbella sphaerica* Lozano-Francisco & Vera-Peláez, p. 110, pl. 2, figs 11-14 (*non* Hervier, 1900).
- *2006 *Columbella castoris* Lozano-Francisco & Vera-Peláez, p. 110, pl. 2, figs 17-22.
- 2020 *Columbella castoris* Lozano-Francisco & Vera-Peláez, 2006 – Landau & Mulder, p. 42, text-fig. 1.
- 2022 *Columbella munizsolisi* Lozano-Francisco & Vera-Peláez in Vera-Peláez & Lozano-Francisco, 2022, p. 10, pl. 1, figs 22-25 (*nom. nov. pro Columbella sphaerica* Lozano-Francisco & Vera-Peláez, 2006, *non* Hervier, 1900).
- 2022 *Columbella castoris* Lozano-Francisco & Vera-Peláez, 2006 – Vera-Peláez & Lozano-Francisco, p. 12, pl. 1, figs 23-26.

Materials and dimensions – Maximum height 27.6 mm, width 13.8 mm. **CO:** NHMW 2022/0201/0001 (1), NHMW 2022/0201/0002 (20), NHMW 2022/0201/0078-0079 (2), RGM.1404320 (1).

Description – Shell large, very broad globose, ovate (AA = 59–83°). Protoconch and earliest whorls decollate in all specimens. Up to three teleoconch whorls preserved; spire whorls low, weakly convex, with periphery at abapical suture, separated by shallow, weakly oblique, linear suture. Surface smooth, except over siphonal fasciole. Last whorl strongly inflated, 77–83% of total height, broadly rounded, periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole short, not delimited from base, bearing a few weak cords. Aperture narrow to moderately narrow, 51–60% of total height, moderate width, elongate pyriform. Outer lip weakly thickened by varix, with bevelled edge, palatal swelling weak, with row of 15–16 small denticles placed at the inner edge; 4–5 denticles placed over palatal swelling only slightly stronger, coalescent in some specimens. Anal canal broad V-shaped notch. Siphonal canal short, open, hardly recurved, shallowly notched at tip. Columella straight, bearing row of about ten denticles, variably developed; no internal folds or

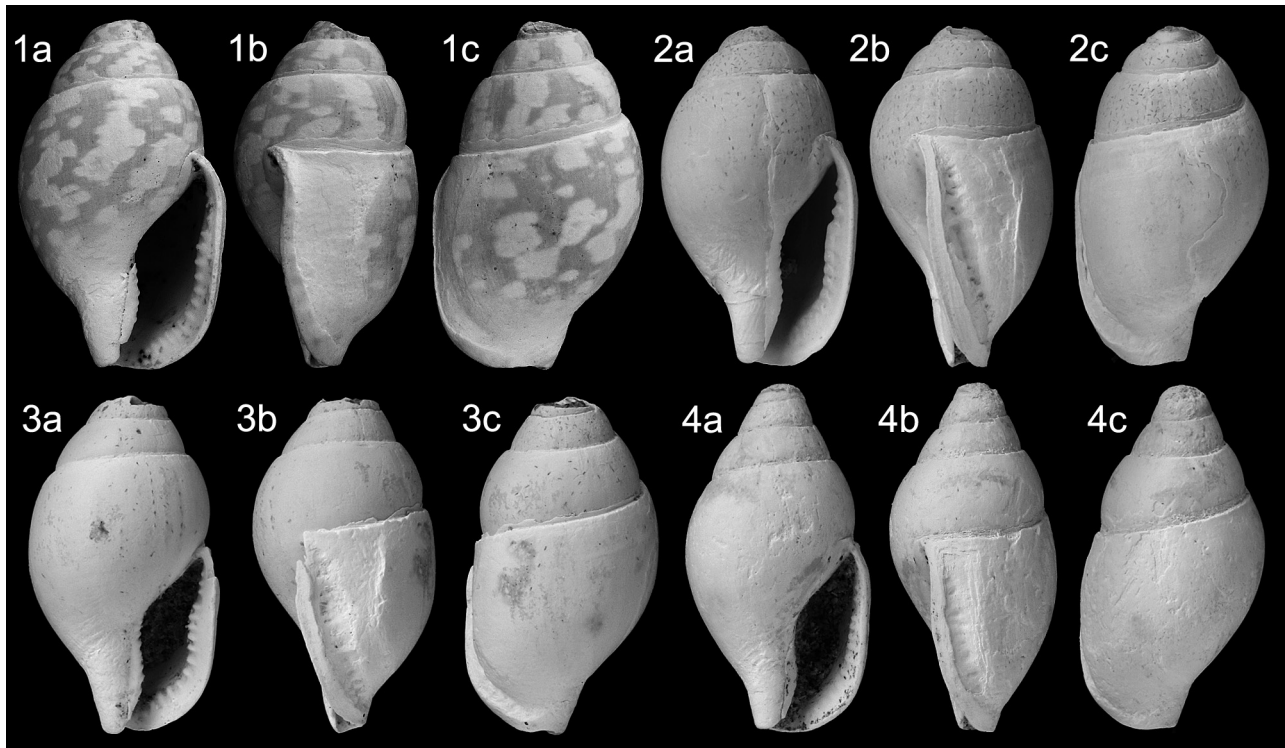


Plate 6. *Mitrella castoris* Lozano-Francisco & Vera-Peláez, 2006. 1. NHMW 2022/0201/0001, height 20.7 mm, width 12.1 mm; 2. NHMW 2022/0201/0078, height 23.1 mm, width 13.1 mm; 3. RGM 1404320, height 21.8 mm, width 12.5 mm; 4. NHMW 2022/0201/0079, height 24.0 mm, width 11.8 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

denticles. Columellar and parietal calluses weakly expanded, discontinuous, mid-portion without any callus. Colour pattern preserved in one specimen (Pl. 6, fig. 1): irregular white coalescent blotches over orange/brown background.

Discussion – Two similar species were described by Lozano-Francisco & Vera-Peláez (2006): *Columbella sphaerica*, (pl. 2 figs. 11-14) and *Columbella castoris*. The only difference given between these species in the original discussion is that *C. sphaerica* was more globose with a narrower aperture. Landau & Mulder (2020) noted that *Columbella sphaerica* was a secondary homonym of *C. sublachryma* var. *sphaerica* Hervier, 1900, and therefore unavailable. They went on to show that the two forms could not be separated using morphometric data and considered *C. castoris* as the valid name for this species. No substitute name was suggested for *Columbella sphaerica* Lozano-Francisco & Vera-Peláez, 2006, as this was considered a subjective synonym.

Vera-Peláez & Lozano-Francisco (2022) stated that the homonymy noted by Landau & Mulder was incorrect and refuted the synonymy.

The first of these points is not a matter for discussion. Both species-group names were published originally in the same genus group (*i.e.*, *Columbella*), and are therefore primary homonyms (ICZN Code, 1999, Art. 53.3). It matters not that Hervier's species is now considered to belong within another genus or family (as argued by Vera-

Peláez & Lozano-Francisco, 2022). Despite believing the homonymy in Landau & Mulder (2020) to be incorrect, they proposed *Columbella munizsolisi* Lozano-Francisco & Vera-Peláez in Vera-Peláez & Lozano-Francisco, 2022 as a replacement name for *Columbella sphaerica* Lozano-Francisco & Vera-Peláez, 2006, *non* Hervier, 1900).

As for the synonymy, those authors continue to give differences in profile as the only distinction between the species, offering further morphometric tables. There is no difference in apertural dentition or sculpture.

This group is represented in the NHMW, RGM and Henk Mulder collections by over 50 adult specimens. What is striking about these specimens, if they are considered two species, are the similarities. 1) They are by far the largest columbellids in the assemblage; 2) they are both quite different in conchological features to any other European/West African Neogene to present-day species; 3) they both decollate their apices, protoconch and early teleoconch whorls, in every specimen seen; although seen in other columbellids (*e.g.*, *Mitrella gervillii* (Payraudeau, 1827), in this species it is more accentuated than in other decollate species; 4) they both become decalcified on the dorsal aspect of the outer lip (taphonomic process) in exactly the same way, which is not often seen in other columbellids in the assemblage, except *Mitrella erythrostroma* (Bellardi, 1848) (this is a taphonomic character); 5) they both have a weak palatal swelling; 6) they both have a row of about ten denticles within the outer lip, those on the palatal swelling only slightly stronger;

and 7) they both occur sympatrically in the same deposit. We continue to consider them two extremes of a single species.

Both *C. sphaerica* and *C. castoris* were placed by Lozano-Francisco & Vera-Peláez (2006, 2022) in the genus *Columbella* Lamarck, 1799. That genus has been used rather indiscriminately in the palaeontological literature for inflated columbellids. True *Columbella* species, however, can be recognised by the following features: a narrow, elongated aperture, the outer lip has a strong palatal swelling, and there are two rows of columellar denticles, one placed at the columellar edge, the other—usually consisting of coarser folds rather than denticles—placed deep within the columella (Landau *et al.*, 2019). This is not the case in the Estepona species, which has a relatively broad aperture, very weak palatal swelling, and no internal folds or denticles. We place it in the genus *Mitrella* in its broadest sense, although it might require a generic group of its own.

It is difficult to find any species to compare this unusual species with. Similarity to the *C. rustica* (Linnaeus, 1758) species group is superficial at best due to the differences discussed the generic assignment above. *Columbella globosa* Millet, 1865 from the Upper Miocene Tortonian of NW France is also superficially similar in having a globose last whorl, but the aperture is narrower and there are folds within the columella, characters of the genus *Columbella*. It may be more closely related to the next largest columbellid in the Estepona assemblages, *Mitrella erythrostoma* (Bellardi, 1848), which also decollates its protoconch and becomes decalcified on the dorsal aspect of the outer lip. However, that species is immediately separated by its taller spire and less inflated last whorl. *Mitrella castoris* is quite unique in shape, and fits neither in *Columbella* nor *Mitrella*. However, *Mitrella*, as used currently, is highly polyphyletic, and we refrain from erecting a monospecific genus.

Distribution – Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Lozano-Francisco & Vera-Peláez, 2006; Landau & Mulder, 2020; Vera-Peláez & Lozano-Francisco, 2022).

Mitrella erythrostoma (Bellardi, 1848)

Plate 7, figs 1-3

- *1848 *Columbella erythrostoma* Bon. Bellardi, p. 9, pl. 1, figs 4, 5.
- 1882 *Columbella erythrostoma?* Bonanni [*sic*] – Wood, p. 6, pl. 1, fig. 10.
- 1890b *Columbella (Mitrella) erythrostoma* Bon. – Sacco, p. 40, pl. 2, fig. 40.
- 1904 *Mitrella erythrostoma* (Bon.) var. *compressula* Sacco, p. 93, pl. 19, figs 51-52.
- 1911 *Columbella (Mitrella) erythrostoma* Bon. – Cerulli-Irelli, p. 256 [306], pl. 23 [40], figs 64, 65.
- 1918 *Columbella (Mitrella) erythrostoma* (Bonelli) – Harmer, p. 306, pl. 33, figs 11, 12.
- 1938 *Columbella (Alia) ligeriana* Peyrot, p. 204, pl. 4, figs 45, 46
- 1952a *Columbella (Alia) erythrostoma* Bonelli, 1825 – Glibert, p. 320, pl. 8, fig. 5.
- 1975 *Mitrella erythrostoma* var. *compressula* Sacco – Fekih, p. 126, pl. 37, fig. 16.
- 1981 *Columbella (Mitrella) erythrostoma* Bellardi, 1848, Bonelli m.s. – Ferrero-Mortara *et al.*, p. 183, pl. 57, fig. 12.
- 1992 *Mitrella semicaudata* (Bellardi, 1848, Bonelli, m.s.) – Cavallo & Repetto, p. 116, fig. 295 [*non Mitrella semicaudata* (Bellardi, 1848)].
- 2011 *Mitrella erythrostoma* (Bellardi, 1848) – Landau *et al.*, p. 28, pl. 13, fig. 19.
- 2017 *Mitrella erythrostoma* (Bellardi, 1848) – Van Dingenen *et al.*, p. 27, pl. 1, fig. 9.
- 2019 *Mitrella erythrostoma* (Bellardi, 1848) – Landau *et al.*, p. 155, pl. 18, figs 1-3.

Materials and dimensions – Maximum height 29.9 mm, width 12.9 mm. **CO:** NHMW 2022/0201/0007-0008 (2), NHMW 2022/0201/0009 (7), RGM.1404321 (1). **EL:** NHMW 2022/0201/0033 (9).

Description – Shell large, broad fusiform (AA = 42-47°). Protoconch decollate in all specimens. Up to five weakly convex teleoconch whorls, with periphery at abapical suture, separated by moderately impressed, weakly

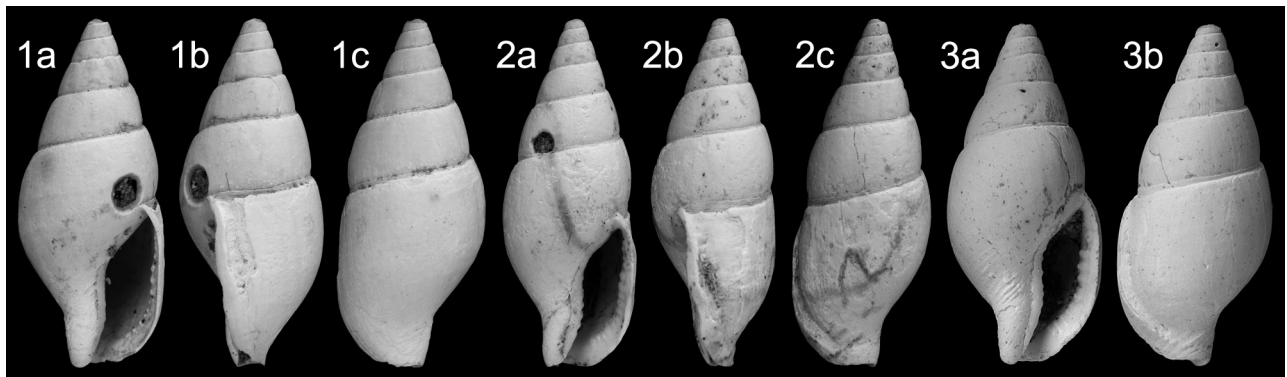


Plate 7. *Mitrella erythrostoma* (Bellardi, 1848). 1. NHMW 2022/0201/0007, height 26.0 mm, width 11.2 mm; 2. NHMW 2022/0201/0008, height 27.8 mm, width 10.9 mm; 3. RGM 1404321, height 23.7 mm, width 10.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

oblique, linear suture. Surface smooth, except over siphonal fasciole. Last whorl moderately inflated, 63-66% of total height, broadly rounded, periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole medium length, not delimited from base, bearing a few weak cords. Aperture narrow to moderately narrow, 40-43% of total height, moderate width, elongate pyriform. Outer lip hardly thickened by varix, slightly pinched inwards just above mid-lip height in area of palatal swelling in some specimens, with bevelled inner edge, palatal swelling weak, with row of 13-15 small denticles placed at the inner edge; 4-5 denticles placed over palatal swelling only slightly stronger. Anal canal V-shaped notch. Siphonal canal moderately short, open, weakly recurved, shallowly notched at tip. Columella straight, bearing row of about twelve tubercles/denticles, variably developed: no internal folds or denticles. Columellar and parietal calluses weakly expanded, continuous or narrowly discontinuous mid-portion, small parietal pad in some specimens. Colour pattern not preserved.

Discussion – *Mitrella erythrostroma* (Bellardi, 1848) is one of the largest-shelled mitrellids in the European Neogene, found from the Middle Miocene to the Upper Pliocene along the European Atlantic frontage and the Mediterranean. Specimens from Estepona are similar in size to those found in other European Pliocene assemblages [*i.e.*, NW France (Van Dingenen *et al.*, 2017), Guadalquivir Basin, Spain (Landau *et al.*, 2011), Italy (Sacco, 1890b)], although specimens from the Upper Miocene of NW France are smaller (Landau *et al.*, 2019). In previous works, we overlooked that both Wood (1882) and Harmer (1918, pl. 33, fig. 10) had illustrated a specimen from the Upper Pliocene Red Crag of England as *M. erythrostroma*. The specimen is incomplete but does indeed seem to represent that species. We are not aware of any further records for the Pliocene North Sea Basin.

Like some other congeners they tend to decollate their apices giving rise to short spired forms, such as Sacco's (1904) variety *compressula*. Apart from the variability in spire height, this species is also variable in degree of inflation and strength of apertural armature. It is highly reminiscent of another highly variable Pliocene to present-day species; *Mitrella gervillii* (Payraudeau, 1827), which also occurs in the Estepona assemblages (see below). That species also decollates its apex, has rather convex whorls, and an outer lip with numerous small denticles. Indeed, some of the smaller specimens are difficult to separate from the more inflated forms of *M. gervillii* (see Giannuzzi-Savelli *et al.*, 2003, figs 575-592 for variability). Nevertheless, *M. erythrostroma* reaches a greater maximum size (30 mm vs. about 19 mm), the last whorl is slightly taller and more inflated, and the base is more strongly excavated.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1952a). Upper Miocene: Atlantic (Tortonian), NW France (Landau *et al.*, 2019); Proto-Mediterranean, Italy (Glibert, 1952a). Lower Pliocene: Atlantic, Atlantic, NW France (Van Dingenen *et*

al., 2017), Guadalquivir Basin, SW Spain (Landau *et al.*, 2011); central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Upper Pliocene: NSB, Red Crag, England (Wood, 1882; Harmer, 1918); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellardi, 1848; Sacco, 1890b, 1904; Cavallo & Repetto, 1992). Upper Pleistocene. Central Mediterranean, Italy (Cerulli-Irelli, 1911).

***Mitrella gervillii* (Payraudeau, 1827)**

Plate 8, figs 1-3

- *1827 *Mitra Gervillii* Payraudeau, p. 165, pl. 8, fig. 21.
- 1844 *Columbella achatina* G.B. Sowerby I, p. 132, pl. 39, fig. 136.
- 1846 *Colombella* [*sic*] *angelia* Duclos, pl. 14.
- 1851 *Colombella* [*sic*] *crossiana* Récluz, p. 257, pl. 7, fig. 5.
- 1865 *Columbella decollata* Brusina, p. 10.
- 1895 *Columbella* (*Mitrella*) *acuta* Monterosato mss. Kobelt, p. 176, pl. 24, figs 8, 9.
- 1960 *Mitrella* (*Mitrella*) *gervillei* [*sic*] (Payraudeau, 1826 [*sic*]) – Malatesta, p. 142, pl. 7, fig. 13.
- 1978 *Mitrella* (*Mitrella*) *gervillei* [*sic*] (Payraudeau, 1826 [*sic*]) – Schirò, p. 8, 9 unnumbered fig. third row.
- 1981 *Mitrella gervillei* [*sic*] (Payraudeau, 1826 [*sic*]) – Sabelli & Spada, unnumbered pages figs 3a-d.
- 1984 *Mitrella gervillei* [*sic*] (Payraudeau, 1826 [*sic*]) – Luque, p. 227, pl. 1, fig. 2.
- 2002 *Mitrella gervillei* [*sic*] (Payraudeau, 1826 [*sic*]) – Chirli, p. 7, pl. 4, figs 1-8.
- 2003 *Mitrella gervillii* (Payraudeau, 1826 [*sic*]) – Chiarelli *et al.*, p. 178, figs 16-24.
- 2003 *Mitrella gervillii* (Payraudeau, 1826 [*sic*]) – Giannuzzi-Savelli *et al.*, p. 18, 246, figs 575-592.
- 2008 *Mitrella gervillii* (Payraudeau, 1826 [*sic*]) – Ceccalupo *et al.*, p. 30, pl. 61, figs 1, 6a, 6b, 7a, 7d.

Materials and dimensions – Maximum height 13.6 mm, width 6.0 mm. CO: NHMW 2022/0201/0021 (1); NHMW 2022/0201/0022 (21), NHMW 2022/0201/0087 (1), RGM. 1404334 (1). EL: NHMW 2022/0201/0036 (4).

Description – Shell moderately small, solid, moderately broad fusiform, with regularly conical spire (AA = 41-46°). Protoconch not preserved. Teleoconch of up to six almost straight-sided whorls, with periphery at abapical suture, separated by superficial linear suture. Surface smooth, except over siphonal fasciole and very fine, irregular subobsolete spirals. Last whorl 60-61% of total height, rather barrel-shaped adapical half, weakly rounded at periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole moderately short, bearing 12-15 weak cords. Aperture moderately narrow, 37-41% of total height, subrectangular elongate. Outer lip weakly thickened by varix, weak palatal swelling, with row of 8-9 relatively strong denticles within; D1-D3 over palatal swelling slightly stronger. Anal canal narrow

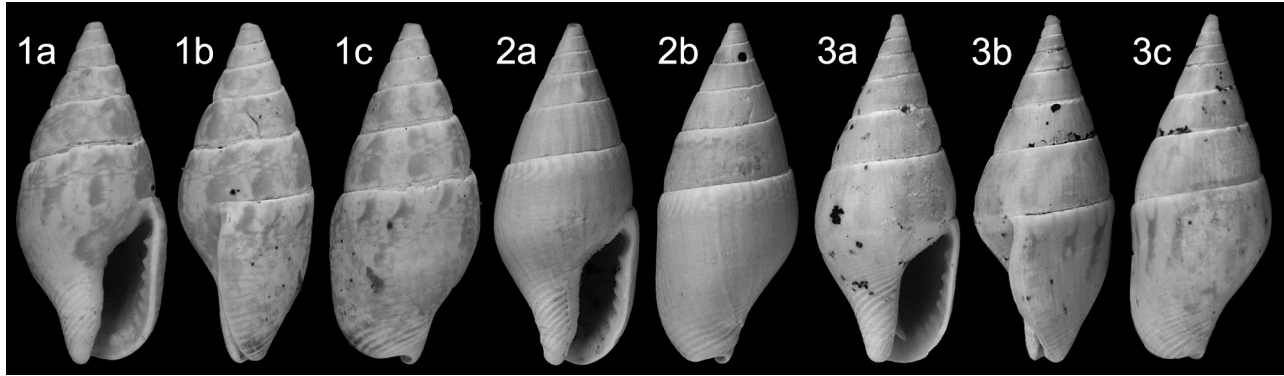


Plate 8. *Mitrella gervillii* (Payraudeau, 1827). 1. NHMW 2022/0201/0021, height 12.3 mm, width 5.4 mm; 2. RGM 1404334, height 13.5 mm, width 5.8 mm; 3. NHMW 2022/0201/0087, height 12.9 mm, width 5.4 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

U-shaped notch. Siphonal canal moderately short, open, shallowly notched at tip. Columella straight, bearing row of 3-4 tubercles/denticles. Columellar callus narrow, thickened, narrowly discontinuous mid-portion, small parietal pad. Colour pattern preserved (Pl. 8, fig. 1): vertically elongated orange/brown flammules and horizontally elongated white blotches; rather variable.

Discussion – The protoconch and earliest part of the first whorl is missing in all the Estepona material. Both Schirò (1978, p. 8) and Luque (1986, p. 227) made the same observation for recent specimens, noting that the apex was almost always decollate. A protoconch was figured by Cecalupo *et al.* (2008, pl. 621, fig. 1) for a specimen from the Gulf of Gabès, Tunisia, and shows it to be paucispiral.

In general shape, apertural characters and colour pattern, these specimens agree with *Mitrella gervillii* (Payraudeau, 1827). The Estepona specimens are similar to those illustrated by Chirli (2002, pl. 4, figs 1-8) as *M. gervillii* [*sic*] from the Italian Lower Pliocene. They differ from extant specimens in having fewer denticles (7-9 vs. 10-12; *vide* Chiarelli *et al.*, 2003). However, in recent populations the number and robustness of the teeth is highly variable (see Giannuzzi-Savelli *et al.*, 2003, figs 575-592). The Pliocene populations seem to have been similarly variable in outline and in strength of apertural armature, as seen in the series illustrated by Chirli (2002) and herein. We therefore consider them conspecific.

Today it lives in the infralittoral zone on algae and sponges (Schirò, 1978), on red coral and a wide range of habitats up to 100 m depth (Chiarelli *et al.*, 2003). In Estepona it is found only in the shallower water assemblages of Velerín conglomerates and El Lobillo.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene, Estepona Basin, Spain (this paper). Lower Pleistocene: central Mediterranean, Sicily (Malatesta, 1960). Present-day: entire Mediterranean and adjacent Atlantic coasts of southern Portugal and Morocco (Sabelli & Spada, 1981; Chiarelli *et al.*, 2003; Cecalupo *et al.*, 2008).

Mitrella minima (Sacco, 1890)

Plate 9, figs 1-2

- *1890b *Columbella* (*Clinurella*) *minima* Sacco, p. 46, pl. 2, fig. 54.
- 1981 *Columbella* (*Clinurella*) *minima* Sacco in Bellardi, 1890 – Ferrero Mortara *et al.*, p. 183, pl. 57, fig. 10.
- ?1981 *Columbella* (*Clinurella*) *vialensis* Sacco in Bellardi, 1890 – Ferrero Mortara *et al.*, p. 183, pl. 57, fig. 12 (?*non* Sacco, 1890).
- 2010 *Mitrella minima* (Sacco, 1890) – Sosso & Dell'Angelo, p. 42, 59 unnumbered fig. top left.
- 2018 *Mitrella vialensis* Sacco in Bellardi, 1890 [*sic*] – Brunetti & Cresti, p. 80, fig. 304 (?*non* Sacco, 1890).

Materials and dimensions – Maximum height 12.1 mm, width 4.1 mm. **CO:** NHMW 2022/0201/0030 (1), NHMW 2022/0201/0031 (1), NHMW 2022/0201/0032 (31). **EL:** NHMW 2022/0201/0039 (4). **VC:** NHMW 2022/0201/0055 (1), NHMW 2022/0201/0056 (50+), RGM.1404333 (5).

Description – Shell moderately small, moderately broad fusiform (AA = 34-37°). Protoconch high conical of about three convex whorls; first 1.5 whorls bearing scattered micropustules, denser towards the suture, later whorls with axial rugae and irregular strongly prosocline riblets just above suture (dp = 525 μ m, hp = 835 μ m, dp/hp = 0.63, dn = 205 μ m, dp1 = 300 μ m). Teleoconch junction with marked by sinusigera. Teleoconch of six weakly convex whorls, with periphery just above abapical suture, separated by deeply impressed linear suture. Surface smooth, except over siphonal fasciole and lower half of base. Last whorl 56-57% of total height, roundly angled at periphery placed about mid-whorl, strongly constricted at base; siphonal fasciole moderately long; weak cords appear on lower half of base, strengthening over fasciole. Aperture wide, 40-41% of total height, ovate. Outer lip moderately strongly thickened by varix, no palatal swelling, with seven or eight denticles within variably developed. Anal

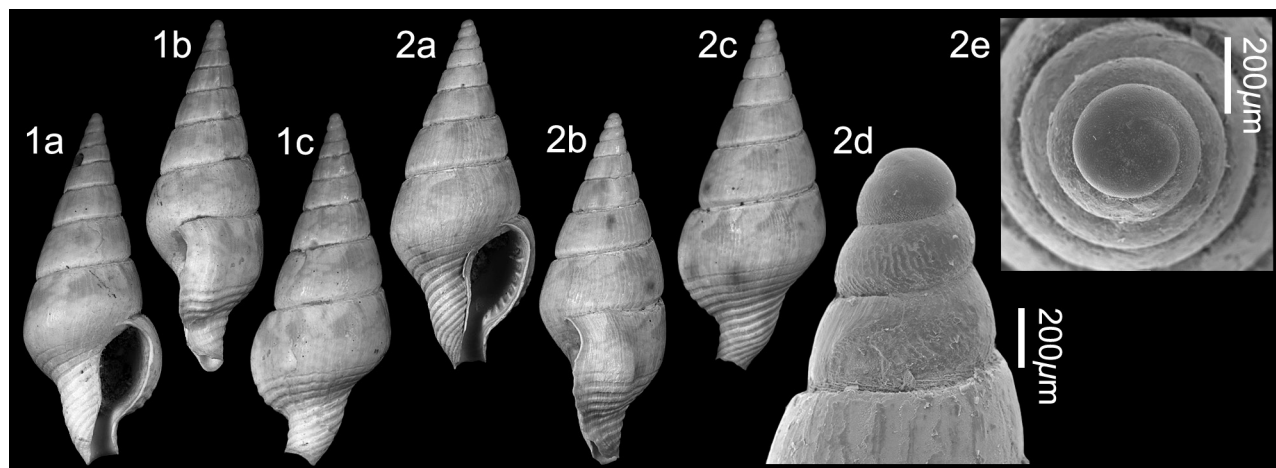


Plate 9. *Mitrella minima* (Sacco, 1890). 1. NHMW 2022/0201/0030, height 9.5 mm, width 3.5 mm (digital images). Velerín conglomerates. 2. NHMW 2022/0201/0055, height 8.0 mm, width 3.2 mm (digital images), 2d, e, detail of protoconch (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

canal broad U-shaped notch. Siphonal canal moderately long, open, bent to left, recurved, shallowly notched at tip. Columella and parietal callus forming very narrow callus margin. Colour pattern preserved: irregular white blotches over darker background, on last whorl horizontal band of larger blotches below suture, row smaller blotches mid-whorl.

Discussion – Sacco (1890b, p. 44) established the subgenus *Clinurella* (type species: *Columbella (Clinurella) scalaris* Sacco 1890, by subsequent designation, Pace, 1902) and included *Columbella (Clinurella) scalaris* (Sacco, 1890), *C. (C.) albucianensis* Sacco, 1890, *C. borsoni* Bellardi, 1848, *C. (C.) vialensis* Sacco, 1890 and *C. (C.) minima* Sacco, 1890. *Columbella borsoni*, *C. minima* and *C. vialensis* have relatively short siphonal canals and only moderately flaring apertures, if at all, and were placed in *Mitrella* (Landau *et al.*, 2013, p. 189; Harzhauer & Landau, 2021, p. 40). They restricted *Clinurella scalaris*, *C. albucianensis* and *C. sophiae* (Boettger, 1902) to *Clinurella*.

Mitrella minima was described from the Upper Pliocene and *M. vialensis* from the Lower Pliocene of Italy [note: Viale, near Montafia is now also considered Upper Pliocene]. Ferrero Mortara *et al.* illustrated syntypes of both species (1981, pl. 57, figs 10 and 12 respectively). According to those authors, the locality of Viale is Piacenzian (1981, p. 183), which is Upper Pliocene, not Lower Pliocene. In our opinion, both specimens selected as syntypes by Ferrero Mortara *et al.* represent the same species that, according to Sacco's original drawings, are closer to *M. minima*.

According to Chirli (2002, p. 13) *M. vialensis* differs only in being larger (10 mm vs. 7 mm, *vide* Sacco, 1890), in having a more acute spire, the last whorl more strongly convex, and especially in having denticles within the outer lip. *Mitrella minima* was said to have a smooth outer lip (Sacco, 1890, p. 46). We refer back to the comment in the Material and methods chapter that columbellids do

not develop labial denticles until fully grown, at which point denticles are formed and the outer lip thickens. Brunetti & Cresti (2018) illustrated specimens identified as *M. minima* and *M. vialensis* that occur together in the Lower Pliocene Orciano Pisano region of Italy. Their specimen of *M. minima* (2018, fig. 300) differs from their specimen of *M. vialensis* (2018, fig. 304) in being smaller, shorter spired, in having a slightly narrower canaliculated suture, subangular base, and in *M. vialensis* having clearly developed denticles within the outer lip. The specimen of *M. minima* illustrated by Sosso & Dell'Angelo (2010, p. 59, unnumbered fig top left) agrees in size with that species (6 mm height) but has strong denticles developed within the outer lip. The specimens of *M. vialensis* illustrated by Chirli (2002, pl. 7, figs 3-8) are relatively large (8.0-9.4 mm height), and all have strong denticles within the outer lip.

Based on the Estepona material, adult height (adult status defined as the presence of a thickened labial varix) ranges from 6.5-12.1 mm. As with many of its congeners, presence or absence of outer lip denticles is not a species-specific character; some specimens are smooth within the outer lip, most have some evidence of denticles that tend to become stronger the larger the specimen, as would be expected if denticles only develop in fully adults. However, even in the most strongly denticulate specimens, they tend to be weak (Pl. X, fig. 2). Convexity of the last whorl is variable; most specimens are subangular (Pl. X, fig. 2), a few are evenly rounded (Pl. X, fig. 1). On balance, the Estepona specimens are closer to *M. minima*.

We are unsure whether *M. minima* and *M. vialensis* represent two different species, or extremes of a single taxon. Further doubt arises as Ferrero Mortara *et al.* (1981) selected syntypes for the two species that represent, in our opinion, *M. minima*. The Estepona specimens are ascribed to *M. minima*, but we stress that their size ranges in the Spanish assemblages overlap, the angulation of the base is variable, and the outer lip is usually denticulate, albeit weakly.

Distribution – Lower Pliocene: central Mediterranean, Italy (Sacco, 1890b; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper), central Mediterranean, Italy (Ferrero Mortara *et al.*, 1981; Sosso & Dell’Angelo, 2010).

***Mitrella pagodiformis* nov. sp.**

Plate 10, figs 1-4

ZooBank registration – urn:lsid:zoobank.org:act:739A33C8-419B-481D-9781-E1A552E17DD1

Type material – **Holotype** NHMW 2022/0201/0027, height 8.4 mm, width 2.8 mm; **paratype 1** NHMW 2022/0201/0028, height 7.3 mm (juvenile); **paratype 2** NHMW 2022/0201/0080, height 8.5 mm, width 3.0 mm; **paratype 3** NHMW 2022/0201/0081, height 7.0 mm (juvenile).

Other material – Known from the type series only.

Type locality – El Lobillo, Estepona, Spain.

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

Etymology – Name reflecting the slightly pagodiform profile of the late teleoconch whorls. *Mitrella* gender feminine.

Diagnosis – *Mitrella* species with small slender shell, protoconch tall, of about 2.25 convex whorls, teleoconch whorls flat-sided, later whorls slightly pagodiform, spirals weak, restricted to siphonal fasciole, outer lip with five denticles.

Materials and dimensions – Maximum height 8.4 mm, width 2.8 mm. **EL:** NHMW 2022/0201/0027-0028, NHMW 2022/0201/0029 (2), NHMW 2022/0201/0080 (3).

Description – Shell small, slender fusiform (AA = 28–30°). Protoconch tall, about 2.25 smooth whorls; nucleus medium sized, post-nuclear whorls tall, convex. Teleoconch junction marked by scar. Teleoconch of 5.5, almost flat-sided whorls, with periphery just above abapical suture, separated by deeply impressed linear suture; periphery on last two whorls subcarinate, somewhat pagodiform, made more evident by narrow swelling of whorl at periphery and deepening of suture. Surface smooth, except over siphonal fasciole and weakly prosocline growth lines and frequent scars. Last whorl 50% of total height, broadly angled at periphery placed about mid-whorl, strongly constricted at base. Siphonal fasciole medium length, bearing weak cords. Aperture wide, 32% of total height. Labial varix and palatal swelling not developed, row of five denticles within, weakening abapically. Anal canal broadly V-shaped notch. Siphonal canal moderate length, open, weakly recurved, notched at tip. Columellar and parietal callus hardly developed, forming narrow callus rim. Colour pattern preserved in some specimens (Pl. 10, fig. 1): large orange/brown blotches over white background.

Discussion – This species is superficially similar to *Mitrella teres* (Bellardi, 1890) from the Lower Pliocene of Italy (holotype illustrated by Ferrero Mortara *et al.*, 1981, pl. 57, fig. 7; also illustrated by Chirli, 2002, pl. 6, figs 7-12) in size and in the character of the tall, elongated protoconch. However, it differs in the profile of the last two whorls, which is slightly concave just below the suture and convex below, slightly swollen in the abapical half in *M. teres*, whereas in the Estepona species the whorl profile is almost straight below the adapical suture and subcarinate just above the abapical one. The last whorl in *M. teres* is taller, rounded rather than angled at the base, and the siphonal canal is much longer than in the Estepona species. Unusually for *Mitrella* species, the outer lip of *M. teres* is not, or hardly, thickened by varix and incomplete in most specimens, but when complete

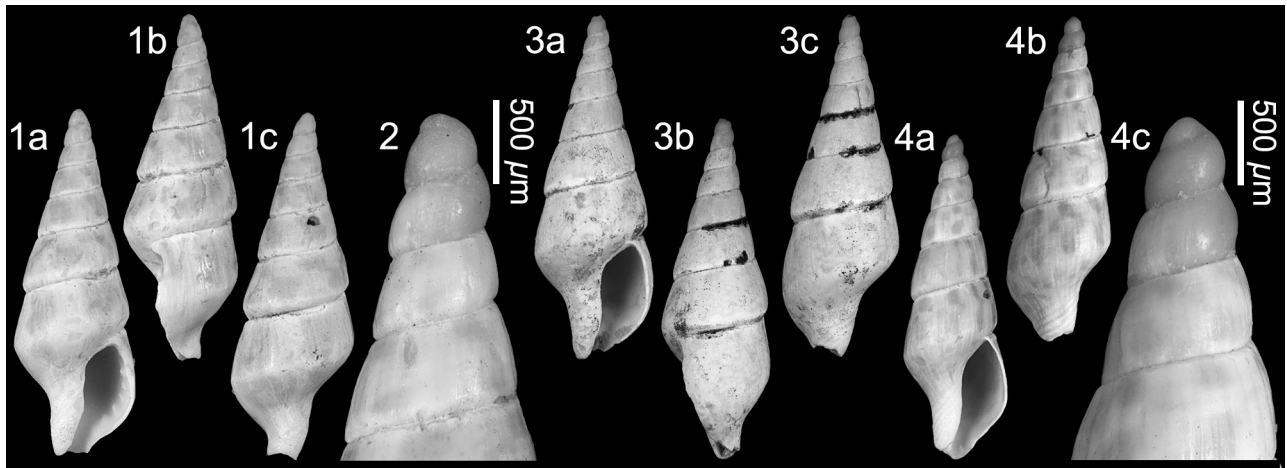


Plate 10. *Mitrella pagodiformis* nov. sp. 1. **Holotype** NHMW 2022/0201/0027, height 8.4 mm, width 2.8 mm; 2. **Paratype 1** NHMW 2022/0201/0028, height 7.3 mm (juvenile), detail of protoconch; 3. **Paratype 2** NHMW 2022/0201/0080, height 8.5 mm, width 3.0 mm. 4. **Paratype 3** NHMW 2022/0201/0081, height 7.3 mm (juvenile), 4c, detail of protoconch (digital images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

does not have denticles within. The *Estepona* species has a broad, weakly thickened labial varix and denticles within.

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

Mitrella scripta (Linnaeus, 1758)

Plate 11, figs 1-2

- *1758 *Murex scriptus* Linnaeus, p. 755.
- 1822 *Buccinum corniculatum* Lamarck, p. 274.
- 1827 *Buccinum linnaei* Payraudeau, p. 161, pl. 8, figs 10-12.
- 1832 *Pisania laevigata* Bivona e Bernardi, p. 12, pl. 2, fig. 7.
- 1848 *Columbella scripta* (Bell. [sic]) – Bellardi, p. 6, pl. 1, fig. 2.
- 1890b *Columbella (Mitrella) scripta* Linn. – Sacco, p. 39, pl. 2, fig. 38.
- 1914 *Columbella scripta* (Linné) – Harmer (*partim*), p. 55, pl. 2, fig. 9 (not fig. 8).
- 1960 *Mitrella (Mitrella) scripta* (Linné, 1766 [sic]) – Malatesta, p. 141, pl. 7, fig. 10.
- 1963 *Mitrella (Mitrella) scripta* (L.) – Venzo & Pelosio, p. 91, pl. 35, fig. 19.
- 1965 *Mitrella (Mitrella) scripta* (L.) – Ruggieri & Greco, p. 53, pl. 9, fig. 7.
- 1979 *Mitrella (Mitrella) scripta* (Linné, 1758) – Montefameglio, p. 189, pl. 1, fig. 2.
- 1986 *Mitrella scripta* (Linné, 1758) – Luque, p. 225, pl. 1, fig. 1.
- ?1992 *Mitrella scripta* (L., 1758) – Cavallo & Repetto, p. 288, fig. 294.
- 2002 *Mitrella scripta* (Linné, 1758) – Chirli, p. 8, pl. 5, figs 1-6.
- 2003 *Mitrella scripta* (Linné, 1758) – Giannuzzi-Savelli *et al.*, p. 18, 244, figs 565-574.
- 2003 *Mitrella scripta* (Linné, 1758) – Chiarelli *et al.*, p. 172, figs 1-3, 29, 36, 40.
- 2011 *Mitrella scripta* (Linné, 1758) – Chirli & Linse, p. 148, pl. 50, fig. 1.

- non 1852 *Columbella scripta* Bell. [sic] – Hörnes, p. 116, pl. 11, figs 12, 14 [= *Mitrella viennensis* Harzhauser & Landau, 2021].
- non 1903 *Columbella scripta* Bell. [sic] – Laskarev, p. 113, pl. 5, figs 24, 25 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1911 *Columbella (Mitrella) scripta* L. – Friedberg, p. 37, pl. 2, fig. 4.
- non 1954 *Mitrella (Mitrella) cf. scripta* (Linne) – Papp, p. 50, pl. 9, fig. 19 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1955 *Columbella (Mitrella) scripta* L. – Moisescu, p. 213, pl. 20, figs 12-14 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1959 *Mitrella scripta* (Bell.) [sic] – Boda, p. 622, 718, pl. 29, figs 3-5 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1960 *Mitrella (Mitrella) scripta* (Linnaeus) – Švagrovský, p. 101, pl. 9, figs 9, 10 [= *Mitrella viennensis* Harzhauser & Landau, 2021].
- non 1964 *Mitrella scripta* L. – Roshka, pl. 2, figs 13, 14 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1968 *Mitrella scripta* (Linné, 1766) – Zelinskaya, p. 207, pl. 48, figs 15, 16.
- non 1971 *Mitrella (Mitrella) scripta* (Bellardi, 1849) [sic] – Švagrovský, p. 379, pl. 66, figs 1-5 [= *Astyris sarmatica* (Kojumdgieva, 1969)].
- non 1993 *Mitrella (Mitrella) scripta* (Linné, 1758) – Iljina, p. 98, pl. 13, figs 4-6 [= *Mitrella viennensis* Harzhauser & Landau, 2021].

Materials and dimensions – Maximum height 16.9 mm, width 6.8 mm. **CO:** NHMW 2022/0201/0023 (1), NHMW 2022/0201/0026 (1), NHMW 2022/0201/0096 (1). **EL:** NHMW 2022/0201/0038 (3).

Description – Shell medium sized, solid, moderately broad fusiform, slightly coeloconoid spire (AA = 38-42°). Protoconch paucispiral, about 1.5 smooth whorls (decollate in most specimens). Teleoconch of six weakly convex whorls, with periphery at abapical suture, separated by narrowly impressed linear suture. Surface smooth, except over siphonal fasciole. Last whorl 59-61% of total height,

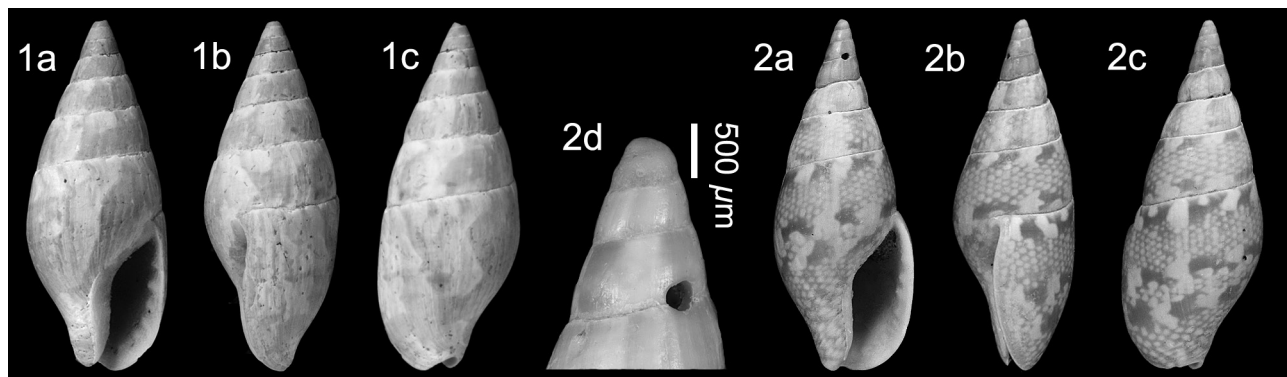


Plate 11. *Mitrella scripta* (Linnaeus, 1758). 1. NHMW 2022/0201/0096 height 16.9 mm, width 6.8 mm; 2. NHMW 2022/0201/0023, height 13.4 mm, width 5.3 mm, 2d, detail of protoconch (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

evenly and weakly convex, periphery placed about mid-whorl, moderately to weakly constricted at base. Siphonal fasciole short, bearing four weak cords. Aperture moderately narrow, 37-41% of total height, pyriform. Outer lip not thickened by varix, weak palatal swelling, with row of 6-8 small denticles within: D2 and D3 only slightly stronger. Anal canal narrow V-shaped notch. Siphonal canal short, open, notched at tip. Columella almost straight, denticles variably developed. Columellar callus thickened, parietal callus weakly thickened, forming continuous narrow callus rim. Colour pattern preserved (Pl. 11, fig. 1): broad, vertical flammules and large blotches below suture; (Pl. 11, fig. 2): horizontally elongated white blotches over darker background; on last whorl two bands of larger blotches, one below suture and one mid-whorl, between these and below mid-whorl broad band of smaller white dots.

Discussion – A small number of specimens from the shallower water assemblages of Velerín conglomerates and El Lobillo we consider conspecific with *Mitrella scripta* (Linnaeus, 1758), today distributed in the Atlantic between Portugal and Morocco, and in the Mediterranean. The specimen figured above (Pl. 11, fig. 1) is typical for the species. The colour pattern of broad vertical flammules is seen in most extant specimens (see Giannuzzi-Savelli *et al.*, 2003, figs 567-569). The second (Pl. 11, fig. 2) is rather unusual in having a rather expanded aperture and thinned outer lip. It is figured primarily for the exceptionally preserved colour pattern, which is also seen in some extant forms of *M. scripta* (see Giannuzzi-Savelli *et al.*, 2003, figs 565, 571). This second form is represented by a single specimen, and we interpret it as an unusual, possibly teratogenic specimen, or damaged during growth.

Mitrella scripta is closely similar to *Mitrella svelta* Kobelt, 1889, but differs in being broader, the spire is slightly coeloconoid as opposed to regularly conical in *M. svelta*, and the siphonal fasciole is shorter and bears fewer cords (4 vs. 6; Chiarelli *et al.*, 2003).

The specimens figured by Cavallo & Repetto (1992, fig. 294) as *M. scripta* might represent this species; the spire is regularly conical rather than coeloconoid and the suture is deeper than usual for the species. Moreover, there are at least ten cords on the siphonal fasciole, whereas in *M. scripta* there are usually 4-5 (Chiarelli *et al.*, 2003). We have provisionally included it in the chresonymy and distribution, with some reservation.

The first reliable stratigraphic record is for the Tortonian Upper Miocene of Italy (Venzo & Pelosio, 1963). Middle Miocene Paratethyan records to *M. scripta* refer to *Mitrella viennensis* Harzhauser & Landau, 2021 or *Astyris sarmatica* (Kojumdgieva, 1969) (see Harzhauser & Landau, 2021).

Today *M. scripta* is a shallow water species living between 1-30m depth on rocky bottoms and living on the rhizomes of *Posidonia* (Chiarelli *et al.*, 2003).

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Venzo & Pelosio, 1963). Lower Pliocene: central Mediterranean, Italy (Montefameglio, 1979; Chirli,

2002). Upper Pliocene, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1890; ?Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Malatesta, 1960; Ruggieri & Greco, 1965); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Atlantic, Portugal to Morocco and entire Mediterranean (Luque, 1986; Giannuzzi-Savelli *et al.*, 2003; Chiarelli *et al.*, 2003).

Mitrella subulata (Brocchi, 1814)

Plate 12, figs 1-3

- *1814 *Murex subulatus* Brocchi, p. 426, pl. 8, fig. 21.
- 1848 *Columbella subulata* Bell. [sic] – Bellardi, p. 14, pl. 1, fig. 12.
- 1890b *Columbella (Terastomella) subulata* (Brocch.) – Sacco, p. 44, pl. 2, fig. 49.
- 1911 *Columbella (Mitrella) subulata* Br. – Cerulli-Irelli, p. 256 [306], pl. 23 [40], figs 64, 65.
- 1955 *Mitrella (Macrurella) subulata* (Brocchi 1814) – Rossi Ronchetti, p. 194, fig. 102.
- 1959 *Pyrene (Mitrella) subulata* (Brocchi) – Ruggieri *et al.*, p. 39, pl. 9, fig. 51.
- 1974 *Mitrella (Macrurella) subulata* (Brocchi 1814) – Malatesta, p. 317, pl. 25, fig. 9.
- 1975 *Atilia (Macrurella) subulata* (Brocchi) – Fekih, p. 129, pl. 38, fig. 20.
- 1975 *Atilia (Macrurella) subulata* var. *convexula* Cerulli-Irelli – Fekih, p. 130, pl. 38, fig. 21.
- 1976 *Mitrella (Columbellopsis) subulata* (Brocchi) – Marasti & Raffi, p. 196, pl. 2, fig. 19.
- 1976 *Mitrella subulata* (Brocchi, 1814) – Caprotti, p. 10, pl. 16, fig. 3.
- 1978 *Murex subulatus* Brocchi, 1814 – Pinna & Spezia, p. 153, pl. 51, fig. 2.
- 1983 *Mitrella subulata* (Brocchi, 1814) – Macri, pl. 3, fig. 9.
- 1990 *Mitrella (Macrurella) subulata* (Brocchi) – Davoli, pl. 5, fig. 9.
- 2002 *Mitrella subulata* (Brocchi, 1814) – Chirli, p. 10, pl. 6, figs 3-6.
- 2011 *Mitrella subulata* (Brocchi, 1814) – Landau *et al.* (partim), p. 28. [not pl. 14, fig. 2 = *Mitrella tetranogostoma* (Fontannes, 1880)].
- 2018 *Mitrella subulata* (Brocchi, 1814) – Brunetti & Cresti, p. 80, fig. 302.
- non 1878 *Columbella subulata* Brocc. – Nyst, pl. 3, fig. 3 [= *Mitrella scaldensis* (Van Regteren Altena, 1956)].
- non 1882 *Columbella subulata* Brocc. – Nyst, p. 36 [= *Mitrella scaldensis* (Van Regteren Altena, 1956)].
- non 1914 *Columbella subulata* (Brocchi) – Harmer, p. 56, pl. 2, figs 11, 12 [= *Mitrella scaldensis* (Van Regteren Altena, 1956)].
- non 2001 *Mitrella subulata* (Brocchi, 1814) – Silva, p. 388, pl. 16, figs 7, 8 [= *Mitrella tetranogostoma* (Fontannes, 1880)].

Materials and dimensions – Maximum height 26.1 mm,

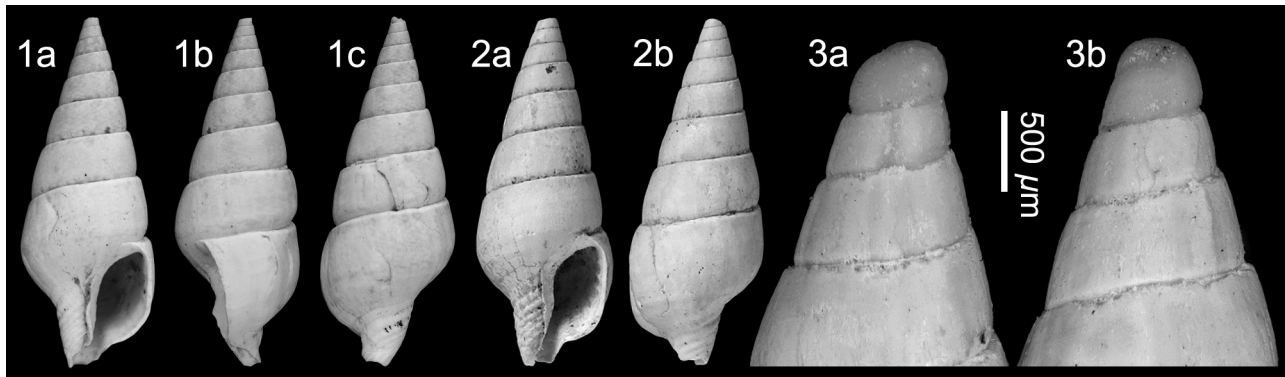


Plate 12. *Mitrella subulata* (Brocchi, 1814). 1. NHMW 2022/0201/0016, height 26.1 mm, width 9.6 mm; 2. RGM.1404322, height 21.2 mm, width 8.1 mm; 3. NHMW 2022/0201/0017, height 11.8 mm, width 4.5 mm, detail of protoconch (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

width 9.6 mm **CO:** NHMW 2022/0201/0016-0017 (2), NHMW 2022/0201/0018 (30), RGM.1404322 (1), RGM.1404323 (2). **EL:** NHMW 2022/0201/0035 (14). **PA:** NHMW 2022/0201/0089 (7).

Description – Shell large, solid, moderately broad fusiform (AA = 32-33°). Protoconch paucispiral, 1.2 smooth whorls with large nucleus. Teleoconch junction marked by scar. Teleoconch of up to eight low, almost flat-sided whorls, with periphery just above abapical suture, separated by deeply impressed linear suture. Surface smooth, except over siphonal fasciole and base in some specimens. Last whorl 50-51% of total height, roundly angled at periphery placed about mid-whorl, strongly constricted at base. Siphonal fasciole medium length, bearing about eight well-developed cords; weak cord delimiting base in some specimens (Pl. 12, fig. 2). Aperture wide, 33-34% of total height, ovate. Outer lip weakly to moderately thickened by broad varix, no palatal swelling, with row of 6-8 denticles within; variably developed. Anal canal broadly V-shaped notch. Siphonal canal moderately short, open, weakly recurved, notched at tip. Columella almost straight, usually smooth; bearing a few subobsolete tubercles in some specimens. Columellar callus sharp, erect, continuous with thin, weakly expanded parietal callus. Colour pattern not preserved.

Discussion – Sculpture on the last whorl is variable. Some specimens lack spiral cords, except for over the siphonal fasciole and the periphery is roundly angled (Pl. 12, fig. 1), whereas in others the periphery bears a subobsolete cord (Pl. 12, fig. 2), and in some the base is covered in further subobsolete cords. Dentition within the outer lip is also variable; relatively strongly developed to absent. Fontannes (1880) described *Strombina* (?) *tetranogostoma* from the Pliocene of France and considered it to differ from *Columbella subulata* in “...dont elle ne se distingue guère que par un dernier tour proportionnellement plus haut et un angle spiral plus ouvert [from which it differs only in having a proportionally taller last whorl and a wider apical angle]” (Fontannes, 1880, p. 94). Brunetti

(2022) recognised this form from the Lower Pliocene of Monte Antico (Italy) and considered the specimen figured by Landau *et al.* (2011, pl. 14, fig. 2) from the Lower Pliocene Guadalquivir Basin of Spain as *Mitrella subulata* to represent *M. tetranogostoma*. Re-examining material at hand from that assemblage, we agree with Brunetti. *Mitrella tetranogostoma* not only has a taller last whorl, but it is more inflated, the apical angle is wider, and the cords on the siphonal fasciole are coarser. However, true *M. subulata* also occurs in the Guadalquivir Basin assemblages together with *M. tetranogostoma*. The latter does not occur in the Estepona assemblages. The specimen from the Upper Pliocene Mondego Basin of Portugal illustrated by Silva (2001, pl. 16, figs 7, 8) as *M. subulata* also represents *M. tetranogostoma*.

Specimens from the Pliocene North Sea Basin identified as *M. subulata* in the historical literature (Nyst, 1878, 1882; Harmer, 1914) represent a separate species endemic to the Pliocene North Sea Basin, *Mitrella scaldensis* (Van Regteren Altena, 1956) that differs from *M. subulata* in being smaller, slenderer, with a less constricted base and a less expanded outer lip.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011). central Mediterranean, Italy (Chirli, 2002; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellardi, 1848; Sacco, 1890; Ruggieri *et al.*, 1959; Malatesta, 1974; Caprotti, 1976). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Marci, 1983).

***Mitrella svelta* Kobelt, 1889**

Plate 13, figs 1-3

1886 *Columbella lanceolata* Locard, p. 102, 539 (*non* Sowerby G.B. I, 1832 in Broderip & Sowerby, G.B. I).

*1889 *Mitrella svelta* Monterosato mss., Kobelt, p. 37, pl. 39, fig. 12-15.

- ?1890b *Columbella (Mitrella) proluxa* Bellardi in Sacco, p. 41, pl. 2, fig. 41.
 1893 *Columbella (Mitrella) spelta* Monterosato, Kobelt, p. 174, pl. 24, figs 3-5, 10 (unjustified emendation).
 1906 *Mitrella syrtiaca* Pallary, p. 207.
 1978 *Mitrella (Mitrella) scripta svelta* «Monterosato» Kobelt, 1901 [*sic*] – Schirò, p. 8, 9 unnumbered fig. second row.
 1981 *Pyrene svelta* Monterosato in Kobelt – Sabelli & Spada, unnumbered pages figs 2a-b.
 ?1981 *Columbella (Mitrella) proluxa* Bellardi, 1890 – Ferrero Mortara *et al.*, p. 181, pl. 56, fig. 10.
 ?2002 *Mitrella proluxa* (Bellardi, 1890) – Chirli, p. 8, pl. 4, figs 9-12.
 2003 *Mitrella lanceolata* (Locard, 1886) – Chiarelli *et al.*, p. 174, figs 4-15, 30, 31, 37, 41, 42.
 2003 *Mitrella lanceolata* (Locard, 1886) – Giannuzzi-Savelli *et al.*, p. 18, 248, figs 593-594.
 2008 *Mitrella lanceolata* (Locard, 1886) – Cecalupo *et al.*, p. 30, pl. 61, figs 5b, 7b, 8, 9a, 9b, 10a.
 2018 *Mitrella lanceolata* (Locard, 1886) – Brunetti & Cresti, p. 80, fig. 299.

Materials and dimensions – Maximum height 19.8 mm, width 6.7 mm. **CO:** NHMW 2022/0201/0019 (1), NHMW 2022/0201/0020 (50+), NHMW 2022/0201/0085 (1), RGM.1404326 (1), RGM.1404327 (2). **EL:** NHMW 2022/0201/0040 (2).

Description – Shell medium sized, very solid, slender fusiform, with tall, regularly conical spire (AA = 31-33°). Protoconch not preserved. Teleoconch of eight, very weakly convex whorls, with periphery at abapical suture, separated by superficial linear suture. Surface smooth, except over siphonal fasciole. Last whorl 52-53% of total height, almost straight sided to periphery, weakly and roundly angled at periphery placed about mid-whorl, weakly constricted at base. Siphonal fasciole short, bearing a few weak cords. Aperture moderately narrow, 33-34% of total height. Outer lip weakly swollen by poorly delimited varix, no palatal swelling, row of about eight denticles within, 2-3 placed mid-lip slightly stronger. Anal canal V-shaped notch. Siphonal canal short, open, weakly recurved, notched at tip.

Columellar callus thickened closely apressed, continuous with thinner parietal callus; no columellar denticles or parietal pad. Colour pattern preserved (Pl. 13, fig. 2): orange/brown background with band of white blotches below suture, row of horizontally elongated dots at periphery last whorl, between these numerous irregular small white dots on darker background.

Discussion – *Mitrella svelta* Kobelt, 1889 is closely similar to *M. scripta* (Linnaeus, 1758), but is slenderer, with a greater height/width ratio last whorl, the spire is regularly conical as opposed to *M. scripta*, which has a slightly coeloconoid spire, it has a greater number of cords on the siphonal fasciole (6 vs. 4), a more tapering siphonal fasciole, and differences in shell colour pattern (see Chiarelli *et al.*, 2003).

This species has usually been recorded in the literature as *Mitrella lanceolata* (Locard, 1886), but Locard's name is a junior homonym of *Columbella lanceolata* Sowerby G.B. I, 1832.

The next available name is *Mitrella svelta* Kobelt, 1889, which Kobelt (1893, p. 37 amended to *spelta*). Chiarelli *et al.* (2003, p. 176) argued that this was a justified emendation, as the name was explicitly changed by Kobelt (1893, p. 174). However, MolluscaBase (2023) considers it an unjustified emendation.

Mitrella svelta has only been recorded in the fossil literature by Brunetti & Cresti (2018, p. 80, fig. 288 under the name *M. lanceolata*) based on specimens from the Lower Pliocene of Italy. However, *M. proluxa* (Bellardi, 1890), described from the Upper Pliocene of Italy is extremely similar. The syntype illustrated by Ferrero Mortara *et al.* (1981, pl. 56, fig. 15) is possibly even slenderer than usual for extant specimens of *M. svelta*, but further specimens from the Pliocene of Italy figured by Chirli (2002, pl. 4, figs 9-12) as *M. proluxa* are, in our opinion, *M. svelta*.

The most similar species is *M. linguloides* (Bellardi, 1890) from the Upper Miocene Proto-Mediterranean of Italy (for illustration of syntype see Ferrero Mortara *et al.*, 1981, pl. 58, fig. 13) and the Middle Miocene eastern Proto-Mediterranean of Turkey (Landau *et al.*, 2013), which differs in being larger shelled and being less constricted at the base.

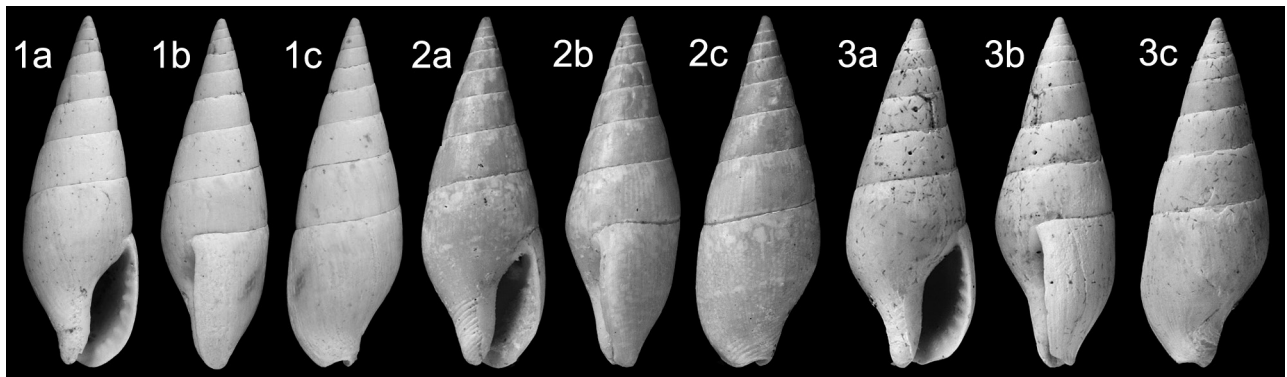


Plate 13. *Mitrella svelta* Kobelt, 1889. 1. NHMW 2022/0201/0019, height 17.8 mm, width 5.7 mm; 2. NHMW 2022/0201/0085, height 15.9 mm, width 5.5 mm; 3. RGM.1404326, height 16.8 mm, width 6.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Today *Mitrella svelta* Kobelt, 1889 is distributed mainly in the Gulf of Gabès, Tunisia, but occasionally found off Sardinia, Sicily, and the coast of Italy.

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); ?central Mediterranean, Italy (Bellardi, 1890). Present-day: western and central Mediterranean, Gulf of Gabès, Tunisia (Schirò, 1978; Sabelli & Spada, 1981; Giannuzzi-Savelli *et al.*, 2003; Cecalupo *et al.*, 2008), rarely eastern Mediterranean (Cecalupo *et al.*, 2008).

Mitrella turgidula (Brocchi, 1814)

Plate 14, figs 1-3

- *1814 *Voluta turgidula* Brocchi, p. 319, pl. 4, fig. 4.
- 1848 *Mitrella turgidula* Bell. [*sic*] – Bellardi, p. 10, pl. 1, fig. 7.
- 1880 *Columbella turgidula* Brocchi – Fontannes, p. 89, pl. 6, fig. 11.
- 1890b *Columbella (Mitrella) turgidula* (Brocch.) – Sacco, p. 37, pl. 2, fig. 33.
- 1904 *Columbella (Conidea) turgidula acutoligustica* Sacco, p. 93, pl. 19, fig. 48.
- 1955 *Mitrella (Macrurella) turgidula* (Brocchi 1814) – Rossi Ronchetti, p. 196, fig. 103.
- 1974 *Mitrella (Mitrella?) turgidula* (Brocchi 1814) – Malatesta, p. 314, pl. 25, fig. 3.
- ?1975 *Atilia (Atilia) turgidula* (Brocchi) – Fekih, p. 127, pl. 38, fig. 4.
- 1978 *Voluta turgidula* Brocchi, 1814 – Pinna & Spezia, p. 171, pl. 67, fig. 1.
- 2002 *Mitrella turgidula* (Brocchi, 1814) – Chirli, p. 12, pl. 7, figs 1, 2.
- non 1928 *Columbella (Mitrella) an turgidula* Brocc. – Friedberg, p. 586, pl. 38, fig. 2 [= *Graphicomassa korytnicensis* (Bałuk, 1995)].
- non 1956 *Pyrene (Mitrella) turgidula* (Brocchi) – Csepregy-Meznerics, p. 402, pl. 7, figs 3-5 [= *Mitrella fallax* (Hoernes & Auinger, 1880)].

non 1966 *Columbella (Mitrella) turgidula* Brocchi, 1814 – Strausz, p. 291, pl. 42, fig. 22 [= *Mitrella fallax* (Hoernes & Auinger, 1880)].

Materials and dimensions – Maximum height 21.1 mm, width 8.3 mm. CO: NHMW 2022/0201/0003-0005 (3), NHMW 2022/0201/0006 (44), RGM.1404323 (2). VC: NHMW 2022/0201/0034 (1).

Description – Shell large, very solid, moderately broad fusiform, with regularly conical spire (AA = 42-43°). Protoconch low dome-shaped, about three smooth whorls; nucleus small. Teleoconch junction marked by opisthocline scar. Teleoconch of 7-8, low, almost flat-sided whorls, with periphery at abapical suture, separated by superficial linear suture. Surface smooth, except over siphonal fasciole. Last whorl 62% of total height, weakly and roundly angled at periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole medium length, bearing weak cords. Aperture very narrow, 40-41% of total height. Outer lip weakly swollen by varix, palatal swelling weak, row of 9-13 denticles within, D2 and D3 over palatal swelling stronger. Anal canal V-shaped notch. Siphonal canal moderate length, open, weakly recurved, shallowly notched at tip. Columellar callus straight, narrow, strongly thickened, bearing row of about eight denticles, narrowly discontinuous mid-portion, small parietal pad. Colour pattern not preserved.

Discussion – *Mitrella turgidula* (Brocchi, 1814) is a very characteristic species; very solid, rather broad with a narrow aperture, further narrowed by the well-developed apertural armature. There is little intraspecific variation. We provisionally include in the chresonymy the juvenile specimen from the Lower Pliocene of Tunisia identified by Fekih (1975) as *A. turgidula*, although this would require confirmation. Paratethyan records to this species refer to *Graphicomassa korytnicensis* (Bałuk, 1995) or *Mitrella fallax* (Hoernes & Auinger, 1880).

Mitrella pseudoturgidula Landau, Ceulemans & Van Dingenen, 2019 from the Upper Miocene Tortonian of NW France is extremely similar in profile and teleoconch characters, however *M. turgidula* has a planktotrophic-

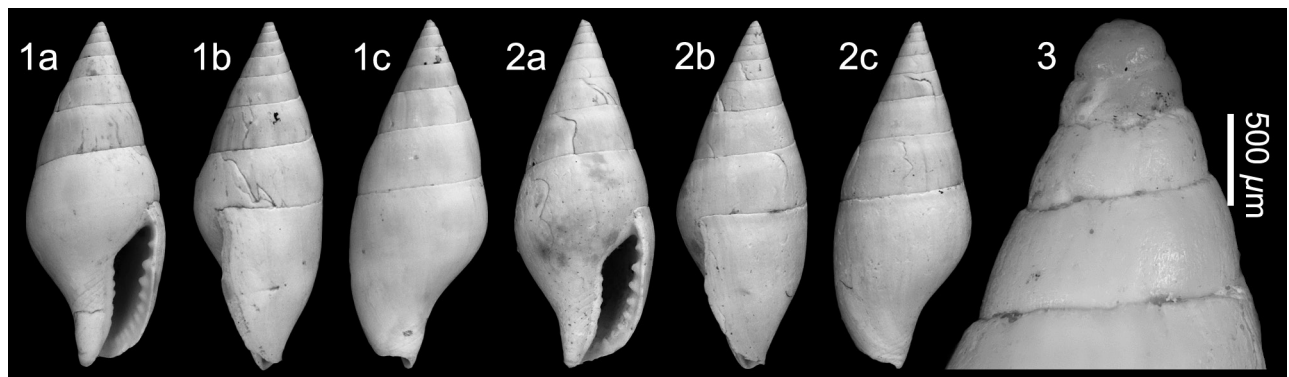


Plate 14. *Mitrella turgidula* (Brocchi, 1814). 1. NHMW 2022/0201/0003, height 20.1 mm, width 8.1 mm; 2. NHMW 2022/0201/0004, height 20.7 mm, width 8.3 mm; 3. NHMW 2022/0201/0005, height 18.9 mm, width 7.7 mm, detail of protoconch (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

type multispiral protoconch with a small nucleus, whereas *M. pseudoturigidula* has a paucispiral protoconch with a large nucleus. The labial denticles are subequal in strength in the French species, whereas in *M. turigidula* D2 tends to be stronger.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Bellardi, 1848). Lower Pliocene: western Mediterranean, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1890, 1904; Chirli, 2002), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Malatesta, 1974).

***Mitrella velerinensis* nov. sp.**

Plate 15, figs 1-3

ZooBank registration – urn:lsid:zoobank.org:act:3FC70EA4-42BE-4459-9135-369099140B1C

Type material – **Holotype** NHMW 2022/0201/0010, height 22.5 mm, width 8.9 mm; **paratype 1** NHMW 2022/0201/0011, height 19.9 mm, width 8.0 mm; **paratype 2** NHMW 2022/0201/0095, height 20.7 mm, width 8.4 mm.

Other material – Maximum height 24.1 mm, width 9.0 mm. **CO:** NHMW 2022/0201/0012 (6).

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

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

Etymology – Name after the type locality of Velerín conglomerates, Estepona, Spain. *Mitrella* gender feminine.

Diagnosis – *Mitrella* species with solid shell, decollate protoconch, cyrtococonoid spire, last two whorls inflated, short relatively wide aperture, 8-9 labial denticles, D2 and D3 usually stronger, columellar callus thickened with

4-5 weak folds, continuous to parietal callus, colour pattern of white blotches over darker background.

Description – Shell large, solid, moderately broad fusiform, slightly cyrtococonoid spire (AA = 38-42°). Protoconch not preserved. Teleoconch of up to seven weakly convex whorls, with periphery at abapical suture, separated by moderately impressed linear suture. Surface smooth, except over siphonal fasciole, and fine weakly prosocline growth lines and frequent growth scars. Penultimate whorl slightly inflated in relation to previous whorls. Last whorl 54-56% of total height, slightly swollen in relation to previous spire whorls, roundly angled at periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole relatively short, bearing up to 15 fine cords. Aperture moderately wide 34-35% of total height, ovate. Outer lip weakly to moderately thickened by varix, weak palatal swelling, with row of 8-9 denticles within; D2 and D3 usually slightly stronger. Anal canal broadly V-shaped notch. Siphonal canal moderately short, open, slightly recurved, shallowly notched at tip. Columella almost straight, bearing 4-5 tubercles. Columellar callus thickened, sharply delimited, narrowly discontinuous mid-portion, small parietal callus. Colour pattern preserved (Pl. 15, fig. 1): irregular horizontally elongated white blotches over darker background.

Discussion – This species is most similar to *Mitrella semicaudata* (Bellardi, 1848), originally described from the Upper Pliocene of Italy (for illustration of syntype see Ferrero Mortara *et al.*, 1981, pl. 56, fig. 11). It differs in having a stouter shell profile, the spire is more strongly cyrtococonoid, the last two whorls more inflated, and the aperture slightly wider. Judging from the specimens of *M. semicaudata* illustrated by Ferrero Mortara *et al.* (1981) and Chirli (2002), that species does not decollate its apex, as seen in *Mitrella velerinensis* nov. sp. Although *M. semicaudata* is fairly widespread in the Mediterranean Pliocene and Lower Pleistocene (Fontannes, 1880; Cerulli-Irelli, 1911; Fekih, 1975; Chirli, 2002; Landau *et al.*, 2011; Chirli & Linse, 2011; Brunetti, 2014, 2022), the name *semicaudata* has been applied to several European Neogene species that are not conspecific.

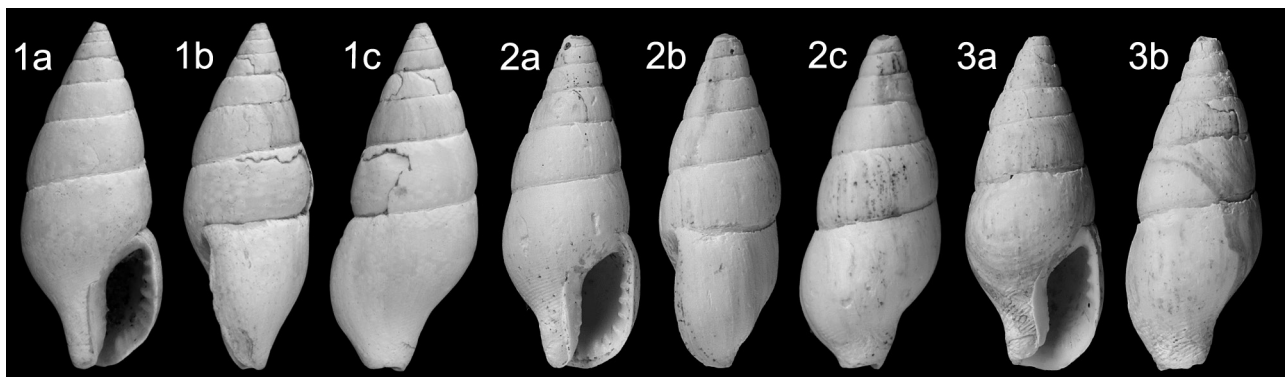


Plate 15. *Mitrella velerinensis* nov. sp. 1. **Holotype** NHMW 2022/0201/0010, height 22.5 mm, width 8.9 mm; 2. **Paratype 1** NHMW 2022/0201/0011, height 19.9 mm, width 8.0 mm; 3. **Paratype 2** NHMW 2022/0201/0095, height 20.7 mm, width 8.4 mm (digital images). Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

We find it useful to give a critical chresonymy of *M. semicaudata* as understood herein:

- *1848 *Columbella semicaudata* Bon. – Bellardi, p. 8, pl. 1, fig. 3.
- 1880 *Columbella semicaudata* var. *serresi* Fontannes, p. 90, pl. 6, fig. 12.
- 1890b *Columbella (Mitrella) semicaudata* Bon. – Sacco, p. 40, pl. 2, fig. 39.
- 1911 *Columbella (Mitrella) semicaudata* Bon. – Cerulli-Irelli, p. 255 [305], pl. 23 [40], figs 60-63.
- 1918 *Columbella (Mitrella) semicaudata* (Bonelli) – Harmer, p. 307, pl. 33, figs 9, ?10.
- 1975 *Mitrella semicaudata* (Bonelli) – Fekih, p. 126, pl. 38, fig. 12.
- 1981 *Columbella (Mitrella) semicaudata* Bellardi, 1848, Bonelli m.s. – Ferrero Mortara *et al.*, p. 180, pl. 56, fig. 11.
- 2002 *Mitrella semicaudata* (Bonelli, 1825) – Chirli, p. 10, pl. 5, figs 7-12, pl. 6, figs 1-2.
- 2011 *Mitrella semicaudata* (Bellardi, 1848) – Landau *et al.*, p. 28, pl. 14, fig. 1.
- 2011 *Mitrella semicaudata* (Bonelli, 1825) – Chirli & Linse, p. 149, pl. 50, fig. 2.
- 2013 *Mitrella semicaudata* (Bellardi, 1848) – Landau *et al.*, p. 192, pl. 29, fig. 10.
- 2014 *Mitrella semicaudata* (Bellardi, 1848, Bonelli, m.s.) – Brunetti, p. 58, unnumbered fig.
- 2022 *Mitrella semicaudata* (Bellardi, 1848, Bonelli, m.s.) – Brunetti, p. 52, fig. 83.
- non 1852 *Columbella semicaudata* Bon. – Hörnes, p. 117, pl. 11, fig. 10 [= *Mitrella complanata* (Sacco, 1890)].
- non 1866 *Columbella semicaudata* Bon. – Pereira da Costa, p. 70, pl. 14, fig. 2.
- non 1911 *Columbella (Mitrella) semicaudata* Bon. – Friedberg, p. 36, pl. 2, fig. 2 [= *Mitrella complanata* (Sacco, 1890)].
- non 1952a *Columbella semicaudata* Bonelli, 1825 – Glibert, p. 321, pl. 8, fig. 6.
- non 1956 *Pyrene (Mitrella) semicaudata* Bon. – Csepregy-Meznerics, p. 403, pl. 7, figs 16-17 [= *Mitrella complanata* (Sacco, 1890)].
- non 1962 *Columbella (Mitrella) semicaudata* Bonelli – Strausz, p. 104, pl. 42, figs 23-24 [= *Mitrella complanata* (Sacco, 1890)].
- non 1966 *Columbella (Mitrella) semicaudata* Bonelli (in Bellardi), 1849 [sic] – Strausz, p. 290, pl. 42, figs 23-24 [= *Mitrella complanata* (Sacco, 1890)].
- non 1968 *Mitrella semicaudata* Bonelli 1825 – Zelinskaya *et al.*, p. 207, pl. 48, figs 17-18 [= *Mitrella complanata* (Sacco, 1890)].
- non 1969 *Columbella (Alia) semicaudata* Bonn – Atanacković, p. 207, pl. 11, fig. 5 [= *Mitrella complanata* (Sacco, 1890)].
- non 1985 *Mitrella (Mitrella) semicaudata* (Bonelli, 1849) – Atanacković, p. 142, pl. 32, figs 3-4 [= *Mitrella complanata* (Sacco, 1890)].
- non 1992 *Mitrella semicaudata* (Bellardi, 1848, Bonelli, m.s.) – Cavallo & Repetto, p. 116, fig. 295 [= *Mitrella*

erythrostroma (Bellardi, 1848)].

non 1993 *Mitrella (Mitrella) semicaudata* Bonelli, 1825 – Iljina, 98, pl. 13, fig. 7 [?= *Mitrella complanata* (Sacco, 1890)].

non 1995 *Pyrene (Mitrella) semicaudata* (Bellardi, 1849 [sic]) – Bałuk, p. 235, pl. 31, figs 1-3 [= *Mitrella viennensis* Hauzhauser & Landau, 2021].

Distribution of M. semicaudata – Middle Miocene: eastern Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.*, 2013). Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011; Brunetti, 2022); western Mediterranean, France (Fontannes, 1880); central Mediterranean, Italy (Cavallo & Repetto, 1992; Chirli, 2002; Brunetti, 2014), Tunisia (Fekih, 1975). ?Upper Pliocene: NSB, Red Crag, England (Harmer, 1918); western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellard, 1848; Sacco, 1890b; Harmer, 1918; Ferrero Mortara *et al.*, 1981). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911), eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011).

Paratethyan Middle Miocene records to this species are incorrect. Most refer to *Mitrella complanata* (Sacco, 1890) that differs in its lower spire, less convex spire whorls, broader columellar callus, and a greater amount of the apex becomes decollate. That species clearly differs from *M. velerinensis* in having almost flat-sided whorls, more of the spire decollate, and a narrower aperture. One specimen (Bałuk, 1995, pl. 31, figs 1-3) refers to *M. viennensis* Harzhauser & Landau, 2021 that differs in having the apex intact, lower spire whorls, and allometric growth rate resulting in a weakly cyrtocoid spire outline (see Harzhauser & Landau, 2021). That species differs from *M. velerinensis* in having a cyrtocoid spire, its more strongly allometric growth, and again having a narrower aperture.

Landau *et al.* (2013, pl. 29, fig. 10) illustrated a specimen from the eastern Proto-Mediterranean Karaman Basin of Turkey as *M. semicaudata*. It probably fits within the variability of that species but may represent a separate taxon. We provisionally include it in the chresonymy with caution. We have excluded from the chresonymy the specimen from the Atlantic Upper Miocene of Portugal illustrated as *Columbella semicaudata* by Pereira da Costa (1866, pl. 14, fig. 2) that seems to have a scalate spire. We have not seen any specimens from that assemblage attributable to this species. Excluded also is the Atlantic Middle Miocene record of the Loire Basin, France (Glibert, 1952a, pl. 8, fig. 6), which is taller spired, the penultimate whorl is not slightly inflated as it is in *M. semicaudata*, and the last whorl is angled at the base. Harmer (1918, pl. 33, fig. 10) illustrated a specimen from the Upper Pliocene Red Crag of England as *M. semicaudata* consisting of only the last whorl. It might represent this species but requires confirmation.

In the extant Mediterranean faunas, *M. velerinensis* is reminiscent of *M. coccinea* (Philippi, 1836), but that species is smaller shelled and the apertural dentition, especially the columellar tubercles, are stronger.

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

***Mitrella villalverniensis* (Sacco, 1890)**

Plate 16, figs 1-2

- *1890b *Columbella (Teratostomella) villalverniensis* Sacco, p. 43, pl. 2, fig. 47.
- 1981 *Columbella (Teratostomella) villalverniensis* Sacco in Bellardi, 1890 – Ferrero Mortara *et al.*, p. 182, pl. 57, fig. 9.
- 2002 *Mitrella villalverniensis* (Sacco in Bellardi, 1890) – Chirli, p. 13, pl. 7, figs 9-12.

Materials and dimensions – Maximum height 10.5 mm, width 3.7 mm. **VC:** NHMW 2022/0201/0057-0058 (figured), NHMW 2022/0201/0059 (11), RGM.1404330 (1), **EL:** NHMW 2022/0201/0076-77 (2).

Description – Shell moderately small, moderately broad fusiform (AA = 33-34°). Protoconch multispiral, 2.5 tall whorls with small nucleus; last whorl microscopically axially rugose (dp = 860 μ m, hp = 1235 μ m, dp/hp = 0.7, dn = 270 μ m, dpl = 510 μ m). Teleoconch junction marked by sinusigera. Teleoconch of five weakly convex whorls, with periphery just above abapical suture, separated by moderately impressed linear suture. Surface smooth, except over siphonal fasciole and axial growth lines. Last whorl 58-59% of total height, roundly and weakly angled at periphery placed about mid-whorl, strongly constricted at base; siphonal fasciole moderately long, bearing very weak cords. Aperture moderately wide, 40-43% of total height, ovate. Outer lip not thickened, no palatal swelling, denticles very weakly developed. Anal canal V-shaped notch. Siphonal canal moderately long, open, bent to left, weakly recurved, shallowly notched at tip. Columella and parietal callus forming very narrow callus margin. Chirli's specimens also show a rather broad, shallow, U-shaped anal canal not seen in the syntype, nor in the Estepona specimens.

Discussion – Compared to the syntype from the Piacenzian Upper Pliocene of Italy (illustrated by Ferrero Mortara *et al.*, 1981, pl. 57, fig. 9) the specimens from Estepona are slenderer and the siphonal canal is a little longer. They fit well with the specimens from the Lower Pliocene of Italy identified as *Mitrella villalverniensis* (Sacco, 1890) by Chirli (2002, pl. 7, figs 9-12). Like the Estepona specimens they are relatively slenderer than the syntype, the siphonal canal is longer, the apertural dentition is very weak, and the angulation of the last whorl at the base varies from weak to subobsolete. The protoconch in one of Chirli's specimens (2002, pl. 7, figs 9-10) is preserved and seems similar to that of the Estepona specimens (protoconch not enlarged nor described in Chirli, 2002).

Distribution – Lower Pliocene: central Mediterranean, Italy (Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1890b; Ferrero Mortara *et al.*, 1981).

Genus *Orthurella* Sacco, 1890

Type species (by subsequent designation, Cossmann, 1901): *Columbella elongata* Bellardi, 1848, Miocene, Italy.

- 1890a *Orthurella* Sacco, p. 224.
- 1890a *Macrurella* Sacco, p. 224. Type species (by subsequent designation, Cossmann, 1901): *Fusus nassoides* Grateloup, 1827, Miocene, France.

Note – Landau *et al.* (2013) considered *Orthurella* Sacco, 1890 and *Macrurella* Sacco, 1890 (in Sacco 1890b) (type species *Fusus nassoides* Grateloup, 1827, Lower Miocene, France) to be synonyms. In contrast to the opinion of Cossmann (1901), the type species of both genera are not conspecific. Therefore, Landau *et al.* (2013, p.193) gave *Orthurella* precedence over *Macrurella* as first revisers.

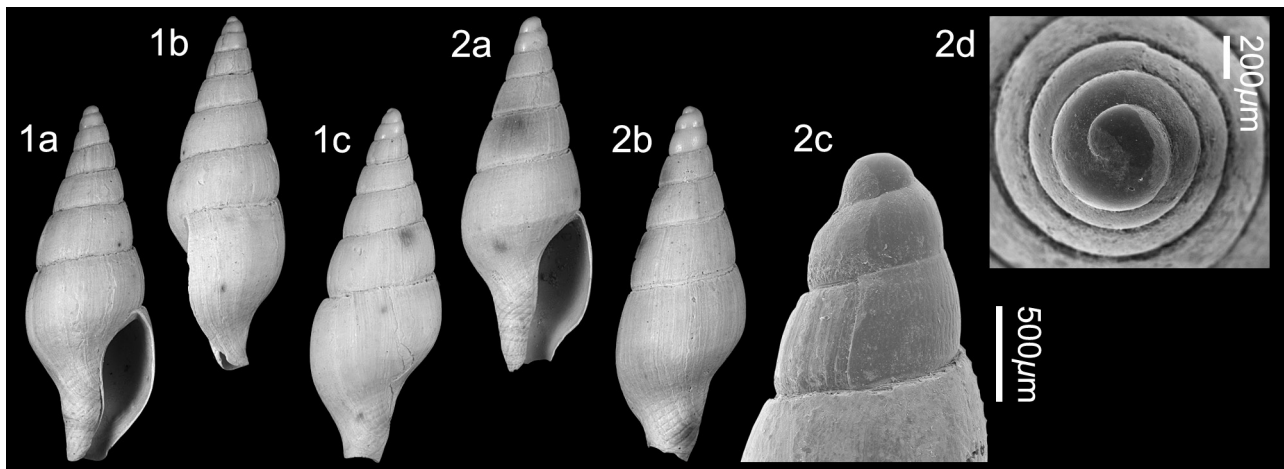


Plate 16. *Mitrella villalverniensis* (Sacco, 1890). 1. NHMW 2022/0201/0057, height 10.5 mm, width 3.7 mm; 2. NHMW 2022/0201/0058, height 8.2 mm, width 2.9 mm (digital images), 2c-d, detail of protoconch (SEM images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Note that Landau *et al.* (2013: 193) in *lapsus* forgot to change *Macrurella* into *Orthurella* in their discussions on *Orthurella nassoides* (Grateloup, 1827), *O. pronassoides* (Sacco, 1890) and *O. attenuata* (Beyrich, 1854), but from the context it is clear that the authors placed these species in *Orthurella*.

Orthurella pronassoides (Sacco, 1890)

Plate 17, figs 1-3

- 1848 *Columbella nassoides* Bell. [*sic*] – Bellardi, p. 16, pl. 1, fig. 13 [*non Orthurella nassoides* (Grateloup, 1827)].
- *1890b *Columbella (Macrurella) pronassoides* Sacco, p. 51, pl. 2, fig. 66.
- 1890b *Columbella (Macrurella) nassoides* (Grat.) – Sacco, p. 51, pl. 2, fig. 67 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1901 *Atilia (Macrurella) nassoides* (Grat.) – Cossmann, p. 244, pl. 10, fig. 25 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1967 *Mitrella (Macrurella) nassoides* (Grateloup) – Pelosio, p. 135 [35], pl. 40, figs 16, 17 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1974 *Mitrella (Macrurella) nassoides* (Grateloup, 1827) – Malatesta, p. 315, pl. 26, fig. 1 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1975 *Atilia Atilia (Macrurella) nassoides* (Grateloup) – Fekih, p. 129, pl. 38, fig. 15 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1976 *Mitrella (Macrurella) nassoides* (Grateloup) – Marasti & Raffi, p. 196, pl. 2, fig. 13 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1976 *Mitrella nassoides* (Grateloup, 1827) – Caprotti, p. 10, pl. 16, fig. 2 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1981 *Columbella (Macrurella) pronassoides* Sacco in Bellardi, 1890 – Ferrero Mortara *et al.*, p. 184, pl. 56, fig. 16.
- 1986 *Mitrella (Macrurella) nassoides* Grateloup – Martinell & Domènech, p. 119, pl. 1, fig. 14 [*non Orthurella nassoides* (Grateloup, 1827)].

- 1988 *Mitrella nassoides* (Grateloup, 1827) – Chirli, p. 21, pl. 8, fig. 2 [*non Orthurella nassoides* (Grateloup, 1827)].
- 1992 *Mitrella nassoides* (Grateloup, 1827) – Cavallo & Repetto, p. 116, fig. 293 [*non Orthurella nassoides* (Grateloup, 1827)].
- 2002 *Mitrella nassoides* (Grateloup, 1827) – Chirli, p. 16, pl. 8, figs 9-12, pl. 9, figs 1-3. [*non Orthurella nassoides* (Grateloup, 1827)].
- 2008 *Mitrella nassoides* (Grateloup, 1827) – Chirli & Richard, p. 43, pl. 7, figs 8-10 [*non Orthurella nassoides* (Grateloup, 1827)].
- 2008 *Mitrella nassoides* (Grateloup, 1827) – Duerr, p. 153, figs 4-6 [*non Orthurella nassoides* (Grateloup, 1827)].
- 2010 *Mitrella nassoides* (Grateloup, 1827) – Sosso & Dell'Angelo, p. 42, 59 unnumbered fig. top centre [*non Orthurella nassoides* (Grateloup, 1827)].
- 2014 *Mitrella nassoides* (Grateloup, 1827) – Brunetti, p. 57, unnumbered fig. [*non Orthurella nassoides* (Grateloup, 1827)].
- 2018 *Mitrella nassoides* (Grateloup, 1827) – Brunetti & Cresti, p. 80, fig. 298 [*non Orthurella nassoides* (Grateloup, 1827)].

Materials and dimensions – Maximum height 27.3 mm, width 9.2 mm. **VC:** NHMW 2022/0201/0014 (1), NHMW 2022/0201/0082 (10). **CO:** NHMW 2022/0201/0013 (1), NHMW 2022/0201/0015 (50+), NHMW 2022/0201/0083 (1), RGM.1404325 (3). **EL:** NHMW 2022/0201/0037 (1).

Description – Shell large, slender fusiform, with high conical spire (AA = 32-33°). Protoconch tall conical of about three convex whorls, last whorl with single spiral thread running just above suture. Teleoconch junction marked by sinusigera. Teleoconch of up to eight almost flat-sided whorls, with periphery at abapical suture, separated by deeply impressed, narrowly canaliculate, linear suture. Surface smooth, except over siphonal fasciole. Last whorl 54-58% of total height, straight sided to periphery placed mid-whorl, very weakly roundly angled and moderately constricted at base. Siphonal fasciole long, bearing weak cords. Aperture very narrow, 39-41%

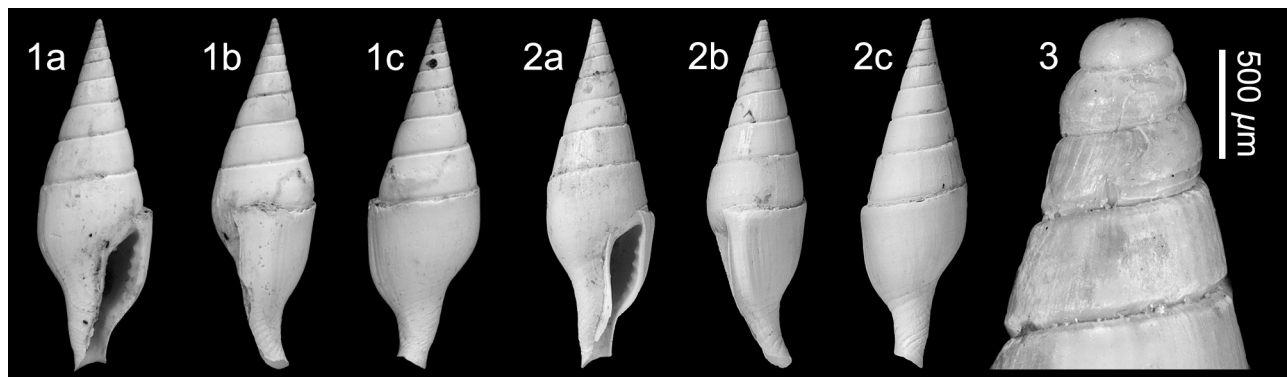


Plate 17. *Orthurella pronassoides* (Sacco, 1890). 1. NHMW 2022/0201/0013, height 25.4 mm, width 8.4 mm; 2. NHMW 2022/0201/0083, height 24.0 mm, width 7.3 mm. Velerín conglomerates. 3. NHMW 2022/0201/0014, height 20.9 mm, width 7.3 mm, detail of protoconch (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

of total height. Outer lip weakly swollen by broad varix, very weak palatal swelling, row of about six denticles within, slightly stronger over palatal swelling. Anal canal narrow V-shaped notch. Siphonal canal long, narrow, open, recurved, notched at tip. Columellar callus straight, narrow, erect, sharp edged, without tubercles or denticles, narrow discontinuous section at upper end, small oblique, straightened parietal callus and pad.

Discussion – This species complex was fully discussed by Landau *et al.* (2013). Historically, superficially similar slender columbellids with a long siphonal fasciole from widely disparate stratigraphic and geologic provenances have been ascribed to *Fusus nassoides* Grateloup, 1827. That species has a relatively stout, fusiform shell, with almost flat-sided whorls and a relatively short, deflected siphonal canal. Mediterranean Pliocene shells ascribed to *F. nassoides* are slenderer with a higher coeloconoid spire, nearly flat whorls and a longer canal compared to Lower Miocene specimens of *Orthurella nassoides*. The name *Orthurella pronassoides* (Sacco, 1890) was used by Landau *et al.* (2013) for these Pliocene Mediterranean specimens. Miocene North Sea Basin shells ascribed to *Fusus nassoides* are smaller than the forms mentioned above, with a deeply impressed, very narrowly canalliculate suture, the aperture is very small, and the siphonal canal is shorter than in any of the above and hardly deflected. The name *Orthurella attenuata* (Beyrich, 1854) is available for this form. Langhian and Serravallian Paratethyan shells usually identified as *Mitrella nassoides*, as well as the Turkish specimens, are characterised by their long, straight siphonal canal, and their gently contracted base, which results in a comparatively long last whorl. The whorls are slightly convex in most specimens (although this character is variable) and tend to be cyrtocooid. The name *Orthurella convexula* Sacco, 1904 can be used for these specimens.

In Estepona *O. pronassoides* is found in both the deep and shallow water deposits.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1890b; Ferrero Mortara *et al.*, 1981). Lower Pliocene: western Mediterranean, France (Martinell & Domènech, 1986); central Mediterranean, Italy (Sacco, 1890b; Pelosio, 1967; Chirli, 2002; Brunetti, 2014; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper), France (Cossmann, 1901; Chirli & Richard, 2008); central Mediterranean, Italy (Marasti & Raffi, 1976; Caprotti, 1976; Chirli, 1988; Sosso & Dell'Angelo, 2010).

Genus *Thiarella* Sacco, 1890

Type species (by subsequent designation, Cossmann, 1899): *Murex thiara* Brocchi 1814, Pliocene, Italy.

- 1890a *Thiarella* Sacco, p. 224.
1899 *Crenisutura* Cossmann, p. 46. Type species (by original designation): *Murex thiara* Brocchi 1814,

Pliocene, Italy. Unnecessary replacement name. Cossmann considered Sacco's name a homonym of *Tiarella* Swainson, 1840 (see Harzhauser & Landau, 2021, p. 43).

Thiarella thiara (Brocchi, 1814)

Plate 18, figs 1-2

- *1814 *Murex thiara* Brocchi, p. 424, pl. 8, fig. 6.
1848 *Columbella thiara* Bon. [*sic*] – Bellardi, p. 19, pl. 1, figs 17, 18.
1880 *Strombina tiara* var. *torcapeli* Fontannes, p. 95, pl. 6, fig. 16.
1890b *Columbella (Thiarella) Rovasendae* Sacco, p. 53, pl. 2, fig. 70.
1890b *Columbella (Thiarella) carinata* (Bon.) Sacco, p. 53, pl. 2, fig. 71.
1890b *Columbella (Thiarella) thiara* (Brocch.) – Sacco, p. 54, pl. 2, fig. 72.
1901 *Atilia (Crenisutura) thiara* (Brocchi) – Cossmann, p. 237, pl. 10, figs 21, 22.
1904 *Columbella (Crenisutura) carinata* var. *recticaudata* Sacco, p. 95, pl. 19, figs 61, 62.
1904 *Columbella (Crenisutura) thiara* var. *eminenticostata* Sacco, p. 95, (= var. A Sacco, 1890b).
1955 *Mitrella (Crenisutura) thiara* (Brocchi 1814) – Rossi Ronchetti, p. 197, fig. 104.
1967 *Mitrella (Crenisutura) thiara* (Brocchi) – Pelosio, p. 136 [36], pl. 40, figs 12-15.
1968 *Mitrella (Crenisutura) carinata* (Bellardi, 1890) – Robba, p. 537, pl. 41, fig. 5.
1973 *Atilia (Crenisutura) thiara* (Brocchi), 1814 – Caprotti & Vescovi, p. 164, pl. 2, fig. 4.
1975 *Atilia (Crenisutura) thiara* (Brocchi) – Fekih, p. 130, pl. 38, fig. 22.
1974 *Atilia (Crenisutura) thiara* (Brocchi), 1814 – Caprotti, p. 26, pl. 20, fig. 6.
1976 *Atilia (Crenisutura) thiara* (Brocchi, 1814) – Caprotti, p. 10, pl. 2, fig. 4.
1976 *Atilia (Crenisutura) thiara* (Brocchi, 1814) – Marasti & Raffi, p. 197, pl. 1, fig. 2.
1978 *Murex thiara* Brocchi, 1814 – Pinna & Spezia, p. 153, pl. 43, fig. 3.
1981 *Columbella (Thiarella) rovasendae* Sacco in Bellardi, 1890 – Ferrero Mortara *et al.*, p. 184, pl. 58, fig. 2.
1981 *Columbella (Thiarella) carinata* Bellardi 1890, Bonelli m.s. – Ferrero Mortara *et al.*, p. 184, pl. 58, fig. 1.
1986 *Mitrella (Crenisutura) thiara* (Brocchi, 1814) – Martinell & Domenèch, p. 119, pl. 1, fig. 4.
1992 *Mitrella thiara* (Brocchi, 1814) – Cavallo & Repetto, p. 116, fig. 296.
2002 *Mitrella (Crenisutura) thiara* (Brocchi, 1814) – Chirli, p. 14, pl. 8, figs 1-8.
2008 *Mitrella thiara* (Brocchi, 1814) – Chirli & Richard, p. 43, pl. 7, figs 11, 12.
2018 *Mitrella thiara* (Brocchi, 1814) – Brunetti & Cresti, p. 80, fig. 303.

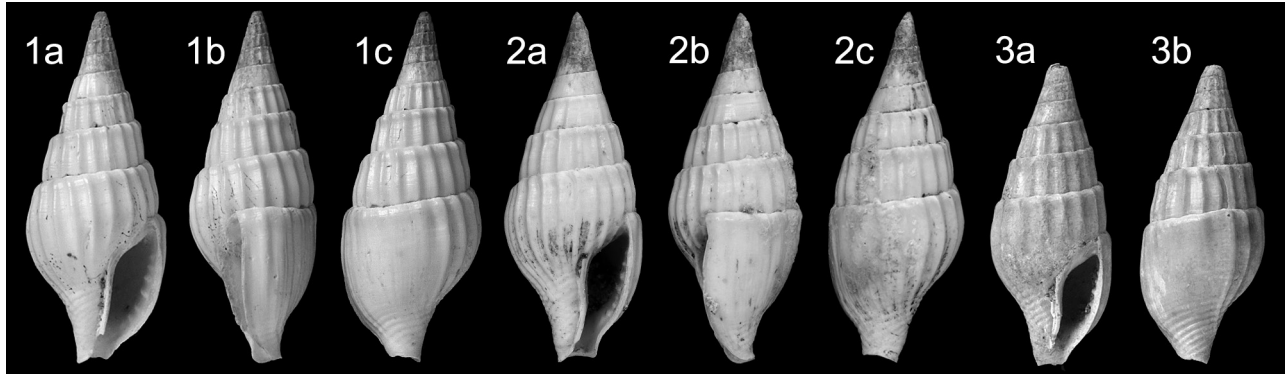


Plate 18. *Thiarella thiara* (Brocchi, 1814). 1. NHMW 2022/0201/0072, height 25.6 mm, width 8.9 mm; 2. NHMW 2022/0201/0073, height 23.2 mm, width 7.6 mm, 2d, detail of protoconch (digital images). Parque Antena, Estepona, Lower Piacenzian, Upper Pliocene.

- non* 1852 *Columbella tiara* Bon. – Hörnes, p. 119, pl. 11, figs 7a-c [= *Thiarella bronni* (Mayer, 1869)].
- non* 1856 *Columbella tiara* Bon. – Hörnes, p. 666, pl. 51, figs 2a-b [= *Thiarella bronni* (Mayer, 1869)].
- non* 1880 *Columbella (Nitidella) tiara* Brocc. – Hoernes & Auinger, p. 94, pl. 11, fig. 3 [= *Thiarella bronni* (Mayer, 1869)].
- non* 1969 *Pyrene (Crenisutura) thiara* (Brocchi)–Csepregy-Meznerics, p. 84, pl. 4, fig. 9 [= *Thiarella bronni* (Mayer, 1869)].

Materials and dimensions – Maximum height 25.6 mm, width 8.9 mm. **CO:** NHMW 2022/0201/0074 (2). **PQ:** NHMW 2022/0201/0072 (1), 2022/0201/0075 (1), NHMW 2022/0201/0073 (3).

Description – Shell large, moderately broad fusiform, with high coeloconoid conical spire (AA = 30–35°). Protoconch tall conical of about three smooth, convex whorls. Teleoconch junction marked by opisthocline scar. Teleoconch of up to nine flat-sided whorls, with periphery at abapical suture, separated by superficial linear suture, weakly undulating on later whorls. Sculpture of opisthocline rounded axial ribs, slightly tuberculate at adapical end, strongly developed on early teleoconch whorls, weakening on mid-portion of spire, strengthening again on last two whorls, adapical end of ribs producing small, pointed tubercles, giving last two whorls somewhat coronate appearance. Spiral sculpture restricted to very fine cord just below the suture running along the apex of tubercles, and fine cords over siphonal fasciole. Last whorl 56–57% of total height, coronate just below suture, concave below, weakly angled at periphery placed about mid-whorl, moderately constricted at base. Siphonal fasciole long, bearing weak cords. Aperture narrow, 38–42% of total height. Outer lip weakly swollen by varix, no palatal swelling, row of about eight subequal denticles within. Anal canal narrow V-shaped notch. Siphonal canal long, narrow, open, straight, unnotched. Columellar and parietal callus moderately thickened, sharply delimited, continuous, forming narrow callus rim; row of small denticles on colu-

mella developed in some specimens; small parietal pad adapically.

Discussion – Sacco (1890b) included *Murex thiara* Brocchi, 1814, from the Tortonian of Stazzano and San Agata (Italy) and the Pliocene of Asti and Vaile (Italy), *Columbella (Thiarella) rosavandae* Sacco, 1890, from the Messinian of Tetti Borelli (Italy), and *Columbella (Thiarella) carinata* Sacco, 1890 (*non* Hinds, 1844), from the Tortonian of Stazzano and San Agata (Italy) and the Messinian of Tetti Borelli (Italy), in his new subgenus *Thiarella*. These taxa co-occur at the same localities and the differences seen in the syntypes seem to be mainly a matter of ontogeny (see Ferrero Mortara *et al.*, 1981, pl. 58, figs 1–2). *Murex thiara* is a highly variable species, as noted by several authors (Pelosio, 1967; Caprotti, 1974), and *Columbella rosavandae* and *C. carinata* were considered subjective junior synonyms of *Thiarella thiara* by Harzhauser & Landau (2021, p. 43). A further variety from the Pliocene of southern France was described by Fontannes (1880) *Strombina tiara* var. *torcapeli*. Brocchi's species was said to differ from Fontannes' form "...que par des côtes longitudinales moins persistantes, plus parallèles à l'axe de la spire, et par un dernier tour relativement plus haut [only in having the axial ribs less persistent, more parallel to the axis of the spire, and in having a relatively higher last whorl]" (Fontannes, 1880, p. 95). We consider these differences not to warrant separation, and place Fontannes' subspecies also in synonymy.

Middle Miocene Paratethyan records to this species refer to *Thiarella bronni* (Mayer, 1869), which differs most notably from *T. thiara* (Brocchi, 1814) in the presence of axial ribs, the rounded, narrowly swollen mid-portion of the last whorl forming the periphery, and the shorter siphonal canal (Harzhauser & Landau, 2021, p. 45).

Thiarella is therefore represented by only two species, *Thiarella thiara* and *Thiara bronni*, forming a continuous lineage from the Langhian to the Pliocene.

Distribution – Upper Miocene: central Proto-Mediterranean, Italy (Sacco, 1890b; Bellardi, 1848; Robba, 1968).

Lower Pliocene: western Mediterranean, France (Sacco, 1890b; Martinell & Domènech, 1986); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1974; Brunetti & Cresti, 2018, Chirli, 2002). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper), France (Cossmann, 1910; Chirli & Richard, 2008); central Mediterranean, Italy (Caprotti & Vescovi, 1973; Marasti & Raffi, 1976; Caprotti, 1976; Cavallo & Repetto, 1992).

Genus *Thiarinella* Sacco, 1890

Type species (by monotypy): *Fusus comptus* Bronn, 1831, Miocene, Italy.

1890a *Thiarinella* Sacco, p. 225.

Note – Cossmann (1901, p. 247) considered *Thiarinella* Sacco, 1890 as synonym of *Scabrella* Sacco, 1890. However, in *Thiarinella* the whorls are coronate, whereas in *Scabrella* (type species: *Columbella (Scabrella) scabra* Sacco, 1890, Miocene, Italy) a subsutural collar is present, but it does not distort the profile (Harzhauser & Landau, 2021, p. 47).

Thiarinella compta (Bronn, 1831)

Plate 19, figs 1-3

- *1831 *Fusus comptus* Bronn, p. 41.
- 1847 *Fusus Brocchii* Michelotti, p. 281, pl. 10, fig. 7.
- 1848 *Columbella compta* Bell. [sic] – Bellardi, p. 18, pl. 1, fig. 16.
- 1890b *Columbella (Thiarinella) compta* (Bronn.) – Sacco, p. 56, pl. 2, fig. 74.
- 1967 *Mitrella (Thiarinella) compta* (Bronn) – Pelosio, p. 137 [37], pl. 40, figs 18-20.
- 1992 *Mitrella compta* (Bronn, 1831) – Cavallo & Repetto, p. 116, fig. 292.
- 2002 *Mitrella (Thiarinella) compta* (Bronn, 1831) – Chirli, p. 16, pl. 9, figs 4-8.
- 2018 *Mitrella compta* (Bronn, 1831) – Brunetti & Cresti, p. 80, fig. 298.

Materials and dimensions – Maximum height 21.6 mm, width 8.4 mm. CO: NHMW 2022/0201/0024-0025 (2). VC: NHMW 2022/0201/0041 (1), NHMW 2022/0201/0084 (1).

Description – Shell large, moderately broad fusiform, with high coeloconoid, slightly scalate, conical spire (AA = 37°). Protoconch not preserved. Teleoconch of up to eight flat-sided whorls, with periphery at abapical suture, separated by narrowly impressed linear suture. Sculpture of narrow, orthocone to opisthocline axial ribs, very slightly tuberculate at adapical end. Spiral sculpture restricted to a siphonal fasciole: extremely fine spiral threads cover whorl on magnification. Last whorl 54% of total height, very weakly coronate just below suture, convex below, rounded at periphery placed about mid-whorl, strongly constricted at base. Axial sculpture fades over last quarter whorl. Siphonal fasciole short, bearing weak cords. Aperture narrow, 36-37% of total height. Outer lip weakly thickened by varix, no palatal swelling, row of 6-7 small subequal denticles within. Anal canal narrow V-shaped notch. Siphonal canal short, narrow, open, slightly recurved, unnotched. Columellar callus straight, narrow, erect, sharp edged, without tubercles or denticles, narrow discontinuous section at upper end, small parietal callus.

Discussion – *Thiarinella compta* (Bronn, 1831) is a highly distinctive species that cannot be confused with any other Estepona columbellid. It is very uncommon in the Estepona assemblages, found rarely in both the shallow and deeper water deposits.

Distribution – Middle Miocene: central Proto-Mediterranean, Italy (Sacco, 1890b). Upper Miocene: central Proto-Mediterranean, Italy (Bellardi, 1848; Sacco, 1890b). Lower Pliocene: central Mediterranean, Italy (Sacco, 1890b; Pelosio, 1967; Chirli, 2002; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper), central Mediterranean, Italy (Cavallo & Repetto, 1992).

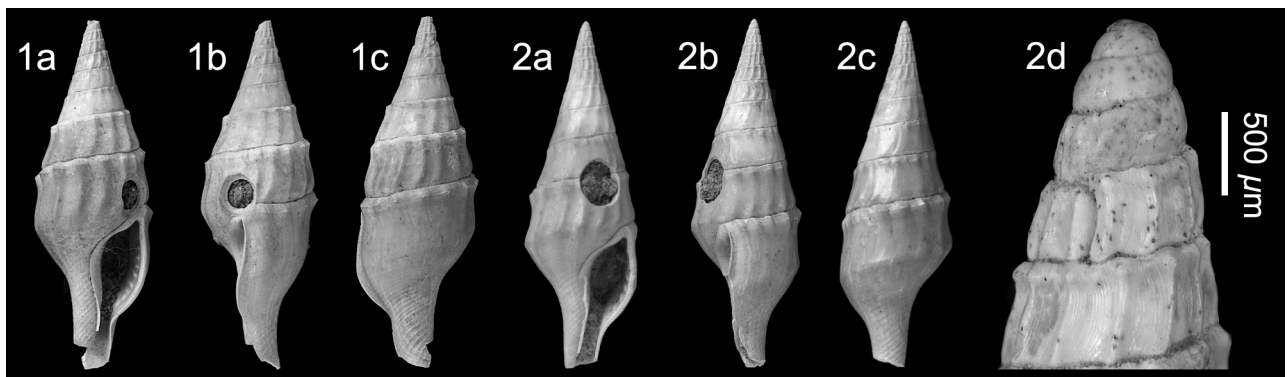


Plate 19. *Thiarinella compta* (Bronn, 1831). 1. NHMW 2022/0201/0024, height 20.9 mm, width 8.4 mm; 2. NHMW 2022/0201/0025, height 21.6 mm, width 8.4 mm. Velerín conglomerates. 3. NHMW 2022/0201/0084, height 19.0 mm, width 7.8 mm (digital images). Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Genus *Zafrona* Iredale, 1916

Type species (by original designation) – *Columbella isomella* Duclos, 1840, present-day, Indo-West Pacific.

1916 *Zafrona* Iredale, p. 32, 33.

Note – Harzhauser & Landau (2021) placed several European Neogene species in the genus *Zafrona* Iredale, 1916 that in fossil literature had historically been placed in the genus/subgenus *Anachis* H. & A. Adams, 1853. The type species *Anachis scalarina* (G.B. Sowerby I, 1832) from the eastern Pacific has quite a different profile, with a gradate spire, swollen mid-portion to the last whorl, and much stronger flexuous axial ribs. A further problem is that the genus *Anachis*, as used today, is highly polyphyletic (deMaintenon & Strong, 2022).

Zafrona species have regularly ovoid to tall-spined shells and strongly resemble the species placed in the genus herein and the Miocene Parathethyan species placed in the genus by Harzhauser & Landau (2021). However, the molecular phylogeny of deMaintenon & Strong (2022) suggested that the Indo-Pacific type species of *Zafrona* formed a separate clade from tropical American species that had previously been placed in *Zafrona* and now belonged to a monophyletic genus *Falsuszafzona*. They also differ in their radular characteristics (Radwin, 1977a; Sleurs, 1987). In the absence of molecular and soft tissue data, and based solely on conchological features, these European Neogene species are closest to *Zafrona*.

***Zafrona harpula* (Michelotti, 1840)**

Plate 20, figs 1-4

- *1840 *Buccinum arpula* Michelotti, p. 26.
- 1848 *Columbella corrugata* Bon. – Bellardi, p. 12, pl. 1, fig. 9 (*non* Brocchi, 1814).
- 1854 *Buccinum Festivum* Millet, p. 165 (*nomen nudum*).
- 1865 *Buccinum festivum* Millet, p. 597.
- ?1880 *Columbella corrugata* Brocchi – Seguenza, p. 105, pl. 11, fig. 16 (only apex figured) (*non* Brocchi, 1814).
- 1880 *Columbella corrugata* Brocchi – Fontannes, p. 91, pl. 6, fig. 13 (*non* Brocchi, 1814).
- 1890b *Columbella (Anachis) corrugata* (Brocch.) – Sacco, p. 59, pl. 2, figs 81, ?82.
- 1901 *Anachis corrugata* (Bon.) – Cossmann, p. 237, pl. 10, figs 6, 7.
- 1904 *Anachis corrugata* var. *brevispirata* Sacco, p. 95 (= var. A Sacco, 1890, fig. 82).
- 1925 *Anachis Lemoinei* Peyrot, p. 65, pl. 1, figs 70, 92.
- 1959 *Pyrene (Anachis) corrugata* (Brocchi) – Ruggieri *et al.*, p. 41, pl. 9, fig. 52.
- 1964 *Anachis corrugata* Bellardi, 1848 – Brébion, p. 405, pl. 9, figs 30, 31.
- 1992 *Anachis (Costoanachis) arpula* (Michelotti, 1840) – Cavallo & Repetto, p. 116, fig. 288.
- 2002 *Anachis recticostata* (Sacco in Bell., 1890) – Chirli, p. 4, pl. 1, figs 3, 4 [*non* *Zafrona recticostata* (Sacco, 1890)].

- 2018 *Anachis arpula* (Michelotti, 1840) – Brunetti & Cresti, p. 80, fig. 305.
- non* 1852 *Columbella corrugata* Bon. – Hörnes, p. 120, pl. 11, fig. 7 [= *Costoanachis guembeli* (Hoernes & Auinger, 1880)].
- non* 1880 *Columbella (Anachis) corrugata* Bell. – Hoernes & Auinger, p. 103, pl. 11, figs 12-14 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1911 *Columbella (Anachis) corrugata* Bell. – Friedberg, p. 41, pl. 2, fig. 7 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1933 *Anachis corrugata* Bell. – Meznerics, p. 341, pl. 14, fig. 8 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1952a *Pyrene (Anachis) lemoinei* Peyrot, 1927 [*sic*] – Glibert, p. 317, pl. 9, fig. 1 (?turrid).
- non* 1952b *Pyrene (Anachis) corrugata* Bellardi, 1849 [*sic*] – Glibert, p. 99, pl. 7, fig. 16 [= *Zafrona hosiusi* (Von Koenen, 1872)].
- non* 1960 *Anachis corrugata* (Bellardi 1849 [*sic*]) – Kojumdgieva *in* Kojumdgieva & Strachimirov, p. 186, pl. 45, fig. 14 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1964 *Anachis (Costoanachis) corrugata* (Brocchi, 1814) – Anderson, p. 247, pl. 22, fig. 181 [= *Zafrona hosiusi* (Von Koenen, 1872)].
- non* 1966 *Columbella (Anachia [*sic*]) terebralis corrugata* Bellardi, 1849 [*sic*] – Strausz, p. 296, text-fig. 133 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1968 *Anachis corrugata* Bellardi – Zelinskaya, p. 208, pl. 48, figs 19-20 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1969 *Anachis corrugata* (Bellardi) – Atanacković, p. 207, pl. 11, figs 7 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].
- non* 1972a *Anachis (Costoanachis) corrugata* (Brocchi, 1814) – Nordsieck, p. 76, fig. 105 [= *Zafrona hosiusi* (Von Koenen, 1872)].
- non* 1982 *Anachis (Costoanachis) corrugata* (Br.) – Anfossi *et al.*, p. 92, pl. 4 [3], figs 18, 19 [?= *Zafrona turbinellus* (Sacco, 1890)].
- non* 1985 *Anachis (Costoanachis) corrugata* (Bellardi, 1849 [*sic*]) – Atanacković, p. 145, pl. 32, figs 15-16 [= *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021].

Materials and dimensions – Maximum height 9.5 mm, width 4.0 mm. **CO**: NHMW 2022/0201/0050-0051 (2); NHMW 2022/0201/0052 (1), NHMW 2022/0201/0053 (30), NHMW 2022/0201/0090-0091, RGM.1404332 (5). **EL**: NHMW 2022/0201/0054 (7).

Description – Shell moderately small, moderately broad fusiform, with conical spire (AA = 49°). Protoconch tall conical of 3.5 convex whorls with small nucleus; microsculpture of opisthocline riblets on last two whorls (probably whole protoconch sculptured, but abraded) (dp = 705 μm, hp = 840 μm, dp/hp = 0.84, dn = 190 μm,

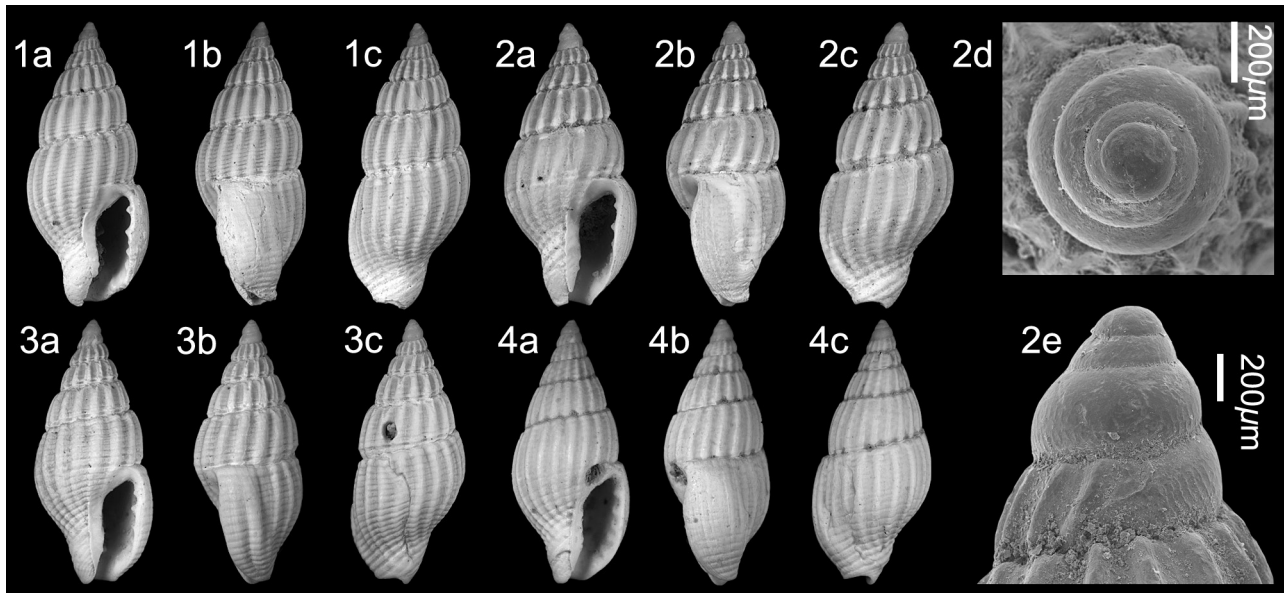


Plate 20. *Zafrona harpula* (Michelotti, 1840). 1. NHMW 2022/0201/0050, height 9.4 mm, width 4.0 mm; 2. NHMW 2022/0201/0051, height 7.7 mm, width 3.6 mm (digital images), 2c-d, detail of protoconch (SEM images); 3. NHMW 2022/0201/0090, height 8.2 mm, width 3.6 mm; 4. NHMW 2022/0201/0091, height 7.0 mm, width 3.4 mm. Velerin conglomerates, Velerin, Estepona, Lower Piacenzian, Upper Pliocene.

dp1 = 255 μ m). Teleoconch junction marked by sinusigera. Teleoconch of up to five convex whorls, with periphery just above abapical suture, separated by deeply impressed V-shaped suture, finely undulating on later whorls. Sculpture of rounded, opisthocline axial ribs extending between sutures, roughly equal in width to their interspaces, 15-17 on penultimate whorl, about 20 on last whorl. Spiral sculpture of fine spiral cords separated by narrow grooves covers entire whorl surface. Last whorl 60-64% of total height, broadly rounded, periphery placed about mid-whorl, moderately constricted at base; axials persisting over base. Siphonal fasciole medium length, bearing stronger cords. Aperture moderately narrow, 39-40% of total height. Outer lip strongly swollen by varix, palatal swelling well developed, row of about six denticles within, D2 strongest. Anal canal U-shaped notch. Siphonal canal moderate length, narrow, open, weakly recurved, shallowly notched at tip. Columellar callus thickened, with row of 3-4 stout tubercles on outer edge and fold delimiting siphonal canal deep within columella; continuous with thinner, moderately expanded parietal callus.

Discussion – Michelotti described this species without a figure based on a Pliocene shell from Astigiana: “*Testa elongata, mitraeformae, anfractibus subconvexis longitudinaliter et oblique plicatis; interstitiis laevigatis, sutura discretis; apertura oblonga, coarctata, labro dentato; columella inferne sulcata, canali non recurvo* [Shell elongate, mitriform, with subconvex whorls axially and horizontally striate; interspaces smooth, sutures discrete; aperture oblong, constricted, with toothed lip; columella striate adapically, canal not recurved]” (1840, p. 26). Bellardi (1848, p. 13), Sacco (1890, p. 59) and Cavallo & Repetto (1992, p.

116) considered Michelotti’s species a synonym of *Columbella corrugata sensu* Bellardi, 1848 (*non* Brocchi). However, *Costoanachis corrugata* (Brocchi, 1814) (*sensu i.e.*, Sacco, 1890b, p. 59; Brébion, 1964, p. 405) is an error initiated by Bellardi (1848, p. 12) who described and illustrated this species under the name *Columbella corrugata* Bon. but referred it to Brocchi (*Buccinum corrugatum*; 1814, p. 652, pl. 15, fig. 16), which is a nassariid.

Cavallo & Repetto (1992) were the first to use Michelotti’s name, presumably realising Brocchi’s name was not available. Brunetti & Cresti (2018, fig 305) illustrated a specimen we consider conspecific with the Estepona specimens illustrated herein as *Zafrona harpula* (Michelotti, 1840). We assume they also meant this as a synonym of *C. corrugata sensu* Bellardi, 1848.

A further complication arises as Michelotti (1840, p. 26) wrote under Spec. N. 8 *Buccinum arpula* [*sic*], and in his discussion and comparison with *B. columbelloides* spelled the trivial name *harpula*. The first spelling is an inadvertent error (*lapsus*) as indicated by the correct spelling a few lines later in the same publication, and must therefore be corrected (ICZN 1999, Art. 32.5).

Subsequently, the trivial name *corrugata* has been applied to several similar *Zafrona* species in widely different European Neogene basins. Paratethyan Middle Miocene specimens were shown not to be conspecific with those from the Mediterranean Pliocene and named *Zafrona sphaerocorrugata* Harzhauser & Landau, 2021. Similarly, Miocene North Sea Basin records (Anderson, 1964; Nordsieck, 1972) were also shown to represent a distinct species; *Zafrona hosiusi* (Von Koenen, 1872). Conversely, specimens from the Upper Miocene of NW France identified as *Z. harpula* by Landau *et al.* (2019, pl. 13, figs 1-4) do seem to represent that species.

Several similar species are present in the Italian Upper Miocene and Pliocene. *Zafrona turbinellus* (Sacco, 1890) (for illustration syntype see Ferrero Mortara *et al.*, 1981, pl. 58, fig. 7) from the Pliocene differs in being smaller shelled, with flatter whorls, fewer, broader and more prominent axial ribs that are continuous along the shell axis and weakly tubercular just below the suture, and separated by broader, smoother, straighter axial interspaces. *Zafrona recticosta* (Sacco, 1890) (for illustration syntype see Ferrero Mortara *et al.*, 1981, pl. 58, fig. 3) from the Upper Miocene differs from the Estepona species in the same characters as *Z. recticosta* (smaller shelled, fewer, stronger axial ribs that are continuous down the shell axis), but in this species the whorls are more inflated mid-whorl, and ribs are straighter than in *Z. recticosta* and weaken more rapidly over the base.

The specimen figured as *Anachis recticostata* by Chirli (2002, pl. 1, figs 3-4) is, in our opinion, not that species. Chirli (2002, p. 4) described 20 ribs on the last whorl, far more than the 12 or so seen in the syntype of *A. recticostata*, that are markedly sinuous over the last whorl, similar to the specimens figured herein (Pl. 20, figs 1-2). Several superficially similar species from present-day West Africa were figured by Pelorce & Boyer (2005) and Rolán (2005) under the genera *Anachis* H. & A. Adams and *Parvanachis* Radwin, 1968, but these species have less convex spire whorls, and the palatal swelling is stronger making the aperture narrower.

Distribution – Middle Miocene: Atlantic (Langhian and Serravallian), Aquitaine Basin (Peyrot, 1925). Upper Miocene: Atlantic (Tortonian), NW France (Landau *et al.*, 2019). Lower Pliocene: western Mediterranean, France (Fontannes, 1880; Cossmann, 1901); central Mediterranean, Italy (Sacco, 1890; Anfossi *et al.*, 1982; Brunetti & Cresti, 2018). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellardi, 1848; Sacco, 1890; Ruggieri *et al.*, 1959; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010).

Discussion

Twenty species of Columbellidae Swainson, 1840 are recorded from the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain, representing seven genera, of which four (20%) are described as new: *Costoanachis malaquiasii* nov. sp., *Mitrella avilai* nov. sp., *Mitrella pagodiformis* nov. sp. and *Mitrella velerinensis* nov. sp. (Figure 1).

Relationships at generic level are difficult to interpret at present due to the probable polyphyletic nature of genera such as *Mitrella* (deMaintenon & Strong, 2022). At genus and species level the assemblage is closely similar to that seen in the rest of the Pliocene Mediterranean with all the genera and 15 (75%) of the species also found in the Pliocene of Italy. However, we note that many of the genera present in the European Miocene did not survive into the Pliocene (*Auingeria* Harzhauser & Landau, 2021, *Bellacolumbella* Harzhauser & Landau, 2021, *Clinurella* Sacco, 1890, *Defensina* Harzhauser & Landau,

2021, *Graphicomassa* Iredale, 1929; *Martaia* Harzhauser & Landau, 2021; *Scabrella* Sacco, 1890; *Sulcomitrella* Kuroda, Habe & Oyama, 1971).

The group is relatively thermophilic, with columbellid diversity drastically reduced in the cooler subtropical Pliocene French-Iberian province to the North, with only two species recorded from the Lower Piacenzian Upper Pliocene of the Mondego Basin of Central-West Portugal (Silva, 2001) and four from the Zanclean Lower Pliocene of NW France (Van Dingenen *et al.*, 2017). Today, columbellid diversity is just over half of what it was during the tropical Mediterranean Pliocene, with 12 species recorded in the Mediterranean Sea, representing five genera (Giannuzzi-Savelli *et al.*, 2003). Moreover, the species do not reach the large size seen in species such *M. castoris* (Lozano-Francisco & Vera-Peláez, 2006) and *M. erythrostoma* (Bellardi, 1848). Only four (20%) of the columbellids found present in the Estepona assemblages are still living today.

Acknowledgements

Our thanks to Carlos Marques da Silva of the University of Lisbon, Portugal, for his advice and help with graphics. An enormous thanks to Pascuale Micali of Fano, Italy for his comments that greatly improved this paper. Thanks also to Leon Hoffman, of the Taxonomy Mollusca, Marine Research Department, Senckenberg Forschungsinstitut Sektion Malakologie for his review, which also improved the paper.

References

- Adams, C.B. 1845. Specierum novarum conchyliorum, in Jamaica repertorium, synopsis. *Proceedings of the Boston Society of Natural History* 2: 1-17.
- Adams, H. & Adams, A. (1853-1858). *The genera of Recent Mollusca; arranged according to their organization*. London, van Voorst. Vol. 1: xl + 484 pp.; vol. 2: 661 pp.; vol. 3: 138 pls. [Published in parts: Vol. 1: i-xl (1858), 1-256 (1853), 257-484 (1854). Vol. 2: 1-92 (1854), 93-284 (1855), 285-412 (1856), 413-540 (1857), 541-661 (1858). Vol. 3: pl. 1-32 (1853), 33-72 (1954), 73-96 (1855), 97-112 (1856), 113-128 (1857), 129-138 (1858)].
- Anderson, H.J. 1964. Die miocene Reinbek-Stufe in Nord- und Westdeutschland und ihre Mollusken-Fauna. *Fortschritte in der Geologie von Rheinland und Westfalen* 14: 31-368.
- Anfossi, S., Brambilla, G. & Mosna, S. 1982. La fauna del Pliocene di Taino (Varese). *Atti dell' Istituto Geologico dell' Universita di Pavia* 30: 83-102.
- Atanacković, M.A. 1969. Paleontološka i biostratigrafska analiza tortonske faune severoistočnog. Potkozarja (okolina sela Turjaka i Miljevića). *Prirodoslovna istraživanja* 36, *Acta Geologica* 6: 149-222.
- Atanacković, M.A. 1985. *Mekušci Morskog Miocena Bosne*. Sarajevo (Geoinženjering): 305 pp.
- Bařuk, W. 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland, 2. *Acta Geologica Polonica* 45: 1-255.

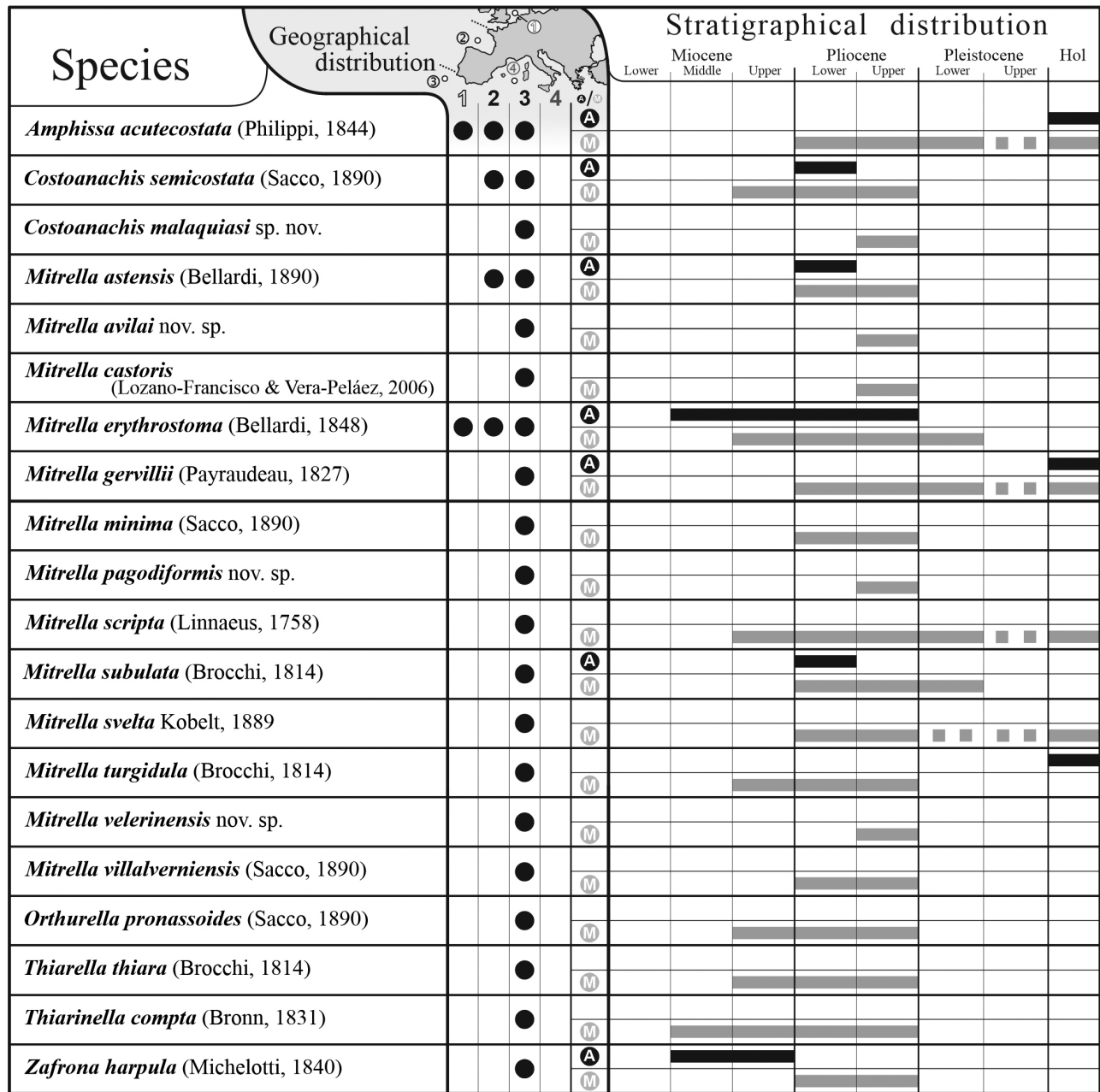


Figure 1. Geography, stratigraphy and distribution of species found in the Upper Pliocene Lower Piacenzian of the Estepona Basin, southern Spain. For Pliocene-present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan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

Bellardi, L. 1848. *Monografia delle Columbelle fossili del Piemonte*. Torino: Stamperia reale. 22 pp.

Beyrich, E. 1853-1856. Die Conchylien des norddeutschen Teritiärgebirges. *Zeitschrift der Deutschen Geologischen Gesellschaft* 5: 273-358, pls. 4-8 (1853); 6: 408-500, 726-781, pls. 9-18 (1854); 8: 21-88, 553-588, pls. 16-28 (1856).

Bivona-Bernardi, Ant. 1832. Caratteri d'un nuovo genere di conchiglie della famiglia delle Columellarie del Signor de Lamarck. *Effemeride Scientifiche e Letterarie per la Sicilia* 2(1): 8-13.

Boda, J. 1959 Das Sarmat in Ungarn und seine Invertebraten-Fauna. *Annales Instituti Regii Hungarici Geologici* 47/3, 569-862.

Boettger, O. 1902. Zur Kenntnis der Fauna der mittelmiozänen Schichten von Kostež im Krassó-Szörényer Komitat. Mit einem Situationsplan der Fundpunkte, 2. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt* 51 (1901): 1-200.

Bonelli, F.A. 1825, 1826 or 1827. *Catalogus Musei zoologici Taurinensis* (Denominationes ineditae testaceorum Musei zoologici Taurinensis (unpublished).

Bouchet, P., Rocroi, J.P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61(1-2): 1-526.

- Bouchet, P. & Warén, A. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). *Bollettino Malacologico* suppl. 1: 121-296.
- Brébion, P. 1964. *Les gastéropodes du Redonien et leur signification*, 1-2. Thèse de doctorat ès-Sciences. Paris (Faculté des Sciences de l'Université de Paris: 775 pp., 15 pls (27 June 1964, unpublished).
- Brocchi, G. 1814. *Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente*, 1-2. Milano (Stamperia Reale): 1-240 (1); 241-712 (2), 16 pls.
- Broderip, W.J. & Sowerby, G.B. I. 1832-1833. [Descriptions of new species of shells from the collection formed by Mr. Cuming on the western coast of South America, and among the islands of the southern Pacific Ocean.]. *Proceedings of the Committee of Science and correspondence of the Zoological Society of London*. Part II for 1832: 25-33 [21 April 1832], 50-61 [5 June 1832], 104-108 [31 July 1832], 113-120 [14 August 1832]; 173-179 [14 Jan. 1833], 194-202 [13 March 1833].
- Bronn, H.G. 1831. *Italiens Tertiär-Gebilde und deren organische Einschlüsse*. Heidelberg (Karl Groos): xii + 176 pp. (part of: Bronn, H.G. 1831. *Ergebnisse meiner naturhistorisch-ökonomischen Reisen*. Heidelberg & Leipzig, 2 vols).
- Brunetti, M.M. 2014. *Conchiglie fossili di Monte Antico (Grosseto, Italia)*. Privately published: 118pp.
- Brunetti, M.M. 2022. *Malacofaune plioceniche della Valle del Guadalquivir, Spagna*. Privately published, Edizione Danaus: 147 pp.
- Brunetti, M.M. & Cresti, M. 2018. *I fossili di Orciano Pisano* [The fossils of Orciano Pisano]. *Atlante iconografico* [An Iconographic Atlas]: 1-232. Edizioni Danaus, Palermo.
- Brusina, S. 1865. Conchiglie dalmate inedite. *Verhandlungen der Kaiserlich-königlichen Zoologisch-botanisch Gesellschaft in Wien* 15: 3-42.
- Cantraine, F.J. 1835. Diagnoses ou descriptions succinctes de quelques espèces nouvelles de mollusques. *Bulletins de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles* 2(11): 380-401.
- Caprotti, E. 1974. Molluschi del Tabianiano (Pliocene inferiore) della Val d'Arda. Loro connessioni temporali e spaziali. *Conchiglie* 10: 1-47.
- Caprotti, E. 1976. Malacofauna dello stratotipo piacentino (Pliocene de Castell'Arquato). *Conchiglie* 12: 1-56.
- Caprotti, E. & Vescovi, M. 1973. Neogastropoda ed Euthyneura dello stratotipo piacentino (Castell'Arquato, Piacenza). *Natura, Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 64: 156-193.
- Cavallo, O. & Repetto, G. 1992. Conchiglie fossili del Roero. *Atlante iconografico. Associazione Naturalistica Piemontese Memorie* (Associazione Amici del Museo 'Federico Eusebio') 2: 1-251.
- Cecalupo, A., Buzzurro, G. & Mariani, M. 2008. Contributo alla conoscenza della macrofauna del Golfo di Gabès (Tunisia). *Quaderni della Civica Stazione Idrobiologica di Milano* 31: 1-173, pl. 1-92.
- Cerulli-Irelli, S. 1911. Fauna malacologica mariana, 5. Cancellariidae, Marginellidae, Mitridae, Fusidae, Chrysodomidae, Buccinidae, Nassidae, Columbelloidae, Muricidae, Tritonidae, Cassidae, Cypraeidae, Chenopodidae. *Paleontographia Italica* 17: 280-325.
- Chiarelli, S., Micali, P. & Quadri, P. 2003 [2002]. Note su alcune specie mediterranee del genere *Mitrella* Risso, 1826 (Gastropoda, Muricidae). *Bollettino Malacologico* 38: 171-183.
- Chirli, C. 1988. *Malacofauna pliocenica di Poggibonsi, Cava delle Piaggiole*. Poggibonsi (Lalli Ed.): 1-89.
- Chirli, C. 2002. *Malacofauna Pliocenica Toscana, 3. Superfamiglia Muricoidea 2° e Cancellarioidea*. Firenze (C. Chirli): 92 pp.
- Chirli, C. & Linse, U. 2011. *The Pleistocene marine Gastropods of Rhodes Island (Greece)*. Grafiche PDB, Tavarnelle V.P. Firenze: 262 pp, 90 pls.
- Chirli, C. & Richard, C. 2008. *Les mollusques plaisanciens de la Côte d'Azur*. Tavarnelle (C. Chirli): 128 pp.
- Cossmann, M. 1899. Rectifications de nomenclature. *Revue Critique de Paléozoologie* 3, 45-46.
- Cossmann, M. 1901. *Essais de paléoconchologie comparé* 4. Paris (Cossmann). 293 pp., 10 pls.
- Cossmann, M. & Peyrot, A. 1909-1935 (after 1924 continued by A. Peyrot). Conchologie néogénique de l'Aquitaine. *Actes de la Société Linnéenne de Bordeaux*, 63: 73-293 (1909); 64: 235-400 (1910), 401-445 (1911); 65: 51-98 (1911). 99-333 (1912); 66: 121-232 (1912), 233-324 (1913); 68: 5-210, 361-435 (1914); 69: 157-365 (1917); 70: 5-180 (1918), 181-491 (1919) 73: 5-321 (1922); 74: 257-342 (1923); 75: 71-318 (1924); 77: 51-256 (1925); 78: 199-256 (1926); 79: 5-263 (1928); 82: 73-126 (1931); 83: 5-116 (1931); 84: 5-288 (1932); 85: 5-71 (1933); 86: 257-353 (1935).
Also published as a 6 volume book with different pagination as Édition in-8°, *Extrait des Actes de la Société Linnéenne de Bordeaux ('Ouvrages couronnés par l'Académie des Sciences, Arts et Belles-Lettres de Bordeaux')*, 1: 1-220 (1909); 221-428 (1911); 429-718 (1912); 2: 1-204 (1913); 205-496 (1914); 3: 1-384 (1917); 385-695 (1919); 4: 1-322 (1922); 323-610 (1924); 5: 1-206 (1927); 207-465 (1928); 6: 1-294 (1931); 295-541 (1932).
- Cox, L.R. 1927. Neogene and Quaternary Mollusca from the Zanzibar Protectorate: 13-102, 171-180, pls 3-19. *In: Report on the Palaeontology of the Zanzibar Protectorate*. Government of Zanzibar, Crown Agents for the Colonies, London.
- Csepregy-Meznerics, I. 1956. Die Molluskenfauna von Szob und Letkés. *Magyar Állami Földtani Intézet Évkönyve (Annales de l'Institut de Géologie Publique de Hongarie)* 45: 361-477.
- Csepregy-Meznerics, I. 1969. Nouvelles gastéropodes et lamellibranches pour la faune hongroise des gisements tortonien inférieurs de la Montagne de Bükk. *Annales Historico-Naturales Musei Nationalis Hungarici Pars Mineralogica et Palaeontologica* 61: 63-127.
- Dall, W.H. 1871. Descriptions of sixty new forms of mollusks from the West coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology* 7(2): 93-159, pls 13-16.
- Dall, W.H. 1916. Notes on West American Columbelloidae. *The Nautilus* 30(3): 25-29.
- Dautzenberg, P. 1889. *Contribution à la faune malacologique des Iles Açores. Resultats des dragages effectués par le*

- yacht l'Hirondelle pendant sa campagne scientifique de 1887. Révision des mollusques marins des Açores. Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco, I. Imprimerie de Monaco. 112 pp.; IV plates.
- Davoli, F. 1990. La collezione di 'Fossili Miocenici di Sogliano' di Ludovico Foresti: Revisione ed illustrazione. *Atti della Società dei Naturalisti e Matematici di Modena* 121: 27-109.
- Doderlein, P. 1863. Cenni geologici intorno la giacitura dei terreni miocenici superiori dell'Italia centrale. *Estratto dagli Atti del X° Congresso degli Scienziati Italiani, Siena 1862*, 1-25, 1 pl. [also, 1864, *Atti del Decimo Congresso degli Scienziati Italiani* 83-107, 223 (errata), 1 pl.].
- Duclos, P.L. 1840. *Histoire naturelle générale et particulière de tous les genres de coquilles univalves marines à l'état vivant et fossile, publiée par monographie. Genre Colombelle*. Didot, Paris, 13 pls.
- Duclos, P.L. 1846-1850. Colombella. In: Chenu, J. C. *Illustrations conchyliologiques ou description et figures de toutes les coquilles connues vivantes et fossiles, classées suivant le système de Lamarck modifié d'après les progrès de la science et comprenant les genres nouveaux et les espèces récemment découvertes*. Volume 4: pls 1-18 [1846]; 19-25, 27 [1848]; 26 [1850].
- Duerr, R. 2008. Two new species of *Mitrella* (Gastropoda: Neogastropoda: Columbelloidea) from the lower Miocene Chipola Formation of northwestern Florida. *The Nautilus* 122: 151-154.
- Fekih, M. 1975. Paleocologie du Pliocène marin au nord de la Tunisie. *Annales des Mines et de la Géologie* 27: 1-195.
- Ferrero Mortara, E.L., Montefameglio, L., Pavia, G. & Tampieri, R. 1981. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, 1. *Museo Regionale di Scienze Naturali di Torino*, Cataloghi 6: 1-327.
- Fontannes, F. 1879-1880. *Les invertébrés du bassin tertiaire du Sud-Est de la France. Les mollusques pliocènes de la Vallée du Rhône et du Roussillon*, 1. *Gastéropodes des formations marines et saumâtres*. Paris (Georg, Lyon & F. Savy): viii + 276 pp., 12 pls (pp. 1-76 published in 1879, remainder in 1880).
- Friedberg, W. 1911-28. *Mięczaki miocenne ziem Polskich (Mollusca Miocena Poloniae)*, 1. *Ślimaki i łódkonogi*, 1. *Gastropoda et Scaphopoda*. Lwow (Muzeum Imienia Dzieduszyckich): 631 pp. (issued in parts: 1, 1-112, pls 1-5 (1911); 2, 113-240, pls 6-14 (1912); 3, 241-360, pls 15-20 (1914); 4, 361-440, pls 21-26 (1923); 5, 441-631, pls 27-38 (1928). Reprinted 1951-55 with slightly different title and pagination, Warszawa (Wydawnictwa Geologiczne).
- Geronimo, I. Di & La Perna, R. 1997. Pleistocene bathyal molluscan assemblages from southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 103 (3): 389-426.
- Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A. & Ebreo, C. 2003. *Atlante delle conchiglie marine del Mediterraneo*, 4(1) (Neogastropoda: Muricoidea). Roma (Edizione de 'La Conchiglia'): 297 pp.
- Glibert, M. 1952a. Gastropodes du Miocène moyen du Bassin de la Loire, 2. *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* 2(46): 241-450.
- Glibert, M. 1952b. Faune malacologique du Miocène de la Belgique, 2. Gastropodes. *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* 121: 1-197.
- Gofas, S., Luque, Á. & Urra, J. 2019. Planktrophic Columbelloidea (Gastropoda) in the northeast Atlantic and the Mediterranean Sea, with description of a new species in the genus *Mitrella*. *Bulletin of Marine Science* 96(1): 145-168.
- González-Delgado, J.A. 1989. Estudio sistemático de los gasterópodos del Plioceno de Huelva (SW de España), 4. Neogastropoda (Muricacea, Buccinoidea). *Studia Geologica Salmanticensia* 26: 269-315.
- Grateloup, J.P.S. de 1827. Description de plusieurs espèces de coquilles fossiles des environs de Dax (Landes). *Bulletin d'Histoire naturelle de la Société Linnéenne de Bordeaux* 2: 3-27.
- Guerra-Merchán, A., Serrano, A. & Ramallo, D., 2002. Evolución sedimentaria y paleogeográfica pliocena del borde septentrional de la cuenca de Alborán en el area de Estepona (provincia de Málaga, Cordillera Bética). *Pliocénica* 2: 31-43.
- Harmer, F.W. 1914-1925. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's monograph of the Crag Mollusca, 1. *Monographs of the Palaeontographical Society*, 1(1): 1-200 (1914); 1(2): 201-302 (1915), 1(3): 303-461 (1918), 1(4): 463-483 (1919), 2(1): 485-652 (1920), 2(2): 653-704 (1921), 2(3): 705-856 (1923), 2(4): 857-900 (1925).
- Harzhauser, M. & Landau, B.M. 2021. The Columbelloidea (Gastropoda, Buccinoidea) in the Miocene Paratethys Sea—striking diversity of a neglected group. *Zootaxa* 5025(1): 001-075.
- Hernández, J.M. & Boyer, F. 2005. Notes on the columbellid fauna from the infralittoral and circalittoral levels of the Canary Islands. *Iberus* 23(2): 69-93.
- Hernández, J.M., Rolán, E. & Swinnen, F. 2011. Parte 3: Gastropoda: Prosobranchia. In: *Moluscos y conchas marinas de Canarias* (E. Rolán, ed.), pp. 54-269. ConchBooks, Hackenheim. 716 pp., 130 pls.
- Hervier, J. 1900 [1899]. Le genre *Columbella* dans l'archipel de la Nouvelle-Calédonie. *Journal de Conchyliologie* 47(4): 305-391, pls 13-14.
- Hinds, R.B. 1844-1845. Mollusca. In: *The zoology of the voyage of H. M. S. "Sulphur", under the command of Captain Sir Edward Belcher, R. N., C. B., F. R. G. S., etc., during the years 1836-42*. Smith, Elder and Co., London, v + 72 pp., 21 pls. [Pp. 1-24, pls. 1-7, July 1844; pp. 25-48, pl. 8-14, October 1844; p. i-v, 49-72, pl. 15-21, January 1845].
- Hoernes, R. & Auinger, M. 1879-91. Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 12: 1-382, 50 pls. Published in parts: 1-52, pls 1-6 (1879); 53-112, pls 7-12 (1880); 113-152, pls 13-16 (1882); 153-192, pls 17-22 (1884); 193-232, pls 23-28 (1885); 233-282, pls 29-36 (1890); 283-330, pls 37-42 (1891); 331-382, pls 43-50 (1891).
- Hörnes, M. 1851-1870. Die fossilen Mollusken des Tertiär-Beckens von Wien. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 3-4: 1-42, pl. 1-5 (1851), 43-208, pl. 6-20 (1852), 209-296, pl. 21-32 (1853), 297-382, pl. 33-40 (1854), 383-460, pl. 41-45 (1855), 461-736, pl. 46-52 (1856) (3); 1-479, pls 1-85 (1870) (4).
- ICZN [International Commission on Zoological Nomenclature]

- re] 1999. *International Code of Zoological Nomenclature. Fourth Edition*. London (International Trust for Zoological Nomenclature): xxix + 306 pp.
- Ilijina (Il'ina), L.B. 1993. Handbook for identification of marine middle Miocene gastropods of Southwestern Eurasia. *Trudi Palaeontological Institute* 255: 1-149 (in Russian).
- Iredale, T. 1916. On some new and old molluscan names. *Proceedings of the Malacological Society of London* 12: 27-37.
- Iredale, T. 1929. Queensland molluscan notes. No. 1. *Memoirs of the Queensland Museum* 9: 261-297.
- Janssen, A.W. 2004. Holoplanktonic molluscan assemblages (Gastropoda, Heteropoda, Thecosomata) from the Pliocene of Estepona (Spain, Malaga). *Palaeontos* 5: 103-131.
- Jeffreys, J.G. 1862-1869. *British conchology*. Vol. 1: pp. cxiv + 341 [1862]. Vol. 2: pp. 479 [1864]. Vol. 3: pp. 394 [1865]. Vol. 4: pp. 487 [1867]. Vol. 5: pp. 259 [1869]. London, van Voorst.
- Jung, P. 1986. Neogene Paleontology in the northern Dominican Republic. 2. The Genus *Strombina* (Gastropoda: Columbellidae). *Bulletins of American Paleontology* 90(324): 1-42.
- Keen, A.M. 1971. Sea Shells of Tropical West America. Marine mollusks from Baja California to Peru. ed. 2. Stanford University Press. xv, 1064 pp., 22 pls.
- Kobelt, W. 1887-1908. *Iconographie der schalentragenden europäischen Meeresconchylien*. 1: 1-171 pl. 1-28 [1887]. Part 2: 1-16 pl. 29-32 [1888] 17-40 pl. 33-38 [1889] 41-104 pl. 39-50 [1900] 105-139 pl. 51-58 [1901]. Part 3: 1-24 pl. 59-62 [1902] 25-200 pl. 63-78 [1903] 201-272 pl. 79-84, 86-87 [1904] 273-406 [1905]. Part 4: 1-80 pl. 99-114 [1906] 81-172 pl. 115-126 [1908].
- Kobelt, W. 1892-1897. Die Familie der Columbellen. In: *Systematisches Conchylien-Cabinet von Martini und Chemnitz, 2nd ed. (Küster H.C., ed.)*. 3(1d): 1-128, pl. 1-18 [1892]; 129-176, pl. 19-24 [1893]; 177-216, pl. 25-30 [1895]; 217-280, pl. 31-36 [1896]; 281-312, pl. 37-42 [1897]; 313-344, pl. 43-44 [1897].
- Koenen, A. von 1872. Das Miozän Nord-Deutschlands und seine Mollusken-Fauna, 1. Einleitung und Palaeontologische Beschreibung der Syphonostomen Gastropoden. *Schriften der Gesellschaft zur Beförderung der Gesammten Naturwissenschaften zu Marburg* 10: 139-262.
- Kojumdgieva, E.M. 1969. *Les Fossiles de Bulgarie. VIII Sarmatien*. Académie des Sciences de Bulgarie, Sofia, 223 pp.
- Kojumdgieva, E.M. & Strachimirov, B. 1960. *Les fossiles de Bulgarie, 7. Tortonien*. Sofia (Académie des Sciences de Bulgarie): 317 pp.
- Kolokotronis, D. 2022. Lectotype Designation for the Extinct *Columbella (Anachis) semicostata* Sacco in Bellardi, 1890 (Columbellidae Gastropoda) with notes on its intraspecific pattern variability and distribution. *European Journal of Zoology* 1(1): 5-10.
- Kuroda, T., Habe, T. & Oyama, K. 1971. *The sea shells of Sagami Bay*. Maruzen, Tokyo, xix + 741 pp. (in Japanese), 489 pp. (in English), 51 pp., 121 pls.
- Lamarck, J.B.P.A. de M. 1799. Prodrôme d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. *Mémoires de la Société d'Histoire Naturelle de Paris* 1: 63-91.
- Lamarck, J.B.P.A. de M. 1815-1822. *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie*. Paris: 7 volumes. Vol. 1 [Introduction]: Verdière, i-xvi, 1-462 [March 1815]; Vol. 2 [les Polypes, les Radiaires]: Verdière, 1-568 [March 1816]; Vol. 3 [suite des Radiaires; les Tuniciers; les Vers]: Verdière, 1-586 [August, 1816]; Vol. 4: Deterville/Verdière, 1-603 [April 1817]; Vol. 5 [les Arachnides; les Crustacés; les Annélides; les Cirrhipèdes; les Conchifères]: Paris, Deterville/Verdière, 1-612 [25 July 1818]; Vol. 6(1) [suite des Conchifères; Les Mollusques]: published by the Author, i-vi, 1-343 [June 1819]; Vol. 6(2) (suite): published by the Author, 1-232 [April 1822]; Vol. 7 (suite): published by the Author, 1-711. [August 1822].
- Landau, B.M., Ceulemans, L. & Van Dingenen, F. 2019. The upper Miocene gastropods of northwestern France, 4. Neogastropoda. *Cainozoic Research* 19: 135-215.
- Landau, B.M., Harzhauser, M., İslamoğlu, Y. & Silva, C.M. da 2013. Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research* 11-13: 3-584.
- Landau, B.M., Marquet, R. & Grigis, M., 2003. The early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 1: Vetigastropoda. *Palaeontos* 3: 1-87, pls 1-19.
- Landau, B.M. & Micali, P. 2021. The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 13: Murchisonelloidea and Pyramidelloidea. *Cainozoic Research* 21(2): 159-351.
- Landau, B.M. & Mulder, H. 2020. Additions and corrections to the Gastropod fauna of the Pliocene of Estepona, southwestern Spain, 4. *Basteria* 84: 26-57.
- Landau, B.M., Silva, C.M. da & Mayoral, E. 2011. The lower Pliocene gastropods of the Huelva Sands Formation, Guadalquivir Basin, southwestern Spain. *Palaeofocus* 4: 1-90.
- Laskarev, V.D. 1903. Die Fauna der Buglowka-Schichten in Volhynien. *Memoires du comite geologique de Saint-Petersbourg, Neue Série* 5, 28, 1.148.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 1. Editio decima, reformata. Holmiae (Laurentii Salvii): 824 pp. [facsimile reprint, British Museum (Natural History), 1956].
- Locard, A. 1886. *Prodrome de malacologie française. Catalogue général des mollusques vivants de France. Mollusque marins*. Lyon, H. Georg & Paris, Baillière: pp. X + 778.
- Locard, A. 1896. Mollusques testacés et brachiopodes. In: Koehler R. 1896. Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne. *Annales de l'Université de Lyon* 26: 129-242, pl. 5-6.
- Locard, A. 1897-1898. Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882 et 1883. *Mollusques testacés. Paris, Masson*. vol. 1 [1897], p. 1-516 pl. 1-22; vol. 2 [1898], p. 1-515, pl. 1-18.
- Lozano-Francisco, M.C. & Vera-Peláez, J.L., 2006. Catálogo del material tipo del Museo Municipal Paleontológico de Estepona, parte I. Mollusca, Gastropoda. Descripción de nuevas especies del Plioceno de las cuencas de Estepona (Málaga) y del Guadalquivir (Huelva) (España). *Pliocénica*

- 5: 105-124.
- Luque, A.A. 1986. El genero *Mitrella* Risso, 1826 (Gastropoda, Columbelloidea) en las costas Ibericas. *Bollettino Malacologico* 22: 223-244.
- Macrì, G. 1983. Contributo alla conoscenza delle argille di Cutrofiano (Lecce). La malacofauna di Cava Signorella. Quaderni del Museo comunale di Paleontologia di Maglie: 112 pp.
- Malatesta, A. 1960. Malacofauna pleistocenica di Grammichele (Sicilia). *Memorie per Servire alla Carta Geologica d'Italia* 12: 1-196.
- Malatesta, A. 1974. Malacofauna pliocenica Umbra. *Memorie per Servire alla Carta Geologica d'Italia* 13: 1-498.
- deMaintenon, M.J. 2016. On the identity of *Graphicomassa albina* (Kiener, 1841) (Gastropoda: Columbelloidea). *Zoosystema* 38(1): 43-48.
- deMaintenon, M.J. & Strong, E.E. 2022. Molecular phylogeny of Columbelloidea (Gastropoda: Neogastropoda). *PeerJ* 10:e13996 <https://doi.org/10.7717/peerj.13996>
- Marasti, R. & Raffi, S. 1976. Osservazioni biostratigrafiche e paleoecologiche sulla malacofauna del Piacenziano di Maiatico (Parma, Emilia Occidentale). *Bollettino della Società Paleontologica Italiana* 15: 189-214.
- Martinell, J. 1982. Estudio de los Buccinoidea (Neogastropoda, Gastropoda) del Plioceno de l'Empordà (Catalunya). Descriptiva y sistemática. *Butlletí de la Institució Catalana d'Història Natural* 48 (sec. Geol. 3): 61-90.
- Martinell, J. & Domènech, R. 1986. Malacofauna du Pliocène marin de Saint-Isidore (Bassin du Var, Alpes-maritimes). *Geobios* 19: 117-121.
- Mayer, C. 1869. Description de Coquilles nouvelles des étages supérieurs des terrains tertiaires. *Journal de Conchyliologie* 17: 82-88, 282-287.
- Meznerics, I. 1933 Die Minutien der tortonischen Ablagerungen von Steinabrunn in Niederösterreich. *Annalen des Naturhistorischen Museums Wien* 46: 319-359.
- Michelotti, G. 1840. Rivista di alcune specie fossili della famiglia dei gasteropodi. *Annali delle Scienze del Regno Lombardo-Veneto. Opera periodica di alcuni collaboratori* 10: 137-162.
- Michelotti, G. 1847. Description des fossiles des terrains miocènes de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem* ser. 2, 3(2): 1-408, 17 pls.
- Millet [de la Turtaudière], P.-A. 1854. *Paléontologie de Maine-et-Loire*. Angers (Cosnier et Lachèse): 187 pp.
- Millet de la Turtaudière, P.A. 1865. *Indicateur du Maine-et-Loire ou indications par commune de ce que chacune d'elles renferme*, 2. Angers (Cosnier et Lachèse): 616 pp.
- Moisescu, G. 1955. Date noi asupra faunei de molluște si brachiopode Tortoniene de la Lăpugiu superior. *Revista Universitatii C. I. Parhon si a Politehnicii Bucuresti* 8: 255-283.
- MolluscaBase eds. (2023). MolluscaBase. *Columbella (Mitrella) spelta* Kobelt, 1893. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=519654> on 2023-06-25.
- Monegatti, P. & Raffi, S. 2001. Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. *Palaeogeography Palaeoclimatology Palaeoecology* 165: 171-193.
- Montefameglio, L. 1979. Associazione a molluschi del Tabiniano del Basso Monferrato (Alba, Italia NW). *Bollettino della Società Paleontologica Italiana* 17: 173-199, 1 pl.
- Nordsieck, F. 1972. *Die miozäne Molluskenfauna von Miste-Winterswijk NL*. Stuttgart (Fischer): 187 pp.
- Nordsieck, F. 1974. Molluschi dei fondali della platea continentale fra la Corsica e la Sardegna. *La Conchiglia* 61: 11-14.
- Nyst, P.H. 1878. Conchyliologie des terrains tertiaires de la Belgique, 1 Terrain Pliocène Scaldisien. *Annales du Musée Royal d'Histoire Naturelle de Belgique, série Paléontologique*, 3: atlas, 28 pls.
- Nyst, P.H. 1882. Conchyliologie des terrains tertiaires de la Belgique, 1. Terrain Pliocène Scaldisien. *Annales du Musée Royal d'Histoire Naturelle de Belgique, série Paléontologique* 3: text, 1-263.
- Olsson, A.A. & Harbison, A. 1953. Pliocene Mollusca of southern Florida, with special reference to those from North Saint Petersburg. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 1-457.
- Pace, S. 1902. Contributions to the study of the Columbelloidea. No. 1. *Proceedings of the Malacological Society of London* 5: 36-154.
- Pallary, P. 1906. Liste des Mollusques marins de la baie de Tripoli. *Annales de la Société Linnéenne de Lyon* 53: 203-213.
- Papp, A. 1954. Die Molluskenfauna im Sarmat des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien* 45: 1-112.
- Pavia, G. 1976. I molluschi del Pliocene inferiore di Monteu Roero (Alba, Italia NW). *Bollettino della Società Paleontologica Italiana* 14: 99-175.
- Payraudeau, B.C. 1827. *Catalogue descriptif et méthodique des annélides et des mollusques de l'île de Corse; avec huit planches représentant quatre-vingt-huit espèces, dont soixante-huit nouvelles*. Paris: 218 pp.
- Pelorce, J. & Boyer, F. 2005. La famille Columbelloidea (Gastropoda; Muricoidea) dans l'infralittoral de la Péninsule du Cap Vert (Sénégal). *Iberus* 23(2): 95-118.
- Pelosio, G. 1967 [1966]. La malacofauna dello stratotipo del Tabianiano (Pliocene inferiore) di Tabiano Bagni (Parma). *Bollettino della Società Paleontologica Italiana* 5: 101-183.
- Pereira da Costa, F.A. 1866-1867. Molluscos fosseis. Gasteropodes dos depositos terciarios de Portugal. *Memória Comissão Geologica de Portugal* 4(1): 1-116 (1866); (2): 117-252 (1867).
- Peyrot, A. 1924-1935 – see Cossmann & Peyrot 1909-1935.
- Peyrot, A. 1938. Les mollusques testacés univalves des depots Helvétiens du Bassin Ligérien. Catalogue critique, descriptive et illustré. *Actes de la Société Linnéenne de Bordeaux* 89: 5-361.
- Philippi, R.A. 1836. *Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit*. Vol. 1. Sumptibus Simonis Schroppii et Sociorum. Berolini [Berlin]. xiv + 267 p., pls. 1-12.
- Philippi, R.A. 1844. *Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit*. Vol. 2. Halle [Halis Saxorum]: Eduard Anton. iv + 303 pp., pls 13-28.
- Pinna, G. & Spezia, L., 1978. Catalogo dei tipi del Museo Civico di Storia Naturale di Milano, 5. I tipi dei Gasteropodi fossili. *Atti della Società italiana di Scienze naturali Museo Civico di Storia naturale* 119: 125-180.

- Radwin, G.E. 1968. New taxa of western Atlantic Columbelloidea (Gastropoda, Prosobranchia). *Proceedings of the Biological Society of Washington* 81: 143-150.
- Radwin, G.E. 1977a. The family Columbelloidea in the western Atlantic. *The Veliger* 19: 403-417.
- Radwin, G.E. 1977b. The family Columbelloidea in the Western Atlantic part IIa. The Pyreninae. *The Veliger* 20: 119-133.
- Raffi, S. & Monegatti, P. 1993. Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climatic-oceanographic and stratigraphic inferences. *Ciências da Terra* 12, 45-50.
- Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palermo (Rafinesque): 223 pp.
- Récluz, C.A. 1851. Description de coquilles nouvelles. *Journal de Conchyliologie* 2: 256-259, pl. 7, fig. 5, pl. 8, fig. 1, 2, 9.
- Reeve, L.A. 1846-1847. Monograph of the genus *Buccinum*. In: *Conchologia Iconica, or, illustrations of the shells of molluscan animals*, vol. 3, pl. 1-14 and unpaginated text. L. Reeve & Co., London. [stated dates: pl. 1-12, December 1846; pl. 13-14, February 1847].
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et principalement de celles des environs de Nice et des Alpes-Maritimes*, 4. *Mollusques*. Paris (Levrault): i-vii, 1-439.
- Robba, E. 1968. I molluschi del Molluschi del Tortoniano-tipo (Piemonte). *Rivista Italiana di Paleontologia e Stratigrafia* 74: 457-646.
- Rolán, E. 2005. Columbelloidea (Gastropoda, Neogastropoda) of the Gulf of Guinea with the description of eight new species. *Iberus* 23(2): 119-156.
- Roshka, V. Kh. 1964. On the Middle Miocene relict forms of mollusks in the Sarmatian of the Moldavian SSR. *zv. Academy of Sciences of the MSSR* 7: 61-67.
- Rossi-Ronchetti, C. 1955. I tipi della 'Conchologia Fossile Subappennina' di G. Brocchi, 2. Gastropodi, Scafofodi. *Rivista Italiana di Paleontologia e Stratigrafia* Memorie 5: 91-343.
- Ruggieri, G., Bruno, F. & Curti, G. 1959. La malacofauna pliocenica di Altavilla (Palermo), 2. *Atti dell'Accademia di Scienze Lettere e Arti di Palermo* 18: 99-129.
- Ruggieri, G. & Greco, A. 1965. Studi geologici e paleontologici su Capo Milazzo con particolare riguardo al Milazziano. *Geologica Romana* 4: 41-88.
- Sabelli, B. & Spada, G. 1981. Guida illustrata all'identificazione delle conchiglie del Mediterraneo. Fam. Columbelloidea II. *Bollettino Malacologico* Suppl. 17(11-12): 3 unnumbered pages.
- Sacchetti, C., Landau, B.M. & Ávila, S. 2023. Pliocene Gastropods of Santa Maria Island. Taxonomy and palaeobiogeographic implications. *Zootaxa* 5295(1): 001-150.
- Sacco, F. 1890a. Catalogo paleontologico del bacino terziario del Piemonte. *Bollettino della Società Geologica Italiana* 8(3): 281-356; 9(2): 185-340.
- Sacco, F. 1890b. I molluschi dei terreni terziari del Piemonte e della Liguria, 6. Volutidae, Marginellidae, Columbelloidea. *Memorie della Reale Accademia delle Scienze di Torino* 2(40): 295-368. [Reprinted by C. Clausen, Torino, Italy, 76 pp, 2 pls.].
- Sacco, F. 1904. I molluschi dei terreni terziari del Piemonte e della Liguria, 30. Aggiunte e correzioni (con 1400 figure). Considerazioni generali. Indice generale dell'opera. Torino (C. Clausen): 203 + xxxvi pp., 31 pls.
- Schirò, G. 1978. Il genere *Mitrella* Risso, 1826 nel Mediterraneo. Parte I. *La Conchiglia* 10 (114-115): 7-8.
- Seguenza, G. 1880. Le formazioni terziarie nella provincia di Reggio (Calabria). *Memorie della Classe di Scienze Fisiche Matematiche e Naturali della Reale Accademia dei Lincei* 6 (1879): 1-446.
- Silva, C.M. da 2001. *Gastropodes pliocénicos marinhos de Portugal: sistemática, paleoecologia, paleobiologia, paleogeografia*. Dissertação de doutoramento. Faculdade de Ciências da Universidade de Lisboa, Lisboa: 747 pp. (unpublished).
- Sleurs, W.J. 1987. The marine micro gastropods from the northern coast of Papua New Guinea (Mollusca: Gastropoda) III. Family Columbelloidea (subfamily Pyreninae), with description of two new species. *Indo-Malayan Zoology* 4:33-68.
- Sosso, M. & Dell'Angelo, B. 2010. *I fossili del Rio Torsero*. Prato (Editing Marginalia, Cartotecnica Beusi srl): 95 pp.
- Sowerby, G.B. I. 1844. Monograph of the genus *Columbella*. In: G. B. Sowerby II (ed.), *Thesaurus conchyliorum, or monographs of genera of shells*. Privately published, London. Vol. 1(4): 109-146bis, pls 36-40.
- Strausz, L. 1962. *Magyarországi Miozén-Mediterrán Csigák Határozója*. Budapest (Akadémiai Kiadó): 370 pp.
- Strausz, L. 1966. *Die Miozän-Mediterranen Gastropoden Ungarns*. Budapest (Akadémiai Kiadó): 692 pp.
- Švagrovský, J. 1960. Biostratigrafia a fauna mäkkýšov vrchného Tortónu východného úpätia slanských Hôr. *Geologické Práce* 57: 1-216.
- Švagrovský, J. 1971. Das Sarmat der Tschechoslowakei und seine Molluskenfauna. *Acta Geologica et Geographica Universitatis Comenianae, Geologica* 20, 1-473.
- Swainson, W. 1840. *A treatise on malacology or shells and shell-fish*. London (Longman). viii + 419 pp.
- Van Dingenen, F., Ceulemans, L. & Landau, B.M. 2017. The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, northwest France), 4. Neogastropoda (in part). *Cainozoic Research* 17: 23-61.
- Van Regteren Altena, C.O. 1956. *Pyrene scaldensis* nova species, a hitherto misunderstood species from the Plio-Pleistocene of western Europe. *Basteria* 20: 79-80.
- Venzo, S. & Pelosio, G. 1963. La malacofauna Tortoniana del Colle di Vigoleno (Preappennino Piacentino). *Palaeontographia Italica* 58: 43-213.
- Vera-Peláez, J.L. & Lozano-Francisco, M.C. 2022. Réplica a "Additions and corrections to the Gastropod fauna of the Pliocene of Estepona, South-western Spain 4" Landau, B.M. & Mulder, H. *Basteria* 84 (1-3) 2020 y "The Early Pliocene Gastropoda (Mollusca) from Estepona (Southern Spain), Part 1: Vetigastropoda" Landau, B.M., Marquet, R. & Grigis, M. *Palaeontos*, 2003. *Pliocénica* 6-7: 1-51.
- Wood, S.V. 1882. Third supplement to the Monograph of the Crag Mollusca, comprising testacea from the upper tertiary of the east of England. Univalves and bivalves. *Monograph Palaeontographical Society of London* 36: 1-24, 1 pl.
- Zelinskaya, V.A., Kulichenko, V.G., Makarenko, D.E. & Sorochan, E.A. 1968. *Paleontologicheskii Spravochnik*, 2. *Bruyukhonogiye 'lopatonogiye mollyuski paleogena' miotsena Ykranini*. (Paleontological Reference Book, 2. *Gastropoda and scaphopod mollusks of the Paleogene and Miocene of Ukraine*). Kiev (Academy of Sciences, Ukrainian SSR, Institute of Geological Sciences): 281 pp.