

The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 23: Colubrariidae, Pisaniidae, Tudicidae, Nassariidae (in part) (Neogastropoda, Buccinoidea)

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In this paper we continue to review the Buccinoidea of the Lower Piacenzian, Upper Pliocene of Estepona, southern Spain, with the description of the families Colubrariidae, Pisaniidae, Tudicidae and Nassariidae (in part). Fifteen species are recorded within seven genera, of which eight are described as new: *Colubraria alboranensis* nov. sp., *Kanamarua ducoi* nov. sp., *Metula moli* nov. sp., *Aplus raveni* nov. sp., *Euthria iberoadunca* nov. sp., *Euthria inflatissima* nov. sp., *Euthria pliovirginea* nov. sp. and *Euthria pouweri* nov. sp., one species is left in open nomenclature. *Pisania baetica* Lozano-Francisco & Vera-Peláez, 2006 is considered a junior subjective synonym of *Pisania magna* (Foresti, 1868) and *Pisania plioalboranensis* Lozano-Francisco & Vera-Peláez, 2006 is considered a junior subjective synonym of *Pisania plioangustata* (Sacco, 1904). The genus *Kanamarua* Kuroda, 1951 is recognised in the European fossil assemblages for the first time.

Just over half (53%) of the species are endemic to the Pliocene Mediterranean Alboran Sea, the rest of the species are also found in the Pliocene of the central Mediterranean Sea. Only one of those Pliocene species survived to the present day.

Two species of *Euthria* from the Atlantic Lower Pliocene Guadalquivir Basin assemblages are described as new: *E. lucenica* nov. sp. and *E. onubensis* nov. sp.

KEY WORDS: southern Spain, Upper Pliocene, Gastropoda, Buccinidae, Pisaniidae, Tudicidae, Buccinoidea, new species

Introduction

In this paper we continue the revision of the Buccinoidea in the diverse Pliocene assemblages of Estepona in south-western Spain, covering the families Colubrariidae Dall, 1904, Pisaniidae Gray, 1857, Tudicidae Cossmann, 1901, and the subfamily Photinae Gray, 1857 within the Nassariidae Iredale, 1916 (1835). Other families within the Buccinidae have already been revised by our team, the Chauvetiidae Kantor, Fedosov, Kosyan, Puillandre, Sorokin, Kano, R. Clark & Bouchet, 2022 (Landau & Micali, 2023), the Columbelloidea Swainson, 1840 (Landau *et al.*, 2023), and the Nassariidae Iredale, 1916 (1835) (excluding Photinae) (Landau *et al.*, 2009), with a few additions in Landau & Mulder (2020). This is the first paper specifically concentrating on these families in the assemblage, although a few species were described by Lozano-Francisco & Vera-Peláez (2006) that are revised

herein. The last remaining family within the superfamily, the Fasciolaridae Gray, 1853 will be revised in a separate paper (Landau & Harzhauser, submitted).

As with other parts of this series, this work is done in tandem with a revision of the Buccinoidea of the Middle Miocene Paratethyan assemblages (Harzhauser & Landau, 2024), which offers a congruous taxonomic framework and a deeper understanding of the similarities and differences between them.

Other works on the Buccinoidea of the Iberian Pliocene are those of Martinell (1982) describing the Mediterranean assemblages of NE Spain, and González-Delgado (1989) for the Atlantic Guadalquivir Basin of SW Spain, also described by Landau *et al.* (2011). However, neither of these assemblages are as diverse as that of Estepona. Important recent works covering the Mediterranean Pliocene of Italy are those of Brunetti & Della Bella (2014, 2016) that showed these groups to be more diverse

that previous acknowledged. In this work we recognise some of the species revised by those authors together with a cohort of species that seem to have been endemic to the Pliocene Alboran Sea, not present in the western or central Mediterranean Pliocene, nor that of the adjacent Atlantic.

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 MPP-MU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al.*, 2011, text-fig. 9).

Material and methods

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

In the descriptions we follow Harzhauser & Landau (2024, p. 6, fig. 1) and categorise the shells as: small (SL < 20.0 mm), medium-sized (20–60 mm), large (>60–100 mm) and very large (SL > 100 mm). We evaluated aperture length (AL), aperture width (AW), aperture height (AH), and last whorl height (LWH). Inner lip denticles numbered D1-D7, where D1 = the anal denticle.

Abbreviations:

CO: Velerín conglomerates; **VC:** Velerín Carretera;
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), updated by Kantor *et al.* (2022).

Subclass Caenogastropoda

Order Neogastropoda

Superfamily Buccinoidea Rafinesque, 1815

Family Colubrariidae Dall, 1904

Genus *Colubraria* Schumacher, 1817

Type species (by monotypy) – *Colubraria granulata* Schumacher, 1817. Present-day, Indo-Pacific.

- 1817 *Colubraria* Schumacher, p. 76, 251.
- 1847 *Columbaria* Gray, p. 133. Incorrect subsequent spelling.
- 1852 *Epidromus* Mörch, p. 107. Type species (by subsequent designation, Cossmann, 1889): *Triton distortus* Schubert & Wagner, 1829, present-day, Indo-Pacific.
- 1925 *Obex* Iredale, p. 259. Type species (by monotypy): *Obex mulveyana* Iredale, 1925, present-day, New South Wales, Australia.
- 2013 *Roquesia* Petuch, p. 200. Type species (by original designation): *Roquesia lindae* Petuch, 2013, present-day, Venezuela.

Note – Two genera with closely similar teleoconchs have been recognised: *Cumia* Bivona e Bernardi, 1838 (type species *Cumia decussata* Bivona e Bernardi, 1838; = *Triton reticulatum* de Blainville, 1829; = *Murex (Fusus) intertextus* Helbling, 1779) and *Colubraria* Schumacher, 1817. Their separation is based on protoconch type, *Cumia* has a very small, paucispiral papillate protoconch, whilst *Colubraria* has a larger, taller multispiral protoconch (Watters, 2009; Monsecour & Monsecour, 2011). However, the importance of protoconch type in generic separation is questionable in the absence of other teleoconch characters, as planktotrophy is lost in so many gastropod genera. The molecular phylogeny of *Colubraria* by Oliverio & Modica (2010, fig. 6) shows *Colubraria reticulata* (= *Cumia intertexta*, type species of *Cumia*) nested amongst other *Colubraria* species such as *Colubraria muricata* ([Lightfoot, 1786]). However, in order to resolve this issue, a larger molecular dataset would be necessary (Yuri Kantor personal comm. MH, 09/10/23). We therefore provisionally accept the separation of *Cumia/Colubraria* based on protoconch morphology, with some scepticism.

Colubraria alboranensis nov. sp.

Plate 1, figs 1-5

ZooBank registration – urn:lsid:zoobank.org:act:B652A5F4-27CC-471F-8F96-0B78B883707B

Type material – Holotype NHMW 2023/0323/0048, height 51.6 mm, width 18.6 mm; paratype 1 NHMW 2023/0323/0049, height 36.1 mm, width 13.7 mm; para-

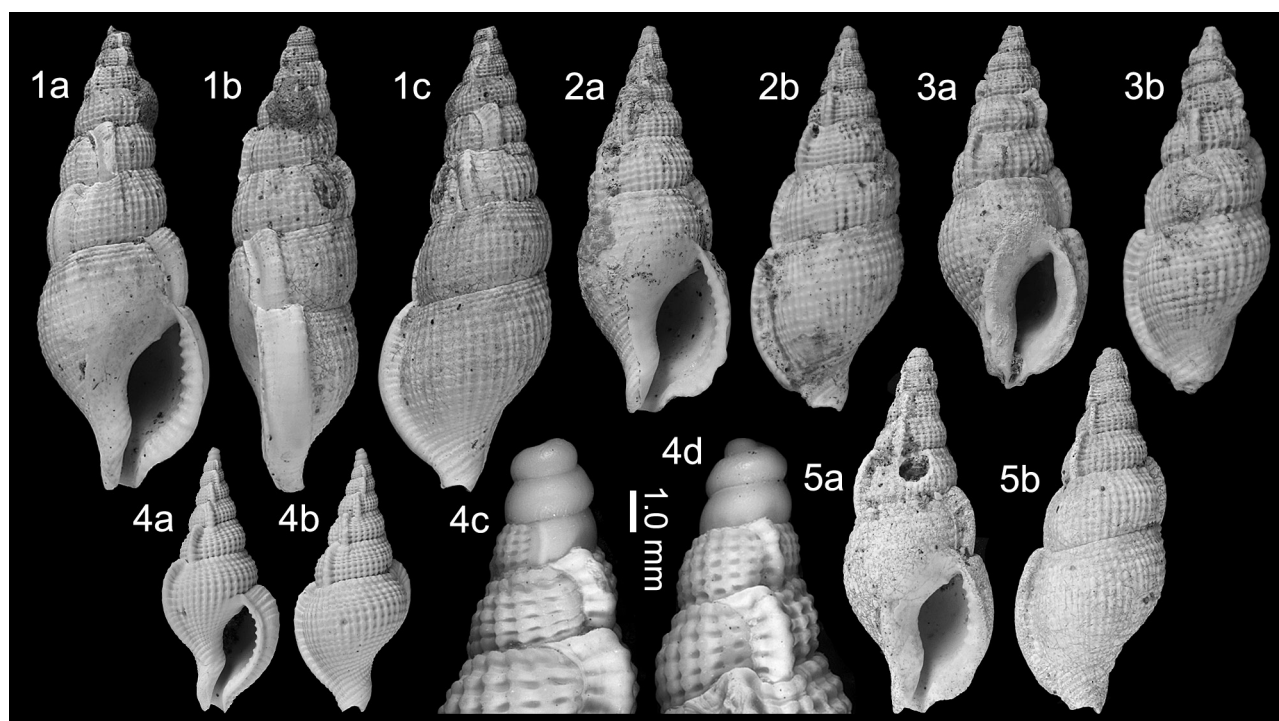


Plate 1. *Colubraria alboranensis* nov. sp.; 1. **Holotype** NHMW 2023/0323/0048, height 51.6 mm, width 18.6 mm; 2. **Paratype 1** NHMW 2023/0323/0049, height 36.1 mm, width 13.7 mm; 3. **Paratype 2** NHMW 2012/0197/0050 height 29.6 mm, width 12.0 mm; 4. **Paratype 3** NHMW 2023/0323/0051, height 28.2 mm, width 11.4 mm, 4 b, c, detail of protoconch; 5. **Paratype 4** RGM.1404366, height 27.3 mm, width 10.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

type 2 NHMW 2012/0197/0050 height 29.6 mm, width 12.0 mm; paratype 3 NHMW 2023/0323/0051 (juvenile), height 28.2 mm, width 11.4 mm; paratype 4 RGM.1404366, height 27.3 mm, width 10.7 mm.

Other material – Maximum height 51.6 mm, width 18.6 mm. **CO:** NHMW 2023/0323/0053 (10).

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

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

Etymology – Named after the Alboran Sea, where it occurred in the Pliocene. *Colubraria*, gender feminine.

Diagnosis – *Colubraria* species of large size, protoconch of 2.5 bulbous whorls, teleoconch growth rate relatively regular, very fine reticulated sculpture, six cords on first teleoconch whorl, that continues strong to aperture, finely reticulated surface pattern with neither axials nor spirals predominant, relatively weak apertural armature.

Description – Shell medium-sized, slender elongate-fusi-form. Protoconch multispiral, composed of 2.5 smooth bulbous whorls. Transition to protoconch marked by strong axial varix. Teleoconch of up to seven convex whorls separated by narrowly impressed suture. Spiral sculpture of six narrow cords on first three whorls, af-

ter which the whorl size grows more rapidly abapically and further spiral cords appear, with secondaries intercalated in some interspaces. Axial sculpture of narrow, rounded, opisthocline ribs, 15 on first whorl increasing in number abapically, roughly equal in width to their interspaces forming finely reticulated surface sculpture in which neither axials nor spirals are predominant, with small, rounded tubercles developed at sculptural intersections. Two strong, elevated varices per whorl on early teleoconch whorls placed about 180° intervals, staggered slightly axially, penultimate varix at about 270°, last varix at 360° to penultimate. Last whorl about 52% of total height, evenly convex, moderately constricted at base, bearing about 40 fine ribs and about 20 cords, three cords below suture closer-spaced, some secondary cords developed in spiral interspaces, base and fasciole poorly delimited, about five stronger cords over fasciole. Aperture elongate-ovate, about 35% of total height, Outer lip sharp edged, bevelled inwards, bearing about 13 small, sharp denticles on inner edge, variably developed; anal sinus small U-shaped notch; siphonal canal medium length, narrow, slightly recurved, Columella broadly excavated mid-aperture, smooth or bearing weak folds in abapical half and small parietal tooth may be present. Columellar callus moderately expanded, weakly to moderately thickened and delimited.

Discussion – As discussed in the generic note, the tall, bulbous multispiral protoconch (Pl. 1, figs 4b, c) places this species in the genus *Colubraria* Schumacher, 1817.

The series illustrated shows quite some variability in adult height. One of the smaller specimens illustrated (Pl. 1, fig. 3) is only about two-thirds maximum size. However, based on the thickness of its apertural armature, we interpret it as being fully adult. The protoconch of this species is similar to that of *C. harryleei* Monsecour & Monsecour, 2011, from present-day Bermuda, but that species is smaller shelled (maximum height 28.8 mm) and has fewer spirals on the first teleoconch whorl (4 vs. 6), there are fewer spirals on the last two whorls (30–32 vs. about 40), and the apertural armature, especially the columellar callus, is more strongly developed.

The genus is present in several European Neogene tropical assemblages, although never abundant. *Colubraria miocaenica* (Michelotti, 1847), originally described from the Lower Langhian Colli Torinesi of Italy is thicker shelled, with more strongly beaded sculpture and thicker apertural armature. Lozouet (2021, pl. 6, figs 8–12) illustrated a juvenile specimen identified as Michelotti's species, with its protoconch, from the Lower Miocene Aquitanian of Meilhan (Vives, France), under the genus *Cumia*. The protoconch is conical, multispiral, and of at least three whorls, placing it in the genus *Colubraria* rather than *Cumia* (see generic note). It is difficult to conclude whether the Miocene Italian and French specimens are conspecific, as Lozouet's juvenile and Michelotti's adult specimens may represent different species. No specimens are at hand from the Meilhan locality. But specimens from Le Peloua (Saucats, France) (NHMW and RGM colls) are smaller than the largest Estepona specimen, lower spired, the first teleoconch whorl has only four spiral cords as opposed to six, axial sculpture is slightly predominant, and the apertural armature thicker, especially in the columellar area where it forms a detached shield. Unfortunately, none of the Le Peloua adult specimens (NHMW coll. at hand) has its protoconch preserved to confirm if they are conspecific with the Meilhan juvenile specimen illustrated by Lozouet.

Colubraria subobscura (Hoernes & Auinger, 1884) from the Middle Miocene Paratethys is even more coarsely beaded than *C. miocaenica* and is squatter and broader than either *C. miocaenica* or *Colubraria alboranensis* nov. sp. Note that the Paratethyan taxa *Triton* (*Epidromus*) *karreri* Hoernes & Auinger, 1884 and *Ranella kostejana* Boettger, 1902 are based on subadult and juvenile specimens of *C. subobscura* respectively (Harzhauser & Landau, 2024, p. 7).

In the Mediterranean Pliocene only *Colubraria reticulata* [= *Cumia intertexta* (Helbling, 1779)] has been recorded from Italy (d'Ancona, 1872; Ruggieri & Greco, 1965; Inzani, 1988; Cavallo & Repetto, 1992; Chirli, 2000; Brunetti & Cresti, 2018) and Rhodes Island (Chirli & Linse, 2011). Unfortunately, none of the Mediterranean Pliocene specimens figured by any of those authors have their protoconch preserved. Similarly, specimens at hand from the Upper Pliocene of Bibbiano (Siena, Italy; NHMW coll.) are without protoconchs. Specimens from the Upper Pliocene of Sicily and Pleistocene of Cyprus (NHMW

coll.) do have their protoconchs preserved and confirm they represent *Cumia intertexta*. That species still occurs in the Mediterranean today and is smaller (maximum size 33.0 mm; *vide* Giannuzzi-Savelli *et al.*, 2003, p. 154), and immediately separated by its paucispiral protoconch (see Oliverio & Tringali, 1991, fig. 1; Giannuzzi-Savelli *et al.*, 2003, fig. 285), character of the genus *Cumia*. Moreover, the growth rate of the intermediate whorls in *Cumia intertexta* is greater, so they appear inflated in relation to the earlier teleoconch whorls and last whorl, whereas in the Estepona species the growth rate is more constant. In the absence of their protoconchs, *C. intertexta* can be separated from *Colubraria alboranensis* nov. sp. by the profile and sculpture of the first teleoconch whorl. In *Cumia intertexta* the first whorl is strongly rounded, with a subsutural area, two cords mid-whorl slightly stronger, below which the whorl profile is concave. In *C. alboranensis* the first whorl is more evenly and less convex, with cords evenly distributed and equal in strength (Pl. 1, figs 4b, c). *Cumia intertexta* has not been found in the Estepona assemblages.

Colubraria does not occur in the Mediterranean today. In the eastern Atlantic and West African faunas *Colubraria canariensis* Nordsieck & García-Talavera, 1979 found from Madeira southwards to Angola is smaller sized, thicker shelled, the protoconch is more conical, consisting of 3–3.5 whorls, the surface beading is coarser and the columellar callus thicker. *Colubraria somalica* Cossignani, 2020 from Somalia is much slenderer than the other congeners discussed above, with more clearly beaded sculpture, and the whorls are tilted in relation to each other resulting in a rather distorted spire. The genus is represented by four species in the tropical western Atlantic (Monsecour & Monsecour, 2011). The largest of these, *C. margarethae* Monsecour & Monsecour, 2011, which attains an even larger maximum size of almost 65 mm, is most like *C. alboranensis* in being relatively thinner shelled and the spire growth rate almost regular, the protoconch has a similar number of whorls, but is lower and more dome shaped. It differs in having the last two whorls less inflated resulting in a narrower aperture, and the sculpture on the last two whorls tends to fade, which is not the case in the Estepona species. The other two species, *C. testacea* (Mörch, 1852) and *C. kathiewayana* Fittkau & Parth, 1993 and both smaller, squatter, with coarser sculpture.

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

Genus *Kanamarua* Kuroda, 1951

Type species (by original designation) – *Colus adonis* Dall, 1919. Present-day, Japan.

1951 *Kanamarua* Kuroda, p. 68.

Note – *Kanamarua* Kuroda, 1951 differs from *Metula* H. Adams & A. Adams, 1853 in having flattened and mod-

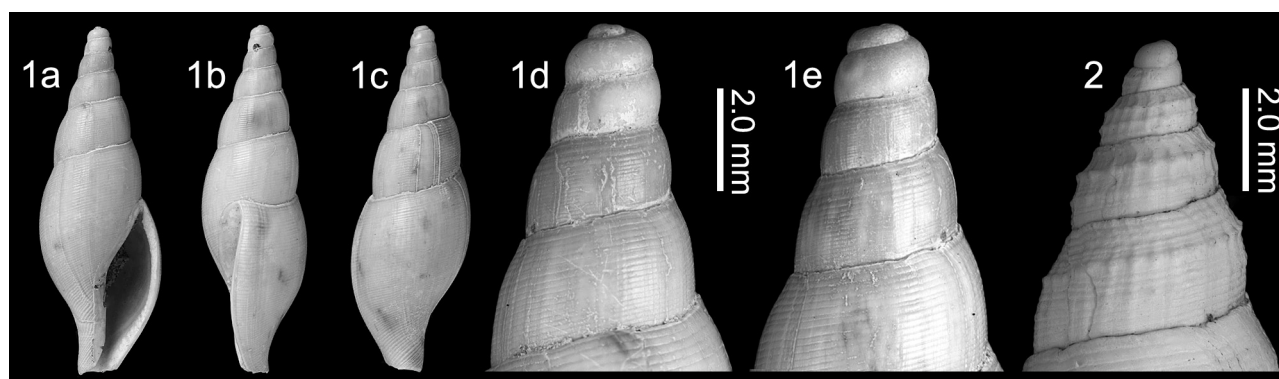


Plate 2. *Kanamarua ducoi* nov. sp.; 1. **Holotype** NHMW 2023/0323/0065, height 25.8 mm, width 8.6 mm, 1d, e, detail of protoconch. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene. 2. *Metula mitraeformis* (Brocchi, 1814), detail of protoconch. Chiavenna Rocchetta, Piacenza, Italy, Piacenzian, Upper Pliocene.

erately broad spiral cords separated by narrow grooves as opposed to granular cords, lacks axial ribs on early teleoconch whorls, a narrower columellar lip, and a smooth paucispiral protoconch of 1-2¼ whorls as opposed to a protoconch of 2-4 whorls with or without spiral sculpture. Today this is a deep water genus widely distributed in the tropical Pacific (Fraussen & Lamy, 2008). The species here described is the first extinct species to be attributed to the genus, and the first record for European assemblages.

Kanamarua ducoi nov. sp.

Plate 2, fig. 1

ZooBank registration – urn:lsid:zoobank.org:act:A744AD27-849A-44AB-89FA-8967B28106E0

Type material – Holotype NHMW 2023/0323/0065, height 25.8 mm, width 8.6 mm.

Other material – Known from the holotype only.

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

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

Etymology – Named after Duco Nieland, oldest grandchild of Wil & Henk Mulder who have contributed enormously to this series. *Kanamarua*, gender feminine.

Diagnosis – *Kanamarua* species of medium size, slender, dome-shaped protoconch of 2.5 whorls with small nucleus, teleoconch sculpture restricted to very fine, crowded spiral cords, anal sinus deep and narrow.

Description – Shell medium sized, slender fusiform; apical angle 27°. Dome-shaped protoconch of 2.5 whorls with small, depressed nucleus; second whorl somewhat swollen, strongly convex (dp = 1.95 mm; hp = 2.13 mm). Junction with teleoconch marked by opisthocline scar.

Teleoconch of 4.5 tall, weakly convex whorls with periphery at abapical suture, sculptured by very fine spiral cords separated by narrow grooves; axial sculpture absent, except for vague axial swellings marking growth halts. Last whorl high, attaining 64% of total height, base slowly constricting, with shallow neck, fasciole indistinct. Aperture narrow, elongate ovate; anal sinus marked by deep, narrow groove, accentuated on labial side by weak anal denticle. Columella weakly excavated. Columellar callus sharply delimited, forming thin, broad rim. Outer lip narrowly and thickened by weak terminal varix, bearing row of small, close-set elongated denticles placed close behind peristome. Siphonal canal moderately long, relatively wide, slightly deflected to the left, shallowly notched.

Discussion – Despite being represented by a single specimen, this species is so different from all known European colubrariids that it warrants description. As discussed in the generic note, the protoconch, early teleoconch whorl sculpture and smooth cords place it in the genus *Kanamarua* Kuroda, 1951 rather than *Metula* H. Adams & A. Adams, 1853. Today *Kanamarua* is a deep water genus, and the single specimen from Estepona was also found in the deeper water deposits of Velerín carretera.

Kanamarua ducoi nov. sp. differs from all superficially similar European Neogene *Metula* species in the generic characters. Of the extant Pacific species *Kanamarua hyatinthus* Shikama, 1973, widely distributed from Somalia, Mozambique, to the Philippines and Vanuatu in the east is most similar in profile but has a relatively taller spire and shorter last whorl and lacks spiral sculpture. *Kanamarua wangae* Monsecour, Fraussen & Fei, 2017 from the South China Sea is also similar in profile and sculpture, but is again slenderer, with more numerous whorls, and has a less inflated last whorl.

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

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

Type species (by subsequent designation) – *Buccinum clathratum* A. Adams & Reeve, 1850 [= *Metula amosi* Vanatta, 1913]. Present-day, Eastern Pacific.

- 1853 *Metula* H. Adams & A. Adams, p. 84.
- 1901 *Acamptochetus* Cossmann, p. 123. Type species (by original designation): *Murex mitraeformis* Brocchi, 1814, Pliocene, Italy.
- 1943 *Antemetula* Rehder, p. 199. Type species (by original designation): *Buccinum metula* Hinds, 1844, present-day, Panamic Pacific.
- 1917 *Antimitra* Iredale, p. 329. Type species (by original designation): *Pleurotoma aegrota* Reeve, 1845, present-day, Philippines.
- 1971 *Colubrarina* Kuroda & Habe in Kuroda, Habe & Oyama, p. 173. Type species (by original designation): *Antemetula (Colubrarina) metulina* Kuroda & Habe in Kuroda, Habe & Oyama, 1971, present-day, northern West Pacific.
- 1972 *Floritula* Olsson & Bayer, p. 921. Type species (by monotypy): *Metula roberti* Olsson, 1967, Pliocene, Florida.

Note – Species within this European Tertiary group have been assigned by authors to the genus *Acamptochetus* Cossmann, 1901, of which *Murex mitraeformis* Brocchi, 1814 is the type species. However, the current ‘accepted opinion’ is that *Acamptochetus* is a synonym of *Metula* H. Adams & A. Adams, 1853 (see MolluscaBase eds, 2023). Fraussen & Lamy (2008, p. 132) described the protoconch of *Metula* as being multispiral and rather sharp, but then went on to recognise that it was quite variable, ranging from 2-4 whorls, with or without spiral sculpture. This is indeed true of the European fossil species that can be paucispiral [e.g., *M. major* (Grateloup, 1845)] or multispiral [e.g., *M. rivulisensis* Lozouet, 2001 and *M. pseudomajor* Lozouet, 2001].

***Metula moli* nov. sp.**

Plate 3, figs 1-3

ZooBank registration – urn:lsid:zoobank.org:act:42AD5680-C817-44ED-9FFC-54B447CCABE0

Type material – Holotype NHMW 2023/0323/0066, height 31.5 mm, width 10.7 mm; paratype 1 NHMW 2023/0323/0066, height 31.3 mm, width 10.4 mm; paratype 2 NHMW 2023/0323/0067, height 31.8 mm, width 10.9 mm.

Other material – Known from type series only.

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

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

Etymology – Named after Dick Mol, Dutch palaeontologist renowned for his vertebrate work, and friend of Henk Mulder. *Metula*, gender feminine.

Diagnosis – *Metula* species of medium size, conical protoconch of 2-2.5 whorls with medium-sized nucleus, teleoconch of six whorls with narrow subsutural ramp, sculpture on early whorls of axial riblets, fading abapically and crowded spiral cords.

Description – Shell medium-sized, moderately slender fusiform; apical angle 35-39°. Conical protoconch of 2-2.5 convex whorls, with medium-sized nucleus (dp = 1.3 mm; hp = 1.52 mm). Junction with teleoconch marked by opisthocline scar. Teleoconch of up to six whorls. Early teleoconch whorls bearing narrow, slightly concave subsutural ramp, angled at shoulder, convex below, with periphery at abapical suture, sculptured by narrow, opisthocline axial ribs, strongly developed over subsutural ramp and shoulder, fading below, not reaching abapical suture, crossed by weak, narrow, close-set, spiral cords forming small, pointed tubercles at shoulder. Abapically, subsutural ramp broadens and weakens, absent or almost so on last two whorls, axial ribs weaken, so that last two whorls bearing only narrow, close-set, flattened cords separated by shallow grooves and poorly delimited axial swelling marking previous growth halts. Suture linear, narrowly impressed, more oblique on last whorl. Last whorl high, attaining 67-68% of total height, weakly and evenly convex, base slowly constricting, with shallow neck, fasciole indistinct. Aperture narrow, elongate ovate; anal sinus marked by moderate width groove, accentuated on labial side by weak anal denticle. Columella weakly excavated. Columellar callus sharply delimited, forming thin, broad rim. Outer lip narrowly thickened by terminal varix, bearing row of small elongated denticles placed close behind peristome; variably developed. Siphonal canal moderately long, relatively wide, slightly deflected to the left, shallowly notched.

Discussion – *Metula moli* nov. sp. is closely similar to the Pliocene Mediterranean *M. mitraeformis* (Brocchi, 1814), and was mislabelled as such in the NHMW collections. However, detailed comparison with specimens from Italy show it not to be conspecific. The Estepona species has a larger protoconch of about an extra half whorl (dp = 0.94 mm, hp = 1.0 mm for *M. mitraeformis*; *hoc opus* Pl. 2, fig. 2). On the early teleoconch whorls the subsutural ramp is narrower and axial ribs are present on the first three whorls, whereas in *M. mitraeformis* axial ribs are absent, or almost so, marked only by tubercles at the shoulder, which is placed lower than in *M. moli*. Profile, spiral sculpture and apertural characters are similar, although *M. moli* is slightly slenderer.

Bouchet (1988) considered *M. mitraeformis* to be the direct ancestor of the extant West African *M. africana* Bouchet, 1988 that differs in having stronger sculpture, a less well developed subsutural ramp, and a narrower siphonal canal. It is certainly a descendent of this species group, although direct lineage is difficult to confirm now that two members

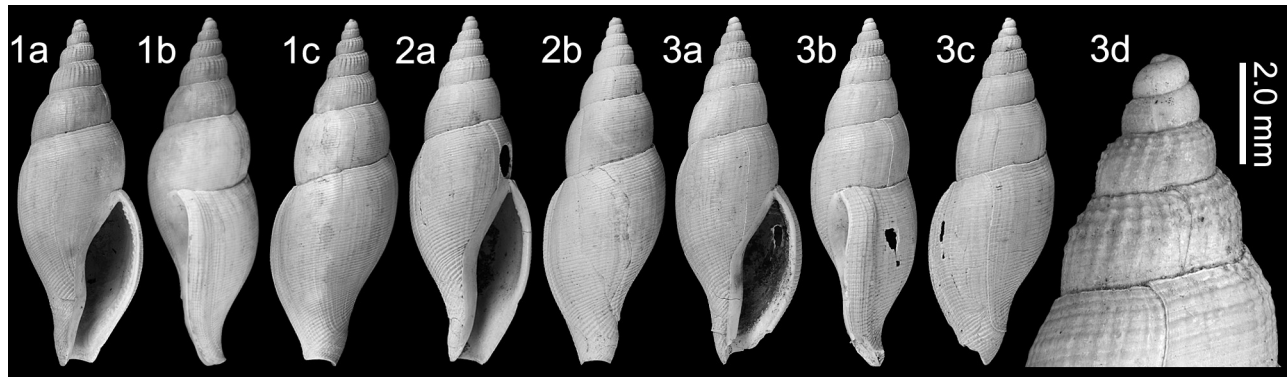


Plate 3. *Metula moli* nov. sp.; 1. **Holotype** NHMW 2023/0323/0066, height 31.5 mm, width 10.7 mm; 2. **Paratype 1** NHMW 2023/0323/0066, height 31.3 mm, width 10.4 mm; 3. **Paratype 2** NHMW 2023/0323/0067, height 31.8 mm, width 10.9 mm, 3d, detail of protoconch. Velerín carretera, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

of this species group are recognised in the Mediterranean Pliocene (*M. mitraeformis* and *M. moli* nov. sp.).

The European fossil *Metula major* (Grateloup, 1845) [= *Acamptochetus submitraeformis* (d'Orbigny, 1852)] from the Burdigalian of the Aquitaine Basin differs in having a paucispiral protoconch, and *M. aliceae* Harzhauser & Landau, 2024 from the Paratethys has tuberculate earliest teleoconch whorls and axial ribs on the early spire whorls.

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

Family Pisaniidae Gray, 1857
Genus *Aplus* De Gregorio, 1885

Type species (by subsequent designation; Vokes, 1971) – *Murex plicatus* Brocchi, 1814. Neogene, Italy.

1885 *Aplus* De Gregorio, p. 279.

For generic synonymy and discussion see Van Dingenen *et al.* (2017, p. 23).

Aplus aequicostatus (Bellardi, 1873)

Plate 4, figs 1-3

- *1873 *Pollia aequicostata* Bellardi, p. 182, pl. 12, fig. 23.
- 1981 *Pollia aequicostata* Bellardi, 1872 [sic] – Ferrero-Mortara *et al.*, p. 48, pl. 6, fig. 8.
- 2014 *Aplus aequicostatus* (Bellardi, 1877 [sic]) – Brunetti & Della Bella, p. 18, figs 5A-F.

non 1964 *Cantharus (Pollia) aequicostata* Bellardi, 1872 [sic] – Brébion, p. 429, pl. 10, figs 24, 25 [= *Aplus scaber* (Millet, 1865)].

Material and dimensions – Maximum height 26.5 mm, width 13.0 mm. **CO:** NHMW 2023/0323/0005-0007 (3), NHMW 2023/0323/0008 (29), RGM.1404370 (5). **EL:** NHMW 2023/0323/0004 (1).

Description – Shell medium-sized, fusiform-biconic. Protoconch low dome-shaped, of 2.25 smooth convex whorls, with periphery at abapical suture, nucleus medium sized; protoconch boundary sharply delimited by beginning of adult sculpture. Teleoconch of six weakly shouldered convex whorls, with broad, steep subsutural ramp, weakly angled at shoulder, convex below: periphery midway between shoulder and lower suture. Suture impressed, undulating. Axial sculpture of 10 broad, rounded, weakly prosocline ribs, wider than their interspaces, weak over subsutural ramp, broader and stronger below shoulder. Spiral sculpture on first teleoconch whorl of three narrow, elevated, rounded cords, adapical weaker; cords override and become strongly swollen over axial ribs; abapically one further primary cord develops over subsutural ramp on second whorl, secondary cords develop immediately above and below lower two primaries giving aspect of tripartite primary cords, with a further secondary intercalated in the centre of the interspaces; tertiary spiral threads irregularly intercalated on last two whorls. Last whorl 65-68% of total height, with two primaries on subsutural ramp, seven tripartite primary cords below shoulder and over base, base moderately constricted, siphonal fasciole broad, flattened bearing about 12 narrower cords. Aperture elongate-ovate, 42-43% of total height; anal canal strongly developed, forming U-shaped groove in labral callus; siphonal canal open, moderate length, weakly posteriorly recurved; outer lip sharp, weakly crenulated by primary spiral cords, bearing seven relatively strongly denticles within: D1 strong, D2 weak, D3 strong, D4-D7 medium strength, weakening abapically; denticles extending within lip in some specimens. Columella deeply excavated in upper third. Columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; three prominent columellar folds present below mid-aperture, three small tubercles developed over primary cords in upper half, and moderately prominent parietal tubercle. Colour pattern preserved consisting of reddish-brown stripes over cords.

Discussion – Van Dingenen *et al.* (2017, p. 24) considered *Aplus aequicostatus* (Bellardi, 1873) a junior subjective

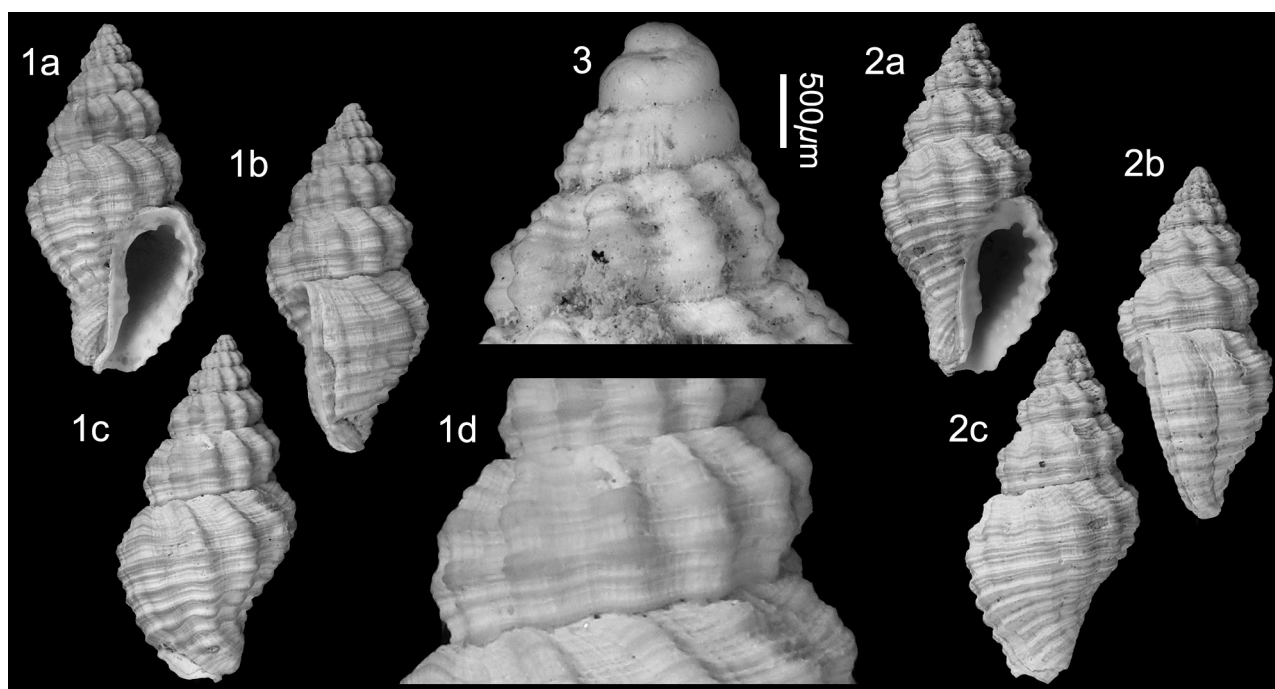


Plate 4. *Aplus aequicostatus* (Bellardi, 1873); 1. NHMW 2023/0323/0005, height 26.1 mm, width 12.8 mm, 1d, detail of teleoconch sculpture; 2. NHMW 2023/0323/0006, height 26.5 mm, width 13.0 mm; 3. NHMW 2023/0323/0007 (juvenile), height 18.8 mm, width 8.5 mm, detail of protoconch. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

synonym of *Aplus scaber* (Millet, 1865). However, with Pliocene material at hand it is clear that this is incorrect. *Aplus aequicostatus* is almost twice the size (maximum height 26.1 mm vs. 11.3 mm), and although the sculpture is similar, the primary cords in *A. scaber* are not tripartite as they are in this species and the swelling of the primary cords over the ribs at the intersections is more pointed. Moreover, there are fewer denticles within the outer lip (85 vs. 7).

In the Miocene Paratethys *Aplus lapugyensis* (Hoernes & Auinger, 1890) is immediately separated by the much greater number of axial ribs on the early teleoconch whorls. *Aplus praedorbignyi* Harzhauser & Landau, 2024 is more closely similar in shape and axial sculpture but differs in the character of its primary cords which are divided not triplets.

A number of Italian Pliocene congeners need to be compared. *Aplus nilus* (De Gregorio, 1884) has a similar protoconch, but differs in having a greater number of axial ribs (12–13 vs. 10), and the primary spiral cords are more rounded and overrun by a greater number of secondary cords. Both *Aplus ansus* (De Gregorio, 1884) and *A. plio-recens* Brunetti & Della Bella, 2014 have sharper primary spiral cords and the shoulder, especially on the last whorl, is more angular. *Aplus plioparvus* (Sacco, 1904) and *A. plio-unifilosus* Brunetti & Della Bella, 2014 are both much smaller species. The Upper Pleistocene to present-day *A. dorbignyi* (Payraudeau, 1827) and the present-day West African *A. assimilis* (Reeve, 1844) are both separated immediately by their paucispiral protoconch (see Brunetti & Della Bella, 2014, fig. 10C; 2016, p. 35). Landau *et al.* (2011) illustrated a specimen from the Atlantic Lower

Pliocene Guadalquivir Basin of southwestern Spain as *A. cf. assimilis*. Brunetti & Della Bella (2016) were fortunate to find a specimen from the same locality with an intact protoconch and named the Guadalquivir Basin species *A. pseudoassilimis*.

The Pliocene species all (except for *A. unifilosus* and *Aplus raveni* nov. sp.) have non-direct developing type protoconchs, whereas the extant Mediterranean/West African species discussed above, plus the Mediterranean *Aplus coccineus* (Monterosato, 1884) [= *A. campisii* (Ardovini, 2015)], *A. nodulosus* (Bivona e Bernardi, 1832), *A. gaillardoti* (Puton, 1856) and *A. scacchianus* (Philippi, 1844) have non-planktotrophic development (Aissaoui *et al.*, 2016). Therefore, planktotrophic development seems to have been lost by the genus since the Pliocene.

Distribution – Lower Pliocene: central Mediterranean, Italy (Brunetti & Della Bella, 2014). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (bouchet, 1873; Brunetti & Della Bella, 2014).

Aplus raveni nov. sp.

Plate 5, figs 1–3

ZooBank registration – urn:lsid:zoobank.org:act:0D921E51-CFAD-4964-BCCE-AE5C036FC38E

Type material – Holotype NHMW 2023/0323/0009, height 16.4 mm, width 7.8 mm; **Velerín conglomerates**. Paratype 1 NHMW 2023/0323/0011, height 16.0 mm,

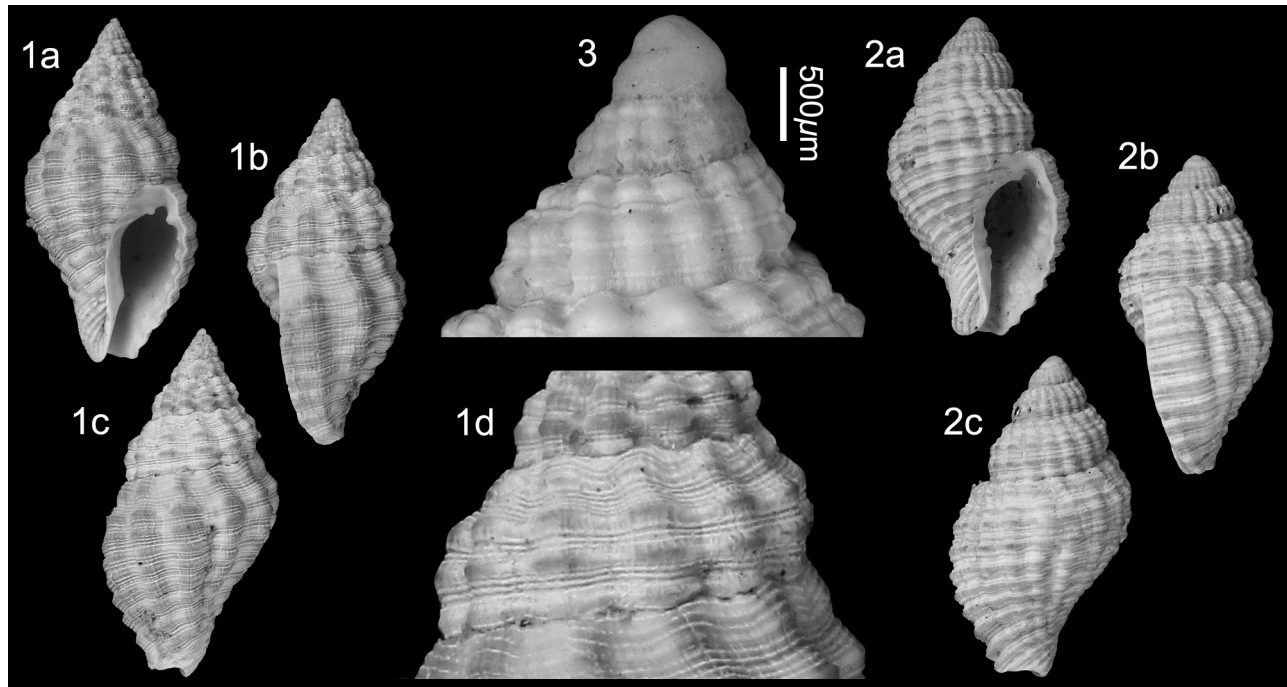


Plate 5. *Aplus raveni* nov. sp.; 1. **Holotype** NHMW 2023/0323/0009, height 16.4 mm, width 7.8 mm, 1d, detail of teleoconch sculpture. Velerín conglomerates, Velerín. 2. **Paratype 1** NHMW 2023/0323/0011, height 16.0 mm, width 8.8 mm; 3. **Paratype 2** NHMW 2023/0323/0012 (juvenile), height 18.8 mm, width 8.5 mm, detail of protoconch. El Lobillo Estepona, Lower Piacenzian, Upper Pliocene.

width 8.8 mm; paratype 2 NHMW 2023/0323/0012 (juvenile), height 18.8 mm, width 8.5 mm; paratype 3 NHMW 2023/0323/0013, height 15.8 mm, width 8.2 mm; paratype 4 NHMW 2023/0323/0014, height 16.7 mm, width 8.5 mm; paratype 5 RGM.1404373, height 14.5 mm, width 7.2 mm; paratype 6 RGM.1404374, height 15.7 mm, width 7.6 mm. **El Lobillo.**

Other material – CO: NHMW 2023/0323/0010 (15). **EL:** NHMW 2023/0323/0015 (10).

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

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

Etymology – Named after the Han Raven, Associate Researcher at the Naturalis Biodiversity Center (Leiden) and Managing Editor of *Cainozoic Research* in recognition of the endless hours of work he has put into the production of this series. *Aplus*, gender masculine.

Diagnosis – Small, ovate-fusiform *Aplus* species with paucispiral protoconch of just over one whorl, rounded unshouldered teleoconch whorls, 11-15 axial ribs, three primary spiral cords on spire whorls, 7-8 labial denticles, three columellar folds in most specimens.

Description – Shell small, ovate-fusiform. Protoconch paucispiral, just over one smooth convex whorl, with large nucleus; protoconch boundary sharply delimited by

beginning of adult sculpture. Teleoconch of 5.5 convex whorls with periphery just above suture, subsutural ramp narrow, weakly delimited. Suture weakly impressed, undulating. Axial sculpture of 11-15 broad, rounded, weakly prosocline ribs, wider than their interspaces. Spiral sculpture on first teleoconch whorl of three elevated, rounded cords, mid-cord strongest; cords override and become strongly swollen over axial ribs; abapically, upper cord weakest, placed just below suture, mid-cord delimits narrow, slightly concave subsutural ramp, lower cord of similar strength forming periphery, very fine secondary and tertiary threads intercalated. Close-set axial growth lines give surface very finely reticulated appearance. Last whorl 70-77% of total height, upper primary forming broad subsutural band, narrow concave subsutural ramp, nine primary cords below shoulder and over base, base moderately weakly constricted, siphonal fasciole broad, flattened bearing about eight sharp, narrow cords. Aperture elongate-ovate, 44-52% of total height; anal canal strongly developed, forming deep U-shaped groove in labral callus; siphonal canal open, moderate length, hardly recurved; outer lip sharp, weakly crenulated by primary spiral cords, bearing 7-8 moderate strength denticles within: D1 strong, D2 weak, D3-D7 or D8 moderately weak, weakening further abapically. Columella deeply excavated in upper third. Columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; 3-4 broad columellar folds variably developed below mid-aperture, small prominent parietal tubercle. Colour pattern preserved consisting reddish-brown stripes over ribs, colour strongest over sculptural intersections.

Discussion – This species is characterised by its small size for the genus, ovate profile with unshouldered whorls, and sculpture of broad rounded ribs and primary spiral cords with numerous fine threads intercalated in the interspaces. It is similar to the extant West African *Aplus assimilis* (Reeve, 1846), but that species is slenderer, the subsutural ramp is even less delimited, there is a single secondary thread intercalated between the more numerous primary spiral cords, and the colour pattern consists of a broad white band on the lower half of the spire whorls and mid-whorl on the last whorl rather than axial colour bands as seen in the Estepona species. *Aplus pseudoassimilis* Brunetti & Della Bella, 2016 from the Atlantic Lower Pliocene Guadalquivir Basin has similar sculpture, but is larger and differs in its wider aperture, with a broader U-shaped anal groove and more numerous labial denticles. *Aplus pliounifilosus* Brunetti & Della Bella, 2014 from the Lower Pliocene of Italy is similar in profile but differs in having fewer cords that are poorly delimited, stronger cords with a single secondary intercalated. *Aplus multicostatus* (Bellardi, 1873) from the Middle Miocene Langhian Colli Torinesi of Italy is the most similar in profile and sculpture, especially to specimens with more numerous ribs (Pl. 5, fig. 2), but the Miocene species differs in having far more numerous denticles within the outer lip. *Aplus raveni* nov. sp. has a paucispiral protoconch of just over one whorl, with a very large nucleus, which suggests direct development. It is very unlikely to be conspecific with the Miocene species and is probably endemic to the Pliocene Alboran Sea.

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

Genus *Enginella* Monterosato, 1917

Type species (by original designation) – *Murex bicolor* Cantraine, 1835 (*non* Risso, 1826; *nec* Valenciennes, 1832) [= *Enginella leucozona* (Philippi, 1844)]. Present-day, Mediterranean.

1917 *Enginella* Monterosato, p. 22.

Enginella pusilla (Bellardi 1873)

Plate 6, figs 1-2

1872 *Murex exiguus* Dujardin – D’Ancona, p. 354, pl. 5, fig. 4 [*non* Broderip, 1833 = *Favartia exigua*; *nec*. Dujardin, 1837].

1873 *Polia pusilla* Bellardi, p. 186, pl. 12, fig. 30.

1981 *Polia pusilla* Bellardi, 1872 [*sic*] – Ferrero-Mortara *et al.*, p. 49, pl. 5, fig. 10.

1995 *Engina pusilla* (Bellardi, 1873) – Forli & Dell’Angelo, p. 16, fig. 6.

2000 *Polia pusilla* Bellardi, 1872 [*sic*] – Chirli, p. 61, pl. 24, figs 10, 11.

2014 *Engina pusilla* (Bellardi, 1877 [*sic*]) – Brunetti & Della Bella, p. 16, figs 11A-E.

non 1964 *Cantharus (Polia) pusilla* Bellardi, 1872 [*sic*] – Brébion, p. 430, pl. 10, figs 26, 27 [= *Engina brunettii* Landau, Ceulemans & Van Dingenen, 2019].

Material and dimensions – Maximum height 12.9 mm, width 6.9 mm. **CO:** NHMW 2023/0323/0001-0002 (2), NHMW 2023/0323/0003 (3), RGM.1404365 (1). **EL:** NHMW 2023/0323/0004 (1).

Description – Shell small, biconic. Protoconch multispiral, low dome-shaped, of just over three smooth convex whorls, with periphery at abapical suture, nucleus small, about three prosocline axial riblets on last quarter protoconch whorl; protoconch boundary sharply delimited by prosocline scar. Teleoconch of five whorls, with broad, concave subsutural ramp, sharply angled at shoulder, convex below: periphery midway between shoulder and lower suture. Suture impressed, shallowly undulating. Axial sculpture of eight broad, rounded, weakly prosocline ribs, wider than their interspaces, weak over subsutural ramp, strengthening below shoulder and slightly nodular at shoulder. Spiral sculpture on first teleoconch whorl of three narrow, elevated, rounded cords; cords override and become strongly swollen over axial ribs; single secondary spiral cord intercalated between primaries on third teleoconch whorl; tertiary threads intercalated on subsutural ramp on penultimate whorl and below

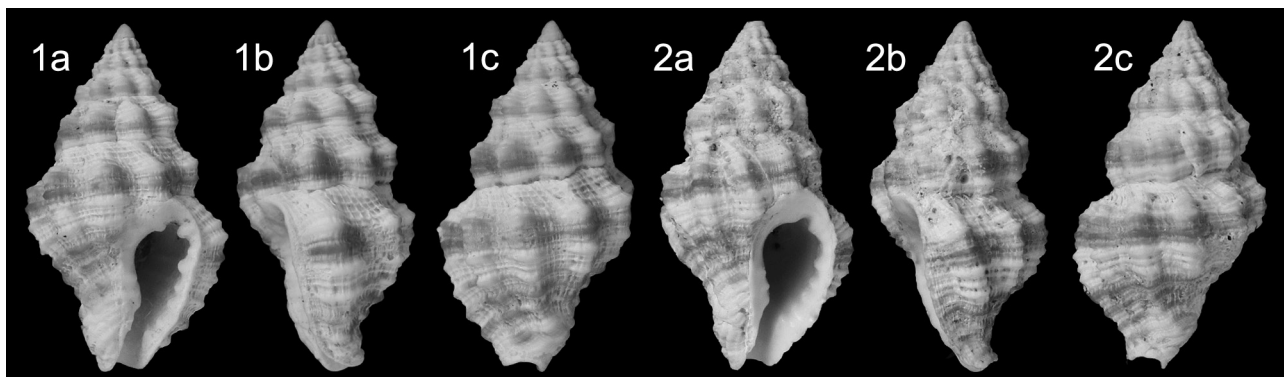


Plate 6. *Enginella pusilla* (Bellardi, 1873); 1. NHMW 2023/0323/0001, height 11.0 mm, width 6.9 mm; 2. NHMW 2023/0323/0002, height 12.9 mm, width 6.9 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

on last whorl. Last whorl 66-67% of total height, bearing six primary spirals intercalated by a single secondary and an irregular tertiary spiral thread in some interspaces, moderately constricted at base, siphonal fasciole broad, flattened, bearing a further six cords. Aperture elongate-ovate, 42-44% of total height; anal canal strongly developed, forming deep, narrow U-shaped groove in labral callus; siphonal canal open, moderate length, posteriorly recurved; outer lip weakly crenulated by primary spiral cords, bearing seven relatively strongly denticles within: D1 (anal denticle) strong, D2 weak, D3 strong, D4-D6 medium strength, D7 strong. Columella deeply excavated in upper third. Columellar callus sharply delimited, adherent, weakly expanded over venter of last whorl; three prominent columellar folds present below mid-aperture and prominent parietal tubercle. Colour pattern preserved consisting of narrow reddish-brown band at periphery and broader band over entire base, colour stronger over primary cords within coloured bands.

Discussion – This species has been placed in the genus *Engina* by authors (Forli & Dell'Angelo, 1995; Brunetti & Della Bella, 2014). However, it should be placed in the genus *Enginella* Monterosato, 1917, as it lacks the radially orientated lirae on the parietal callus present in *Engina* (see Cernohorsky, 1975; Vermeij, 2001, 2004). The rest of the apertural structures are similar to those found in *Engina* (see Landau & Vermeij, 2012, fig. 1).

The protoconch figured by Brunetti & Della Bella (2014, fig. 11E) is multispiral, and identical to that seen in the Estepona specimens, and the colour pattern was also described in Italian shells by Forli & Dell'Angelo, 1995, p. 16).

Specimens from the Atlantic Upper Miocene of north-western France identified as *Cantharus (Pollia) pusilla* by Brébion (1964) are not that species and were described as *Engina brunettii* Landau, Ceulemans & Van Dingenen, 2019. They differ in having a protoconch of only two whorls as opposed to just over three whorls in *E. pusilla*, the spire is less scalate, the teleoconch whorls separated by a shallower suture, and the outer lip denticles are less numerous (5 vs 7). Moreover, the French species is an *Engina* species, with parietal lirae (see Landau *et al.*, 2019, pl. 45, figs 1a, 2a, 3), absent in *Enginella*.

The present day Mediterranean *Enginella leucozona* (Philippi, 1844) differs in having a paucispiral protoconch of only about 1.5 whorls and slightly slenderer profile. It is quite possible that *E. pusilla* lost its mode of planktotrophic development at the end of the Pliocene and evolved into the direct developing *E. leucozona*.

We are not aware of any molecular data confirming the separation of the genera *Engina* and *Enginella*, but the fact that since at least the Pliocene only *Enginella* has been present in the Mediterranean, whereas *Engina* was present along the European Atlantic frontage supports their separation.

Distribution – Lower Pliocene: central Mediterranean, Italy (Forli & Dell'Angelo, 1995; Chirli, 2000; Brunetti & Della Bella, 2014). Upper Pliocene: western Mediter-

anean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Bellardi, 1873; Brunetti & Della Bella, 2014).

Genus *Pisania* Bivona e Bernardi, 1832

Type species (by subsequent designation; ICZN Opinion 740, 1965) – *Pisania striatula* Bivona e Bernardi, 1832. Present-day, Mediterranean.

- 1832 *Pisania* Bivona e Bernardi, p. 8.
- 1904 *Colubraria (Taeniola)* Dall, p. 137. Type species (by original designation): *Triton decollatus* G.B. Sowerby I, 1833, present-day, Polynesia. Junior homonym of *Taeniola* Pallas, 1760 [Cestoda].
- 1912 *Jeannea* Iredale, p. 220. Type species (by original designation): *Jeannea hedleyi* Iredale, 1912, present-day, Kermadec Is.
- 1929 *Appisania* Thiele, p. 314. Type species (by monotypy): *Pisania montrouzieri* Crosse, 1862, present-day, New Caledonia.
- 1966 *Sukunaia* Cernohorsky, p. 229. Type species (by original designation): *Sukunaia jenningsi* Cernohorsky, 1966, present-day, Fiji.

***Pisania magna* (Foresti, 1868)**

Plate 7, figs 1-3

- *1868 *Pisania maculosa* var. *magna* Foresti, p. 23, pl. 1, figs 6, 7.
- 1868 *Pisania maculosa* var. *subangulata* Foresti, p. 23, pl. 1, figs 8, 9.
- 1872 *Pisania striatula* Bivona – d'Ancona (*partim*), p. 173, pl. 10, figs 2, 3 [*non* Bivona e Bernardi, 1832, = *Pisania striata* (Gmelin, 1791)].
- 1901 *Pisania maculosa* var. *magna* Foresti – Cossmann, p. 164, pl. 6, fig. 18.
- 1904 *Pisania maculosa* var. *pliostratissima* Sacco, p. 58, pl. 14, fig. 64.
- 1997 *Pisania striata* (Gmelin) – Cirone *et al.*, p. 165, pl. 1, figs 11, 12 [*non* *Pisania striata* (Gmelin, 1791)].
- 2006 *Pisania baetica* Lozano-Francisco & Vera-Peláez, p. 109, pl. 2, figs 3-8.
- 2010 *Pisania maculosa magna* Foresti, 1868 – Ceregato *et al.*, p. 62, pl. 2, figs 46-47.
- 2010 *Pisania maculosa subangulata* Foresti, 1868 – Ceregato *et al.*, p. 62, pl. 2, figs 46-47.
- 2016 *Pisania magna* (Foresti, 1868) – Brunetti & Della Bella, p. 19, figs 11A-G.

Material and dimensions – Maximum height 20.2 mm, width 11.6 mm. CO: NHMW 2023/0323/0016-0018 (3), NHMW 2023/0323/0019 (9), RGM.1404368 (2).

Description – Shell small to medium-sized, ovate-fusiform. Protoconch and early teleoconch whorls abraded. Four teleoconch whorls preserved. Spire whorls convex

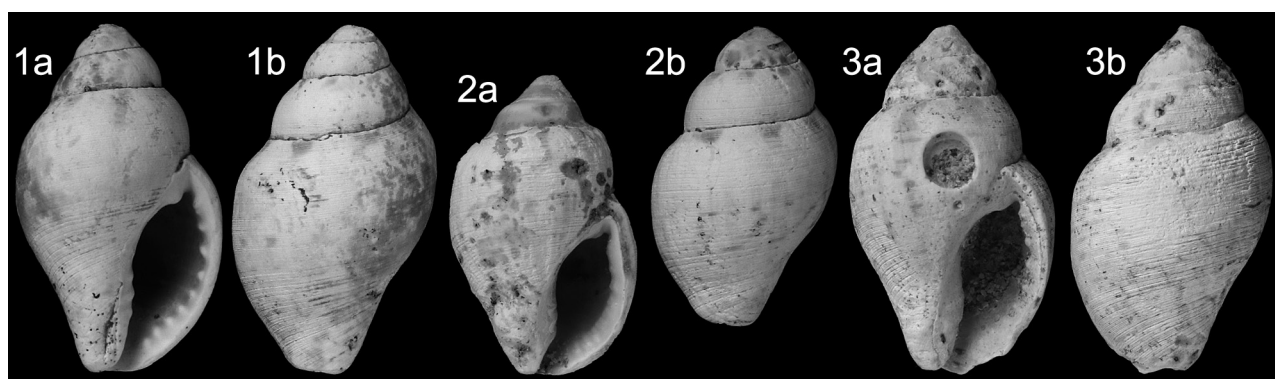


Plate 7. *Pisania magna* (Foresti, 1868); 1. NHMW 2023/0323/0016, height 20.0 mm, width 11.4 mm; 2. NHMW 2023/0323/0017, height 20.0 mm, width 12.3 mm; 3. NHMW 2023/0323/0018, height 18.6 mm, width 10.5 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

with periphery at abapical suture, penultimate whorl roundly shouldered in some specimens. Sculpture restricted to extremely fine, crowded spiral threads. Last whorl 79–83% of total height, roundly shouldered to evenly rounded, weakly constricted at base, entire surface covered in subequal fine spiral threads, slightly stronger and wider over base and fasciole; siphonal fasciole not delimited. Aperture 47–52% of total height, anal sinus deeply and narrowly notched; siphonal canal moderately short, narrow, bent to left, open; outer lip bearing 8–9 small denticles within, D1 slightly stronger, D1 and D2 fused in some specimens. Columella broadly excavated mid-aperture. Columellar callus narrow, weakly thickened, bearing three folds below mid-whorl and stout parietal tooth. Colour pattern of red blotches just below suture on last whorl preserved in some specimens.

Discussion – In their review of the genus in the Pliocene of Italy, Brunetti & Della Bella (2016) separated *Pisania magna* (Foresti, 1868) from the Lower Pliocene to present-day Mediterranean *P. striata* (Gmelin, 1791) most importantly by the character of its very fine spiral sculpture. The whorls tend also to be more rounded, and there are more numerous teeth within the outer lip that tend to be lyrate rather than denticulate. Specimens from Estepona concur closely to the species concept of *P. magna*, as suggested by Brunetti & Della Bella (2016), also Foresti's var. *subangulata* is present (Pl. 7, fig. 2). Lozano-Francisco & Vera-Peláez (2006) erected the taxon *Pisania baetica* for this species from Estepona. Their species description and discussion highlights the differences between these Estepona specimens and *P. striata*, so that *P. baetica* is clearly a subjective junior synonym of *P. magna*.

Distribution – Lower Pliocene: central Mediterranean, Italy (Foresti, 1868; Sacco, 1904; Brunetti & Della Bella, 2016). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Lozano-Francisco & Vera-Peláez, 2006); central Mediterranean, Italy (Brunetti & Della Bella, 2016).

Pisania plioangustata (Sacco, 1904)

Plate 8, figs 1–4

- *1904 *Pisania maculosa* var. *plioangustata* Sacco, p. 58, pl. 14, fig. 64.
- 2000 *Pisania striata* (Gmelin, 1791) – Chirli (*partim*), p. 57, pl. 25, figs 11, 12 [*non Pisania striata* (Gmelin, 1791)].
- 2006 *Pisania plioalboranensis* Lozano-Francisco & Vera-Peláez, p. 108, pl. 2, figs 15, 16.
- 2013 *Pisania striata* (Gmelin, 1791) – Landau *et al.*, p. 168, pl. 25, figs 8, 9, pl. 64, fig. 7 [*non Pisania striata* (Gmelin, 1791)].
- 2016 *Pisania plioangustata* (Sacco, 1904) – Brunetti & Della Bella, p. 18, figs 10A–G.

Material and dimensions – Maximum height 32.5 mm, width 15.3 mm. **CO:** NHMW 2023/0323/0020–0023 (4), NHMW 2023/0323/0024 (7), RGM.1404367 (2).

Description – Shell medium-sized, fusiform. Protoconch not preserved. Teleoconch consisting of six whorls separated by superficial linear suture. First three teleoconch whorls broadly conical, weakly convex, with periphery at abapical suture, bearing about 15 prosocline rounded ribs, wider than their interspaces, overrun by three narrow spiral cords. At end of third whorl axial sculpture rapidly weakens, spirals become irregular with secondary threads intercalated, so that last three whorls sculptured by fine irregular spiral cords and threads of roughly alternating strength. Last three whorls with weak concavity below suture in area of subsutural ramp, increasingly convex below. Last whorl 75–77% of total height, weakly concave below suture to non-delimited shoulder, convex below, moderately constricted at base; surface entirely covered in fine spiral cords and threads and several conspicuous growth halts or varices; siphonal fasciole relatively long, broad, weakly rounded, bearing slightly stronger cords. Aperture ~50% of total height; anal sinus forming prominent notch; siphonal canal moderate length, wide, bent to left, open; outer lip bearing 11–13 weak, lyrate denticles within, D1 slightly stronger. Colu-

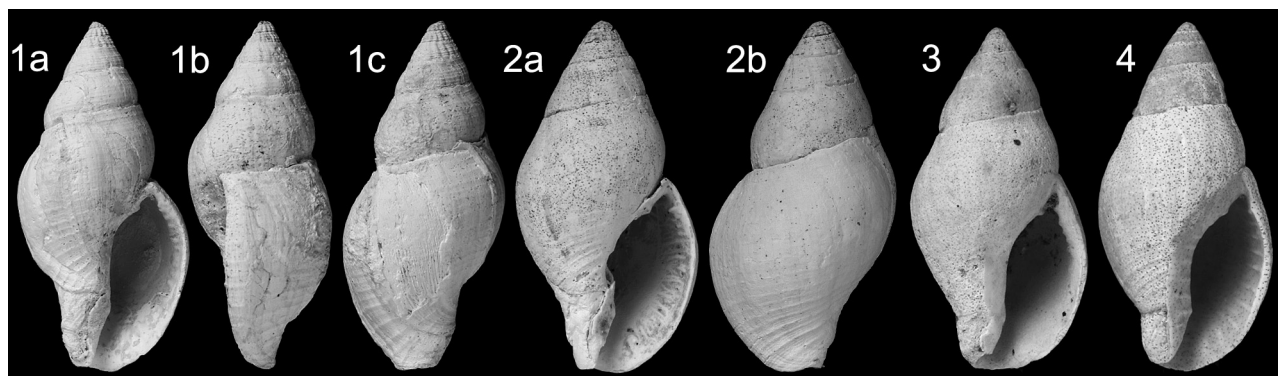


Plate 8. *Pisania plioangustata* (Sacco, 1904); 1. NHMW 2023/0323/0020, height 32.5 mm, width 15.0 mm; 2. NHMW 2023/0323/0021, height 30.1 mm, width 14.8 mm; 3. NHMW 2023/0323/0022, height 29.3 mm, width 14.0 mm; 4. NHMW 2023/0323/0023, height 27.2 mm, width 12.8 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

mella broadly excavated mid-aperture. Columellar callus narrow and weakly thickened in abapical half, thin and poorly delimited adapically, bearing irregular folds below mid-aperture in some specimens, along entire length in others and small parietal tooth.

Discussion – The specimens from Estepona agree closely with the description for the species given by Brunetti & Della Bella (2016, p. 18). The number of ribs and cords on the first three teleoconch whorls are similar. The Italian specimens figures also show the numerous lyrate denticles within the outer lip and the folds on the columella covering the entire columella in some specimens or restricted to the abapical half in others (2016, figs 10A-F). Unfortunately, the protoconch is not preserved in the Estepona material, but it is multispiral and typical for species with planktotrophic development (2016, fig. 10G). This species was described by Lozano-Francisco & Vera-Peláez (2006) as *Pisania plioalboranensis*, which we consider a subjective junior synonym.

Brunetti & Della Bella (2016) suggested that specimens from the Serravallian Middle Miocene eastern Proto-Mediterranean Karaman Basin of Turkey illustrated by Landau *et al.* (2013, pl. pl. 25, figs 8, 9, pl. 64, fig. 7) as *Pisania striata* (Gmelin, 1791) might represent *P. plioangustata*. Both have a similar protoconch, profile, and teleoconch sculpture, although we note that the axial ribs extend slightly further over the teleoconch in the Turkish specimens. Nevertheless, we accept this synonymy.

Pisania plioangustata (Sacco, 1904) differs from *P. striata* (Gmelin, 1791) in its more elongated fusiform profile and in the character of the sculpture, composed of thicker cords in *P. striata*. *Pisania magna* (Foresti, 1868) differs in its squatter profile, even finer sculpture and in having fewer and stouter denticles within the outer lip.

Distribution – Middle Miocene: eastern Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.*, 2013). Lower Pliocene: central Mediterranean, Italy (Sacco, 1904; Brunetti & Della Bella, 2016). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Lozano-Francisco & Vera-Peláez, 2006).

Pisania striata (Gmelin 1791)

Plate 9, figs 1-3

- *1791 *Voluta striata* Gmelin, p. 3255.
- 1791 *Voluta syracusana* Gmelin, p. 3456.
- 1822 *Buccinum maculosum* Lamarck, p. 269.
- 1826 *Purpura variegata* Risso, p. 167 (*non* Röding, 1798).
- 1829 *Purpura variegata* Schubert & Wagner, p. 148 (*non* Röding, 1798).
- 1832 *Pisania striatula* Bivona e Bernardi, p. 11, pl. 2, fig. 6.
- 1832 *Voluta Gualtierii* Scacchi, p. 1 [unnumbered].
- 1866 *Buccinum maculosum* Sow. (*non* Linn.) – Pereira da Costa, p. 116, pl. 16, fig. 20.
- 1872 *Pisania striatula* Bivona – d'Ancona (*partim*), p. 173, pl. 10, fig. 4.
- 1900 *Pisania maculosa* var. *elongata* Pallary, p. 268.
- 1900 *Pisania maculosa* var. *obesa* Pallary, p. 268, pl. 7, fig. 11.
- 1904 *Pisania maculosa* (Lk.) – Sacco, p. 58, pl. 14, fig. 62.
- 1904 *Pisania maculosa* var. *plio brevis* Sacco, p. 58, pl. 14, fig. 63.
- 1912 *Pisania maculosa* var. *trigonostoma* Pallary, p. 91, pl. 15 [1], fig. 38.
- 1963 *Pisania (Pisania)* cfr. *maculosa* (Lk.) – Venzo & Pelosio, p. 94, pl. 35, fig. 16.
- 1965 *Pisania (Pisania) maculosa* (L.) – Ruggieri & Greco, p. 53, pl. 2, fig. 4.
- ?1974 *Pisania (Pisania) maculosa* (Lamarck, 1822) – Malatesta, p. 313, pl. 25, fig. 6.
- 1991 *Pisania striata* (Gmelin, 1791) – Poppe & Goto, p. 148, pl. 30, fig. 3.
- 1992 *Pisania striata* (Gmelin, 1791) – Cavallo & Repetto, p. 100, fig. 224.
- 2000 *Pisania striata* (Gmelin, 1791) – Chirli (*partim*), p. 57, pl. 25, figs 13, 14.
- 2003 *Pisania striata* (Gmelin, 1791) – Giannuzzi-Savelli *et al.*, p. 160, figs 299-310.
- 2016 *Pisania striata* (Gmelin, 1791) – Brunetti & Della Bella, p. 16, figs 8A-F.

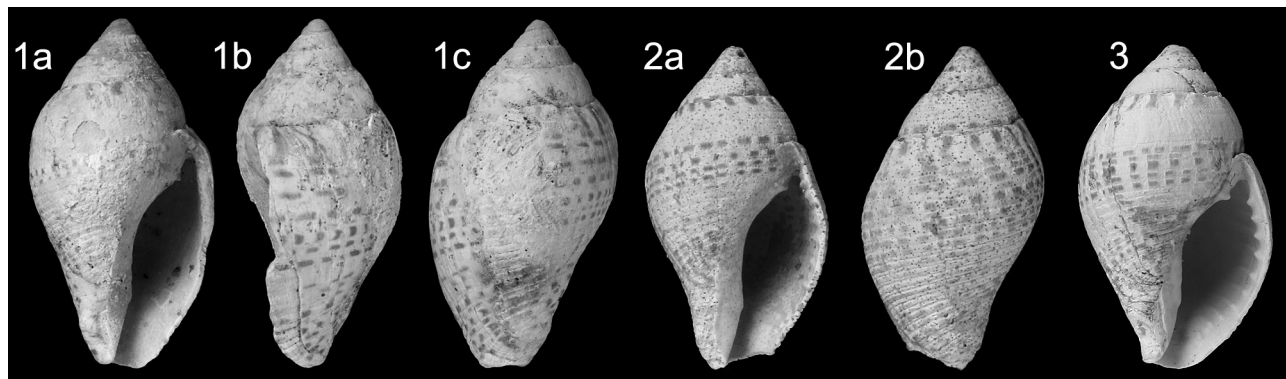


Plate 9. *Pisania striata* (Gmelin 1791); 1. NHMW 2023/0323/0025, height 28.4 mm, width 14.7 mm; 2. NHMW 2023/0323/0026 (juvenile), height 19.4 mm, width 10.3 mm; 3. NHMW 2023/0323/0064 (subadult), height 22.2 mm, width 12.6 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

non 1997 *Pisania striata* (Gmelin) – Cirone *et al.*, p. 165, pl. 1, figs 11, 12 [= *Pisania magna* (Foresti, 1868)].

non 2013 *Pisania striata* (Gmelin, 1791) – Landau *et al.*, p. 168, pl. 25, figs 8, 9, pl. 64, fig. 7 [= *Pisania plioangustata* (Sacco, 1904)].

Material and dimensions – Maximum height 28.4 mm, width 14.7 mm. **CO:** NHMW 2023/0323/0025-0026 (2), NHMW 2023/0323/0064 (1), RGM.1404369 (2).

Description – Shell medium-sized, ovate-fusiform. Protoconch and early teleoconch whorls abraded. Five teleoconch whorls preserved. Spire whorls low, convex, with periphery at abapical suture. Sculpture of flattened cords of alternating strength covers entire surface. Last whorl ~80% of total height, roundly shouldered, weakly constricted at base; siphonal fasciole weakly delimited. Aperture ~60% of total height, anal sinus deeply and narrowly notched; siphonal canal moderate length, wide, straight, open; outer lip bearing about ten lyrate denticles within, D1 slightly stronger. Columella broadly and shallowly excavated mid-aperture. Columellar callus narrow, weakly thickened, bearing well developed parietal fold. Colour pattern of elongated red dots over primary cords preserved.

Discussion – The Estepona material is scant, represented by one subadult and one juvenile. Nevertheless, they agree in profile, sculpture, and colour pattern with *Pisania striata* (Gmelin 1791). As with *P. plioangustata* (Sacco, 1904), early whorls of extant specimens are costate (see Brunetti & Della Bella, 2016, fig. 8E-F). However, in all fossil material seen the early whorl surface is abraded. The Italian fossil specimens illustrated by those authors (2016, figs 8B, D) illustrate the same colour pattern preserved in the Estepona specimens.

The oldest confirmed record for the species is that of Pereira da Costa (1866) for the Atlantic Tortonian of Cacela, Portugal. Specimens at hand from that locality (NHMW coll.) confirm the identification.

Distribution – Upper Miocene: Atlantic, Cacela, Portugal (Pereira da Costa, 1866); central Mediterranean, Italy

(Venzo & Pelosio, 1963). Lower Pliocene: central Mediterranean, Italy (Sacco, 1904; Chirli, 2000; Brunetti & Della Bella, 2016). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1904; ?Malatesta, 1974; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Ruggieri & Greco, 1965). Present-day: Mediterranean (Poppe & Goto, 1991; Giannuzzi-Savelli *et al.*, 2003). Today this is an intertidal species, or just below the tideline, found on rocky shores (Poppe & Goto, 1991, p. 149).

Family Tudicidae Cossmann, 1901

Genus *Euthria* Gray, 1850

Type species (by subsequent designation; Petit, 2012) – *Murex corneus* Linnaeus, 1758. Present-day, Mediterranean.

1850 *Euthria* Gray, p. 67.

Note – Some of the new species described herein (*i.e.*, *Euthria pliovirginea* nov. sp. and *E. onubensis* nov. sp.) and *Euthria virginea* (Grateloup, 1833) (see Harzhauser & Landau, 2024) approximate in shell features to the antipodean genus *Aeneator* Finlay, 1926 [Type species by original designation (Finlay, 1926, p. 414): *Verconella marshalli* Murdoch, 1924, Pliocene New Zealand] also placed in the family Tudicidae. They have angular spire whorls, a relatively thin outer lip, deep anal notch, rather broad columellar callus that also extends along the siphonal canal, and a longer siphonal canal than usual for *Euthria*. We do not think they are conspecific with that genus but mention it as a possible link between the Mediterranean and Pacific faunas, or more likely a case of convergence.

***Euthria iberoadunca* nov. sp.**

Plate 10, figs 1-6

ZooBank registration – urn:lsid:zoobank.org:act:D662A0B7-EECD-4DFB-8450-FE7922879F3D

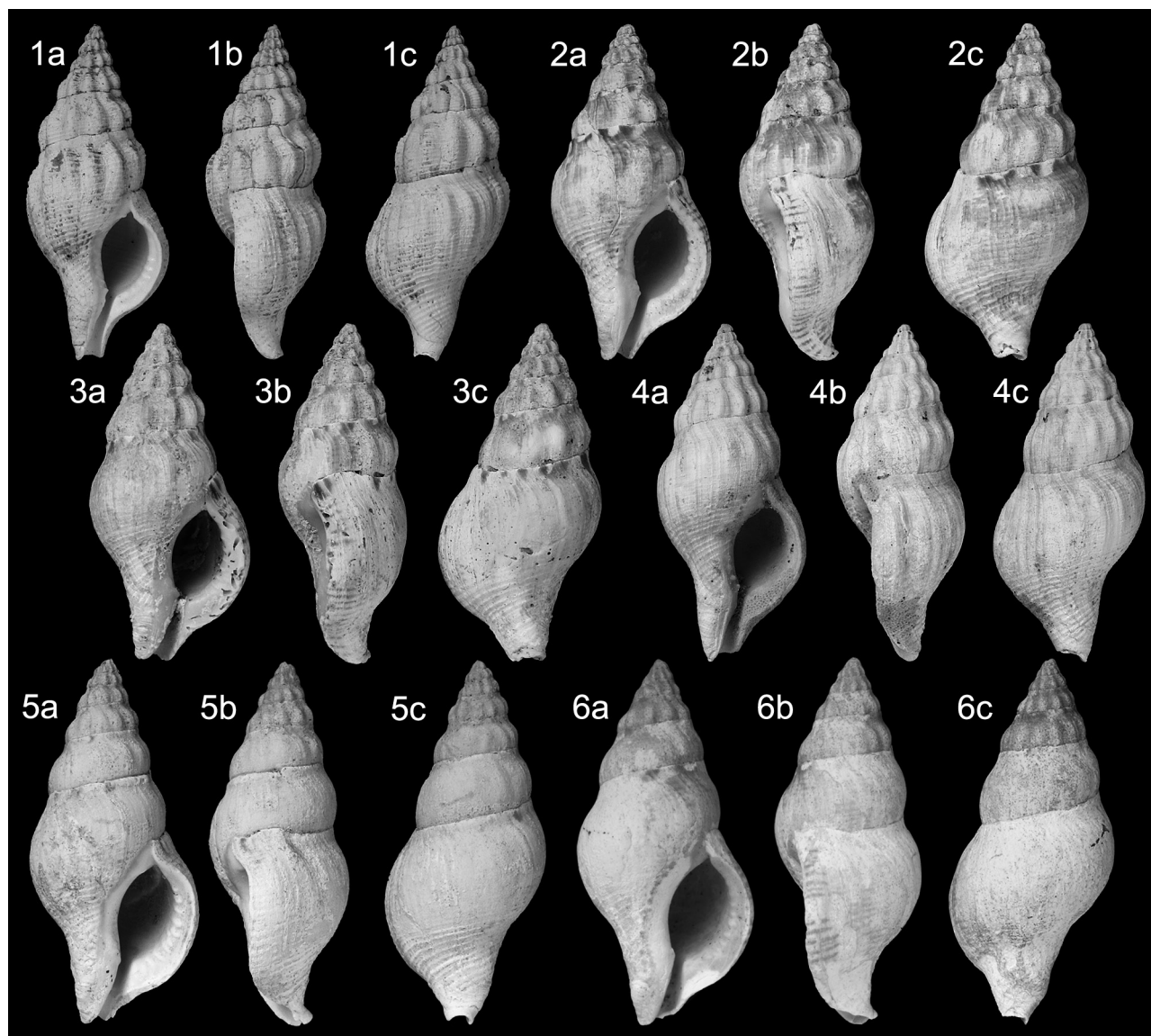


Plate 10. *Euthria iberoadunca* nov. sp.; 1. **Holotype** NHMW 2023/0323/0030, height 37.4 mm, width 14.8 mm; 2. **Paratype 1** NHMW 2023/0323/0031, height 36.0 mm, width 16.1 mm; 3. **Paratype 2** NHMW 2023/0323/0032, height 35.1 mm, width 15.6 mm; 4. **Paratype 3** NHMW 2023/0323/0033, height 39.4 mm, width 16.2 mm; 5. **Paratype 4** NHMW 2023/0323/0041, height 46.3 mm, width 19.9 mm; 6. **Paratype 5** NHMW 2023/0323/0042, height 50.5 mm, width 22.1 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Type material – Holotype NHMW 2023/0323/0030, height 37.4 mm, width 14.8 mm; paratype 1 NHMW 2023/0323/0031, height 36.0 mm, width 16.1 mm; paratype 2 NHMW 2023/0323/0032, height 35.1 mm, width 15.6 mm; paratype 3 NHMW 2023/0323/0033, height 39.4 mm, width 16.2 mm; paratype 4 NHMW 2023/0323/0041, height 46.3 mm, width 19.9 mm; paratype 5 NHMW 2023/0323/0042, height 50.5 mm, width 22.1 mm; paratype 6 RGM.1404372, height 38.9 mm, width 17.7 mm.

Other material – Maximum height 50.5 mm, width 22.1 mm. **CO:** NHMW 2023/0323/0034 (8).

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

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

Etymology – Named reflecting the type locality in the Iberian Peninsula and similarity to *Euthria adunca* (Bronn, 1831). *Euthria*, gender feminine.

Diagnosis – *Euthria* species of medium size, thick shelled, teleoconch of six whorls, sculpture of 11-12 rounded axial ribs fading on the last 1-2 whorls, spiral sculpture very weak, outer lip moderately flared bearing 8-9 small, short denticles within, siphonal canal narrow, medium length.

Description – Shell medium-sized, very solid, fusiform. Protoconch not preserved. Teleoconch of six convex

whorls with very narrow, steep, narrow subsutural ramp, convex below, periphery at abapical suture. Suture weakly impressed, undulating. Axial sculpture of 11-12 rounded axial ribs, roughly equal in width to their interspaces, narrow and weak over subsutural ramp, broadening towards abapical suture, fading on last two whorls in gerontic specimens. Spiral sculpture of narrow spiral cords that overruns ribs, with threads of secondary and tertiary strength regularly intercalated. Last whorl 70-72% of total height, slightly concave below suture, rounded at periphery, moderately constricted at base; axial sculpture weakens on last whorl, ribs not covering base and usually absent from last half whorl, although persisting to outer lip in some specimens; siphonal fasciole broad, flattened, not delimited from base. Aperture ~ 45% of total height, ovate; anal canal marked by small, narrow notch; siphonal canal long, open, narrow, bent slightly to left and recurved; outer lip moderately flared, rounded, bearing 8-9 weak denticles within, variably developed. Columella broadly and evenly excavated. Columellar callus narrow, slightly thickened, bearing prominent denticle at upper end of siphonal fasciole, small parietal denticle, denticles and tubercles between these variably developed. Colour pattern of large irregular orange flammules preserved in many specimens.

Discussion – *Euthria iberoadunca* nov. sp. is closely similar to the central Mediterranean Upper Miocene to Pliocene *Euthria adunca* (Bronn, 1831). The differences are subtle, but consistent. The Estepona species is composed of fewer whorls (6 vs. 9-10), slightly lower spired and, most importantly has a considerably shorter siphonal canal. Axial sculpture in the two species is comparable, but fades earlier in most specimens of *E. iberoadunca*, so that the last one or two whorls are more evenly rounded, and not weakly shouldered as they are in *E. adunca*. The spiral sculpture is weaker than *E. adunca*, most notably in the subsutural area and base, the aperture is slightly smaller, and lastly, the labial denticles are short, whereas in *E. adunca* they are lirate (see Brunetti & Della Bella, 2016, figs 5A-F). Unfortunately, the protoconch is not preserved in the Estepona material. That of *E. adunca* is paucispiral, composed of two smooth convex whorls (Brunetti & Della Bella, 2016, fig. 5F).

Specimens from the Middle Miocene Paratethys ascribed to *E. adunca* by authors (e.g., Hoernes & Auinger, 1890; Nikolov, 1994; Bałuk, 1995; Kovács, 2022) are not that species, but a Paratethyan endemic *E. brunettii* Harzhauser & Landau, 2024. That species differs from *E. adunca* in having a multispiral protoconch of about 2.7 whorls vs. 2 in *E. adunca*, and spiral sculpture is weaker and fades earlier in ontogeny. *Euthria brunettii* differs from *E. iberoadunca* in having more convex spire whorls separated by a deeper suture, slightly greater number of axial ribs on early spire whorls, although there is some overlap (12-14 vs. 11-12), the profile of the last whorl is more notably concave at the subsutural ramp and swollen mid-whorl, and the siphonal canal is longer. Specimens identified by Kovács & Vicián (2023, p. 253, fig. 13A) as *E. adunca* represent another Paratethyan endemic *Euthria*

fraussenii Harzhauser & Landau, 2024 that clearly differs from any of the species discussed above, in the very early disappearance of both axial and spiral sculpture, leaving the last four or five whorls totally smooth.

Our works so far on European Neogene basins shows *Euthria* to be a relatively endemic genus (Van Dingenen *et al.*, 2017; Landau *et al.*, 2019; Harzhauser & Landau, 2024; Landau *et al.*, in prep.; *hoc opus*), as would be expected from a group reproducing by direct development. Specimens from the Atlantic Lower Pliocene Guadalquivir Basin of southwestern Spain illustrated as *E. cornea* (Linnaeus, 1758) by Landau *et al.* (2011, pl. 12, fig. 1) and Brunetti & Della Bella (2016, fig 4E) may represent a further species, but unfortunately, we have insufficient material at hand to reach a firm conclusion.

Brunetti & Della Bella (2016, p. 16) are almost certainly correct to separate Lower and Middle Miocene Italian specimens originally described by Sacco (1890) as varieties of *E. adunca*, *E. praecedens* and *E. tauromontis* that are here considered at full species rank.

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

Euthria inflatissima nov. sp.

Plate 11, figs 1-2

ZooBank registration – urn:lsid:zoobank.org:act:CED80848-783C-424E-B277-93B30B1D216F

Type material – Holotype NHMW 2023/0323/0045, height 65.8 mm, width 31.6 mm; paratype 1 NHMW 2023/0323/0054, height 61.6 mm, width 28.6 mm; paratype 2 NHMW 2023/0323/0046, height 50.6 mm, width 24.1 mm; paratype 3 NHMW 2023/0323/0055, height 66.6 mm, width 33.9 mm (siphonal canal and apex incomplete).

Other material – Known from type series only.

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

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

Etymology – Name reflects the very inflated shape of the last whorl. *Euthria*, gender feminine.

Diagnosis – *Euthria* species of large size, axial ribs on first 2-3 teleoconch whorls, last whorl strongly inflated, siphonal canal long, strongly bent, aperture large, expanded outer lip, weakly denticulate, and deeply excavated columella.

Description – Shell medium-sized to large, moderately solid, broad fusiform. Protoconch not preserved. Teleoconch of six convex whorls separated by shallowly impressed linear suture.

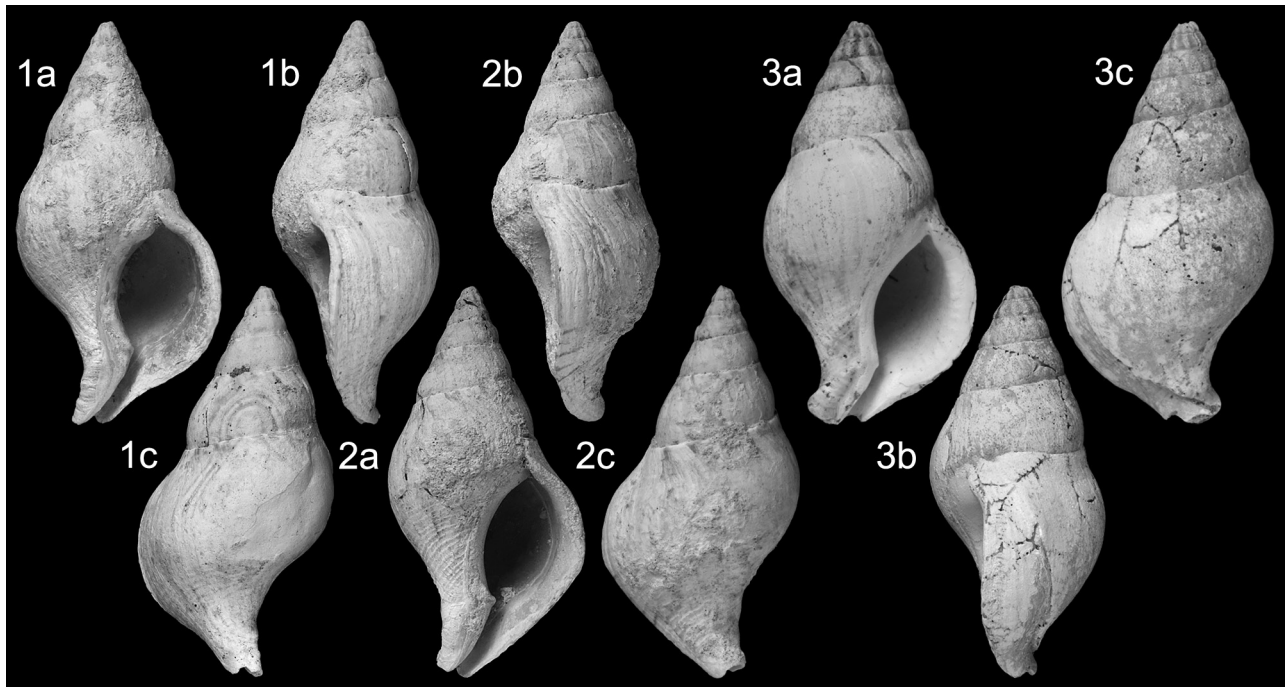


Plate 11. *Euthria inflatissima* nov. sp.; 1. **Holotype** NHMW 2023/0323/0045, height 65.8 mm, width 31.6 mm (small area of repair dorsum right); 2. **Paratype 1** NHMW 2023/0323/0054, height 61.6 mm, width 28.6 mm. 3. **Paratype 2** NHMW 2023/0323/0046, height 50.6 mm, width 24.1 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Early teleoconch whorls weakly convex, bearing about ten prosocline axial ribs, narrower than their interspaces crossed by fine spiral cords. Abapically whorls become more strongly inflated with narrow subsutural concavity, strongly convex below; on second to third whorl axials rapidly weaken and fade, weak spiral sculpture covers entire surface. Last whorl 71-75% of total height, slightly concave below suture, strongly inflated and rounded at periphery, strongly constricted at base; spirals slightly stronger over base; siphonal fasciole broad, rounded, moderately delimited from base. Aperture 47-50% of total height, roundly ovate; anal canal marked by small, narrow notch; siphonal canal long, open, narrow, strongly bent to left and slightly recurved; outer lip expanded, bearing about 12 very weak denticles within, variably developed. Columella broadly, deeply and evenly excavated. Columellar callus narrow, strongly thickened, sharply delimited, bearing prominent denticle at upper end of siphonal fasciole, small parietal pad. Colour pattern of row of small orange blotches just below suture on last two whorls.

Discussion – *Euthria inflatissima* nov. sp. is the largest *Euthria* sp. in the Estepona assemblages and differs from all its congeners in having a strongly inflated last whorl and expanded outer lip, and the siphonal canal very strongly bent to the left. It is most like *Euthria curvirostris* (Gratoloup, 1845) from the Atlantic Middle and Upper Miocene of France in its strongly recurved siphonal canal, but that species is higher spired, axial sculpture disappears even earlier in ontogeny, has more strongly developed, albeit weak, spiral sculpture, and the last

whorl and aperture are not as strongly inflated. Landau *et al.* (2013, p. 165, pl. 25, figs 2, 3, pl. 64, fig. 5, pl. 79, fig. 10) illustrated specimens from the Serravallian Middle Miocene eastern Mediterranean Karaman Basin of Turkey as *E. curvirostris* that on further examination are not conspecific. The Turkish species is thicker shelled, lower spired, spiral sculpture is almost completely absent, and the canal is not as recurved. The taxon *Euthria yesimae* Harzhauser & Landau, 2024 was erected for these Turkish specimens (see Harzhauser & Landau, 2024, p. 91 for further discussion and comparison).

In the Italian Pliocene *Euthria perpiniana* (Fontannes, 1879) originally described from the Mediterranean Pliocene of southern France, but also recognised in the Italian Pliocene assemblages (Brunetti & Della Bella, 2016), is similar in size and also has axial sculpture restricted to the early teleoconch whorls but differs in the characters described. *Euthria plioelongata* (Sacco, 1890) from the Lower Pliocene is smaller and slenderer. *Euthria ceddensis* Brunetti & Della Bella, 2016 differs in having its axial sculpture extending further over the spire, the last whorl, whilst also inflated, is less evenly so, the inflation restricted to mid-whorl and roundly angled at the shoulder and base, and the siphonal canal is less bent.

In the Middle Miocene Paratethys *Euthria odiosa* Harzhauser & Landau, 2024 is similar in having sculpture fade early in ontogeny, but that species is smaller shelled (maximum height 49.9 mm), slenderer, with a taller spire composed of more numerous whorls (8 vs. 6), and the outer lip is not as strongly flared as in the Estepona species resulting in a smaller aperture and more

strongly denticulate/lirate within. *Euthria carpathica* Harzhauser & Landau, 2024, also a Paratethyan endemic, also loses its sculpture early in ontogeny and is composed of a similar number of whorls, but again is slenderer and the aperture lacks the characteristic expansion seen in *Euthria inflatissima*.

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

***Euthria pliovirginea* nov. sp.**

Plate 12, figs 1-4

ZooBank registration – urn:lsid:zoobank.org:act:2CACBAF0-05CD-4C2D-853F-0F376ACDA651

Type material – Holotype NHMW 2023/0323/0060, height 42.3 mm, width 15.0 mm; paratype 1 NHMW 2023/0323/0061, height 44.7 mm, width 16.9 mm; paratype 2 NHMW 2023/0323/0062, height 39.1 mm, width 14.5 mm, **Velerín carretera**; paratype 3 NHMW 2023/0323/0059, height 53.6 mm, width 18.5 mm, **Velerín conglomerates**.

Other material – Maximum height 53.6 mm, width 18.5 mm. **VC**: NHMW 2023/0323/0063 (1).

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

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

Etymology – Name reflecting the resemblance to *Euthria virginea* (Grateloup, 1833). *Euthria*, gender feminine.

Diagnosis – *Euthria* species with slender fusiform shell, low-dome-shaped protoconch of two smooth whorls with first whorl depressed, angular teleoconch whorls with axial sculpture reduced to small, pointed tubercles at shoulder, spiral sculpture very weak, very long, almost straight siphonal canal, moderately expanded outer lip very weakly denticulate within.

Description – Shell medium-sized, relatively solid, slender fusiform. Protoconch low dome-shaped, of two smooth, convex whorls, first whorl somewhat flattened. Transition to teleoconch marked by prosocline scar. Teleoconch of six angular whorls, with broad concave subsutural ramp delimited by slightly strengthened shoulder cord; shoulder forming periphery placed at about one-quarter to one-third whorl height, whorl profile straight below, tapering inwards to suture. Suture narrowly impressed, linear. Sculpture of axial ribs most marked on first teleoconch whorl forming pointed tubercles at shoulder and fading over subsutural ramp and below shoulder. Abapically ribs subobsolete, represented by 10-11 small, pointed tubercles at shoulder. Spiral sculpture weak, numerous fine cords of alternating strength covering entire surface, fading abapically. Last whorl about 75% of total

height, with broad concave subsutural ramp delimited by weak shoulder cord, rounded below, strongly constricted at base; shoulder tubercles weaken towards aperture, obsolete on last half whorl in some specimens, primary spirals slightly stronger over base and fasciole; siphonal fasciole flattened, not delimited from base. Aperture ~ 60% of total height, ovate; anal canal marked by small, narrow notch; siphonal canal extremely long, open, narrow, straight or slightly bent, not recurved; outer lip moderately flared, rounded, very weakly denticulate within. Columella broadly excavated. Columellar callus moderate width, thickened, smooth except for small to subobsolete denticle at upper end of siphonal fasciole and small parietal denticle.

Discussion – *Euthria pliovirginea* nov. sp. belongs within the *E. virginea* species group characterised by their slender fusiform shells and very long siphonal canals. As discussed by Harzhauser & Landau (2024, p. 85) there is enormous confusion in the literature surrounding *Fusus virgineus* Grateloup, 1833 due to: 1) its traditional placement in the genus *Euthriofusus* Cossmann, 1901 (Tudicidae), 2) the poor illustration of the species by Grateloup (1845) that lead to 3) most illustrated specimens identified as *Euthriofusus virgineus* coming from Middle Miocene Paratethyan deposits (e.g., Hörnes, 1853; Hoernes & Auinger, 1890; Bałuk, 1995; Schultz, 1998; Kovács & Vicián, 2023; *inter alia*), which was shown not to be that species but *Euthria stuetzii* (Naumann, 1852) (see Harzhauser & Landau, 2024, p. 82). Indeed, the only reliable illustration of Grateloup's species is that of Peyrot (1928, pl. 8, figs 7-8).

Harzhauser & Landau (2024) revised generic placement of the *Fusus virgineus* species group and argued for their placement within the genus *Euthria* Gray, 1850. Within this group, *Euthria virginea* from the Serravallian of Salles (France) is slenderer than *E. pliovirginea* with a taller spire and convex whorls in which the shoulder is poorly delimited. *Euthria stuetzii* from the Middle Miocene Paratethys is more similar to the Estepona species in having small spinous tubercles at the shoulder in some specimens, but differs in being larger, more solid, the whorls are less angled at the shoulder and the ribs are more numerous and persist longer, forming more numerous tubercles at the shoulder. As discussed by Harzhauser & Landau (2024), *Euthria stuetzii* (Naumann, 1852) is highly reminiscent of the extant *Euthriostoma saharicum* (Locard, 1897) from western Africa, which differs mainly in its strongly shouldered whorls, the smooth inner lip and the wider siphonal canal. *Euthriostoma* Marche-Marchad & Brébion 1977 [type species *Euthriostoma gliberti* Marche-Marchad & Brébion, 1977 = *Euthriostoma saharicum* (Locard, 1897)] is probably a junior synonym of *Euthria*, but we refrain from formally synonymising the two until molecular data is available.

Euthria anatolica (Toula, 1901), from the Serravallian of the Karaman Basin is also similar in shape and in forming sharp tubercles at the shoulder, but again is bigger and thicker shelled than the Estepona species and differs

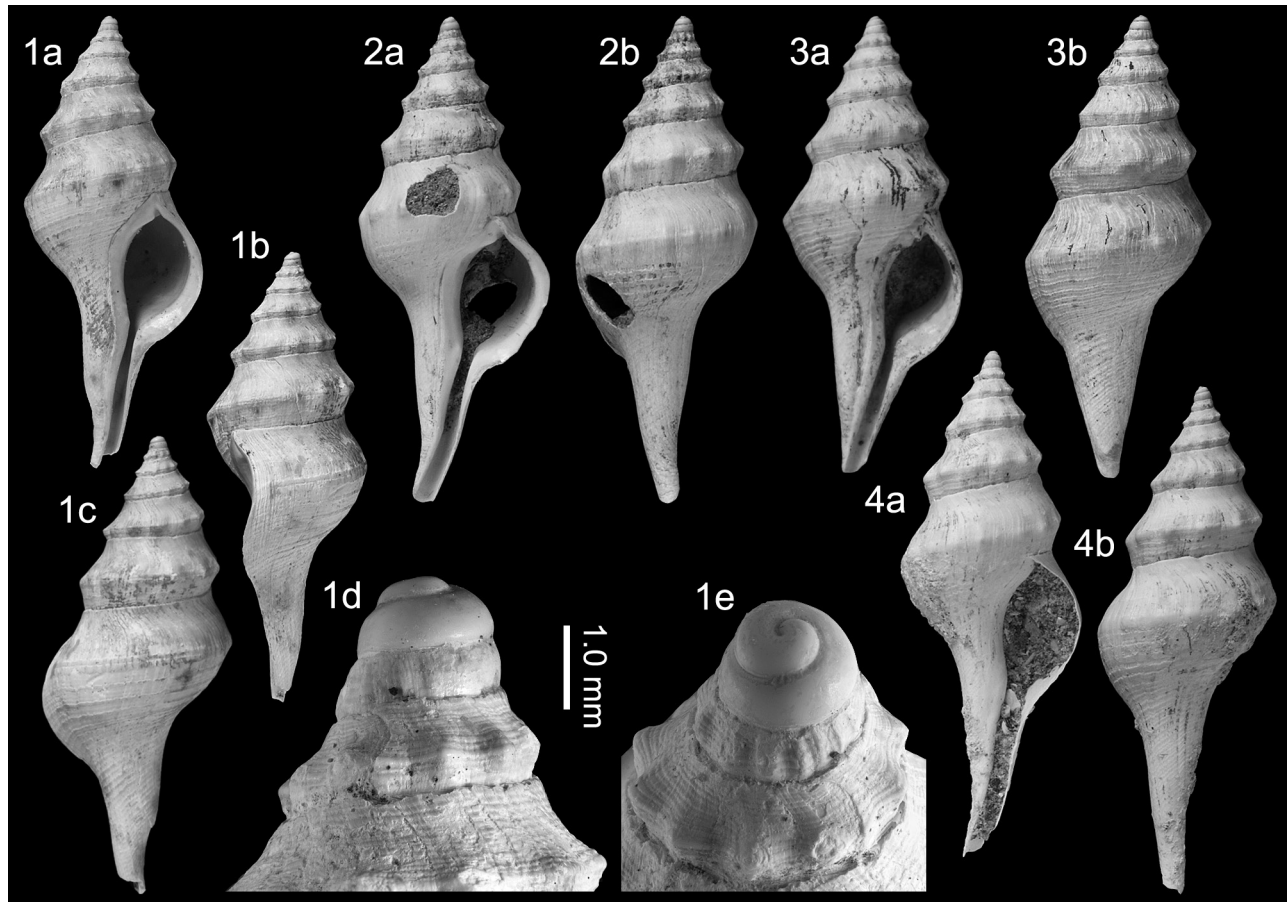


Plate 12. *Euthria pliovirginea* nov. sp., 1. **Holotype** NHMW 2023/0323/0060, height 42.3 mm, width 15.0 mm; 2. **Paratype 1** NHMW 2023/0323/0061, height 44.7 mm, width 16.9 mm; 3. **Paratype 2** NHMW 2023/0323/0062, height 39.1 mm, width 14.5 mm, Velerín carretera. 4. **Paratype 3** NHMW 2023/0323/0059, height 53.6 mm, width 18.5 mm, Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

in its even longer siphonal canal and in the character of its protoconch that is not depressed. The Turkish species often forms a double row of spines at the shoulder, not see in *E. pliovirginea* (see Landau *et al.*, 2013 for further discussion).

A further species in this group from the Atlantic Lower Pliocene Guadalquivir Basin assemblages of southwestern Spain was illustrated by Landau *et al.* (2011, pl. 14, figs 7-8) as *Euthriofusus* cf. *virgineus* and is described at *Euthria onubensis* nov. sp. herein. For comparison see under that species.

We note that despite being uncommon in Estepona, almost all specimens of *E. pliovirginea* (except for one) come from the deeper water deposits of Velerín carretera, as opposed to all its congeners that are found only in the shallower water deposits. Indeed, this and *Kanamarua ducoi* nov. sp. are the only species in the families covered in this monograph to be found in the deeper water deposits.

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

***Euthria pouweri* nov. sp.**

Plate 13, figs 1-5

ZooBankregistration—urn:lsid:zoobank.org:act:9AE3AE40-EF4F-49AD-93D9-29273A5D1243

Type material – Holotype NHMW 2023/0323/0035, height 24.6 mm, width 12.0 mm; paratype 1 NHMW 2023/0323/0036, height 29.0 mm, width 13.2 mm; paratype 2 NHMW 2023/0323/0037, height 30.4 mm, width 14.0 mm; paratype 3 NHMW 2023/0323/0038, height 27.8 mm, width 12.9 mm; paratype 4 NHMW 2023/0323/0039, height 21.7 mm, width 11.7 mm; paratype 5 RGM.1404371, height 19.5 mm, width 10.2 mm.

Other material – Maximum height 31.5 mm, width 14.9 mm. **CO:** NHMW 2023/0323/0040 (24).

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

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

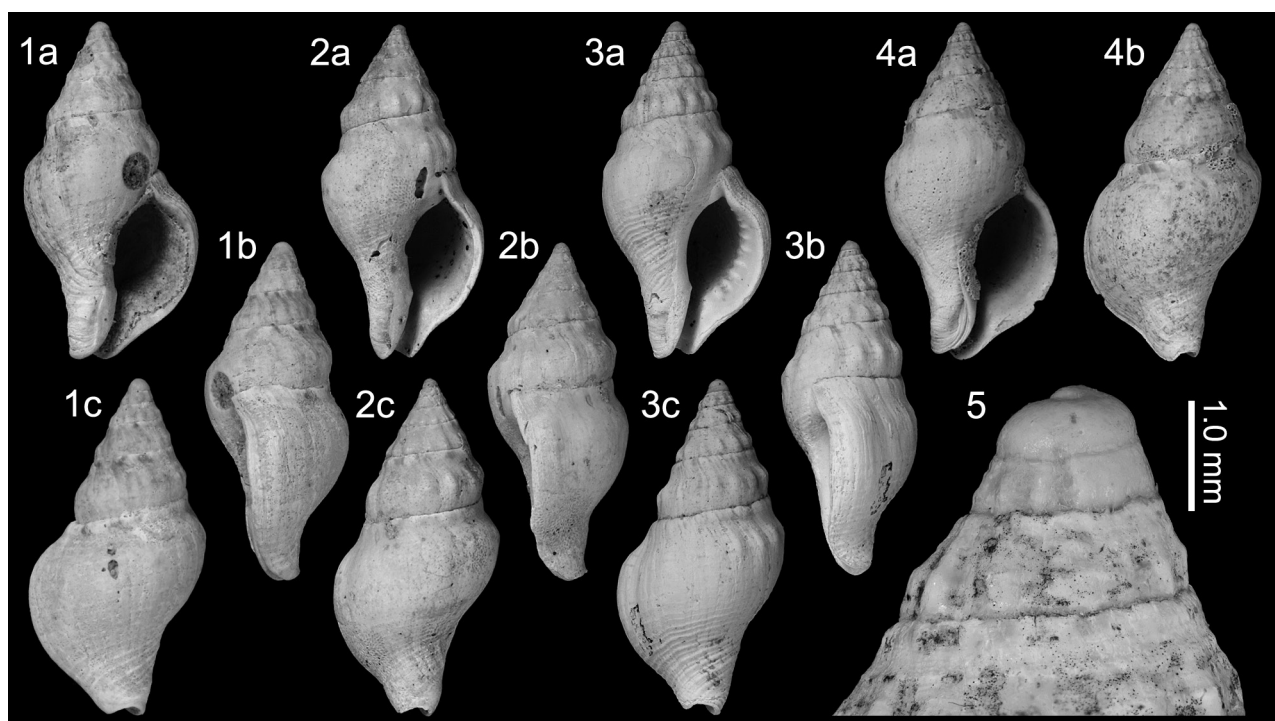


Plate 13. *Euthria pouweri* nov. sp.; 1. **Holotype** NHMW 2023/0323/0035, height 24.6 mm, width 12.0 mm; 2. **Paratype 1** NHMW 2023/0323/0036, height 29.0 mm, width 13.2 mm; 3. **Paratype 2** NHMW 2023/0323/0037, height 30.4 mm, width 14.0 mm; 4. **Paratype 3** NHMW 2023/0323/0038, height 27.8 mm, width 12.9 mm; 5. **Paratype 4** NHMW 2023/0323/0039, height 21.7 mm, width 11.7 mm. Velerín conglomerates, Velerín, Estepona, Lower Piacenzian, Upper Pliocene.

Etymology – Named after Ronald Pouwer, Collection Manager Cainozoic Mollusca at the Naturalis Biodiversity Center (Leiden) and Production Editor of Cainozoic Research in recognition of his work and skill in making these publications so aesthetically pleasing as well as scientifically meaningful. *Euthria*, gender feminine.

Diagnosis – *Euthria* species of small size, low dome-shaped protoconch of two whorls, teleoconch whorls bearing 12–13 ribs developing tubercles at shoulder, usually fading on first half of last whorl, last whorl shouldered, aperture small, outer lip with 10–11 relatively strong lyrate denticles, columella relatively shallowly excavated, and siphonal canal moderately short.

Description – Shell medium-sized, very solid, relatively squat fusiform. Protoconch depressed dome-shaped, of 2.1 smooth convex whorls with medium sized nucleus. Junction with teleoconch delimited by beginning of axial sculpture. Teleoconch of six whorls separated by narrowly impressed, linear or weakly undulating, weakly oblique. First three whorls low, with very broad, weakly concave subsutural ramp, shouldered short distance above suture, bearing 12–13 broad, low, rounded ribs, subobsolete over subsutural ramp, somewhat tubercular at shoulder, stronger below; spiral sculpture restricted to fine threads over entire surface. Last two increasingly oblique suture resulting in increased whorl height and more of whorl below shoulder exposed. Axial ribs fade abapically and disappear in most specimens at some stage after third whorl, but remain devel-

oped to the outer lip in some specimen. Last whorl ~ 73% of total height, strongly concave subsutural ramp, roundly angled at shoulder, convex below, moderately strongly constricted at base; axial sculpture present or absent, when present only developed as axially elongated tubercles at shoulder, spiral sculpture very weak, slightly stronger over fasciole; siphonal fasciole broad, flattened, not delimited from base. Aperture ~ 48% of total height, ovate; anal canal marked by small notch; siphonal canal moderately long, open, narrow, bent slightly to left and recurved; outer lip concave below subsutural ramp, roundly angled at shoulder, bearing 10–11 weak lyrate denticles within, variably developed. Columella broadly and evenly excavated. Columellar callus narrow, slightly thickened, bearing fold at upper end of siphonal canal, small parietal pad without denticle. Colour pattern preserved in some specimens consisting of row of small red blotches over subsutural ramp.

Discussion – *Euthria pouweri* nov. sp. is highly variable in sculpture; some specimens with the first three whorls weakly ribbed and almost smooth later whorls, whereas in others the ribs continue developed to the outer lip represented as elongated tubercles at the shoulder. As with other *Euthria* species, denticulation within the outer lip is variable, but always weak and lyrate.

The present-day *Euthria cornea* (Linnaeus, 1758) differs by its smaller protoconch (1.5 whorls), the transition to the teleoconch is marked by the start of the teleoconch sculpture of 5 or 6 fine spiral cords, the more convex upper spire whorls (instead of shouldered), and the greater

number (16 or more) of internal lirae (lyrate denticles) within the aperture.

The Estepona species seems most similar to the Upper Miocene Tortonian *E. nodosa* Bellardi, 1873 in being relatively small and having elongated tubercles developed at the shoulder. However, that species seems to be slenderer and has a longer siphonal canal, and the tubercles are well developed on all whorls (which happens in the occasional Estepona specimen). Unfortunately, the Italian species was not illustrated by Ferrero-Mortara *et al.* (1981), we have no information regarding its variability, and the specimen illustrated by Montanaro (1935, pl. 6, fig. 17) represents a juvenile. Nevertheless, the rather squat profile typical for the Estepona species is quite different from that of Bellardi's species. In the Atlantic Middle Miocene Serravallian of the Loire Basin *E. turoniensis* Peyrot, 1938 is similar in size and profile, but less solid, and has stronger and more numerous ribs that persist onto the last whorl in all specimens. *Euthria palumbensis* Van Dingenen, Ceulemans & Landau, 2017 from the Lower Pliocene of NW France is also similar in size, but slenderer, with stronger axial and spiral sculpture, and a smaller aperture. None of the Miocene Paratethyan *Euthria* species are closely similar to *E. pouweri*; *Euthria zboroviensis* Friedberg, 1912, from the Middle Miocene of Ukraine and Hungary is somewhat similar but differs in its smaller size and squatter shape (see Kovács & Vicián 2023 p. 254, figs 13J-N; Harzhauser & Landau, 2024, figs 47A-B).

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

Euthria sp.

Plate 14, fig. 1

Material and dimensions – Height 39.5 mm, width 17.6 mm. **EL:** NHMW 2023/0323/0047 (1).

Description – Shell medium-sized, very solid, fusiform. Protoconch not preserved. Teleoconch of six whorls, decreasing in convexity abapically, separated by superficial linear suture. Early whorls bearing ten rounded ribs, roughly equal in width to their interspaces, widening towards abapical suture. On second half of fourth whorl ribs weaken rapidly and disappear. Spiral sculpture of fine cords very weak (partly abraded). Last whorl 70% of total height, evenly rounded at periphery, moderately constricted at base; spirals slightly stronger over base and fasciole; siphonal fasciole flattened, not delimited from base. Aperture 45% of total height, ovate; anal canal marked by small, narrow notch; siphonal canal moderate length, open, narrow, bent slightly to left and recurved; outer lip rounded, bearing 12 weak lyrate denticles within. Columella broadly and evenly excavated. Columellar callus narrow, slightly thickened, bearing prominent denticle at upper end of siphonal fasciole, weak parietal pad.

Discussion – Unfortunately, this species is represented by a single specimen with its surface sculpture abraded. It is

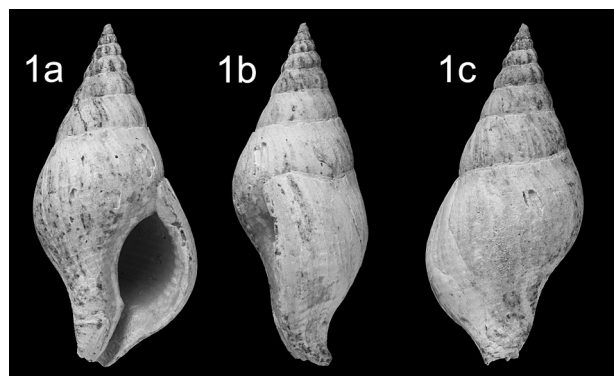


Plate 14. *Euthria* sp.; 1. NHMW 2023/0323/0047, height 39.5 mm, width 17.6 mm. El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

reminiscent of *Euthria plioelongata* (Sacco, 1890) from the Zanclean Lower Pliocene of Italy, but in that species, there is a poorly delimited, but distinct, subsutural concavity, absent in the Estepona species, and the axial ribs do not extend as far down the teleoconch (see Brunetti & Della Bella, 2016, figs 2A-E). In the character of the last two whorls in which the suture is very superficial and there is no subsutural ramp, it is similar to the Italian Upper Miocene Tortonian *E. patula* Bellardi, 1873, but that species is squatter, with a lower spire. Interestingly, *E. patula* may occur in the Bizcornil assemblage (San Pedro de Alcantara, Estepona) (NHMW coll.). This locality was considered Lower Pliocene by Guerra Merchán *et al.* (2002, p. 34). It lies about 14 km east of Velerín and has not been extensively sampled by our team, and therefore material from this locality is not included in this Estepona series and needs deeper study. Some of the Miocene Paratethyan species need to be compared. *Euthria depressospira* Bandat, 1943 has a similarly shaped last whorl, but as its trivial name would suggest, is characterised by its low spire. *Euthria odiosa* Harzhauser & Landau, 2024 is also similar in the character of the last whorl and sculpture fades on the fourth whorl in both species. However, the spire is more acute in the Estepona species.

We await further material to better characterise this species and leave it in open nomenclature.

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

Euthria lucenica nov. sp.

Plate 15, figs 1-4

- 2011 *Euthria cornea* (Linnaeus, 1758) – Landau *et al.*, p. 24, pl. 12, fig. 1 [*non Euthria cornea* (Linnaeus, 1758)].
- 2016 *Euthria* sp. – Brunetti & Della Bella, p. 12, fig. 4E.
- 2022 *Euthria* sp. – Brunetti, p. 50, fig. 77.

ZooBank registration – urn:lsid:zoobank.org:act:77C2B688-3B57-4B14-97C1-D351AD8A83D2

Type material – Holotype NHMW 2010/0054/0108, height 52.0 mm, width 25.9 mm; paratype 1 NHMW 2023/0323/0069, height 47.1 mm, width 22.3 mm; paratype 2 NHMW 2023/0323/0070, height 48.3 mm, width 23.1 mm; paratype 3 NHMW 2023/0323/0071, height 34.8 mm, width 16.5 mm.

Other material – Maximum height 52.0 mm, width 25.9 mm. NHMW 2023/0323/0071 (3).

Type locality – Lucena del Puerto, Huelva, Spain.

Type stratum – Arenas de Huelva Formation, Zanclean, Lower Pliocene.

Etymology – Named after the type locality of Lucena del Puerto, Huelva. *Euthria*, gender feminine.

Diagnosis – *Euthria* species with broad fusiform shell, six teleoconch whorls, spire whorls bearing ten ribs that weaken adapically forming broad tubercles at periphery, spiral sculpture weak, last whorl somewhat inflated, tubercles fade on entire to last half whorl, outer lip denticles weak, siphonal canal medium length.

Description – Shell medium sized, relatively solid and

broad fusiform; apical angle 48.5–50°. Protoconch not preserved. Teleoconch of up to six whorls separated by narrowly impressed initially undulating, later linear, suture. Early teleoconch whorl bearing about ten rounded axial ribs, slightly narrower than their interspaces. Later spire whorls with broad, steep, weakly concave subsutural ramp, poorly delimited by rounded shoulder placed below mid-whorl, periphery short distance above abapical suture. Ribs obsolete over subsutural ramp, broad and rounded below, weakening towards suture, forming axially elongated nodes at periphery. Spiral sculpture of fine spiral cords (mostly abraded). Last whorl somewhat inflated, about 70% of total height, with broad concave subsutural ramp, rounded at weak shoulder, convex below, moderately constricted at base, fasciole rounded, moderately delimited; ribs reduced to ten elongated nodes at shoulder, fading on first half of last whorl in most specimens; spiral cords slightly stronger over base and fasciole. Aperture about 47% of total height, ovate; anal canal marked by small notch; siphonal canal moderate length, narrow, open, bent to left and slightly recurved; outer lip sinuous in profile, roundly angled at shoulder, flared abapically, bearing row of weak elongated denticles beginning some distance within peristome. Columella broadly and shallowly excavated, bearing denticle at upper end of siphon.

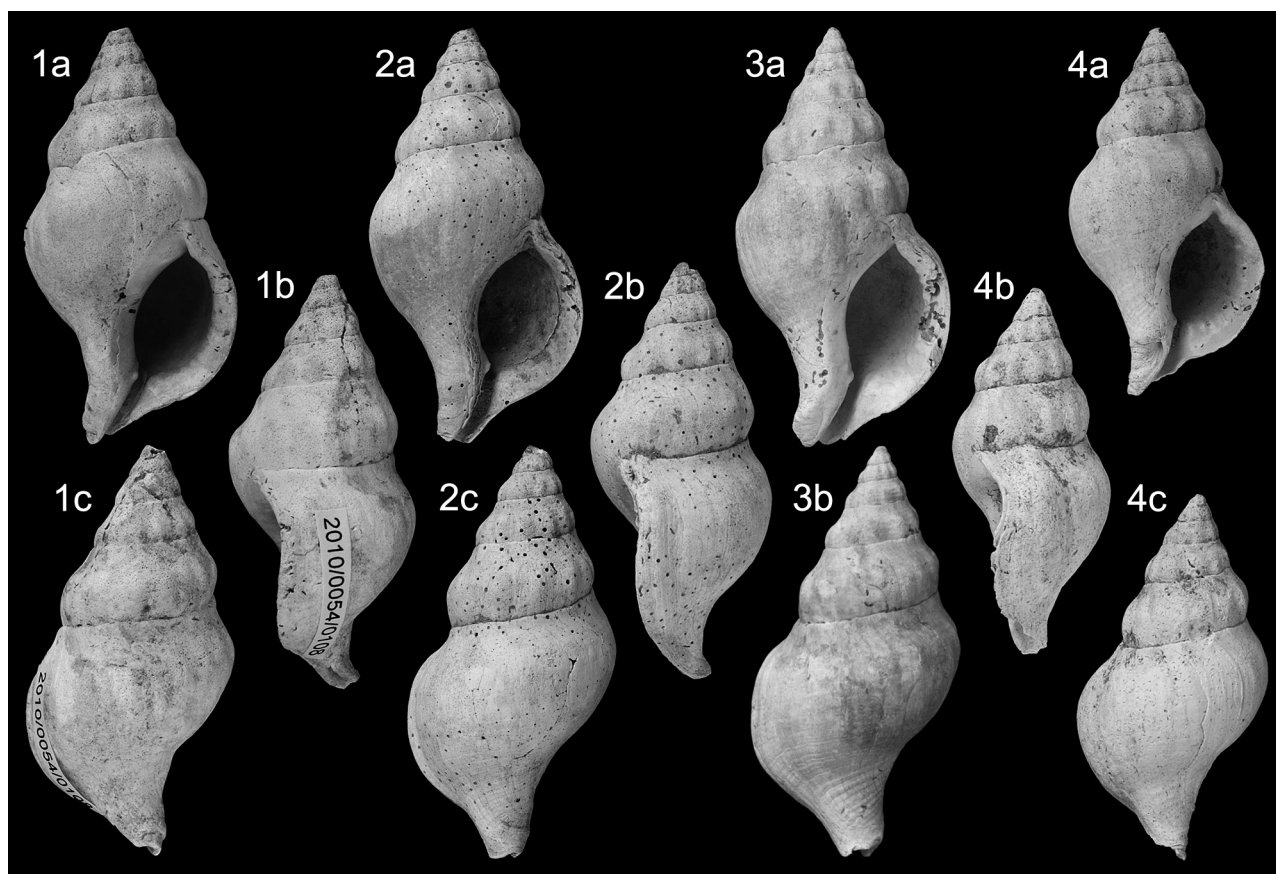


Plate 15. *Euthria lucenica* nov. sp.; 1. **Holotype** NHMW 2010/0054/0108, height 52.0 mm, width 25.9 mm; 2. **Paratype 1** NHMW 2023/0323/0069, height 47.1 mm, width 22.3 mm; 3. **Paratype 2** NHMW 2023/0323/0070, height 48.3 mm, width 23.1 mm; 4. **Paratype 3** NHMW 2023/0323/0071, height 34.8 mm, width 16.5 mm. Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, Lower Pliocene.

nal canal; very weak parietal denticle or pad in some specimens. Columellar callus moderate width, thickened, sharply delimited.

Discussion – *Euthria lucenica* nov. sp. shows some variability in the strength and persistence of the ribs on the last whorl; they are obsolete on the entire to last half whorl in most specimens, persist to the aperture in some, and the inflation of the last whorl, varying from moderately to relatively strongly inflated, but never as strongly as in *E. inflatissima* nov. sp. from Estepona (see above). It differs from all the Italian Pliocene species reviewed by Brunetti & Della Bella (2016) in having the axial sculpture persisting longer. The Upper Miocene Tortonian specimen of *E. adunca* (Bronn, 1831) illustrated by those authors (2016, figs 5D-E) shows similar sculpture, but the last whorl is not inflated, the outer lip not flared, and the siphonal canal is straighter. Landau *et al.* (2011) erroneously ascribed these specimens to *Euthria cornea* (Linnaeus, 1758), but that species, although highly variable, is usually slenderer, with a better developed subsutural collar and ramp, and ribs disappear earlier in ontogeny, although occasional specimens may have tubercles at the shoulder on the last whorl. The last whorl is usually less inflated, resulting in a less flared outer lip, and the siphonal canal is less bent to the left.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011; Brunetti & Della Bella, 2016; Brunetti, 2022).

***Euthria onubensis* nov. sp.**

Plate 16, figs 1-4

2011 *Euthriofusus* cf. *virgineus* (Grateloup, 1832 [sic]) – Landau *et al.*, p. 28, pl. 14, figs 7, 8 [*non Euthria virginea* (Grateloup, 1833)].

ZooBank registration – urn:lsid:zoobank.org:act:0C0C77A4-6F45-4118-B9D8-3258114CEC39

Type material – Holotype NHMW 2010/0054/0162, height 44.8 mm, width 18.7 mm; paratype 1 NHMW 2010/0054/0163, height 46.6 mm, width 22.5 mm; paratype 2 NHMW 2023/0323/0056, height 45.5 mm, width 20.0 mm; paratype 3 NHMW 2023/0323/0057, height 43.5 mm, width 20.1 mm.

Other material – Maximum height 45.5 mm, width 20.0 mm. NHMW 2023/0323/0058 (1).

Type locality – Lucena del Puerto, Huelva, Spain.

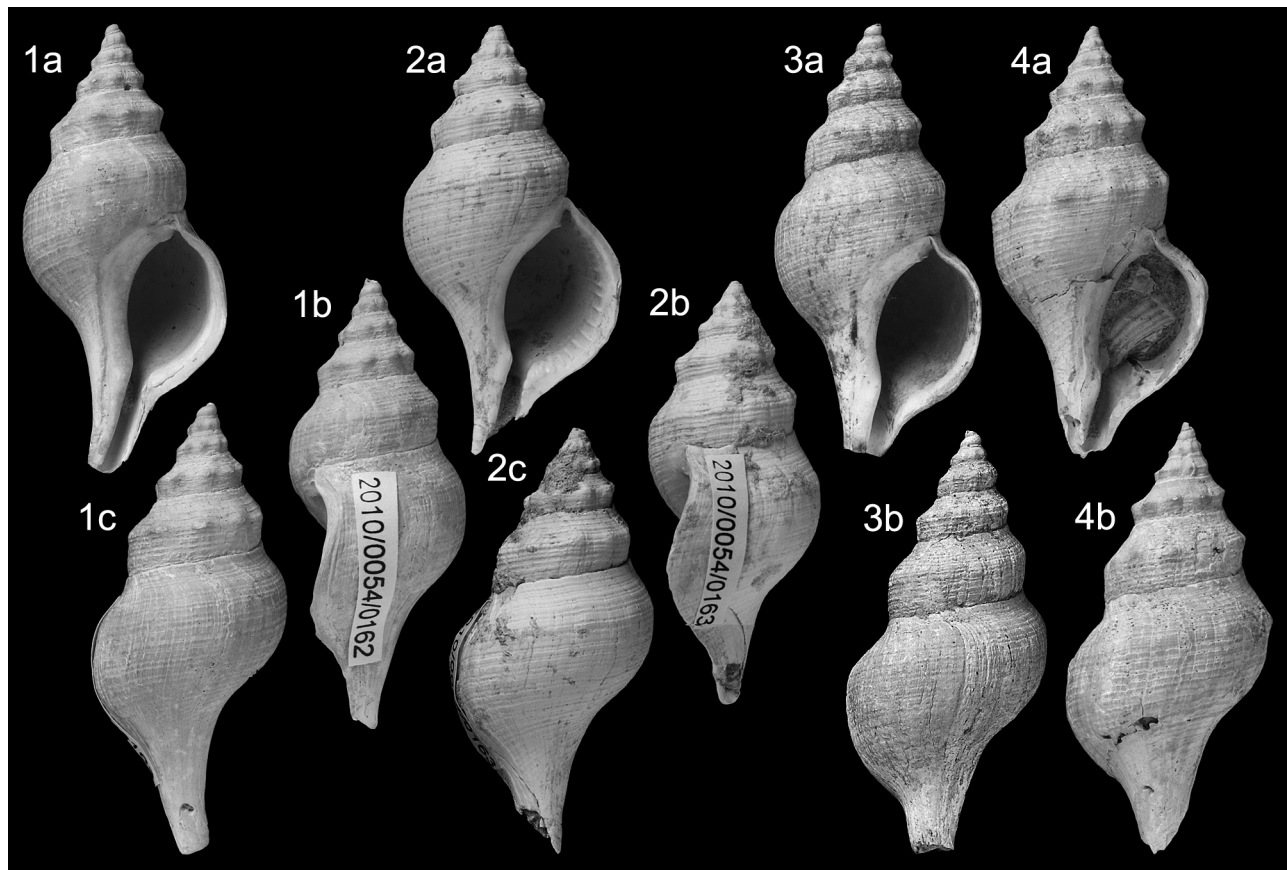


Plate 16. *Euthria onubensis* nov. sp.; 1. **Holotype** NHMW 2010/0054/0162, height 44.8 mm, width 18.7 mm; 2. **Paratype 1** NHMW 2010/0054/0163, height 46.6 mm, width 22.5 mm; 3. **Paratype 2** NHMW 2023/0323/0056, height 45.5 mm, width 20.0 mm; 4. **Paratype 3** NHMW 2023/0323/0057, height 43.5 mm, width 20.1 mm. Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, Lower Pliocene.

Type stratum – Arenas de Huelva Formation, Zanclean, Lower Pliocene.

Etymology – Named after the ancient Latin name for Huelva, *Onuba*. *Euthria*, gender feminine.

Diagnosis – *Euthria* species with broad fusiform shell, five teleoconch whorls, spire whorls angled at shoulder placed mid-whorl bearing ten pointed tubercles, ribs subobsolete, spiral sculpture weak, last whorl somewhat inflated, tubercles fade on entire to last half whorl, outer lip denticles weak to absent, long siphonal canal.

Description – Shell medium-sized, relatively thin-shelled, broad fusiform. Protoconch not preserved. Teleoconch of five whorls separated by narrowly impressed linear suture. Spire whorls with broad concave subsutural ramp delimited by angled shoulder forming periphery placed at about mid-whorl height, whorl profile straight below, tapering slightly inwards to suture. Sculpture of ten subobsolete axial ribs forming somewhat pointed, horizontally elongated tubercles at shoulder and fading rapidly over subsutural ramp and below shoulder. Spiral sculpture weak, numerous fine cords, alternating or of irregular strength covering entire surface, shoulder cord slightly broader. Last whorl 74% of total height, with broad concave subsutural ramp delimited by weakly angled to rounded shoulder, convex and somewhat inflated mid-whorl, strongly constricted at base; shoulder tubercles weaken rapidly, obsolete on entire to half or last whorl, spirals weak over entire last whorl surface; siphonal fasciole flattened, not delimited from base (only complete in holotype). Aperture 53% of total height, wide, ovate; anal canal marked by small, narrow notch; siphonal canal long, open, narrow, slightly bent to the left, not recurved; outer lip flared, weakly thickened, rounded, smooth or with row of about 18 weak denticles within. Columella broadly and weakly excavated. Columellar callus broad, slightly thickened, sharply delimited, smooth except for subobsolete denticle at upper end of siphonal canal and small parietal denticle.

Discussion – *Euthria onubensis* nov. sp. is included in the *Euthria virginea* species group characterised by their long siphonal canal. Note that only the holotype has its siphonal canal complete. This character clearly separates it from *E. lucenica* nov. sp., with which it co-occurs, but it is also thinner shelled than that species and the shoulder tubercles are much smaller.

It is most similar to *Euthria pliovirginea* nov. sp. from the Estepona assemblages in its tubercular shoulder sculpture and long siphonal canal, but clearly differs in being thinner shelled, its lower, broader spire, the shoulder is placed mid-whorl as opposed to closer to the abapical suture in *E. pliovirginea*, the last whorl is more strongly inflated resulting in a wider aperture, the shoulder tubercles fade slightly earlier, and the siphonal canal is not as long.

This group of *Euthria* species with long siphonal canals, widespread in the European Miocene, seems to have been

restricted to the westernmost Mediterranean (*E. pliovirginea* nov. sp.) and adjacent Atlantic (*E. onubensis* nov. sp.) and did not extend its range further into the Pliocene Mediterranean (see Brunetti & Della Bella, 2016), nor further North along the Eastern European Frontage (see Van Dingenen *et al.*, 2017; Landau *et al.*, in prep).

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, SW Spain (Landau *et al.*, 2011).

Family Nassariidae Iredale, 1916 (1835)

Subfamily Photinae Gray, 1857

Genus *Europhos* Landau, Harzhauser, İslamoğlu & Silva, 2013

Type species (by original designation) – *Buccinum polygonum* Brocchi, 1814. Pliocene, Italy.

2013 *Europhos* Landau, Harzhauser, İslamoğlu & Silva, p. 170.

Europhos polygonus (Brocchi 1814)

Plate 17, figs 1-3

- *1814 *Buccinum polygonum* Brocchi, p. 344, pl. 5, fig. 10.
- 1847 *Nassa polygona* Brocchi – Michelotti, p. 207, pl. 13, fig. 2.
- 1879 *Phos polygonum* Brocchi – Fontannes, p. 55, pl. 5, fig. 1.
- 1882 *Phos polygonus* (Brocch.) – Bellardi, p. 8, pl. 1, fig. 5.
- 1901 *Phos polygonum* (Brocchi) – Cossmann, p. 158, pl. 5, figs 20, 21.
- 1904 *Phos polygonum* var. *acutespirata* Sacc., Sacco, p. 58, pl. 14, figs 57-59.
- 1904 *Phos polygonum* var. *percostata* Sacc., Sacco, p. 58, pl. 14, figs 60, 61.
- ?1927 *Phos polygonum* (Brocchi) – Peyrot, p. 228, no. 970, pl. 4, figs 31-34.
- 1939 *Phos polygonum* (Br.) – Montanaro, p. 182, pl. 7, figs 16, 17.
- 1955 *Phos polygonum* (Brocchi 1814) – Rossi-Ronchetti, p. 202, fig. 107.
- 1958 *Phos (Phos) polygonus* (Brocchi, 1814) – Beer-Bistrický, p. 45, pl. 1, fig. 4.
- 1973 *Phos (Phos) polygonus* (Brocchi), 1814 – Caprotti & Vescovi, p. 165, pl. 1, fig. 16.
- 1974 *Phos (Phos) polygonus* (Brocchi, 1814) – Malatesta, p. 308, pl. 24, fig. 10.
- 1974 *Phos (Phos) polygonus* (Brocchi) 1814 – Caprotti, p. 27, pl. 2, fig. 3.
- 1976 *Phos (P.) polygonus* (Brocchi) – Pavia, p. 112, pl. 6, fig. 20.
- 1976 *Phos (Phos) polygonus* (Brocchi, 1814) – Caprotti, p. 11, pl. 15, fig. 16.
- 1978 *Buccinum prismaticum* Brocchi, 1814 – Pinna & Spezia, p. 132, pl. 10, fig. 2.

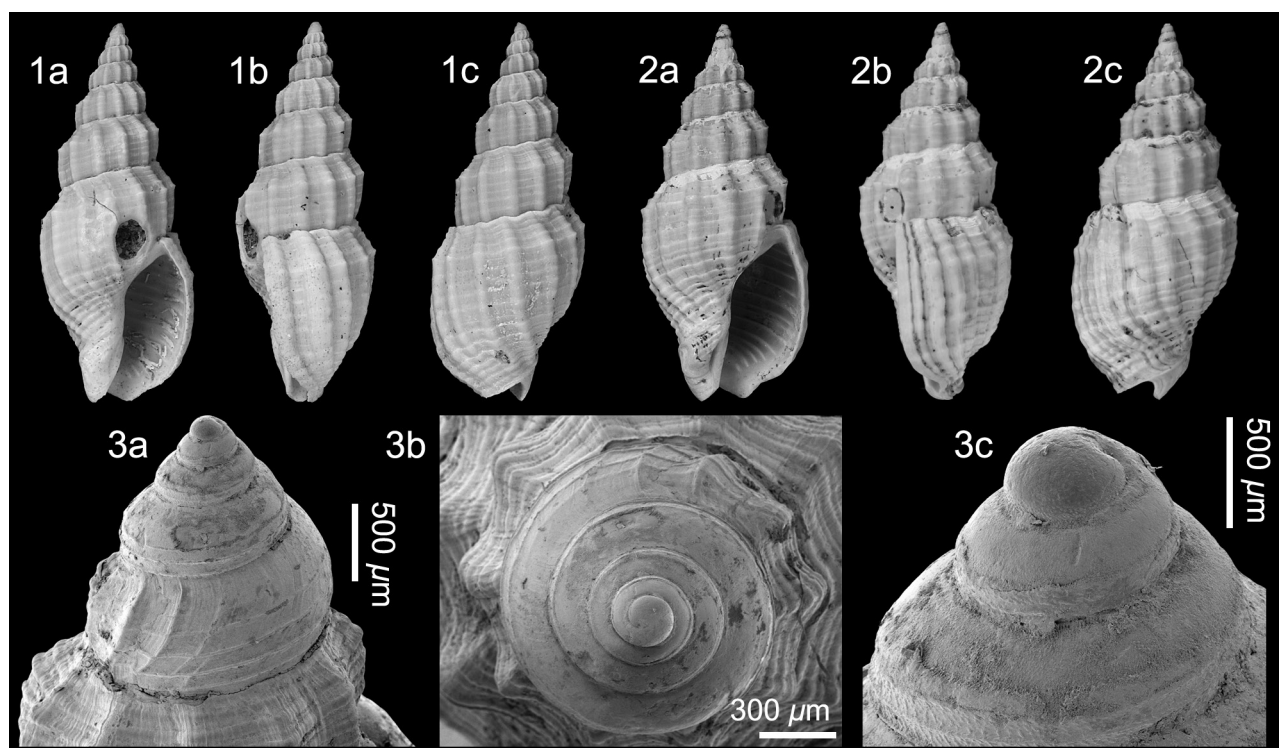


Plate 17. *Europhos polygonus* (Brocchi, 1814); 1. NHMW 2023/0323/0027, height 33.3 mm, width 14.4 mm; 2. NHMW 2023/0323/0028, height 29.5 mm, width 12.8 mm (digital images); 3. NHMW 2012/0197/0011 (juvenile), detail of protoconch (SEM images). El Lobillo, Estepona, Lower Piacenzian, Upper Pliocene.

- 1982 *Phos polygonum* (Brocchi, 1814) – Martinell, p. 66, pl. 1, figs 5, 6.
 1989 *Phos (Phos) polygonus* (Brocchi, 1814) – González Delgado, p. 279, pl. 2, figs 6-7.
 1992 *Phos polygonus* (Brocchi, 1814) – Cavallo & Repetto, p. 98, fig. 223.
 1997 *Phos cf. polygonus* (Brocchi) – Ruiz Muñoz, p. 176, pl. 35, figs 11, 12.
 2000 *Phos polygonus* (Brocchi, 1814) – Chirli (*partim*), p. 55, pl. 21, figs 1-7.
 2010 *Phos polygonus* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 39, p. 57, unnumbered fig. top left.
 2011 '*Phos*' *polygonus* (Brocchi, 1814) – Landau *et al.*, p. 24, pl. 12, fig. 2.
 2013 *Europhos polygonus* (Brocchi, 1814) – Landau *et al.*, p. 170, text-fig 23, pl. 25, fig. 12.
 2016 *Europhos polygonus* (Brocchi, 1814) – Brunetti & Della Bella, p. 22, figs 13A-H.
 2022 *Europhos polygonus* (Brocchi, 1814) – Brunetti, p. 50, fig. 78.
- non 1852 *Buccinum polygonum* Brocc. – Hörnes, p. 160, pl. 13, figs 14, 15 [= *Phos hoernesii* (Semper, 1861)].
 non 1866 *Bucinum polygonum* Brocc. – Pereira da Costa, p. 109, pl. 15, figs 13, 14 [= *Phos connectens* (Bellardi, 1882)].

Material and dimensions – Maximum height 33.3 mm, width 14.4 mm. **EL:** NHMW 2012/0197/0011 (juvenile), NHMW 2023/0323/0027-0028 (2), NHMW 2023/0323/0029 (1).

Description – Shell medium-sized, elongate, turriculate, with tall spire and angular whorls. Protoconch multispiral, composed of 4.25-4.5 whorls with small nucleus. Postnuclear whorls shouldered bearing three spiral cords below shoulder and micropustules in the spiral interspaces. 2-3 opisthocyrt axial riblets on last part of protoconch just before sinusigera. Teleoconch of six sharply angled whorls, with broad, weakly concave subsutural ramp, sharply angled by shoulder cord, weakly convex below, periphery mid-way between shoulder and suture. Suture impressed, shallowly undulating. Axial sculpture of narrow prosocline ribs, about eleven on penultimate whorl. Spiral sculpture of very weak cords and secondary threads override axials, shoulder cord slightly spinous at intersections. Last whorl 61-63% of total height, concave subsutural ramp, weakly convex below, moderately constricted at base; axials weaken, and spirals strengthen over base; siphonal fasciole broad, flattened, bearing spiral cords. Aperture ~ 40% of total height; anal sinus not developed, siphonal fasciole moderately short, broad, open; outer lip angled at shoulder, lyrate within. Columella moderately excavated in upper third, twisted at fasciole. Columellar callus slightly thickened abapically, reduced to callus wash mid-aperture, slightly thicker in parietal region, with fold abapically delimiting siphonal canal. Colour pattern preserved in some specimens consisting of broad orange band below shoulder on spire whorls and two narrower bands, one placed just below shoulder, second over base, on last whorl.

Discussion – The protoconch of this species was illustrated by Landau *et al.* (2013, text-fig. 23) based on a specimen from El Lobillo. All the European ‘Phos’ species have a multispiral protoconch with 2–3 spiral cords from the second protoconch whorl and axial riblets on at least part of the last protoconch whorl. *Phos* de Montfort, 1810 is an exclusively Indo-West Pacific genus, characterised by shells with a smooth multispiral protoconch (Fraussen & Poppe, 2005, p. 77). Species of the tropical American Neogene to present-day genus *Antillophos* Woodring, 1928 have protoconchs of 3.5–4 whorls and the teleoconch differs from *Europhos* in having a less well defined shoulder that is not spinose, and in *Antillophos* the sculpture is more evenly reticulate in most species, whereas it is predominantly axial in *Europhos* (see Landau *et al.*, 2013, p. 170; 2016, p. 137). *Buccinum polygonum* Brocchi, 1814 also has sculpture of micropustules, clearly seen where the surface is not eroded (Pl. 17, fig. 3c).

For comparison with other congeners, see Landau *et al.* (2013, p. 171).

Europhos polygonus is uncommon in Estepona, where it is found only in the shallow water assemblage at El Lobillo. The shells are typical for the species, as illustrated by Brunetti & Della Bella (2016, figs 13A–H), and show little intraspecific variability.

Distribution – Middle Miocene: Atlantic (Langhian and Serravallian), Aquitaine Basin, France (Peyrot, 1927); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Proto-Mediterranean (Tortonian): Po Basin, Italy (Bellardi, 1882; Montanaro, 1939). Lower Pliocene: northeastern Atlantic, Guadalquivir Basin, Spain (González Delgado, 1989; Ruiz Muñoz, 1997; Landau *et al.*, 2011; Brunetti, 2022); north-east Spain (Martinell, 1982), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Bellardi, 1882; Pavia, 1976; Chirli, 2000; Brunetti & Della Bella, 2016). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1904; Caprotti & Vescovi, 1973; Caprotti, 1974; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & dell’Angelo, 2010; Brunetti & Della Bella, 2016).

Discussion

The Colubrariidae are represented by three species (Figure 1), all of which are new: *Colubraria alboranensis* nov. sp., *Kanamarua ducoi* nov. sp. and *Metula moli* nov. sp. The large *Colubraria* species represents the first record of the genus in the Pliocene Mediterranean, as today only the genus *Cumia* is present. It is also the first record of the deep-water genus *Kanamarua* Kuroda, 1951 in the European fossil assemblages and oldest known member of the genus which is now widespread in the tropical Pacific.

The two genera are distinguished primarily by their protoconch type, although the validity of this character needs to be tested based on molecular data.

The Pisaniidae are represented by six species representing three genera, of which one is described as new *Aplus raveni*

nov. sp. and the Tudicidae by five species of which four are new: *Euthria iberoadunca* nov. sp., *Euthria inflatissima* nov. sp., *Euthria pliovirginea* nov. sp., *Euthria pouweri* sp., and one species is left in open nomenclature. These genera reproduce by direct development, or possibly have a short lecithotrophic stage, and it is therefore not surprising to find species endemic to the western Mediterranean Alboran Sea and, *vice versa*, most of the species within these families recorded by Brunetti & Della Bella (2016) from the Italian Pliocene do not occur in Estepona. These insights into the endemic character of the genus *Euthria* led us to review the genus in the Atlantic Lower Pliocene Guadalquivir Basin of SE Spain, which results in the description of two further endemic species, *E. lucenica* nov. sp. and *E. onubensis* nov. sp. One species is recorded in the subfamily Photinae (family Nassariidae), *Europhos polygonus* (Brocchi 1814), which was widespread in the Pliocene Mediterranean and adjacent Atlantic. This species was omitted by us in the monograph covering the Nassariidae (Landau *et al.*, 2009), and is included herein for completion. *Europhos polygonus* has a protoconch suggesting planktotrophic development, which supports the wide geographic range observed.

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References

- Adams, H. & Adams, A. 1853–1858. *The genera of recent Mollusca; arranged according to their organization*. London (John van Voorst), 1:1–256, pls 1–32, 1853, 257–484, 1854; 2:1–284, pls 33–96, 1855a, 285–412, pls 97–112, 1856, 413–540, pls 113–128, 1857, 541–660, pls 129–138, 1858.
- Adams, A. & Reeve, L.A. 1848–1850. Mollusca. In: Adams, A. (ed.) *The zoology of the voyage of H.M.S. Samarang, under the command of Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S., during the years 1843–1846*. Reeve & Benham, London, x + 87 pp., 24 pls. [Pt. I. Preface to Mollusca (iii–x, by Adams only), 1–24, pls. 1–9, 1848; Pt. II, 25–44, pls. 10–17, 1850; Pt. III, Preface and plate explanations (i–xv), 45–87, pls. 18–24, 1850].
- Aissaoui, C., Puillandre, N., Bouchet, P., Fassio, G., Modica, M.V. & Oliverio, M. 2016. Cryptic diversity in Mediterranean gastropods of the genus *Aplus* (Neogastropoda: Buccinidae). *Scientia Marina* 80(4): 521–533.
- Ancona, C. d’ 1872. Malacologia pliocenica italiana. Fascicolo II. Generi: *Pisania*, *Ranella*, *Triton*, *Fasciolaria*, *Turbinella*, *Cancellaria*, *Fusus*. pp. 55–141, pl. 8–15. G. Barbèra, Firenze. [reissued 1873: *Memorie per servire alla Descrizione della Carta Geologica d’Italia* 2: 173–259, pl. 8–15].
- Ardovini, R. 2015. Descrizione di una nuova specie di *Politia* dalla Sicilia Sud-orientale. *Malacologia Mostra Mondiale* 86: 12–13.

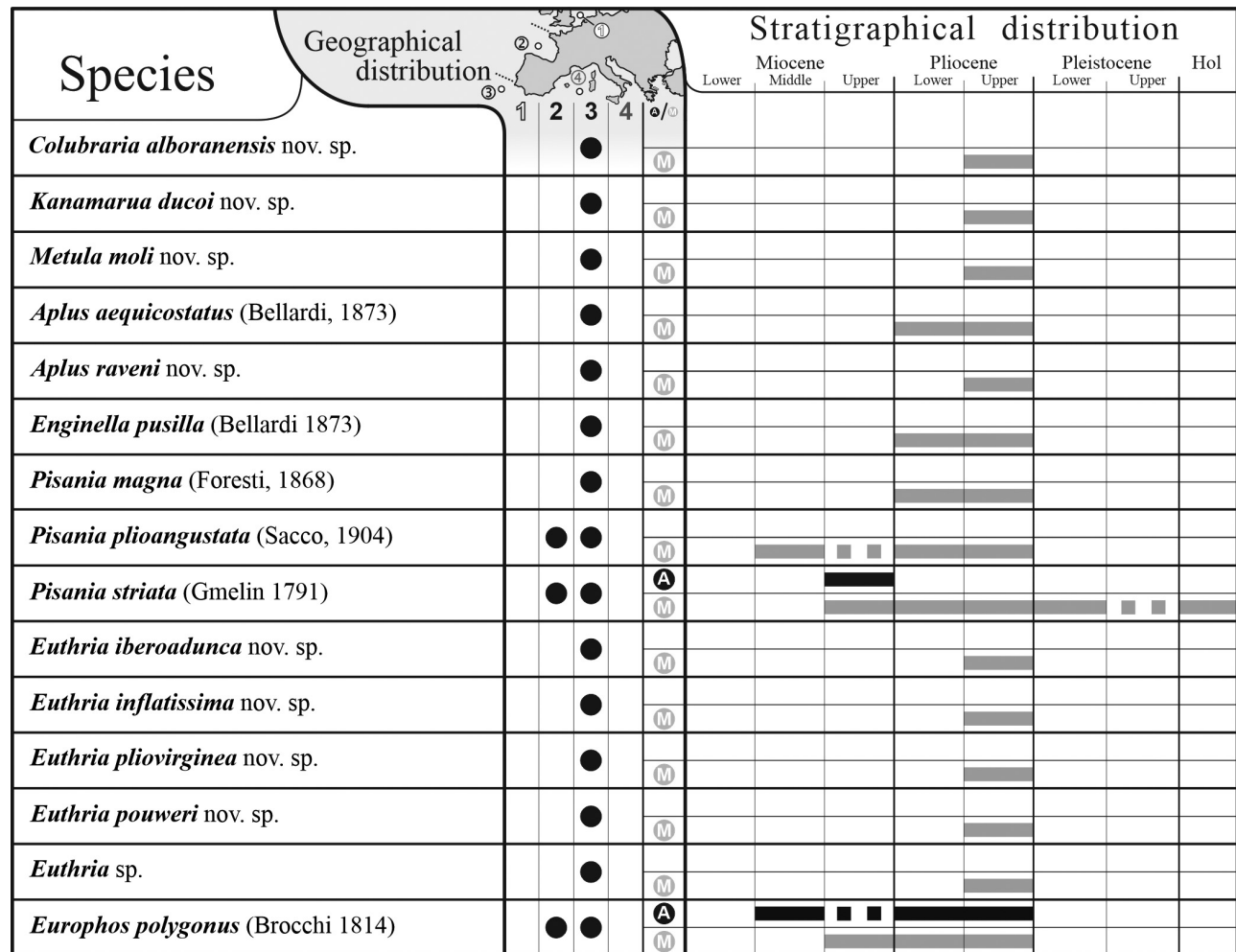


Figure 1. Geography, stratigraphy and distribution of species found in the Upper Pliocene Lower Piacenzian of the Estepona Basin, southern Spain. For present-day geographic distribution designated by biogeographical province: 1 = Boreal-Celtic Province, 2 = French-Iberian Province, 3 = Mediterranean-Moroccan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

Bałuk, W. 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part II. *Acta Geologica Polonica* 45: 153-255.

Bandat, H. 1943. Újharmadkori csigák Délalbániából (Tertiary gastropods from South Albania). *Földtani Szemle* 1(6): 289-367.

Beer-Bistriczky, E. 1958. Die miozänen Buccinidae und Nassariidae des Wiener Beckens und Niederösterreichs. *Mitteilungen der Geologischen Gesellschaft in Wien* 49 (1956): 41-84.

Bellardi, L. 1873. I molluschi dei terreni terziarii del Piemonte e della Liguria, 1. Cephalopoda, Pteropoda, Heteropoda, Gasteropoda (Muricidae e Tritonidae). *Memorie della Reale Accademia delle Scienze di Torino* (2)27 (1873): 33-294 (reprint 264 pp.) (June 10, 1873).

Bellardi, L. 1882. I molluschi dei terreni terziarii del Piemonte e della Liguria, 3. Gasteropoda (Buccinidae, Cyclopsidae, Purpuridae, Coralliophilidae, Olividae). *Memorie della Reale Accademia delle Scienze di Torino* (2)34 (1883): 219-469 (reprint 253 pp.) (December 10, 1882).

Bivona e Bernardi, A. 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.

Bivona e Bernardi, A. 1838. Generi et specie di molluschi descritti dal Barone Antonio Bivona e Bernardi. Lavori postumi pubblicati dal figlio Andrea dottore in medicina con note ed aggiunte. *Giornale di Scienze Lettere e Arti per la Sicilia* 61: 211-227 [stated date March 1838]; 63: 319-324 [stated date September 1838] [also as reprint, 16 pp, 1 pl., tipografia del Giornale Letterario, Palermo].

Blainville, H.M.D. de 1828-1830. Malacozoaires ou Animaux Mollusques. [in] *Faune Française*. Levrault, Paris 320 p., 48 pl. [livr. 18 (29 Nov. 1828), p. 1-80; livr. 20 (7 March 1829), p. 81-170; livr. 23 (1 Aug. 1829), p. 171-240; livr. 28 (3 July 1830), p. 241-320].

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.

Bouchet, P. 1988. Two new species of *Metula* (Gastropoda: Buccinidae) with a description of the radula of the genus. *Nautilus* 102(4): 149-153.

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.
- 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 January 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. 2022. *Malacofauna plioceniche della Valle del Guadalquivir, Spagna*. Privately published, Edizione Danaus: 147 pp.
- Brunetti, M.M. & Della Bella, G. 2014. La famiglia Buccinidae Rafinesque, 1815 nel Plio-Pleistocene italiano: i genere *Aplus* De Gregorio, 1884, *Engina* Gray, 1839 e *Gemophos* Olsson & Harbison, 1953 (Gastropoda). *Bollettino Malacologico* 40: 11-32.
- Brunetti, M.M. & Della Bella, G. 2016. Revisioni di alcuni generi della famiglia Buccinidae Rafinesque, 1815 nel Plio-Pleistocene del Bacino Mediterraneo, con descrizione di tre nuove specie. *Bollettino Malacologico* 52: 3-37.
- 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.
- 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 di 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.
- Ceregato, A., Scarponi, D. & Bella, G. della 2010. The Neogene mollusc type material from the collection of Lodovico Foresti preserved in the "Giovanni Capellini" Museum of Geology of Bologna University, Italy. *GeoActa* 9: 53-65.
- Cernohorsky, W.O. 1966. A new genus and species of Buccinidae from the Fiji Islands (Mollusca: Gastropoda). *The Veliger* 9(2): 229-232.
- Cernohorsky, W.O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaniinae (Mollusca: Gastropoda). *Records of the Auckland Institute and Museum* 12: 175-211.
- Chirli, C. 2000. *Malacofauna Pliocenica Toscana, 2 Superfamiglia Muricoidea*. Firenze (C. Chirli): 142 pp.
- Chirli, C. & Linse, U. 2011. *The Pleistocene marine Gastropods of Rhodes Island (Greece)*. Grafiche PDB, Tavarnelle V.P. Firenze: 262 pp, 90 pls.
- Cirone, G., Raineri, V. & Brunetti, M. 1997. Osservazioni su alcune specie della collezione Foresti del Museo "G. Doria" di Genova. *Bollettino della Società Paleontologica Italiana* 36, 161-167.
- Cossmann, M. 1889. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. *Annales de la Société Royale Malacologique de Belgique* 24: 3-381, pl. 1-12.
- Cossmann, M. 1901. *Essais de paléoconchologie comparée*, 4. The author and Société d'Éditions Scientifiques, Paris: 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).
- Cossignani, T. 2020. *Colubraria somalica*: nuove specie dalla Somalia. *Malacologia Mostra Mondiale* 108: 20-21.
- Crosse, H. 1862. Description d'une espèce nouvelle appartenant au genre *Pisania*. *Journal de Conchyliologie* 10: 251-252, pl. 10, fig. 5.
- Dall, W.H. 1904. An historical and systematic review of the frogshells and tritons. *Smithsonian Miscellaneous Collections* 47: 114-144.
- Dall, W.H. 1919. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum* 56 (2295): 293-371.
- De Gregorio, A. 1884-1885. Studi su talune conchiglie mediterranee viventi e fossili con una rivista del genere *Vulsella*. *Bollettino della Società Malacologica Italiana* 10: 36-128 [1884], 129-288 [1885], pl. 1-5.
- Dujardin, F. 1837. Mémoire sur les couches du sol en Touraine, et description des coquilles de la craie et des faluns. *Mémoires de la Société Géologique de France* 2(2): 211-311, pls 15-21.
- 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.
- Finlay, H.J. 1926. A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Insti-*

- tute 57: 320-485, pls 18-23 [dated 1927, published Dec, 1926].
- Fittkau, E.J. & Parth, M. 1993. *Colubraria kathiewayana* sp. nov. from Brazil. *Spixiana* 16(2): 189-190.
- 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).
- Foresti, L. 1868. Catalogo dei molluschi fossili pliocenici delle Colline Bolognesi. Parte 1: gasteropodi. *Memoire della Accademia delle Scienze dell'Instuto di Bologna* serie 2, 7: 541-637, 2 pls.
- Forli, M. & Dell'Angelo, B. 1995. Segnalazione di Gasteropodi poco frequenti per il Pliocene toscano. *Notiziario CISMA* 17: 15-19.
- Fraussen, K. & Lamy, D. 2008. Revision of the genus *Kanamarua* Kuroda, 1951 (Gastropoda: Colubrariidae) with the description of two new species. *Novapex* 9(4): 129-140.
- Fraussen, K. & Poppe, G.T. 2005. Revision of *Phos* and *Antillophos* (Buccinidae) from the Central Philippines. *Visaya* 1(5): 76-115.
- Friedberg, W. 1911-28. *Mięczaki mioceńskie ziem Polskich (Mollusca Miocaenica 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).
- Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A. & Ebreo, C. 2003. *Atlante delle conchiglie marine del Mediterraneo, vol. 4 (Neogastropoda: Muricoidea)*. Evolver, Roma 298 pp.
- Gmelin, J.F. 1791. Vermes. In: Gmelin J.F. (Ed.) *Caroli a Linnaei Systema Naturae per Regna Tria Naturae*, Ed. 13. Tome 1(6). G.E. Beer, Lipsiae [Leipzig]. pp. 3021-3910. *Systema Naturae. Linnaeus (ed.). Ed. 13*. 1: pars. 6.
- González-Delgado, J.A. 1989. Estudio sistemático de los gasterópodos del Plioceno de Huelva (SW de España), 4. Neogastropoda (Muricea, Buccinacea). *Studia Geologica Salmanticensia* 26: 269-315.
- Grateloup, J.P.S. de 1828-35. Tableau des coquilles fossiles qu'on rencontre dans les terrains calcaire tertiaires (faluns) des environs de Dax, dans le Département des Landes, 1-12. *Bulletins d'Histoire Naturelle de la Société Linnéenne de Bordeaux* 2(9): 72-109 (1828a) (1); 2(10): 123-158 (1828b) (2); 2(10): 192-204 (1828c) (3). *Actes de la Société Linnéenne de Bordeaux* 5(27): 192-204 (1832a) (4); 5(29): 263-282 (1832b) (5); 5(30): 314-344 (1832c) (6); 6(32): 31-48 (1833a) (7); 6(33): 90-100 (1833b) (8); 6(34): 159-164 (1833c) (9); 6(35): 188-212 (1834a) (10); 6(37): 270-320 (1834b) (11); 7(39): 101-114 (1835) (12).
- Grateloup, J.P.S. de 1845-1847. *Conchyliologie fossile des terrains tertiaires du Bassin de l'Adour (environs de Dax)*, 1. *Univalves*. Atlas. Bordeaux (Th. Lafargue): pls. 1-45 (1840); i-xx, 12 pp.; pls. 46-48 (1846). Note: For dates of the plates we follow Lesport *et al.* (2012). All plates published 1845, except plates 2, 4, 11 (1847).
- Gray, J.E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London* (1847): 129-219.
- Gray, J.E. 1850 [text]. In: Gray, M. E., *Figures of molluscan animals, selected from various authors*. Longman, Brown, Green and Longmans, London. Vol. 4, iv + 219 pp. (August) [Frontispiece (portrait of Mrs. Gray); pp. ii-iv (preface); 1-62 (explanation of plates 1-312 in Volumes 1-3); pp. 63-124 (systematic arrangement of figures); 127-219 (reprint of Gray 1847)].
- Gray, J.E. 1853. On the division of ctenobranchous gasteropodous Mollusca into larger groups and families. *Annals and Magazine of Natural History* (2)11: 124-132.
- Gray, J.E. 1857. *Guide to the systematic distribution of Mollusca in the British Museum, Part I*. Taylor & Francis, London. xii + 230 pp.
- 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.
- Harzhauser, M. & Landau, B.M. 2024. The Colubrariidae, Eosiphonidae, Melongenidae, Pisaniidae, Proditiidae and Tudicidae (Gastropoda, Buccinoidea) of the Miocene Paratethys Sea. *Zootaxa* 5427 (1): 001-110.
- Helbling, G.S. 1779. Beiträge zur Kenntniß neuer und seltener Konchylien. Aus einigen Wienerischen Sammlungen. *Abhandlungen einer Privatgesellschaft in Böhmen, zur Aufnahme der Mathematik, der vaterländischen Geschichte, und der Naturgeschichte* 4: 102-131, pl. 1-4.
- Hinds, R.B. 1844. Descriptions of new shells, collected during the voyage of the Sulphur, and in Mr. Cuming's late visit to the Philippines. *Proceedings of the Zoological Society of London* (1844) 11: 149-168.
- Hoernes, R. & Auinger, M. 1879-1891. Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der Österreich-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 12: 1-382, pls 1-50 [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 29-29-36 (1890); 283-332, pls 37-50 (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).
- International Commission on Zoological Nomenclature (ICZN) 1965. Opinion 740. *Pisania* Bivona, 1832 (Gastropoda): Designation of a type-species under the plenary powers. *Bulletin of Zoological Nomenclature* 22: 171-172.
- Inzani, A. 1988. La famiglia Cymatiidae nel pliocene italiano. The Cymatiidae family during the Italian Pliocene. *Hobby Fauna International News* 4(1): 19-26, 28-31.
- Iredale, T. 1912. New generic names and new species of marine Mollusca. *Proceedings of the Malacological Society of London* 10(3): 217-228, pl. 9.
- Iredale, T. 1916. On two editions of Duméril's *Zoologie Analytique*. *Proceedings of the Malacological Society of London* 12: 79-84.
- Iredale, T. 1917. More molluscan name changes, generic and specific. *Proceedings of the Malacological Society of London* 12: 322-330.
- Iredale, T. 1925. Mollusca from the continental shelf of eastern Australia. *Records of the Australian Museum* 14(4): 243-270, pls 41-43.

- Janssen, A.W. 2004. Holoplanktonic molluscan assemblages (Gastropoda, Heteropoda, Thecosomata) from the Pliocene of Estepona (Spain, Malaga). *Palaeontos* 5: 103-131.
- Kantor, Y.I., Fedosov, A.E., Kosyan, A.R., Puillandre, N., Sorokin, P.A., Kano, Y., Clark, R. N. & Bouchet, P. 2022 [nomenclatural availability: 2021]. Molecular phylogeny and revised classification of the Buccinoidea (Neogastropoda). *Zoological Journal of the Linnean Society* 194: 789-857.
- Kovács, Z. 2022. Middle Miocene Buccinoidea (Neogastropoda) assemblage from the Făget Basin (Romania) in the collection of the Hungarian Natural History Museum, Budapest. *Fragmenta Palaeontologica Hungarica* 37 (2021): 65-99.
- Kovács, Z. & Vicián, Z. 2023. Buccinoidea (Neogastropoda) assemblage from the Lower Badenian (Middle Miocene) deposits of Letkés (Hungary). *Bollettino Malacologico* 59(2): 222-259.
- Kuroda, T. 1951. Descriptions of a new genus of a marine gastropod, *Kanamarua*, gen. n., and a new species of a bivalve, *Abra kanamarui*, sp. n. dedicated to Mr T. Kanamaru on his 60th birthday. *Venus* 16(5-8): 68-72.
- Kuroda, T., Habe, T. & Oyama, K. 1971. *The sea shells of Sagami Bay collected by His Majesty the Emperor of Japan*. Maruzen Co., Tokyo. pp. i-xix, 1-741 (Japanese), 121 pls., 1-489 (English), 1-51.
- Lamarck, J.B.P.A. de M. 1822. *Histoire naturelle des animaux sans vertèbres, présentant des caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principaux 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*, 7. Paris (de Lamarck): 711 pp.
- 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. (submitted). The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 24: Fasciolaridae (Neogastropoda, Buccinoidea). *Cainozoic Research*.
- 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., Harzhauser, M. & Monsecour, K. 2023. The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 20: Columbidae (Buccinoidea). *Cainozoic Research* 23(2): 279-313.
- 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. & Micali, P. 2023. The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 19: Chauvetiidae (Buccinoidea). *Cainozoic Research* 23(2): 245-278.
- 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 & Harzhauser, M. (in prep.). The genus *Euthria* (Gastropoda: Tudicidae) in the Atlantic Pliocene Mondego Basin of Portugal, a highly endemic genus in the European Neogene.
- Landau, B.M., Silva, C.M. da & Gili, C. 2009. The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 8, Nassariidae. *Palaeontos* 17: 1-101.
- Landau, B., Silva, C.M. da & Heitz, A. 2016. Systematics of the gastropods of the Lower-Middle Miocene Cantaure Formation, Paraguaná Formation, Paraguaná peninsula, Venezuela. *Bulletins of American Paleontology* 389-390: 1-581.
- 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.
- Landau, B. & Vermeij, G.J. 2012. The genera *Engina* and *Ameranna* nov. gen. (Mollusca: Gastropoda, Buccinoidea, Buccinidae, Pisaniinae) from the Western Atlantic Neogene. *Cainozoic Research* 9: 121-133.
- [Lightfoot, J.] 1786. *A Catalogue of the Portland Museum, lately the property of the Dutchess Dowager of Portland, deceased; which will be sold by auction by Mr. Skinner & Co.* [book]. London. viii + 194 pp.
- 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. 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.
- Lozouet, P. 2021. Buccinoidea (Mollusca, Gastropoda, Neogastropoda) de l'Oligocène supérieur (Chattien) du bassin de l'Adour (Sud-Ouest de la France). *Cossmanniana* 22: 3-129.
- Malatesta, A. 1974. Malacofauna pliocénica Umbra. *Memorie per Servire alla Carta Geologica d'Italia* 13: 1-498.
- Marche-Marchad, I. & Brebion, P. 1977. Sur un Buccinidé nouveau d'affinité miocène vivant au large du Sénégal. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, série D, 285(4): 339-342.
- Martinell, J. 1982. Euthyneura del Plioceno del Empordà (Girona). Descriptiva y sistemática. *Studia Geologica Salmanticensia* 16: 223-233.
- 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. 1865. *Indicateur du Maine-et-Loire ou indications par commune de ce que chacune d'elles renferme*, 2. Angers (Cosnier et Lachèse): 616 pp.
- MolluscaBase eds. 2023. MolluscaBase. *Metula* H. Adams & A. Adams, 1853. World Register of Marine Species. [https://marinespecies.org/aphia.php?p=taxdetails&id=225377]
- Monegatti, P. & Raffi, S. 2001. Taxonomic diversity and stratigra-

- phic distribution of Mediterranean Pliocene bivalves. *Palaeogeography Palaeoclimatology Palaeoecology* 165: 171-193.
- Monsecour, D., Fraussen, K. & Fei, W. 2017. A new *Kanamarua* (Gastropoda: Colubrariidae) with a remarkable shape from the Spratly Islands, South China Sea. *Gloria Maris* 55(4): 105-110.
- Monsecour, D. & Monsecour, K. 2011. The family Colubrariidae Dall, 1904 in the western Atlantic, including the description of two new species. *Gloria Maris* 50(5): 107-123.
- Montanaro, E. 1935. Studi monografici sulla malacologia Miocenica Modenese, 1. I molluschi Tortoniani di Montegibbio. *Palaeontographia Italica* 35 (nuova serie 5): 1-84.
- Montanaro, E. 1939. Studi monografici sulla malacologia Miocenica Modenese, 3. I molluschi Tortoniani di Montegibbio. *Palaeontographia Italica* 39 (n. s. 5): 101-142.
- Monterosato, T.A. di 1884. *Nomenclatura generica e specifica di alcune conchiglie mediterranee*. Palermo (Virzi): 152 pp.
- Monterosato, T.A. di. 1917. Molluschi viventi e quaternari raccolti lungo le coste della Tripolitania dall'ing. Camillo Crema. *Bollettino della Società Zoologica italiana* ser. 3, 4: 1-28, pl. 1.
- Montfort, D. de 1810. *Conchyliologie systématique, ou classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Coquilles univalves, non cloisonnées*. Paris (F. Schoell): 676 pp.
- Mörch, O.A.L. 1852-1853. *Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra & Gadea Comes de Yoldi, Regis Daniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Tertii Eques. Fasc. 1, Cephalophora*, 170 pp. [1852]; *Fasc. 2, Acephala, Annulata, Cirripedia, Echinodermata*, 74 [+2] pp. [1853]. Hafniae [Copenhagen]: L. Klein.
- Murdoch, R. 1924. Some Tertiary Mollusca, with descriptions of new species. *Transactions and Proceedings of the Royal Society of New Zealand* 55: 157-160, pls 8-10.
- Naumann, C.F. 1852. *Atlas zu C.F. Naumann's Lehrbuch der Geognosie. Zweite Hälfte*. Wilhelm Engelmann, Leipzig, pls 27-70.
- Nikolov, P.I. 1994. Some molluscs from the Badenian (Middle Miocene) west of Pleven (Central Northern Bulgaria). II. Gastropoda: order Neogastropoda. *Geologica Balcanica* 24: 45-70.
- Nordsieck, F. & García-Talavera, F. 1979. *Moluscos Marinos de Canarias y Madera (Gastropoda)*. Aula de Cultura, Tenerife, 208 pp., 46 pls.
- Oliverio, M. & Modica, M.V. 2010. Relationships of the haemaphysagous marine snail *Colubraria* (Rachiglossa: Colubrariidae), within the neogastropod phylogenetic framework. *Zoological Journal of the Linnean Society* 158: 779-800.
- Oliverio, M. & Tringali, L.P. 1991. *Fusus intertextus* and (?) *Fusus* sp. in the Mediterranean Sea (Neogastropoda; Buccinidae; Pisaniniinae). *Notiziario C.I.S.M.A.* 13: 38-40.
- Olsson, A.A. 1967. *Some Tertiary mollusks from south Florida and the Caribbean*. Paleontological Research Institution, Ithaca, N.Y. 61 pp., 9 pls. [Reprinted 1993 in Paleontological Research Institution Special Publication No. 19].
- Olsson, A.A. & Bayer, F.M. 1972. American Metulas (Gastropoda: Buccinidae). *Bulletin of Marine Science* 22: 900-925.
- Orbigny, A. d' 1852. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique*, 3. Paris (Victor Masson): 1-196, index 1-189.
- Pallary, P. 1900. Coquilles marines du littoral du département d'Oran. *Journal de Conchyliologie* 48(3): 211-422.
- Pallary, P. 1912. Catalogue des mollusques du littoral méditerranéen de l'Égypte. *Mémoires de l'Institut d'Égypte* 7(3): 69-207, pls 15-18.
- Pallas, P.S. 1760. *Dissertatio medica inauguralis de infestis viventibus intra vivenda, Lugduni Batavorum*. Th. Haak: 62 pp.
- 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.
- Pereira da Costa, F.A. 1866-1867. Molluscos fosseis. Gastropodes dos depositos terciarios de Portugal. *Memória Comissão Geologica de Portugal* 4(1): 1-116 (1866); (2): 117-252 (1867).
- Petit, R.E. 2012. John Edward Gray (1800-1875): his malacological publications and molluscan taxa. *Zootaxa* 3214: 1-125.
- Petuch, E.J. 2013. *Biogeography and biodiversity of western Atlantic mollusks*. CRC Press. 252 pp.
- Peyrot, A. 1924-1935 – see Cossmann & Peyrot 1909-1935.
- Peyrot, A. 1938. Les mollusques testacés univalves des dépôts Helvétiques du Bassin Ligérien. Catalogue critique, descriptive et illustré. *Actes de la Société Linnéenne de Bordeaux* 89: 5-361.
- Philippi, R.A. 1844. *Enumeratio molluscorum siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit auctor, 2. Continens addenda et emendanda, nec non comparisonem faunae recentis siciliae cum faunis aliarum terrarum et cum fauna periodi tertiariae*. Halis Saxonum (E. Anton): iv + 303 pp.
- 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.
- Poppe, G.T. & Goto, Y. 1991. *European seashells, 1. Polyplacophora, Caudofoveata, Solenogastrea, Gastropoda*. Wiesbaden (Verlag Christa Hemmen): 352 pp.
- Puton, E. 1856. Lettre au docteur Mougeot sur les Mollusques de Syrie, envoyés au musée des Vosges par M. le docteur Gaillardot. *Annales de la Société d'Émulation du Département des Vosges* 1856: 219-231.
- 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.
- Reeve, L.A. 1843-1846. Monograph of the genus *Pleurotoma*. In: *Conchologia Iconica, or, illustrations of the shells of molluscos animals*, vol. 1, pl. 1-40 and unpaginated text. L. Reeve & Co., London. [stated dates: pls 1-2, January 1843; pls 3-6, February 1843; pls 7-8, March 1843; pls 9-10, April 1843; pls 11-12, May 1843; pls 13-14, June 1843; pl.

- 15, July 1843; pl. 16, August 1843; pl. 17, November 1843; pl. 18, December 1843; pl. 19; January 1844; pls 20-26, October 1845; pls 26-27, November 1845; pls 28-33, December 1845; pls 34-38, January 1846; pls 39-40, April 1846].
- Reeve, L.A. 1846-1847. Monograph of the genus *Buccinum*. In: *Conchologia Iconica, or, illustrations of the shells of molluscous 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].
- Rehder, H.A. 1943. New marine mollusks from the Antillean Region. *Proceedings of the United States National Museum* 93(3161): 187-203.
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Tome quatrième*. Levrault, Paris, vii + 439 pp., pls 1-12.
- Röding, P.F. 1798. *Museum Boltenianum, sive catalogus cimeliorum e tribus regnis naturae quae olim collgera Joa. Fried. Bolten, M.D.p.d. per XL annos proto physicus Hamburgensis, 2. Conchylia sive Testacea univalvia, bivalvia et multivalvia*. Hamburgi (Johan. Christi. Trappii): 199 pp.
- Rossi-Ronchetti, C. 1955. I tipi della 'Conchiologia Fossile Subapennina' di G. Brocchi, 2. Gastropodi, Scafopodi. *Rivista Italiana di Paleontologia e Stratigrafia* Memorie 5: 91-343.
- Ruggieri, G. & Greco, A. 1965. Studi geologici e paleontologici su Capo Milazzo con particolare riguardo al Milazziano. *Geologica Romana* 4: 41-88.
- Ruiz Muñoz, F., González-Regalado Montero, M.L. & Redondo Sanz, J.L. 1997. *Guía de fósiles del sur de la provincial de Huelva*. Diputación Provincial de Huelva (Imprenta Diputación): 204 pp.
- Sacco, F. 1890. Catalogo paleontologico del bacino terziario del Piemonte. *Bollettino della Società Geologica Italiana* 8(3): 281-356; 9(2): 185-340.
- 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.
- Scacchi, A. 1832. *Lettera di Arcangelo Scacchi dottore in medicina su vari testacei napolitani al Sig. D. Carlo Tarentino prof. di storia naturale nel R. Liceo di Catanzaro*. Napoli [privately printed] 6 p.
- Schubert, H.G. & Wagner, J.A. 1829. *Neues Systematisches Conchylien-Cabinet Angefangen von Martini und Chemnitz. Vol. 12*. Bauer & Raspe, Nürnberg, xii + 196 pp., pls. 214-237.
- Schultz, O. 1998. *Tertiärfossilien Österreichs*. Goldschneck-Verlag, Weinstadt, 159 pp.
- Schumacher, C.F. 1817. *Essai d'un nouveau système des habitations des vers testacés*. Schultz, Copenhagen: iv + 288 pp., 22 pls.
- Semper, O. 1861. Beiträge zur Kenntniss der Tertiärformation. *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg* 15: 221-409.
- Shikama, T. 1973. Description of New Marine Gastropoda from the East and South China Seas. *Science Reports of the Yokohama National University* (sec.2) 20: 1-8.
- Sosso, M. & Dell'Angelo, B. 2010. *I fossili del Rio Torsero*. Prato (Editing Marginalia, Cartotecnica Beusi srl): 95 pp.
- Sowerby, G.B. I 1833-1834. [Characters 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 South Pacific Ocean]. *Proceedings of the Zoological Society of London* 1833: 16-22, 34-38 [17 May]; 52-56 [24 May]; 70-74 [20 September]; 82-85 [8 September]; 134-139. [16 April 1834].
- Swainson, W. 1840. *A treatise on malacology or shells and shell-fish*. London (Longman). viii + 419 pp.
- Thiele, J. 1929-1935. *Handbuch der systematischen Weichtierkunde*. Jena, Gustav Fischer, 1154 pp. Vol. 1 part 1: 1-376 [between 4 September and 21 October 1929]; Vol. 1 part 2: 377-778 [before 31 October 1931]; Vol. 2 part 3: 779-1022 [before 19 January 1934]; Vol. 2 part 4: i-iv, 1023-1154, i-vi for volume 1 [before 27 March 1935].
- Toula, F. 1901. Eine marine Neogenfauna aus Cilicien. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 51: 247-263.
- Valenciennes, A. 1832. Coquilles univalves marines de l'Amérique équinoxiale, recueillies pendant le voyage de MM. A. de Humboldt et A. Bonpland. In: *Humboldt, A. von & Bonpland, A. (Eds), Recueil d'observations de zoologie et d'anatomie comparée: faites dans l'océan atlantique, dans l'intérieur du nouveau continent et dans la mer du sud pendant les années 1799, 1800, 1801, 1802 et 1803*. Vol. 2: 262-339, pl. 57.
- 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(1): 23-61.
- Vanatta, E.G. 1913. Descriptions of new species of marine shells. *Proceedings of the Academy of Natural Sciences of Philadelphia* 65: 22-27.
- Venzo, S. & Pelosio, G. 1963. La malacofauna Tortoniana del Colle di Vigoleno (Preappennino Piacentino). *Palaeontographia Italica* 58: 43-213.
- Vermeij, G.J. 2001. Taxonomy, distribution, and characters of pre-Oligocene members of the *Cantharus* group of Pisaniinae (Neogastropoda: Buccinoidea). *Journal of Paleontology* 75: 295-309.
- Vermeij, G.J. 2004. The *Cantharus* group of pisaniine buccinid gastropods: Review of the Oligocene to Recent genera and description of some new species of *Gemophos* and *Hesperisternia*. *Cainozoic Research* 4: 71-96.
- Vokes, E.H. 1971. Catalogue of the genus *Murex* Linné (Mollusca: Gastropoda); Muricinae, Ocenebrinae. *Bulletins of American Paleontology* 61: 1-141.
- Watters, G.T. 2009. A revision of the western Atlantic Ocean genera *Anna*, *Antillophos*, *Bailya*, *Caducifer*, *Monostiolium*, and *Parviphos*, with description of a new genus, *Dianthiphos*, and notes on *Engina* and *Hesperisternia* Gastropoda: Buccinidae: Pisaniinae and *Cumia* (Colubrariidae). *The Nautilus* 123(4): 225-275.
- Woodring, W.P. 1928. *Miocene mollusks from Bowden, Jamaica, 2. Gastropods and discussion of results*. Washington (Carnegie Institution of Washington, DC): 564 pp.