

The Pliocene Gastropoda (Mollusca) of Estepona, southern Spain. Part 14: Clavatulidae (Gastropoda, Conoidea)

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Received 22 December 2021, revised version accepted 23 April 2022.

In this paper we review the Clavatulidae of the lower Piacenzian, upper Pliocene of Estepona, southern Spain. Ten clavatulid species; nine within the ‘*Clavatula*’ genus group representing the genera *Clavatula* (s.s.), ‘*Clavatula*’ (s.l.) and *Granulatocincta*, of which three are new: ‘*Clavatula*’ *iberica* nov. sp., ‘*Clavatula*’ *pliogradata* nov. sp., and ‘*Clavatula*’ *nana* nov. sp. One species is present representing the ‘*Perrona*’ genus group, which is described as new: *Tomellana postjouannetii* nov. sp.

Tomellana onubensis nov. sp. is described from the Atlantic lower Pliocene Guadalquivir Basin assemblage of Huelva, southwestern Spain. *Clavatula raffaëlei* Cipolla, 1914 is considered a junior subjective synonym of ‘*Clavatula*’ *romana* (Defrance, 1826). *Clavatula rugata* Bellardi, 1877 is considered a junior subjective synonym of *Granulatocincta rustica* (Brocchi, 1814).

In the Pliocene tropical Mediterranean-West African Palaeobiogeographical Province clavatulid diversity during MPPMU1 increases immediately adjacent to the Strait of Gibraltar on both the Mediterranean and Atlantic sides, and in the Atlantic decreases rapidly further north in the subtropical French-Iberian Province, reflecting the strongly thermophilic nature of the group that today is restricted to tropical West African waters. Clavatulids in the Estepona assemblages are strongly endemic (60%), which is in keeping with their non-planktotrophic mode of development.

KEY WORDS: southern Spain, upper Pliocene, Gastropoda, Clavatulidae, Conoidea, new species

Introduction

In this paper we continue to revise the astoundingly diverse Pliocene assemblage of Estepona in south-western Spain (see Landau & Micali, 2021, p. 160 for other references to this series). The Clavatulidae from Estepona were initially discussed in a doctoral thesis submitted to the University of Malaga (date of thesis 1996 or 1997; both dates quoted in the taxonomic chresonymies of Vera-Peláez, 2002, but dated 1996 in the references section of that paper; the year 1996 used herein, which is the date on the front page of the copy available to the present authors). Subsequently his findings were published together with his wife in Vera-Peláez & Lozano-Francisco (2001a) together with a description of the Clavatulidae from the Atlantic lower Pliocene Guadalquivir Basin of south-western Spain. This was followed in the same year by a synthesis paper on the palaeobiogeography and palaeoecology of the group in the Iberian Pliocene (Vera-Peláez & Lozano-Francisco, 2001b).

Traditionally, the European Neogene clavatulids have been divided into two main groups by all authors: *Clavatula* Lamarck, 1801 for sculptured forms, and *Perrona*

Schumacher, 1817 for more or less smooth species. Other genera such as *Pusionella* Gray, 1847 have also been recognised in the European Neogene, but do not occur in the European Pliocene. Many authors have adopted a relatively wide species concept for some species [e.g.: *Clavatula interrupta* (Brocchi, 1814), *C. rustica* (Brocchi, 1814), *Perrona jouannetii* (Des Moulins, 1842)], which on closer examination represent several species that are in some cases not even closely related. Moreover, these identifications of the same species in geographically and stratigraphically disparate deposits have been uncritically repeated by subsequent authors giving many species an artificially wide distribution and geological longevity.

In this work we adopt a similar taxonomic methodology as that used by Harzhauser *et al.* (2022) in their revision of the clavatulids from the Miocene Paratethys and critically revise their distribution, especially in relation to their presence in the Miocene Paratethys.

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 (Landau & Jansen, 2015a, 2015b Landau *et al.*, 2015; Landau & Mulder, 2020; Landau & Micali, 2021) we have dated the assemblages as earliest Piacenzian, early late Pliocene, an age corroborated by the assemblage of Euthecosomata (Janssen, 2004). Either way, they form part of the Mediterranean ecostratigraphic unit MPPMU1 of Raffi & Monegatti (1993) and Monegatti & Raffi (2001), which includes the Zanclean and earliest Piacenzian (see Landau *et al.*, 2011, text-fig. 9).

Material and methods

The material described herein was collected from several localities around Estepona by the senior author (BL; 1997-2020) and by Henk Mulder (between 2008-2021), to whom we are extremely grateful for his tireless efforts and generosity in making his collection available to us. For a map of localities see Landau *et al.* (2003, p. 4, text-fig. 1). The material is housed in the Natural History Museum Vienna (NHMW).

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

The protoconch of almost all known clavatulid species is paucispiral, or possibly lecithotrophic, and almost always

unsculptured (exceptions occur such as *Scaevatula* Gofas, 1990, which has a ribbed protoconch, but does not occur in the Mediterranean Pliocene). This paucispiral type of protoconch is suggestive of direct development, or at least a short planktotrophic phase, which tends to lead to stratigraphically short lived and geographically restricted species. This is certainly the pattern that emerges once their classification in the fossil assemblages is critically revised and is still seen today where many clavatulid species have relatively restricted geographical distributions.

Following Harzhauser *et al.* (2022) increased taxonomic significance has been given to the neanic whorls.

We have adopted the shell terminology used by Harzhauser *et al.* (2022, p. 8; Fig. 1 *hoc opus*) in which the shells are categorised as small (SL < 20.0 mm), medium-sized (20-40 mm), moderately large (40.1-60 mm), large (60.1-80 mm), and very large (SL > 80.1 mm). For the statistical analysis of the morphometric data, we evaluated aperture length (AL), aperture width (AW), last whorl height (LWH), aperture height (AH), aperture length (AL) and length of siphonal canal (SiL) to derive following ratios (Fig. 2): SL/MD, AH/SL, AL/AW and AH/SiL. The SL/MD ratio is an expression of slenderness of the shell. To be objective in the descriptions we define shell shapes of the Estepona Clavatulidae as follows: broad (SL/MD < 2.5), moderately broad, (SL/MD = 2.5-2.7), moderately slender (SL/MD = > 2.7-3.3), slender (SL/MD > 3.3). The relative width of the aperture is calculated as aperture length (AL) versus aperture width (AW). Apertures are described as moderately narrow (AL/AW > 4.0), moderately wide (AL/AW = 4.0-3.1) and wide (AL/AW < 3.1). The siphonal canal length is categorised

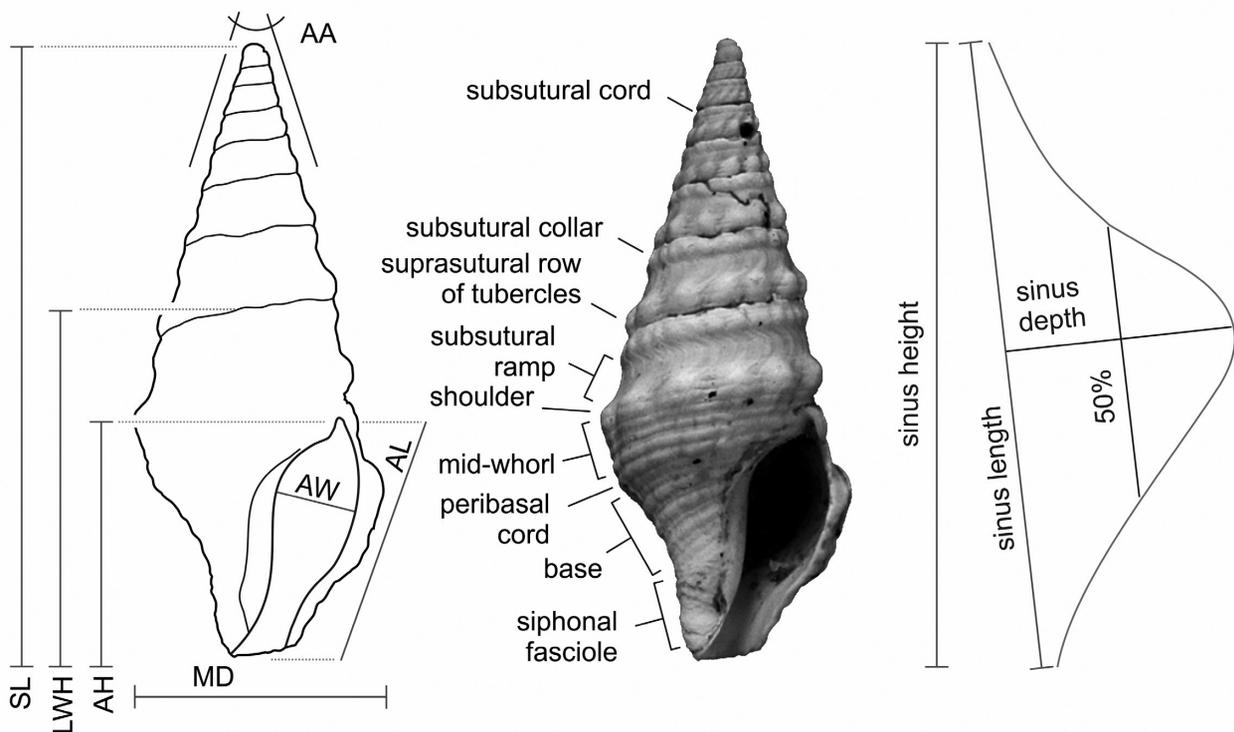


Figure 1. Descriptive terms used in descriptions and measurements to shell morphology, whorl profiles and anal sinus. SL: shell length, MD: maximum diameter, AA: apical angle, LWH: last whorl height, AH: aperture height. AL: aperture length. AW: aperture width (adapted from Harzhauser *et al.*, 2022).

as follows: long (SL/SiL <4.2), moderately long (SL/SiL = 4.2-<5.3), moderately short (SL/SiL = 5.3-<6.8), short (AH/SiL \geq 6.8). The depth of the anal sinus is described as deep (SinW/SinD = <2.5), moderately deep (SinW/SinD = 2.5->3.5), moderately shallow (SinW/SinD = 3.5-5) and very shallow (SinW/SinD = >9) (note that the category between 5 and 9 is not realised in our data set). The width of the anal sinus is evaluated by the ratio between the maximum width of the sinus (SinW) and the width of the sinus at the half of its depth (SinW50). It is categorised as wide (SinW/SinW50 = <1.5), moderately wide (SinW/SinW50 = 1.5-2.0), moderately narrow (SinW/SinW50 = >2-2.5) and narrow (SinW/SinW50 = >2.5).

In all Conoidea the anal sinus is an important character, and often useful for separation at both generic and species level. In clavatulids the sinus is well-developed and clearly preserved in all species. There is some variability in the shape of the sinus, as seen in Fig. 2, where three sinuses have been drawn for each species. Nevertheless, it remains a useful taxonomic character.

On early teleoconch whorls the sinus can be represented by comma-shaped axial riblets mid-whorl, sometimes swollen, but these are not ribs. Ribs are uncommon in clavatulids, and when present are poorly defined and formed by axially aligned rows of tubercles (*i.e.*, ‘*Clavatula nana*’ nov. sp.) and are only present on the last whorl below the shoulder. For further discussion on the anal sinus and other clavatulid shell morphology, see Harzhauser *et al.* (2022, p. 12-19).

Abbreviations:

CO: Velerín conglomerates; **PA:** Rio del Padrón; **VC:** Velerín Carretera; **VA:** Velerín Antena; **PQ:** Parque Antena; **EL:** El Lobillo; see Landau *et al.* (2004, p. 4, text-fig. 1).
NHMW Natural History Museum Vienna (Austria)
MMPE Museo Municipal de Paleontología de Estepona (Málaga).
RGM Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

Protoconch measurements:

dp = diameter protoconch, **hp** = height protoconch, **dp/hp** = diameter/height protoconch, **dv1** = diameter first protoconch whorl, **n** = diameter nucleus.

Superfamily Conoidea J. Fleming, 1822

Family Clavatulidae Gray, 1853

In their molecular phylogeny Puillandre *et al.* (2011, p. 269) found Clavatulidae to be a well-supported clade, further supported by Abdelkrim *et al.* (2018, p. 2359). In their (Puillandre *et al.*, 2011) work on the extant species, four genera were recognised: *Clavatula* Lamarck, 1801 and *Perorona* Schumacher, 1817 were considered genetically very similar. *Pusionella* Gray, 1847, is not present in the Estepona assemblages, and *Turricula* Schumacher, 1817, which has been used by recent authors (*e.g.*, Chirli, 1997; Scarponi & Della Bella, 2004; Bařuk, 2003; *inter alia*) for several Pliocene Mediterranean species. These species should be placed in the genera *Knefastia* Dall, 1919 or *Comitas* Finlay, 1926 (both Pseudomelatomidae), and are excluded herein. More recent molecular data of Nicolas Puillandre (pers. comm. 2021, *in* Harzhauser *et al.*, 2022, p. 19) suggests that *Clavatula*, as currently perceived, is not monophyletic, but consists of several clades, which was supported by Harzhauser *et al.* (2022, p. 20) based on conchological data.

These authors distinguished the following clades (all based on present-day species):

1. *Clavatula* (*C. regia*, *C. muricata*, *C. rubrifasciata*, *C. lelieuri*)
2. *caerulea*-clade (‘*C.*’ *caerulea*, ‘*C.*’ *pyramidata*)
3. *mystica*-clade (‘*C.*’ *mystica*)
4. *bimarginata*-clade (‘*C.*’ *bimarginata*)
5. *taxea*-clade (‘*C.*’ *taxea*, ‘*C.*’ *tripartita*)
6. *diadema*-clade (‘*C.*’ *diadema*)

For further discussion on these clades see Harzhauser *et al.* (2022).

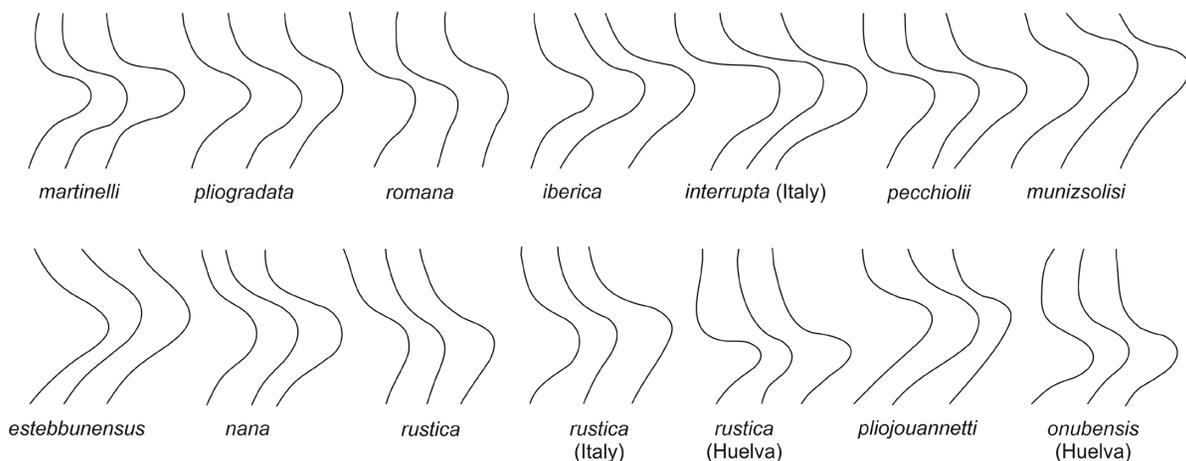


Figure 2. Anal sinus morphology of Estepona Clavatulidae. Three sinuses drawn per species to illustrate intraspecific variability (adapted from Harzhauser *et al.*, 2022).

In the fossil literature two genera have been recognised: *Clavatula* Lamarck, 1801 and *Perrona* Schumacher, 1817. Although neither of these are monophyletic, we provisionally divide the genera and species groups in the *Clavatula*-like species groups that are usually strongly sculptured and the *Perrona*-like species groups that are usually smooth, or almost so, have a rounded shoulder and poorly delimited base and siphonal fasciole.

Clavatula-like species groups

Genus *Clavatula* Lamarck, 1801

Type species – *Clavatula coronata* Lamarck, 1801 [= *Turris regia* Röding, 1798], by monotypy, present-day, West Africa.

1801 *Clavatula* Lamarck, p. 84.

Note – Harzhauser *et al.* (2022) considered a bipartite neanic whorl sculpture, with a weak, smooth adapical subsutural cord and a prominent suprasutural cord bearing large beads as diagnostic for the genus. The fossil record will need to be re-evaluated, but the oldest confirmed species is *Clavatula sorini* Harzhauser, Landau & Janssen, 2022 from the Langhian of the Central Paratethys. Today it is represented by *C. regia* Röding, 1798 (= *C. coronata* Lamarck, 1801), *C. muricata* (Lamarck, 1822), *C. rubrifasciata* (Reeve, 1845), and *C. lelieuri* (Récluz, 1851). This group is not represented in the Mediterranean Pliocene.

'*Clavatula*' (s.l.): *Clavatula caerulea* (Weinkauff in Weinkauff & Kobelt, 1875) clade

Note – Species placed in the *caerulea*-clade are characterised by their medium-small sized shell, slender fusiform profile with a relatively high spire and short last whorl, and bipartite early whorl sculpture. The *caerulea*-clade comprises the West African species '*Clavatula caerulea*' (Weinkauff in Weinkauff & Kobelt, 1875) and

'*Clavatula*' *pyramidata* (Kiener, 1840). Both differ from *Clavatula* in their slenderer shells and the higher spire. '*Clavatula*' *martinelli* Vera-Peláez & Lozano-Francisco, 2001 is most similar to members of this clade in which we provisionally place it. It would be the oldest member of the clade, which is not represented further east within the Pliocene Mediterranean.

'*Clavatula*' *martinelli* Vera-Peláez & Lozano-Francisco, 2001

Pl. 1, figs 1-3.

1996 *Clavatula* sp. 1 – Vera-Peláez, p. 234, pl. 11, figs 6-14.

*2001a *Clavatula martinelli* Vera-Peláez & Lozano-Francisco, p. 13, pl. 3, figs 1-9, pl. 4, figs 4-5, pl. 8, fig. 13.

Material and dimensions – Maximum height 17.2 mm, width 6.4 mm. **CO:** NHMW 2020/0171/0304-0306 (3), NHMW 2020/0171/0307 (50+). **EL:** NHMW 2020/0171/0308 (5)

Description – Shell small, moderately broad, with tall, conical spire (spire angle ~34°) and relatively short last whorl. Protoconch small, paucispiral, composed of two convex whorls, with large nucleus, junction marked by sinusigera (dp = 750-800 μm, hp = 550-600 μm, dp/hp = 1.33-1.36, dV1 = 450-500 μm, n = 300-400 μm). Teleoconch of up to eight whorls, concave mid-whorl, with periphery at suprasutural cord, separated narrowly impressed, irregular suture. Sculpture on first teleoconch whorl of arcuate riblets crossed by three cords. On second whorl riblets weaken mid-whorl and become swollen above abapical suture. From third whorl sculpture bipartite; narrow beaded subsutural cord, smooth concave mid-portion, suprasutural cord bearing row of larger, rounded tubercles. Last whorl moderately short, 53-56% total height, with narrow, rounded subsutural collar bearing small to medium-sized tubercles; mid-width concave subsutural ramp delimited by shoulder bearing 12-15 strong, rounded tubercles; convex below, moderately constricted

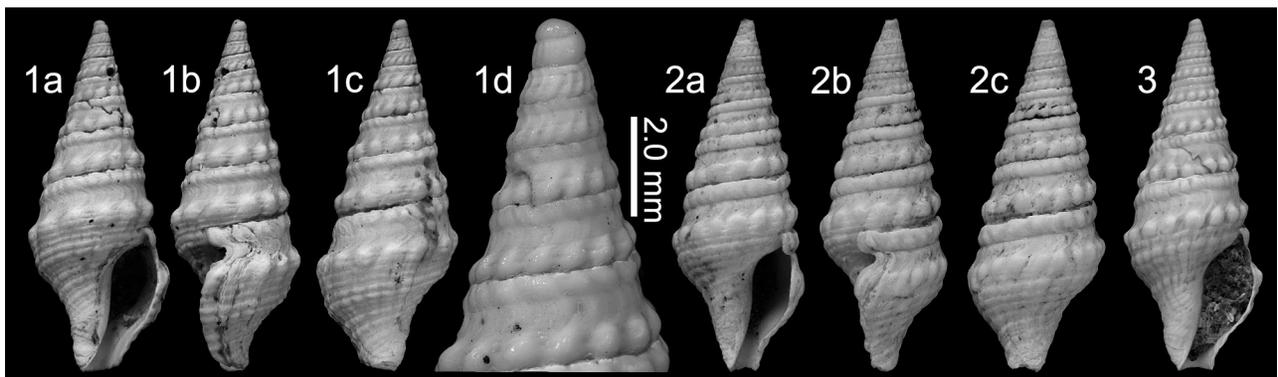


Plate 1. '*Clavatula*' *martinelli* Vera-Peláez & Lozano-Francisco, 2001; 1. NHMW 2020/0171/0304, height 15.8 mm, width 6.5 mm, 1d, detail of protoconch; 2. NHMW 2020/0171/0305, height 16.9 mm, width 6.5 mm; 3. NHMW 2020/0171/0306, height 15.6 mm, width 6.1 mm (digital images). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene.

at base, sculpture below shoulder of weakly tubercular cords, peribasal cord developed variably. Siphonal fasciole weakly delimited, flattened, bearing finer non-tubercular cords. Aperture moderately wide, relatively short, 35-38% total height, outer lip simple; anal sinus deep, narrow, symmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately short, open, recurved, unnotched. Columella excavated in adapical third, straight below, twisted at siphonal canal. Columellar callus thickened forming narrow callus margin.

Discussion – ‘*Clavatula*’ *martinelli* Vera-Peláez & Lozano-Francisco, 2001 is similar in profile and sculpture to the extant West African ‘*C.*’ *caerulea* (Weinkauff in Weinkauff & Kobelt, 1875), but the present-day species has an even higher spire, comparatively lower last whorl, the shoulder tubercles are less well developed than in ‘*C.*’ *martinelli*, and the siphonal canal is wider. ‘*Clavatula*’ *pyramidata* (Kiener, 1839), is even more similar, with similar strength tubercles developed on the suprasutural cord and shoulder, but differs again in having a higher coeloconoid spire, shorter last whorl, and wider siphonal canal. There are no particularly similar species in the Mediterranean Pliocene. *Clavatula ruida* Bellardi, 1877 originally described from the upper Miocene of Italy, but also recorded from the Pliocene (see Scarponi & Della Bella, 2004, figs 25, 26), is superficially similar in profile, but has finely beaded rather than tubercular sculpture. The neanic whorls differ in that the axial ribs are strong along the entire whorl height forming tubercles at each suture, larger at the abapical, whereas in ‘*C.*’ *martinelli* the ribs fade mid-whorl from the second whorl and the neanic whorl sculpture is bipartite. *Clavatula ruida* does not belong within the ‘*C.*’ *caerulea* clade.

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

‘*Clavatula*’ (*s.l.*): *Clavatula bimarginata* (Lamarck, 1822) clade

Note – Species placed in the *bimarginata*-clade are char-

acterised by their slender fusiform profile, bipartite neanic whorl sculpture with a granulose subsutural cord and suprasutural spiral cord of equal strength with indistinct, bifid beads, separated by a moderately concave interspace bearing prominent, comma-shaped axial riblets formed by growth lines. Spiral threads form a somewhat cancellate pattern especially in the abapical half of the whorls.

‘*Clavatula*’ *pliogradata* nov. sp.

Pl. 2, fig. 1.

2004 *Clavatula* aff. *gradata* (Defrance, 1826) – Scarponi & Della Bella, p. 32, pl. 4, figs 19-20, 46.

Type material – Holotype NHMW 2020/0171/0309, height 17.4 mm, width 6.5 mm.

Other material – Known from holotype and specimens illustrated by Scarponi & Della Bella (2004, pl. 4, figs 19-20, 46) from “Villa Filicaia”, Montaione, Firenze, Italy (5 specimens).

Type locality – El Lobillo, Estepona, Spain.

Type stratum – unnamed formation of early Piacenzian age.

Etymology – Compound name reflecting similarity to the species *Clavatula gradata* (Defrance, 1826). *Clavatula* gender feminine.

Diagnosis – *Clavatula* species of relatively small size, broad biconic, bipartite early whorls with abapical row of tubercles stronger than adapical, riblets mid-whorl, later whorls with narrow beaded subsutural cord, smooth concave mid-portion, broad suprasutural band overrun by 2-4 cords, anal sinus moderately deep, narrow, asymmetrically U-shaped, siphonal canal moderately short.

Description – Shell small, solid, broad biconic, with tall, conical spire (spire angle 37°). Protoconch small, paucispiral (dp = 400 μm, hp = 340 μm, dp/hp = 1.18; surface abraded). Teleoconch of up to eight whorls, separated by

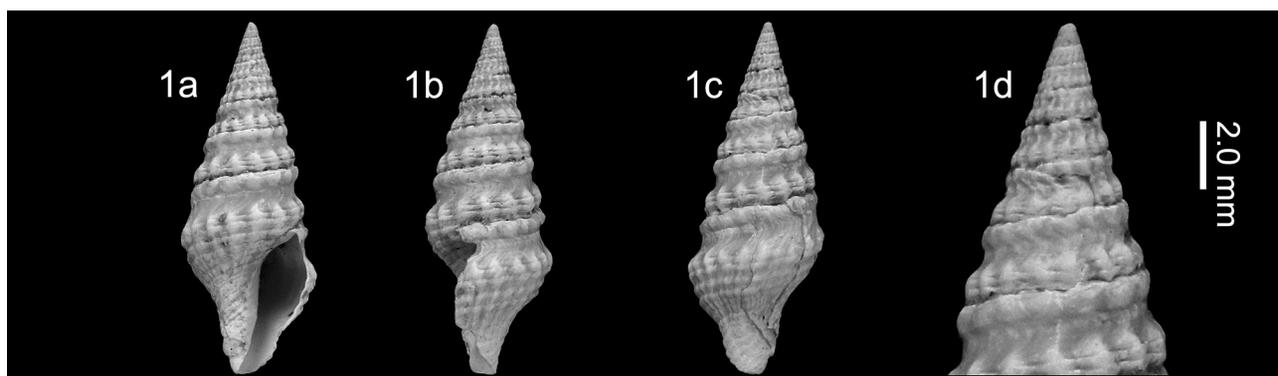


Plate 2. ‘*Clavatula*’ *pliogradata* nov. sp.; 1. **Holotype** NHMW 2020/0171/0309, height 17.4 mm, width 6.5 mm, 1d, detail of early teleoconch whorls (digital images). El Lobillo, Estepona, lower Piacenzian, upper Pliocene.

deeply impressed undulating suture. Sculpture on early whorls bipartite with granulose subsutural spiral cord and slightly broader, more strongly granulose, abapical cord, central portion concave bearing prominent opisthocyrt axial riblets formed by growth lines. On later whorls subsutural collar rounded, relatively narrow, tubercles coalescent on last two whorls; riblets on concave mid-portion weaken, smooth on last two whorls; abapical band broadest, overrun by 2-4 spiral cords, interrupting tubercles. Last whorl 55-57% of total height, with moderately developed subsutural collar, concave subsutural ramp, shoulder moderately angled, bearing 16-18 tubercles, weakly convex below, weakly constricted at base, sculpture on shoulder and below of relatively broad, weakly tubercular spiral cords of roughly alternating strength, peribasal cord weakly developed. Siphonal fasciole weakly delimited, flattened, bearing non-tubercular spiral cords. Aperture moderately wide, elongated, 40% total height, outer lip simple; anal sinus moderately deep, narrow, asymmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately short, open, slightly twisted to left, unnotched. Columella shallowly excavated, twisted at siphonal canal. Columellar callus weakly thickened forming narrow callus margin.

Discussion –The shell, profile and neanic whorl sculpture place this species in the ‘*Clavatula*’ *bimarginata* (Lamarck, 1822) clade. It differs from the extant West African ‘*C.*’ *bimarginata* in having less well-developed tubercles on the subsutural collar and having much weaker spiral sculpture, especially below the shoulder on the last whorl.

The specimen from Estepona is undoubtedly conspecific with that illustrated by Scarponi & Della Bella (2004, pl. 4, figs 19-20, 46) as *Clavatula* aff. *gradata* (Defrance, 1826) from the lower Pliocene of Italy.

Pleurotoma gradata erected by Defrance (1826, p. 393) includes several distinct species from: “*Sienna, environs de Bordeaux et d’Angers*”. Bellardi (1847, p. 29, pl. 2, fig. 4) stated the locality only as “*colle di Torino*” (= Colle della Maddalena), without specifying the locality of his figured specimen. Bellardi (1877, p. 185) considered his specimen earlier identified as *P. gradata* to represent a juvenile specimen of *Clavatula defrancii* Bellardi, 1877. Glibert (1954, p. 19) referred to Siena as the first locality cited and therefore regarded the Pliocene form as typical by citing Bellardi 1877. However, he went on to say “*il me semble que la véritable gradata est la coquille d’Italie décrite et figurée par L. Bellardi, en 1877*”. Bellardi does not state where the figured specimen is from. Only for his ‘variety A’ he gives the locality of Stazzano, Tortonian, upper Miocene. If one regards Glibert’s statement as a first revisers action and restrict the name to the Pliocene form, this would neglect the fact that Bellardi’s figure (1877, pl. 5 f. 39) actually refers to his Var. A from Stazzano, *i.e.* the Tortonian form. The locality was confirmed by Ferrero Mortara *et al.* (1981, p. 77), and is the type of Sacco’s (1904, p. 48) var. *carinulata*. Therefore, the Pliocene form has not been explicitly redescribed or figured by early Italian authors, but the name usually applied to Tortonian material for which the correct name is ‘*Clavatula*’ *carinulata*

Sacco, 1904. In the Aquitaine Basin of France the taxon has not been mentioned again, however, it was described and figured in the middle Miocene Langhian Loire Basin by Peyrot (1938, p. 266, pl. 4, fig. 17). These specimens were renamed *C. neogradata* by Glibert, 1954, p. 18) under the assumption that typical *gradata* was a Pliocene species. Peyrot (1938, p. 266) said that he had examined syntypes of *gradata* and therefore one can assume that his interpretation of this taxon is correct. He mentions its occurrence at Sceaux (= environs d’Angers) as common (see also Landau *et al.*, 2020, p. 84, pl. 74, figs 1-4).

In order to resolve this issue, we suggest that the taxon *gradata* should be restricted to the population of the Loire Miocene, with the type locality of Sceaux-d’Anjou. *Clavatula neogradata* Glibert, 1954 therefore becomes a synonym of ‘*C.*’ *gradata*. The Pliocene form is described as ‘*Clavatula*’ *pliogradata* nov. sp. We would like to thank Ronald Janssen for helping us untangle this complicated historic taxonomy.

Montanaro (1937, pl. 8, figs 39-50) illustrated numerous specimens from the Tortonian of Montegibbio (Italy), which refer to ‘*Clavatula*’ *carinulata* Sacco, 1904. The Miocene species differs from the Pliocene form in having much narrower and less elevated adsutural cords resulting in a broader concave mid-portion, and the peribasal cord is well developed.

Distribution – Lower Pliocene: central Mediterranean, Italy (Scarponi & Della Bella, 2004). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper).

***Clavatula* (s.l.): *Clavatula mystica* (Reeve, 1843) clade**

Note – Species placed in the *mystica*-clade are characterised by shells with a slender to stout biconic profile, the first teleoconch whorls are flat-sided, bearing weak opisthocline axial ribs, grading into three spiral rows of beads (tripartite sculpture), the suprasutural spiral row most prominent. On later whorls the shoulder is prominent (Harzhauser *et al.*, 2022, p. 29). Species in this group differ from *Clavatula* (s.s.) in having tripartite early whorl sculpture, *Clavatula* (s.s.) has bipartite neanic whorls. The only Paratethyan species placed in this group is ‘*Clavatula*’ *romana* (Defrance, 1826) which also occurs throughout the Pliocene Mediterranean and is an unusually long-lived and widely distributed clavatulid. Today the group is represented in West Africa by ‘*Clavatula*’ *mystica* (Reeve, 1843)

‘*Clavatula*’ *romana* (Defrance, 1826)

Pl. 3, figs 1-6.

- *1826 *Pleurotoma romana* Defrance, p. 393.
- 1861 *Pleurotoma exoleta* Costa, p. 85, pl. 3, fig. 9.
- 1862 *Pleurotoma asperulatum* Lk. – Brugnone, p. 11, pl. 1, fig. 5 [*non Clavatula asperulata* (Lamarck, 1822)].

- 1864 *Pleurotoma Mortilleti* (Mayer) – Mortillet, p. 335, 344 (*nomen nudum*).
- 1864 *Pleurotoma Mortilleti* Mayer, p. 163, pl. 8, fig. 3.
- 1866 *Pleurotoma stozzii* Semper, p. 280.
- 1875 *Pleurotoma Mortilleti* var. *minor* Seguenza, p. 206 [*nom. nov. pro Pleurotoma asperulatum* Brugnone, 1862, *non* Lamarck, 1822]
- 1877 *Clavatula romana* (Defr.) – Bellardi, p. 172, pl. 5, fig. 36.
- 1891 *Pleurotoma* (8. *Clavatula*) *Romana* Defr. – Hoernes & Auinger, p. 339, pl. 43, fig. 4.
- 1896 *Clavatula romana* (Defr.) – Cossmann, p. 65, pl. 5, fig. 2.
- 1914 *Clavatula Raffaëlei* Cipolla, p. 127 [23], pl. 12 [1], fig. 19.
- 1914 *Clavatula Romana* Defrance [*sic*] – Cipolla, p. 128 [24], pl. 12 [1], fig. 20.
- 1938 *Clavatula romana* Defrance [*sic*] – Stchepinsky, p. 86, pl. 8, fig. 14.
- 1959 *Clavatula raffaëlei* Cipolla, 1914 – Ruggieri & Curti, p. 122, pl. 30, fig. 172.
- 1959 *Clavatula romana minor* (Seguenza) – Ruggieri & Curti, p. 122, pl. 30, fig. 173, 174.
- 1967 *Clavatula (Clavatula) romana* (Defrance, 1826) – Palla, p. 995, pl. 75, fig. 7.
- 1974 *Trachelochetus romanus* (Defrance, 1826) – Malatesta, p. 415, pl. 31, fig. 20.
- 1978 *Clavatula romana* Defrance – Cuscani Politi, p. 50, pl. 6 figs. 18-19.
- 1979 *Trachelochetus romanus* (Defrance, 1826) – Malatesta, p. 415, pl. 31, fig. 20.
- 1996 *Trachelochetus romanus* (Defrance, 1826) – Vera-Peláez, p. 255, text-figs 8a-c, 9f, pl. 13, figs 10-13; pl. 15, fig. 3.
- 1997 *Trachelochetus romanus* (De France [*sic*], 1826) – Chirli, p. 32, pl. 9, figs 1-4.
- 2001a *Clavatula romana* (Defrance, 1826) – Vera-Peláez & Lozano-Francisco: p. 11, pl. 1, figs 12-13, pl. 6, figs 7-8, pl. 8, fig. 6.
- 2004 *Clavatula (Trachelochetus) romana* (Defrance, 1826) – Scarponi & Della Bella, p. 35, figs 29-31, 50.
- 2018 *Clavatula romana* (Defrance, 1826) – Brunetti & Cresti, p. 88, fig. 347.
- 2022 ‘*Clavatula*’ *romana* (Defrance, 1826) – Harzhauser *et al.*, p. X, figs 12A₁–A₃, 4E, 5, 7.
- non 1993 *Clavatula (Trachelochetus) cf. romana* (Defrance, 1826) – González Delgado, p. 28, pl. 2, figs 7, 8 (= *Clavatula iberoechinata* Vera-Peláez & Lozano-Francisco, 2001a).
- non 1997 *Clavatula cf. romana* (Defrance) – Ruiz Muñoz *et al.*, p. 100, pl. 39, figs 1, 2 (= *Clavatula landaui* Vera-Peláez & Lozano-Francisco, 2001a).

Material and dimensions – Maximum height 39.0 mm, width 14.6 mm. **CO:** finely sculptured form: NHMW 2020/0171/0312-0314 (3), NHMW 2020/0171/0315 (1), coarsely sculptured form: NHMW 2020/0171/0316-0318 (3), NHMW 2020/0171/0319 (1).

Description – Shell medium-sized, solid, biconic, moderately broad, with tall, conical spire (spire angle rather variable, 34.5-40°). Protoconch not preserved (paucispiral, composed of about two convex whorls, with large nucleus, junction marked by sinusigera, *vide* Scarponi & Della Bella, 2004, fig. 50). Teleoconch of up to nine whorls, concave mid-whorl, with periphery at suprasutural cord, separated by narrow, irregularly undulating suture. Early teleoconch whorls flat-sided with tripartite sculpture; indistinctly beaded subsutural spiral cord, central cord of similar width, suprasutural cord with slightly larger beads. Beads arranged axially into opisthocline ribs. On fifth to sixth whorl adapical row forms sharply delimited subsutural collar bearing small tubercles, central row weakens leaving concave mid-portion of whorl smooth, except for deeply sinuous axial growth lines, suprasutural row of beads become larger and less numerous. Reduction in number of beads variable, resulting in finely sculptured (Pl. 3, figs 1-3) and coarsely sculptured (Pl. 3, figs 5-6) forms with intermediate specimens (Pl. 3, fig. 4). Last whorl tall, 61-65% total height, subsutural collar with small tubercles weakening towards aperture, concave subsutural ramp with a few weaker secondary cords developed, delimited by strongly tubercular shoulder bearing 15-18 (coarsely sculptured form) – up to 32 (finely sculptured form) tubercles, convex below, moderately constricted at base, sculpture below shoulder of weakly tubercular cords, peribasal cord developed variably. Siphonal fasciole not delimited, flattened, bearing non-tubercular spiral cords. Aperture moderately wide, elongated, 44- 47% total height, outer lip simple, bearing lirae deeply within in some specimens; anal sinus moderately shallow, narrow, asymmetrically U-shaped, with apex mid-ramp; siphonal canal moderately short, open, slightly recurved, unnotched. Columella straight, twisted at siphonal canal. Columellar callus weakly thickened forming narrow callus margin.

Discussion – This species is problematic. Both in the Italian Pliocene and in the Pliocene of Estepona a finely (Pl. 3, figs 1-3; Scarponi & Della Bella, 2004, pl. 5, fig. 31) and coarsely (Pl. 3, figs 5-6; Scarponi & Della Bella, 2004, pl. 5, fig. 30) sculptured form is present. These would seem to represent different species; however, intermediate forms occur (Pl. 3, fig. 5; Scarponi & Della Bella, 2004, pl. 5, fig. 29) and the early whorls are indistinguishable (Pl. 3, fig. 1c, 4c). Moreover, the presence or absence of lirae within the outer lip seems to be an intraspecifically variably feature in this species. It is also an unusually long-lived and geographically extensive species, as the specimen from the middle Miocene Paratethys of Slovakia illustrated by Harzhauser *et al.* (2022, p. 31, fig. 12 A₁–A₃) is identical to coarsely sculptured form. We therefore follow Scarponi & Della Bella (2004, p. 35) in considering ‘*C.*’ *romana* a highly variable species.

The genus/subgenus *Trachelochetus* Cossmann, 1889 (Type species *Pleurotoma desmia* Edwards, 1857, Eocene, France) was based on having a high spire, a short last whorl, a mid-whorl angulation on the spire whorls, lirae within the outer lip, and a straight siphonal canal. *Pleu-*

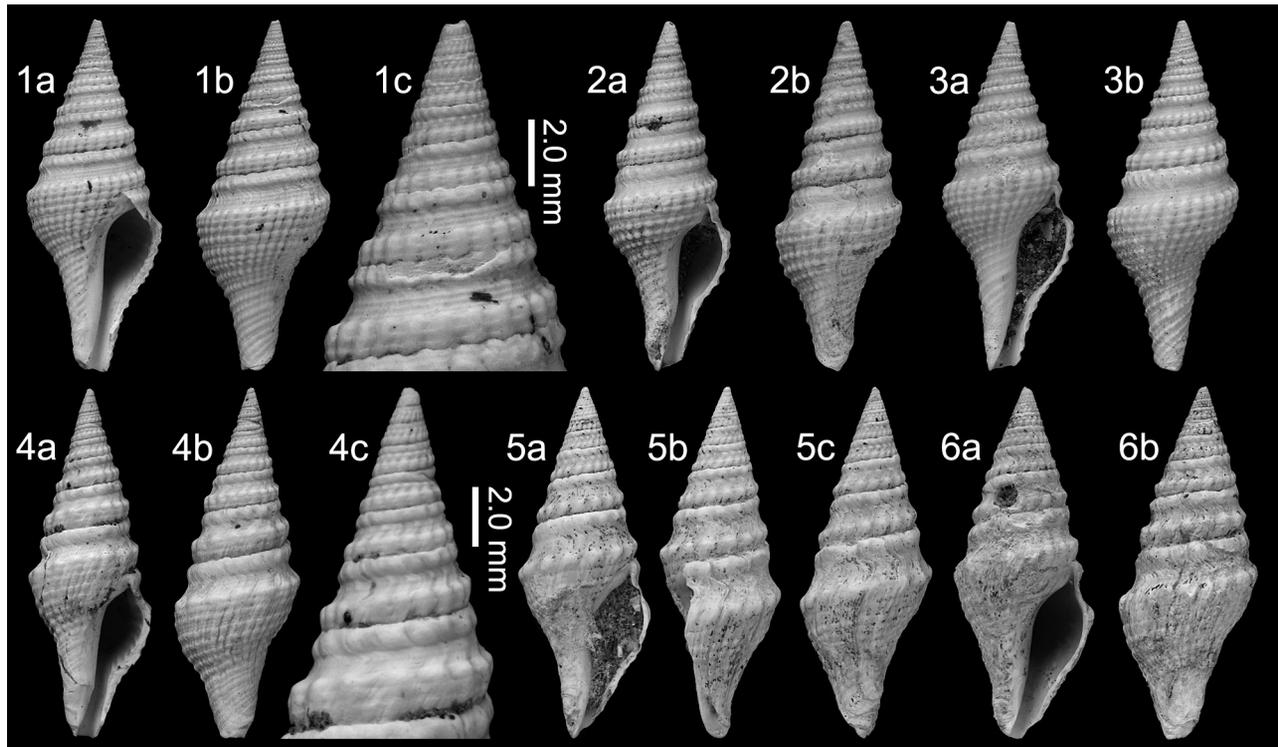


Plate 3. *Clavatula romana* (DeFrance, 1826); 1-3. Finely sculptured form; 1. NHMW 2020/0171/0312, height 32.4 mm, width 12.3 mm, 1c, detail of early teleoconch whorls; 2. NHMW 2020/0171/0313, height 34.8 mm, width 12.3 mm; 3. NHMW 2020/0171/0314, height 32.5 mm, width 11.9 mm; 4-6. Coarsely sculptured form; 4. NHMW 2020/0171/0316, height 28.7 mm, width 9.5 mm, 4c, detail of early teleoconch whorls; 5. NHMW 2020/0171/0317, height 25.7 mm, width 9.1 mm; 6. NHMW 2020/0171/0318, height 28.8 mm, width 11.3 mm (digital images). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene.

rotoma romana DeFrance, 1826 has been placed in that genus by authors (e.g., Scarponi & Della Bella, 2004; *inter alia*) due to the unnotched siphonal canal and the presence of lirae within the outer lip, absent in *Clavatula* species (Powell, 1966, p. 58). However, the overall shell shape is quite different, and any similarities are most likely superficial.

Clavatula romana shares a similar tripartite neanic whorl sculpture with *C. interrupta* (Brocchi, 1814). It differs however in its later teleoconch whorls which are more angular, the mid-portion of the whorls more deeply concave, fewer, less tuberculose axial ribs, and lacking well-developed beaded cords below the shoulder on spire whorls (for further discussion see below under *Clavatula interrupta* group).

In Estepona this species is found only in the shallower water deposits, which agrees with the infra- and circalittoral distribution given by Scarponi & Della Bella (2004). *Clavatula raffaëlei* Cipolla, 1914 was erected based on a single specimen from the Italian upper Pliocene of Altavilla (same specimen illustrated by Ruggieri & Curti, 1959, pl. 30, fig. 173, 174). It seems to the present authors to represent a very strongly and coarsely sculptured form of *C. romana* and is considered a junior subjective synonym herein.

Clavatula iberoechinata Vera-Peláez & Lozano-Francisco, 2001 from the Atlantic lower Pliocene Guadal-

quivir Basin of Spain is superficially similar in having a broad biconic profile, but differs in being even more broadly biconic, with coarser sculpture, fewer and even larger tubercles developed at the periphery than in the coarser variety of *C. romana*, and the subsutural row of tubercles develops open spines. The neanic whorls are usually poorly preserved in the Guadalquivir Basin material, but they are quite different from those of the *Clavatula mystica* (Reeve, 1843) clade in having arcuate riblets on the first one or two whorls and later whorls bipartite, on third whorl subsutural cord with small tubercles, suprasutural row with larger tubercles, mid-portion with narrow arcuate riblets that fade by the fourth whorl leaving weakly concave mid-portion. *Clavatula landaui* Vera-Peláez & Lozano-Francisco, 2001 is another broadly biconic species from the Atlantic lower Pliocene Guadalquivir Basin of Spain that differs from both *C. romana* and *C. iberoechinata* in having much reduced finely tubercular sculpture. Although the first teleoconch whorl is worn in all specimens, later neanic whorls are clearly bipartite, with a narrow finely beaded subsutural cord, suprasutural cord with slightly larger tubercles; beads and tubercles subobsolete in some specimens, mid-portion very broad, concave, and smooth, except for inconspicuous arcuate growth lines.

Distribution – Middle Miocene: Paratethys, Slovakia

(Hoernes & Auinger, 1891; Harzhauser *et al.*, 2022). Upper Miocene: central Proto-Mediterranean, Tunisia (Stchepinsky, 1938). Lower Pliocene: western Mediterranean, eastern Spain (Marquina, 1988a); central Mediterranean: Italy (Chirli, 1997; Scarponi & Della Bella, 2004; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996; Vera-Peláez & Lozano-Francisco, 2001a); central Mediterranean: Italy (Bellardi, 1877; Cipolla, 1914; Ruggieri & Curti, 1959; Malatesta, 1974, 1979; Scarponi & Della Bella, 2004).

'*Clavatula*' mystica-clade: '*Clavatula*' interrupta group

Harzhauser *et al.* (2022, p. 30) recognised a species group within the *mystica*-clade that shared the tripartite neanic whorl sculpture of the *mystica*-clade, but differed in having a weaker subsutural collar, deeply concave mid-portion and more prominent, beaded suprasutural cord, the anal sinus is deeper than in the *mystica*-clade, the last whorl more strongly shouldered and more strongly constricted at the base. They included in the '*Clavatula*' *interrupta* group several Paratethyan species and considered the group type to be the well-known Mediterranean Miocene species '*Clavatula*' *interrupta* (Brocchi, 1814), which occurs in the middle Miocene Paratethys and Pliocene central Mediterranean but does not seem to occur in Estepona.

'*Clavatula*' iberica nov. sp.

Pl. 4, figs 1-3.

- 1993 *Clavatula* (*Clavatula*) *interrupta* (Brocchi, 1814) – González Delgado, p. 23, pl. 2, figs 3, 4 [*non* Brocchi, 1814].
- 1996 *Clavatula interrupta* (Brocchi, 1814) – Vera-Peláez (*partim*), p. 223, pl. 10, figs 1-7, 9 (only) [not pl. 10, figs 8, 10, pl. 15, fig. 1 = *Clavatula interrupta* (Brocchi, 1814)].
- 2001a *Clavatula interrupta* (Brocchi, 1814) – Vera-

Peláez & Lozano-Francisco (*partim*), p. 6, pl. 1, figs 3-7 (only), pl. 4, figs 1-3, pl. 8, figs 1-2 [not figs 1-2 = *Clavatula interrupta* (Brocchi, 1814)].

- 2011 *Clavatula interrupta* (Brocchi, 1814) – Landau *et al.*, p. 37, pl. 20, fig. 4 [*non* Brocchi, 1814].

Type material – Holotype NHMW 2020/0171/0295, height 30.6 mm, width 9.9 mm; paratype 1 NHMW 2020/0171/0296, height 29.5 mm, width 9.1 mm; paratype 2 NHMW 2020/0171/0297, height 35.0 mm, width 11.2 mm; paratype 3 NHMW 2020/0171/0298 (juvenile).

Other material – CO: NHMW 2020/0171/0299 (41). 'Yellow sands' (of Landau, 1984): NHMW 2010/0054/0202 (1), NHMW 2020/0171/0582 (10); 'Grey sands' (of Landau, 1984): NHMW 2020/0171/0583 (16). Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, lower Pliocene.

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

Type stratum – unnamed formation of early Piacenzian age.

Etymology – Named after the Iberian Peninsula. *Clavatula* gender feminine.

Diagnosis – '*Clavatula*' species of medium size, slender conical spire, tripartite early whorls with abapical row of tubercles stronger than adapical, mid-whorl beads weakest, later whorls with narrow beaded subsutural cord, smooth concave mid-portion, broad suprasutural band overrun by 2-4 cords, anal sinus deep, moderately narrow, symmetrically U-shaped, siphonal canal moderately short.

Description – Shell medium-sized, solid, and moderately slender, with tall conical spire (spire angle 26.9-29.2 °). Protoconch small, paucispiral, composed of 1.5 convex whorls, with large nucleus, junction marked by beginning of axial sculpture (dp = 660 µm, hp = 560 µm, dp/

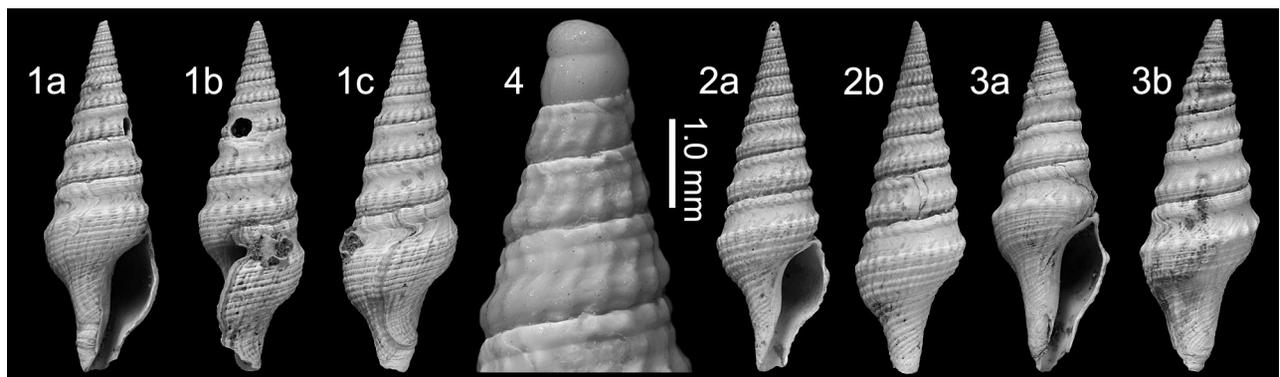


Plate 4. '*Clavatula*' *iberica* nov. sp.; 1. **Holotype** NHMW 2020/0171/0295, height 30.6 mm, width 9.9 mm; 2. **Paratype 1** NHMW 2020/0171/0296, height 29.5 mm, width 9.1 mm; 3. **Paratype 2** NHMW 2020/0171/0297, height 35.0 mm, width 11.2 mm; 4. **Paratype 3** NHMW 2020/0171/0298, detail of protoconch and early teleoconch whorls (digital images). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene.

hp = 1.18, dV1 = 530 μm , n = 230 μm). Teleoconch of up to ten whorls, with relatively broad concave portion mid-whorl, separated by deeply impressed, finely undulating suture. Sculpture on early whorls consisting of arcuate ribs bearing three rows of tubercles; adapical and mid-whorl row poorly defined, adapical row stronger. On the third or fourth whorl mid-row tubercles weakens, increasing number of fine spiral cords intersect adapical row of tubercles. Later whorls bearing row of small adapical tubercles, subobsolete on later whorls to form a narrow subsutural cord; relatively broad, smooth subsutural ramp below; abapical band about one-third whorl height, bearing axially elongated tubercles cut by fine secondary spirals. Last whorl 50-55% of total height, with moderately developed subsutural collar, concave subsutural ramp, shoulder moderately angled, bearing 18-26 tubercles, convex below, moderately constricted at base, sculpture on shoulder and below of fine, irregular, weakly tubercular spiral cords of roughly alternating strength, peribasal cord weakly developed. Siphonal fasciole weakly delimited, flattened, bearing non-tubercular spiral cords. Aperture moderately wide, elongated, 36-39% total height, outer lip simple; anal sinus deep, moderately narrow, symmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately short, open, slightly recurved and twisted to left, unnotched. Columella shallowly excavated, twisted at siphonal canal. Columellar callus weakly thickened forming narrow callus margin.

Discussion – The Iberian Pliocene specimens identified as ‘*Clavatula interrupta*’ (Brocchi, 1814) by Vera-Peláez & Lozano-Francisco (2001a) and followed by Landau *et al.* (2011) are not that species. The Iberian specimens are about half the maximum size (maximum height 35.4 mm vs. 70+ mm for ‘*C. interrupta*’), the spire angle is narrower (27-29° vs. 35-38° for ‘*C. interrupta*’), sculpture on the early spire whorls is similar, but the middle row of tubercles disappears earlier in ontogeny (3-4th whorl vs. 5th-6th whorl in ‘*C. interrupta*’), the central concave portion in the Spanish specimens is wider and smoother than in *C. interrupta* that bears elevated axial sinus lines that are often swollen at their flexure, the spiral sculpture on the suprasutural band and below the shoulder are far more weakly beaded than in ‘*C. interrupta*’, the shoulder is more coarsely beaded (18-26 tubercles vs. 32-40 in ‘*C. interrupta*’), and the siphonal canal is shorter (apertural height 36-39% vs. for 43-47% for *C. interrupta*). The anal sinus is symmetrically U-shaped in both species, but deeper in ‘*C. interrupta*’ (see Fig. 2). For these Estepona specimens we erect the name ‘*Clavatula iberica*’ nov. sp. The Iberian specimens are similar to ‘*Clavatula modesta*’ (Pecchioli, 1864, non G.B. Sowerby I, 1834; see below), but that species differs in having a broader, rounded subsutural cord, stronger spiral sculpture that is also present on the concave portion of the whorl, and axial riblets at the shoulder than persist onto the base. Another closely similar member of the ‘*Clavatula interrupta*’ group is ‘*C. implexa*’ Bellardi, 1877, described from the lower Pliocene of Italy. Vera-Peláez & Lozano-Francisco (2001a, p. 47,

tab. 17; 2001b, p. 193, tab. 2) recorded this species from Velerín, but there is no record or discussion of the species occurring in the Estepona assemblages in their taxonomic discussion, but according to those authors it occurs in the Atlantic Guadalquivir Basin (2001a, p. 17-18). ‘*Clavatula implexa*’ differs from ‘*C. iberica*’ in having a much more strongly developed and broader subsutural collar, narrower subsutural ramp, and the suprasutural cord and shoulder are subobsolete. This broad subsutural collar also distinguishes ‘*C. implexa*’ from ‘*C. interrupta*’, as well as a shorter siphonal canal.

Other members of the ‘*Clavatula interrupta*’ group from the Paratethys Miocene: ‘*C. hirmetzli*’ Kovács & Vicián, 2021 is more biconic, with coarser sculpture, ‘*C. irisae*’ Harzhauser, Landau & Janssen, 2022 is broader with lirae within the outer lip, ‘*C. sophiae*’ (Hoernes & Auinger, 1891) is broader and has small, pointed tubercles developed on the subsutural collar, and ‘*C. vitalisi*’ Strausz, 1955 is much broader with a shorter siphonal canal. In the middle Miocene Karaman Basin of Turkey ‘*C. ariejansseni*’ Harzhauser, Landau & Janssen, 2022 has similar sculpture, but is broader with lirae within the outer lip.

Distribution – Lower Pliocene: Atlantic: Guadalquivir Basin, S. Spain (González Delgado, 1993; Vera-Peláez & Lozano-Francisco, 2001a; Landau *et al.*, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996; Vera-Peláez & Lozano-Francisco, 2001a).

‘*Clavatula modesta*’ (Pecchioli, 1864)

Pl. 5, figs 1-3.

- *1864 *Pleurotoma modesta* Pecchioli, p. 516, pl. 5, figs 17, 18 (non G.B. Sowerby I, 1834).
- 2004 *Clavatula modesta* (Pecchioli, 1864) – Scarponi & Della Bella, p. 33, fig. 24.
- non 1896 *Clavatula modesta* Simonelli, p. 331, fig. 2 [secondary homonym; = ‘*Perrona simonellii*’ nov. nom].
- non 1963 *Clavatula modesta* Simonelli, 1896 – Venzo & Pelosio, p. 117, pl. 40, figs 15, 17 [= ‘*Perrona simonellii*’ nov. nom].

Material and dimensions – Maximum height 43.4 mm, width 12.9 mm. CO: NHMW 2020/0171/0300-0302 (4), NHMW 2020/0171/0303 (1).

Description – Shell medium-sized to moderately large, solid, and moderately slender, with tall, conical spire (apical angle 32-33°). Protoconch not preserved. Teleoconch of up to ten whorls, with narrow weakly concave portion mid-whorl, separated by narrow, finely undulating suture. Sculpture on early whorls tripartite; adapical and mid-whorl row smaller, poorly defined, adapical row stronger. On fifth whorl mid-row tubercles weakens leaving narrow, but well-defined cord in centre of concave

portion mid-whorl, two spiral cords bisect adapical row of tubercles; further narrow secondary spirals appear irregular in position and strength. Last whorl 55-60% of total height, with rounded subsutural collar bearing 32-36 tubercles, overrun by 4-5 fine cords, concave subsutural ramp with well-developed sinuous axial growth lines and four cords, central cord stronger, delimited by finely tubercular shoulder, convex below, moderately strongly constricted at base, sculpture below shoulder of narrow tubercular cords of roughly alternate strength, peribasal cord very weakly developed. Siphonal fasciole not delimited, flattened, bearing non-tubercular spiral cords. Aperture moderately wide, elongated, 44-45% of total height, outer lip simple; anal sinus moderately deep, narrow, asymmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately long, open, straight, unnotched. Columella shallowly excavated, twisted at siphonal canal. Columellar callus weakly thickened forming narrow callus margin.

Discussion –*Pleurotoma modesta* Pecchioli, 1864 is a junior primary homonym of *P. modesta* G.B. Sowerby I, 1834 and under ICZN (1999) art. 57.2 would be invalid. However, exception by art. 23.9.5 according to which “the junior name can be maintained as valid if both homonyms are still in use and since 1899 no longer in the same genus. The case then should to be submitted to the ICZN for a ruling...”. In this case conditions of art. 23.9.5 are fulfilled, as *P. modesta* Sowerby is regarded as valid species of *Turridrupa* Hedley, 1922.

Similarly, *Clavatula modesta* Simonelli, 1896 from the upper Miocene Tortonian of Vigoleno, Italy, is also a secondary homonym. However, it represents a ‘*Perrona*’ species, and replacement name is unnecessary as ICZN (1999) art. 59.2 states that younger secondary homonyms need not to be replaced if they are no longer congeneric. This species was considered a form of and synonymised with ‘*Clavatula interrupta*’ (Brocchi, 1814) (De Stefani, 1874, p. 49) until Scarponi & Della Bella (2004, fig. 24) figured a specimen from Italy and considered it a valid species, without entering into discussion. ‘*Clavatula modesta*’ (Pecchioli, 1864) was said to differ from ‘*C. interrupta*’ in having the subsutural collar wider than the suprasutural

one, the mid-whorl portion less concave, the sculpture generally finer, the last whorl less inflated and the siphonal canal straighter, longer and narrower. In the Estepona material, the sculpture is not finer than in ‘*C. interrupta*’, but the cords are not granular as they are in Brocchi’s species. The species is known from very few specimens, but the Estepona material at hand and the Italian specimens are only half the size of fully grown ‘*C. interrupta*’. A further difference not previously mentioned is that spiral sculpture runs along the concave mid-whorl portion, whereas in ‘*C. interrupta*’ the mid-whorl part has no spiral sculpture. These spirals are clearly seen in the holotype (Pecchioli, 1864, figs 17, 18) and the specimen from San Gimignano (Siena) illustrated by Scarponi & Della Bella (2004, fig. 24). The subsutural collar does not seem particularly wider than the suprasutural one in the Estepona specimens, nor in the specimen illustrated by Scarponi & Della Bella. It is possible that this is merely an unusual form of ‘*C. interrupta*’, as suggested by De Stefani, but the separation here is made based mainly on smaller size, the presence of spirals mid-whorl and the non-granular cords that form poorly defined riblets from the shoulder onto the base on the last whorl. ‘*Clavatula modesta*’ is more similar in size to ‘*C. iberica*’ nov. sp. (see that species for comparison). ‘*Clavatula interrupta*’, ‘*C. modesta*’ and *C. iberica* belong to the same ‘*Clavatula interrupta*’ species group that is no longer represented in extant faunas.

Another species belonging to the ‘*C. interrupta*’ group described from the lower Pliocene of Italy, but also recorded in the Atlantic lower Pliocene Guadalquivir Basin of Spain (Vera-Peláez & Lozano-Francisco, 2001a; Landau *et al.*, 2011), is ‘*C. implexa*’ Bellardi, 1877. We are uncertain on the early whorl sculpture in that species, as they are always abraded in the Huelva material, but in the earliest whorls preserved it is similar to other species in the ‘*C. interrupta*’ group. ‘*Clavatula implexa*’ differs from ‘*C. interrupta*’ in having a broader, more elevated subsutural collar and in having a shorter siphonal canal. ‘*Clavatula implexa*’ differs from ‘*C. modesta*’ in having a wider apical angle, the subsutural and suprasutural bands are more elevated resulting in a more deeply concave central portion, and it lacks spiral cords on the central portion.

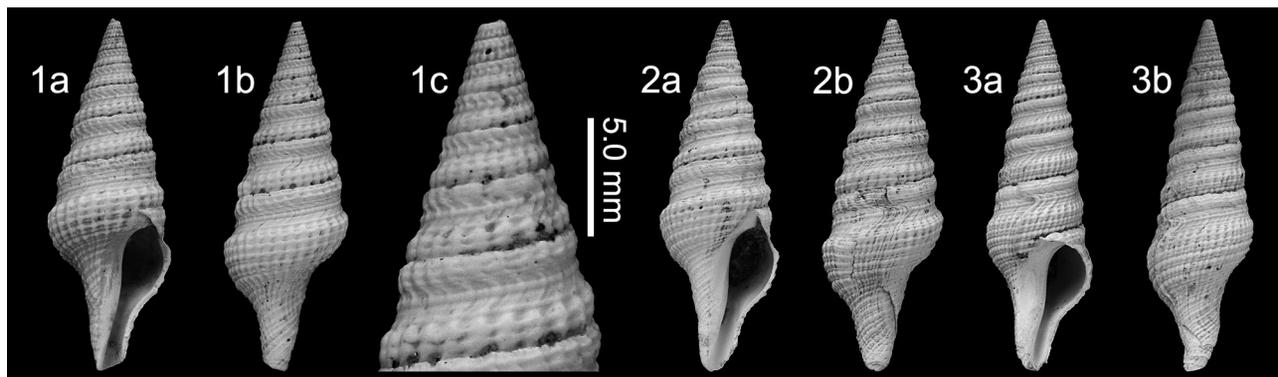


Plate 5. ‘*Clavatula modesta*’ (Pecchioli, 1864); 1. NHMW 2020/0171/0300, height 29.2 mm, width 10.3 mm, 1c, detail of early teleoconch whorls; 2. NHMW 2020/0171/0301, height 36.4 mm, width 12.0 mm; 3. NHMW 2020/0171/0302, height 43.4 mm, width 12.9 mm (digital images). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene.

Distribution – Lower Pliocene: central Mediterranean, Italy (Scarponi & Della Bella, 2004). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (this paper), central Mediterranean, Italy (Scarponi & Della Bella, 2004).

***Clavatula* (s.l.): *Clavatula carinulata* Sacco, 1904 species group**

This species group comprises species that have a regularly conical spire and short last whorl, moderately short siphonal canal, the neanic whorls have deeply sinuous axial riblets that form beads at the sutures, more strongly so at the abapical suture, and on later whorls the subsutural cord remains weak, never forming a well-defined collar, the mid-portion is wide, broadly concave, and smooth, and the suprasutural row of beads or tubercles is moderately well developed to subobsolete. On the last whorl the subsutural collar is weak to obsolete, the subsutural ramp broad, sharply delimited by shoulder carina, and the base is delimited by a perifasciolar band.

We include in the group '*Clavatula carinulata* Sacco, 1904 from the upper Miocene Proto-Mediterranean of Italy, '*Clavatula*' cf. *munizsolisi* Vera-Peláez & Lozano-Francisco, 2001 from the Atlantic lower Pliocene Guadalquivir Basin of southern Spain, '*Clavatula*' *munizsolisi* Vera-Peláez & Lozano-Francisco, 2001 and '*Clavatula*' *estebunensis* (Vera-Peláez & Lozano-Francisco, 2001) from the Mediterranean upper Pliocene of Estepona. This group is not represented in the Miocene Paratethys, nor in the extant West African fauna.

'*Clavatula*' *munizsolisi* (Vera-Peláez & Lozano-Francisco, 2001)

Pl. 6, figs 1-5.

- 1996 *Clavatula* sp. 2 – Vera-Peláez, p. 237, pl. 12, figs 1-8, pl. 15, fig. 4.
- 1996 *Perrona* (*Perrona*) sp. – Vera-Peláez, p. 252, pl. 14, figs 2, 4, 6, 8, 11, 12, 14.
- 2001a *Clavatula carinulata* Sacco, 1890 [*sic*] – Vera-Peláez & Lozano-Francisco (*partim*), p. 23, pl. 2, figs (?non 8-10), 11-13, pl. 4, figs 6-8, pl. 8, figs (?non 11) 12 [not figs 6-7, pl. 8, figs 10 = *Clavatula carinulata* Sacco, 1904].
- *2001a *Perrona* (*Perrona*) *munizsolisi* Vera-Peláez & Lozano-Francisco, p. 41, pl. 3, figs 16-21, pl. 4, figs 9-11, pl. 9, fig. 9.
- 2001b *Clavatula munizsolisi* (Vera-Peláez & Lozano-Francisco, 2001) – Vera-Peláez & Lozano-Francisco, p. 191, 192, 193.
- ?non 2011 *Clavatula carinulata* Sacco, 1890 – Landau *et al.*, p. 37, pl. 19, figs 8, 9 (?undescribed *Clavatula* species).

Material and dimensions – Maximum height 32.0 mm, width 12.2 mm (exceptional, most specimens 16-22

mm height). **CO:** NHMW 2020/0171/0281 (1), NHMW 2020/0171/0282 (9), NHMW 2020/0171/0290 (50+). **EL:** NHMW 2020/0171/0291-0293 (3), NHMW 2020/0171/0294 (2). **PQ:** NHMW 2020/0171/0283 (1), NHMW 2020/0171/0284 (3).

Description – Shell medium-sized, medium-thickness, broad, with tall, conical spire (spire angle ~31.5-33.5°) and relatively short last whorl. Protoconch small, paucispiral, composed of 1.5-1.75 convex whorls, with large nucleus, junction marked by sinusigera (Estepona specimens; dp = 1000 µm, hp = 800 µm, dp/hp = 1.25, dV1 = 700 µm, n = 500 µm). Teleoconch of up to ten whorls, broadly concave mid-whorl, with periphery at suprasutural cord, separated by shallow, irregular suture. Sculpture on early teleoconch whorls of deeply sinuous axial ribs, slightly swollen just below adapical suture, narrow over upper third concave portion of whorl, swelling again towards abapical suture. On 4th or 5th whorl adapical portion weakens leaving subobsolete subsutural collar, mid-portion becomes smooth or at most bearing deeply sinuous growth lines, abapical row of tubercles placed just above suture; suture strengthens (T2 = 16-18, TP = 16-18). Fine irregular spiral threads cover entire surface and overrun tubercles, in some specimens absent on concave mid-portion of whorl. Last whorl moderately short, 53-55% total height, with weak to subobsolete subsutural collar, broad concave subsutural ramp delimited by moderately tubercular shoulder, tubercles subobsolete on last half whorl, straight-sided below to peribasal angulation, strongly constricted at base, sculpture below shoulder of narrow subequal spiral cords separated by narrow grooves. Siphonal fasciole weakly delimited, bearing fine spiral cords. Aperture wide, relatively short, 37 % total height, outer lip simple; anal sinus deep, moderately narrow, asymmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately short, open, recurved and bent adaxially, unnotched. Columella excavated in adapical third, straight below, twisted at siphonal canal. Columellar callus thickened forming narrow callus margin.

Discussion – Vera-Peláez & Lozano-Francisco (2001a, pl. 2, figs 6-7) illustrated a lectotype of *Clavatula gradata* var. *carinulata* Sacco, 1904 from the Tortonian upper Miocene of Stazzano, Italy and considered some of the specimens from the shallow water assemblages of Estepona conspecific with the Italian Miocene species, whilst noting that there were differences. The Estepona specimens differed from the Tortonian shell illustrated by Sacco (1904, pl. 12, figs 65-66) in having a slightly shorter siphonal canal and fewer axial ribs (tubercles at the carina on later teleoconch whorls; last whorl 16 vs. 22). We further note that the Tortonian shells have a broader spire (apical angle lectotype 38.3° vs. 31.5-33.5° for Estepona specimens).

Vera-Peláez & Lozano-Francisco (2001a) also considered this species to occur in the Atlantic lower Pliocene Guadalquivir Basin deposits of southern Spain, where the population differed again in being larger shelled, with a slightly longer siphonal canal, and having even fewer

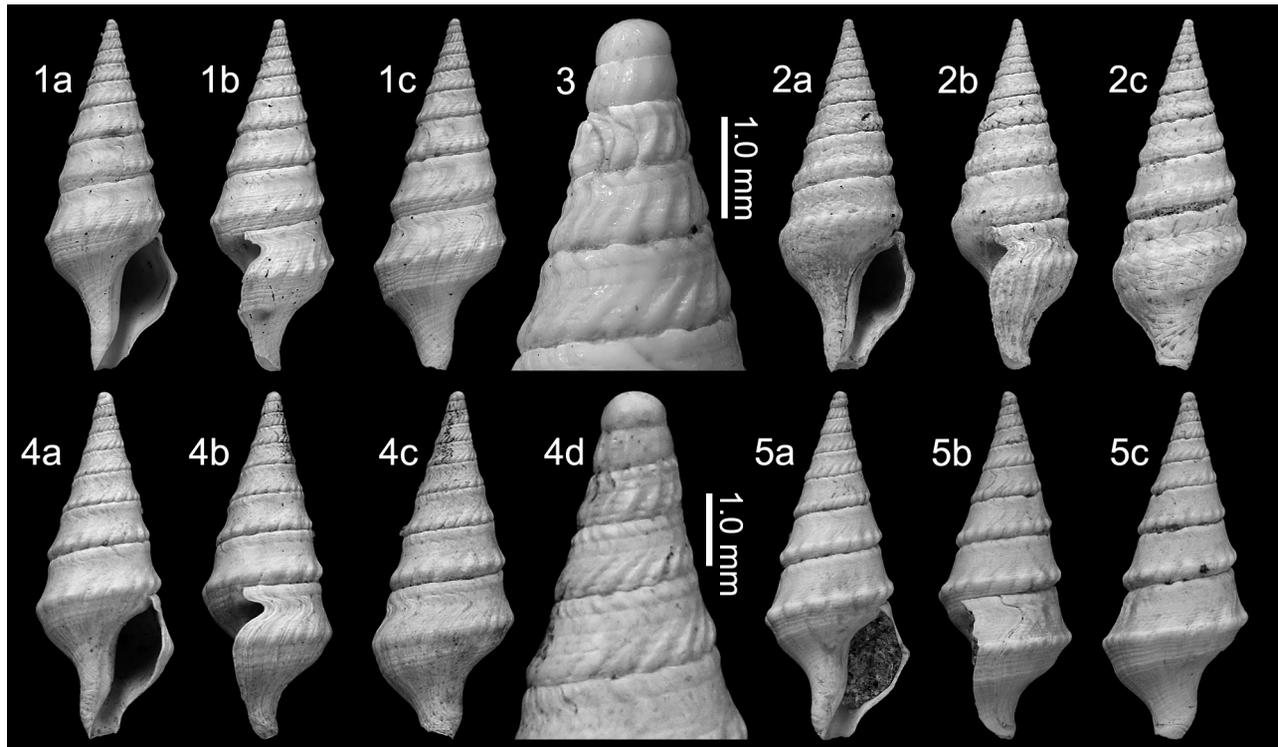


Plate 6. '*Clavatula*' *munizsolisi* (Vera-Peláez & Lozano-Francisco, 2001); 1. NHMW 2020/0171/0291, height 23.8 mm, width 8.7 mm; 2. NHMW 2020/0171/0292, height 25.5 mm, width 9.7 mm; 3. NHMW 2020/0171/0293, detail of protoconch and early teleoconch whorls. El Lobillo. 3. NHMW 2020/0171/0283, height 18.2 mm, width 7.2 mm, 1d, detail of protoconch and early teleoconch whorls. Parque Antena. 4. NHMW 2020/0171/0281, height 10.0 mm, width 7.4 mm (digital images). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene.

(11-14), more strongly developed abapical rows of tubercles at the periphery and peribasal cord. We note that the Guadalquivir Basin specimens are highly variable, and the tubercles can be robust to subobsolete. In most specimens there is a further weaker cord delimiting the siphonal fasciole, absent in the Estepona specimens (see Landau *et al.*, 2011, pl. 19, figs 8, 9).

In the same work Vera-Peláez & Lozano-Francisco (2001a) described *Perrona* (*Perrona*) *munizsolisi* Vera-Peláez & Lozano-Francisco, 2001 from the deeper water assemblage of Parque Antena. Although these specimens have opisthocline ribs on the neanic whorls, they are not of the comma-shaped type typical of *Perrona* species (see Harzhauser *et al.*, 2022, p. 100). Indeed, the two Spanish authors changed the generic assignment of this species to *Clavatula* (Vera-Peláez & Lozano-Francisco, 2001b), without discussion.

There is no consistent difference between the deeper-water specimens described by Vera-Peláez & Lozano-Francisco as *P. (P.) munizsolisi* and those from shallower Estepona assemblages identified by those authors as *Clavatula carinulata*. Their neanic whorls are identical (compare Pl. 6, figs 3 and 4d).

Clavatulids are usually restricted both geographically and stratigraphically. We consider it unlikely that the Tortonian Proto-Mediterranean, lower Pliocene Atlantic and upper Pliocene western Mediterranean represent shells of a single species, and it is more likely to represent

a species complex. The differences discussed above are sufficient to consider the Estepona specimens a distinct species for which the name '*Clavatula*' *munizsolisi* is available. The Guadalquivir Basin specimens probably represent yet another species for which it needs further characterisation.

This distinctive species cannot be confused with any of its Iberian Pliocene congeners.

In Estepona, '*C.*' *munizsolisi* is found in the both the deeper and shallower water facies suggesting a wide bathymetric range for the species.

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

'*Clavatula*' *estebunensis* (Vera-Peláez & Lozano-Francisco, 2001)

Pl. 7, figs 1-2

1996 *Perrona* (*Perrona*) cf. *theodori* (Toula, 1910) [*sic*] – Vera-Peláez, p. 248, pl. 14, figs 1, 3, 5, 7, 9, 10, 13, pl. 15, fig. 6 [*non Clavatula theodori* (Toula, 1910)].

*2001a *Perrona* (*Perrona*) *estebunensis* Vera-Peláez & Lozano-Francisco, p. 38, pl. 3, figs 10-15, pl. 4, figs 12-14, pl. 9, fig. 6.

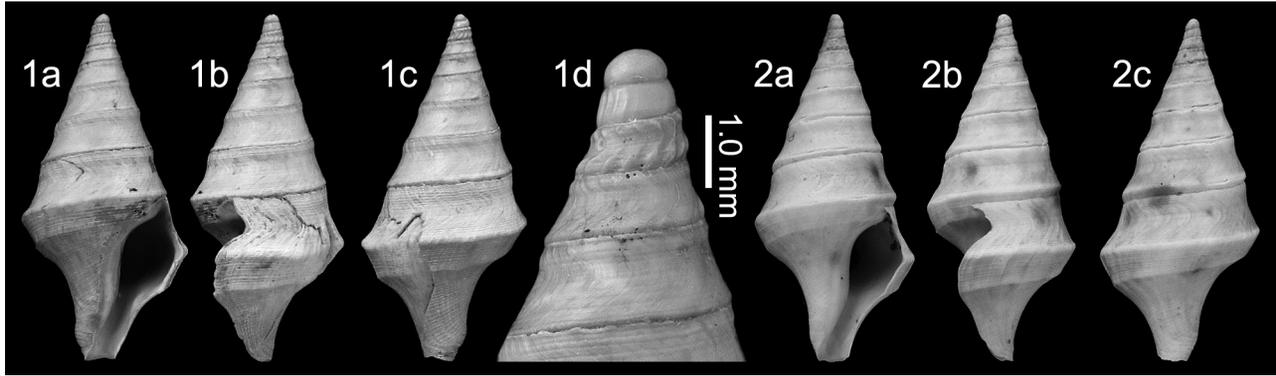


Plate 7. ‘*Clavatula*’ *estebunensis* (Vera-Peláez & Lozano-Francisco, 2001); 1. NHMW 2020/0171/0275, height 20.0 mm, width 9.3 mm, 1d, detail of protoconch; 2. NHMW 2020/0171/0276, height 21.4 mm, width 9.3 mm (digital images). Velerín carretera, Velerín, Estepona, lower Piacenzian, upper Pliocene.

Material and dimensions – Maximum height 27.0 mm, width 10.7 mm. **CO**: NHMW 2020/0171/0280 (1). **VC**: NHMW 2020/0171/0275-0276 (2), NHMW 2020/0171/0277 (9). **PQ**: NHMW 2020/0171/0278 (11). **EL**: NHMW 2020/0171/0279 (1).

Description – Shell medium sized, broad, with regularly conical spire (apical angle 38.7-38.9°). Protoconch paucispiral, composed of 1.5 smooth bulbous whorls, with large nucleus (dp = 560-600 μ m, hp = 500-560 μ m, dp/hp = 1.07-1.12, dV1 = 380-500 μ m, n = 340-400 μ m). Junction with teleoconch marked by series of axial riblets. Teleoconch of seven concave whorls, with periphery at abapical suture, separated by superficial, linear suture. Sculpture on first teleoconch whorl of deeply sinuous axial ribs, very slightly swollen just below adapical suture, narrow over upper third concave portion of whorl, swelling again towards abapical suture. Weak spirals cover entire whorl surface. On second whorl axials fade, subsutural cord forms poorly delimited subsutural cord, suprasutural cord disappears. Abapically sculpture restricted to very faint spiral cords most evident towards the sutures, with smooth central portion to whorls. Last whorl 60% of total height; subsutural collar subobsolete, broad, concave subsutural ramp delimited by elevated, sharp shoulder carina placed at level of insertion of outer lip, straight-sided below to weaker peribasal cord delimiting base, strongly constricted at base, siphonal fasciole slightly rounded, poorly delimited; spiral sculpture of very fine cords more strongly developed below shoulder and on base. Aperture wide, ovate, outer lip sharp; anal sinus deep, moderately wide, asymmetrically U-shaped, with apex mid-ramp; siphonal canal moderately short, bent adaxially, shallowly notched at tip. Columella moderately excavated in upper half, straight below, twisted at fasciole, smooth. Columellar and parietal callus moderately thickened, adherent, forming broad callus rim; small parietal pad developed adapically.

Discussion – Vera-Peláez & Lozano-Francisco (2001) described this species under the genus *Perrona* Schumacher, 1817 probably based on the much reduced teleoconch

sculpture. Harzhauser *et al.* (2022, p. 100) restricted the use of the genus to species with neanic whorl sculpture consisting of a smooth, flat to moderately convex subsutural cord and opisthocline, comma-shaped axial riblets. The neanic whorl sculpture of this species does not agree with that of *Perrona*. The axials are deeply sinuous and there is no smooth subsutural cord. In our opinion this species is best placed in ‘*Clavatula*’ *sensu lato*, and belongs within the ‘*Clavatula*’ *carinulata* Sacco, 1904 group. It differs from other members of the group in being broader and having the axial sculpture fade far earlier, by the second teleoconch whorl, and in having the shoulder smooth, devoid of tubercles.

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

‘*Clavatula*’ *sensu lato*, unassigned

‘*Clavatula*’ *nana* nov. sp.

Pl. 8, figs 1-2.

Type material – Holotype NHMW 2020/0171/0591, height 9.7 mm, width 4.3 mm; paratype 1 NHMW 2020/0171/0592, height 8.8 mm, width 4.1 mm; paratype 2 NHMW 2020/0171/0593, height 8.0 mm, width 3.5 mm.

Other material – **EL**: NHMW 2020/0171/0594 (3 incomplete specimens).

Type locality – El Lobillo, Estepona, Spain.

Type stratum – unnamed formation of lower Piacenzian age.

Etymology – Latin ‘*nanus*, -a, -i’, adjective meaning dwarf. *Clavatula* gender feminine.

Diagnosis – *Clavatula* species of small size, broad biconic, early whorls with sinuous axial ribs, on later whorls

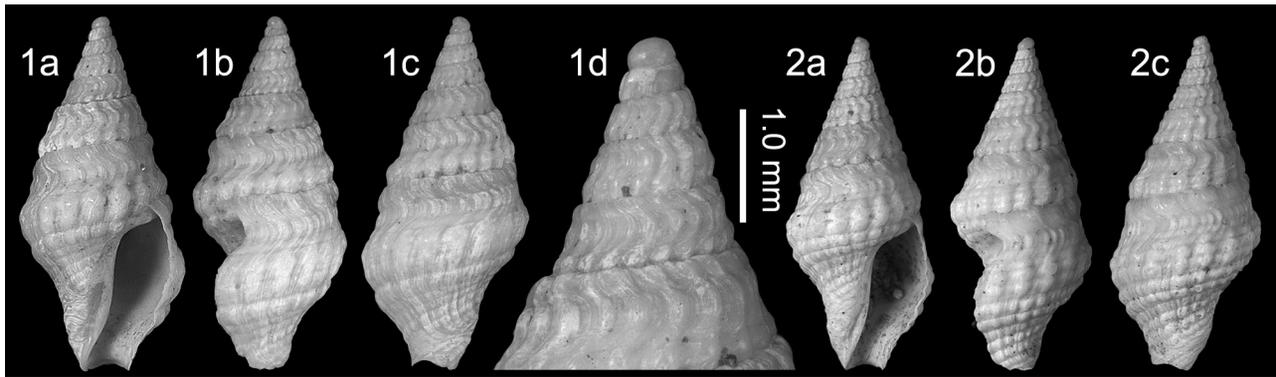


Plate 8. ‘*Clavatula*’ *nana* nov. sp.; 1. **Holotype** NHMW 2020/0171/0591, height 9.7 mm, width 4.3 mm, 1d, detail of early teleoconch whorls; 2. **Paratype 1** NHMW 2020/0171/0592, height 8.8 mm, width 4.1 mm (digital images). El Lobillo, Estepona, lower Piacenzian, upper Pliocene.

subsutural collar poorly developed, ribs over collar and ramp, shoulder with large bifid tubercles, tubercular cords over base, moderately deep, moderately wide, symmetrically U-shaped, moderately short siphonal canal.

Description – Shell small, solid, broad squat biconic, with broad, conical spire (spire angle 40-45.6°). Protoconch small, paucispiral, composed of two convex whorls, with large nucleus, junction marked by beginning of axial sculpture (dp = 320-350 μ m, hp = 280-310 μ m, dp/hp = 1.13-1.14, dV1 = 240-260 μ m, n = 140 μ m). Teleoconch of up to six whorls, separated by narrowly impressed finely undulating suture. First and second teleoconch whorls very weakly convex, with sculpture of elevated sinuous ribs, with deepest portion of arc at two-thirds whorl height. Third and penultimate whorls; shallow groove delimits subsutural cord, mid-portion weakly concave, ribs develop small tubercle above abapical suture. Last whorl 62-64% of total height, with weakly developed subsutural collar, concave subsutural ramp; elevated sinuous growth lines cover subsutural collar and ramp, shoulder roundly angled, bearing 16-18 rounded bifid tubercles bisected by spiral groove, convex below, moderately constricted at base; sculpture of tubercular spiral cords mid-whorl and base of subequal strength separated by narrow grooves, tubercles aligned axially in sinuous rows. Peribasal and perifasciolar cords not developed. Siphonal fasciole moderately delimited, rounded, bearing a few cords, forming very narrow umbilical chink. Aperture wide, pyriform, 43-44% total height, outer lip simple; anal sinus moderately deep, moderately wide, symmetrically U-shaped, with apex just below subsutural collar; siphonal canal moderately short, open, wide, slightly twisted to left, notched. Columella deeply excavated in upper third, twisted at siphonal canal. Columellar callus weakly thickened forming narrow callus margin.

Discussion – Despite being small and represented by few specimens, this species is quite unlike any of its Estepona congeners. We are uncertain whether these shells represent fully adult specimens, but the types are remarkably

similar in size and thick-shelled. The siphonal fasciole is well developed, which usually only occurs in adult specimens.

‘*Clavatula*’ *nana* nov. sp. is separated from the other Estepona ‘*Clavatula*’ species not only by its small size, but by having neither bipartite nor tripartite neanic whorls, but having sinuous axial riblets extending between the sutures. The subsutural cord only appears on the third teleoconch whorl by a shallow spiral groove cutting the ribs a short distance below the suture. The tubercular cords and short siphonal canal are reminiscent of members of the genus *Granulatocincta* Harzhauser, Landau & Janssen, 2022, but that genus is distinguished by its tripartite early whorl sculpture. In the extant faunas ‘*C.*’ *diadema* (Kiener, 1839) also has early whorls with axial ribs, but these are opisthocline rather than sinuous and the adult shell with its spinous shoulder and long siphonal canal is quite different from ‘*C.*’ *nana*. We have also not seen this type of early whorl sculpture in the Paratethyan fauna and cannot ascribe this species to any particular clavatulid group.

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

Genus *Granulatocincta* Harzhauser, Landau & Janssen, 2022

Type species – *Pleurotoma granulato-cincta* Münster in Goldfuss, 1841, by original designation, middle Miocene, Langhian, Central Paratethys Sea, Austria.

2022 *Granulatocincta* Harzhauser *et al.*, p. 45.

Original description – “Small to large, solid, broad fusiform to buccinoid with conical to weakly coronate spire. Protoconch paucispiral. Teleoconch of up to ten whorls. Early teleoconch whorls flat-sided, with tripartite sculpture; finely beaded subsutural cord, beaded mid-whorl cord, and axially elongate, opisthocline beads on suprasutural cord cut by one or two narrow spiral

grooves making beads bifid or trifid. Later teleoconch whorls flat-sided or weakly concave; subsutural collar weakly swollen; suprasutural cord weak, largely covered by subsequent whorl, mid-portion entirely covered by narrow, finely beaded spiral cords. Adsutural cords usually coarsely, beaded (G. callim, G. contorta, G. sotterii) although beads overrun by secondary and tertiary spiral cords in some species (G. pelliscrocodili). Last whorl 55–70% of total height; subsutural collar beaded or finely coronate, shoulder obtusely angled by finely tubercular shoulder cord, convex below, siphonal fasciole short, rounded, twisted. Aperture wide, ovate; outer lip not thickened by varix, smooth or lirate within; anal sinus wide, moderately deep, asymmetrically U-shaped; apex coinciding with middle row of beads; siphonal canal short to moderately short, shallowly notched at tip. Columella weakly excavated in upper third, weakly twisted below, smooth. Columellar and parietal callus thickened, sharply delimited, forming relatively broad callus rim, often with pseudumbilical chink.” (Harzhauser *et al.*, 2022, p. 45).

Discussion – Species in the genus *Granulatocincta* Harzhauser, Landau & Janssen, 2022 differ from *Clavatula* (s.s.) Lamarck, 1801 in having tripartite early teleoconch sculpture; bifid in *Clavatula*, and the dense, granulate spiral sculpture covering the entire whorl, which is unknown in any extant Clavatulidae. In *Granulatocincta* the whorl profile below the shoulder on the last whorl is squatter and more rounded compared to *Clavatula* due to the comparatively wider periphery and much shorter siphonal canal. Members of the ‘*Clavatula*’ *interrupta* group also have tripartite early whorl sculpture but are fusiform and not bucciniform in profile and have a much longer siphonal canal, as well as lacking the granulate spiral sculpture covering the entire whorl.

***Granulatocincta rustica* (Brocchi, 1814)**

Pl. 9, figs 1-2; Pl. 10, figs 1-6.

- *1814 *Murex rusticus* Brocchi, p. 428, pl. 9, fig. 4.
- 1847 *Pleurotoma rustica* Brocchi (*Murex*) – Bellardi, p. 28, pl. 1, fig. 17.
- 1861 *Pleurotoma fimbriata* O.G. Costa, p. 84, pl. 1, fig. 17.
- 1877 *Clavatula rustica* (Brocch.) var. A – Bellardi, p. 152, pl. 5, fig. 9.
- 1877 *Clavatula rugata* Bellardi, p. 155, pl. 5, fig. 10.
- 1890 *Clavatula rustica pliosubspinosa* Sacco, p. 273 (= *Clavatula rustica* (Brocch.) var. A of Bellardi, 1877).
- 1898 *Pleurotoma (Clavatula) subruidum* Almera & Bo-fill: p. 38, pl. 5, fig. 3.
- 1904 *Clavatula rustica* (Brocchi) – Sacco, p. 47, pl. 12, figs 57, 58.
- 1914 *Clavatula rustica* Brocchi [sic] – Cipolla, p. 127 [23], pl. 12 [1], fig. 18.
- 1955 *Clavatula (Melatoma) rustica* (Brocchi 1814) – Rossi Ronchetti, p. 307, fig. 164.
- 1959 *Clavatula rustica* Brocchi [sic] – Ruggieri & Curti, p. 121, pl. 30, fig. 179.
- 1974 *Clavatula (Clavatula) rustica* (Brocchi, 1814) – Malatesta, p. 414, pl. 31, fig. 19.
- 1975 *Clavatula rugata gigantea* Fekih, p. 137 (*nomen nudum*).
- 1978 *Clavatula rustica* Brocchi [sic] – Cuscani Politi, p. 50, pl. 6, fig. 20.
- 1978 *Murex rusticus* Brocchi, 1814 – Pinna & Spezia, p. 152, pl. 39, fig. 3.
- 1979 *Clavatula rustica* (Brocchi, 1814) – Malatesta, p. 414, fig. 35, pl. 31, fig. 19.
- 1981 *Clavatula rugata* Bellardi, 1877 – Ferrero Mortara *et al.*, p. 74, pl. 12, fig. 13.
- 1992 *Clavatula rustica* (Brocchi, 1814) – Cavallo & Repetto, p. 132, fig. 349.
- 1996 *Clavatula rustica* (Brocchi, 1814) – Vera-Peláez, p. 229, pl. 11, figs 1-5, pl. 15, fig. 2.
- 1997 *Clavatula rustica* (Brocchi, 1814) – Chirli, p. 30, pl. 8, figs 7-10.
- 2001a *Clavatula rustica* (Brocchi, 1814) – Vera-Peláez & Lozano-Francisco, p. 9, pl. 1, figs 8-11, pl. 5, figs 1-2, pl. 8, fig. 3.
- 2001a *Clavatula rugata* Bellardi, 1877 – Vera-Peláez & Lozano-Francisco, p. 16, pl. 2, figs 1-5, pl. 8, fig. 8 [non Bellardi, 1877].
- 2004 *Clavatula rustica* (Brocchi, 1814) – Scarponi & Della Bella, p. 34, figs 27-28, 49.
- 2013 *Clavatula rugata* Bellardi, 1877 – Landau *et al.*, p. 37, pl. 20 fig. 7 [non Bellardi, 1877].
- 2018 *Clavatula rustica* (Brocchi, 1814) – Brunetti & Cresti, p. 88, fig. 348.

Material and dimensions – Maximum height 35.6 mm, width 12.0 mm. **CO:** NHMW 2020/0171/0287-0288 (2), NHMW 2020/0171/0289 (4).

Description – Shell medium sized, bucciniform, moderately slender, with tall, regularly conical spire and short last whorl. Protoconch not preserved (paucispiral, 1.5 convex whorls: *fide* Scarponi & Della Bella, 2004, fig. 49). Teleoconch of up to nine whorls, initially straight-sided, later whorls concave mid-whorl, with periphery at abapical suture, separated by shallow, finely undulating suture. Sculpture on early teleoconch whorls tripartite: finely beaded subsutural cord, beaded mid-whorl cord, and axially elongate, opisthocline beads on suprasutural cord cut by a narrow spiral groove making beads bifid. On later whorls subsutural cord widens, rounded and elevated, tubercles weaken and disappear by 4th or 5th whorl; mid-portion becomes concave with arcuate riblets bearing small tubercles in the centre of the concavity, suprasutural cord equal in width to subsutural cord, less elevated, overrun by two, later three spiral cords slightly swollen at intersections. Spiral sculpture deeply interrupted by strong, deeply sinuous riblets and growth lines, making all cords irregularly and weakly tubercular. Last whorl short, 53-56% total height, with elevated, rounded, non-tubercular subsutural collar, narrow concave subsutural ramp bearing row of beads at centre, poorly delimit-

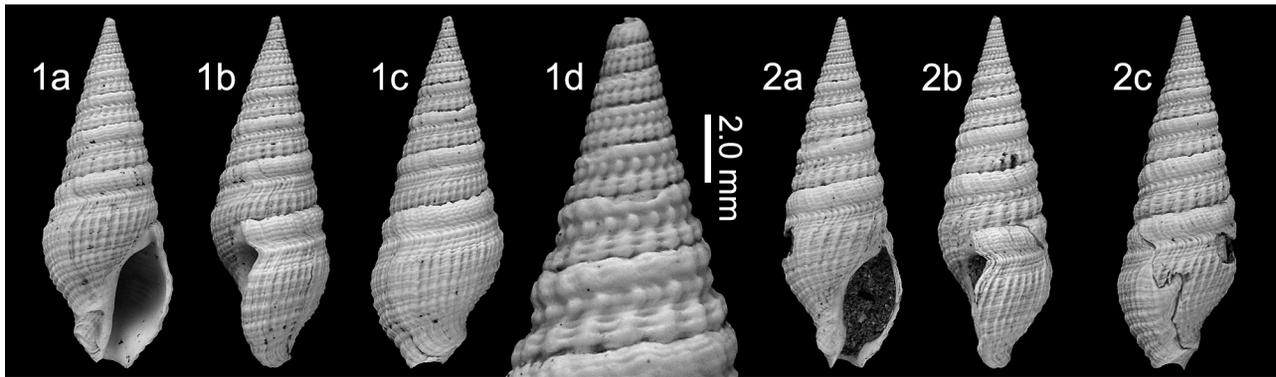


Plate 9. *Granulatocincta rustica* (Brocchi, 1814); 1. NHMW 2020/0171/0287, height 35.0 mm, width 12.3 mm, 1d, detail of early teleoconch whorls; 2. NHMW 2020/0171/0288, height 35.6 mm, width 12.0 mm (digital images). Velerín conglomerates, Velerín, Estepona, lower Pliocenez, upper Pliocene.

ited by weak, rounded shoulder, convex below, weakly constricted at base; sculpture below shoulder of rows for small tubercles, peribasal cord developed variably, but always weak. Siphonal fasciole sharply delimited, rounded, bearing about five non-tubercular spiral cords. Aperture wide, short, 35 % total height, outer lip simple; anal sinus moderately shallow, narrow, asymmetrically U-shaped, with apex on abapical half of ramp; siphonal canal short, wide, open, widely notched at tip. Columella straight, smooth, oblique. Columellar callus slightly thickened forming narrow callus margin.

Discussion – *Granulatocincta rustica* (Brocchi, 1814) is quite unlike any other *Estepona* clavatulid separated by its bucciniform shape and very short siphonal canal. These features, and its tripartite early teleoconch whorl sculpture, place it in the genus *Granulatocincta* Harzhauser, Landau & Janssen, 2022 (see generic note). Two species have been described in the Mediterranean: one in the upper Miocene: *G. rugata* (Bellardi, 1877), and one in the Pliocene: *G. rustica*. The Pliocene species *G. rustica* is highly variable in sculpture; the *Estepona* specimens are finely sculptured compared to some of those from Italian assemblages (see Scarponi & Della Bella, 2004, pl. 5, fig. 28), but similarly finely sculptured specimens also occur in Italy (see Chirli, 1997, fig. 9).

Vera-Peláez & Lozano-Francisco (2001a) considered all the lower Pliocene specimens from the Arenas de Huelva Formation of Atlantic southern Spain to represent the upper Miocene *G. rugata*. Those authors wrote that they differed from *Clavatula rustica* in “*presentar el ombligo y fasciola sifonal mucho más pequeños o ausentes, una escultura no reticulada y menor talla* [having a smaller umbilicus and siphonal canal or absent, a non-reticulated sculpture, and smaller size]” (Vera-Peláez & Lozano-Francisco, 2001a, p. 17). This position was followed by Landau *et al.* (2013, p. 37). However, on further examination of the material at hand from Huelva and further Tortonian material illustrated herein (Pl. 10, fig. 6), these differences do not hold up to scrutiny. The umbilicus and siphonal canal are only strongly developed in fully adult specimens, and in the Huelva, specimens figured (Pl. 10,

figs 1-3) they are no weaker than in the specimens from Italy figured by Chirli (1997, pl. 8, figs 8-10). The sculpture is coarser in the Huelva specimens than in the *Estepona* ones, but probably fits within the variability in sculpture seen in *G. rustica* (see Chirli, 1997; Scarponi & Della Bella, 2004; *hoc opus* Pl. 10, figs 4, 5). The largest *G. rugata* specimen from Huelva is 48.7 mm height, larger than any of the Italian *G. rustica* specimens illustrated by Chirli (1997) or Scarponi & Della Bella (2013) and almost 2.5x the size of *C. rugata*. The holotype of *C. rugata* from the Tortonian of Stazzano, Italy (figured by Ferrero Mortara *et al.*, 1981, pl. 12, fig. 13) does not have an umbilicus or siphonal fasciole but may not be fully grown. The sculpture could fit within the variability of *G. rustica*.

One can, in some cases, see small differences in sculpture between populations; the *Estepona* specimens (Pl. 9, figs 1-2) tend to be finer sculptured, the Huelva specimens (Pl. 10, figs 1-3) are coarsely sculptured, with the tubercles coalescent. The shape of the anal sinus is different between the *Estepona* and Huelva specimens, more deeply U-shaped in the Huelva specimens (see Fig. 2). The Italian specimens seem rather variable in sculpture (Pl. 10, figs 4, 5). It is possible that *G. rustica* represents a species complex. However, intraspecific variability within populations from one locality are so great that we prefer to consider them a single variable species. We note that the type species *G. granulocincta* (Münster in Goldfuss, 1841) is similarly variable (see Harzhauser *et al.*, 2022). The scant material seen from the upper Miocene of Italy identified in collections as *Clavatula rugata* (NHMW coll.; RGM coll.) also fits within the variability of *G. rustica*, and we therefore consider it a junior subjective synonym. Bellardi (1877, p. 154) also recorded the species in the middle Miocene of Italy. We have included this record in the distribution but are unable to confirm it.

Clavatula delgadoi Vera-Peláez & Lozano-Francisco, 2001 described from Atlantic Guadalquivir Basin of southwestern Spain also has tripartite early whorl sculpture and a very short siphonal canal and belongs in the genus *Granulatocincta*. It differs from *G. rustica* in having smoother sculpture, the adsutural cords bearing few-

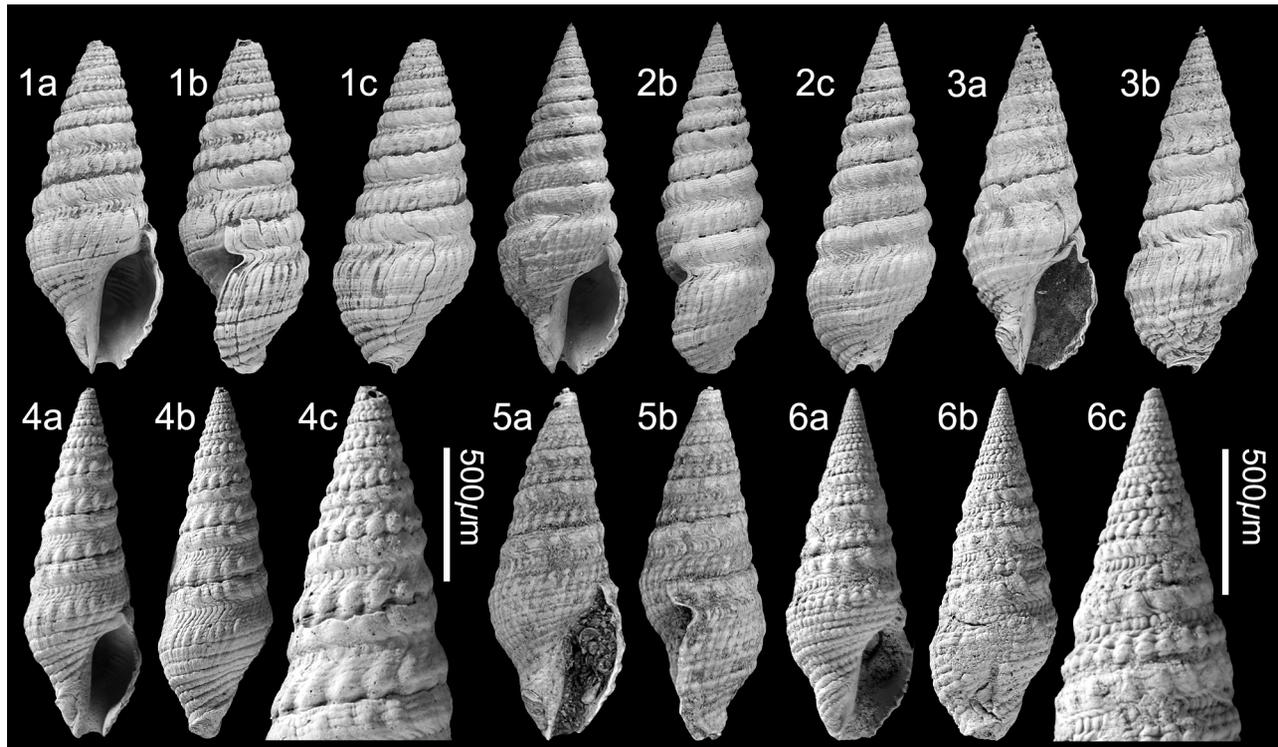


Plate 10. *Granulatocincta rustica* (Brocchi, 1814); 1. NHMW 2020/0171/0574, height 35.5 mm, width 14.2 mm; 2. NHMW 2020/0171/0575, height 43.1 mm, width 14.9 mm; 3. NHMW 2020/0171/0576, height 45.8 mm, width 16.7 mm (digital images). Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, lower Pliocene. 4. NHMW coll. (unnumbered), height 31.4 mm, width 10.5 mm, Asti, Italy, Pliocene. 6. RGM.811074, height 24.1 mm, width 9.5 mm, Bologna, Italy, Pliocene. 5. NHMW coll. (unnumbered), height 23.5 mm, width 8.6 mm, Santa Agata, Italy, Tortonian, upper Miocene.

er, larger tubercles, weak axial riblets extend from the shoulder to the base absent in *G. rustica*, and in lacking a siphonal fasciole and umbilicus.

In the Estepona deposits *G. rustica* has not been found in the deeper water deposits, which agrees with the infralittoral habitat described by Scarponi & Della Bella (2004, p. 35).

Distribution – Middle Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Upper Miocene: Proto-Mediterranean, Italy (Bellardi, 1877). Lower Pliocene: western Mediterranean, NE Spain (Almera & Bofill, 1898; Marquina, 1988a; Gili & Martinell, 1993); central Mediterranean: Italy (Bellardi, 1877; Montefameglio *et al.*, 1979; Chirli, 1997; Scarponi & Della Bella, 2004; Brunetti & Cresti, 2018), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Vera-Peláez, 1996; Vera-Peláez & Lozano-Francisco, 2001a); central Mediterranean: Italy (Bellardi, 1877; Cipolla, 1914; Ruggieri & Curti, 1959; Malatesta, 1974, 1979; Cavallo & Repetto, 1992; Scarponi & Della Bella, 2004).

***Perrona*-like species groups**

We place here species that tend to have smooth mid- and later whorls, devoid of axial sculpture, which at most consists of coarse tubercles on the subsutural collar. The

shoulder of these species is poorly delimited and broadly rounded, and the base usually lacks a distinct peribasal cord, which separates them from *Clavatula*-like species groups.

Genus *Perrona* Schumacher, 1817

Type species – *Perrona tritonium* Schumacher, 1817 [= *Perrona perron* (Gmelin, 1791)], by monotypy, present-day, West Africa.

1817 *Perrona* Schumacher, p. 66, 218.

Note – In addition to the generic description given by Powell (1966, p. 57), Harzhauser *et al.* (2022, p. 102) considered the neanic whorl sculpture consisting of a smooth, flat to moderately convex subsutural cord and opisthocline, comma-shaped axial riblets below, to be diagnostic of the genus. Adopting this stricter genus concept, none of the species in the Estepona assemblages can be ascribed to this genus.

Genus *Tomellana* Wenz, 1943

Type species – *Clavatula lineata* Lamarck, 1816, by typification of replaced name, present-day, West Africa.

- 1840 *Tomella* Swainson, p. 314. Type species (by subsequent designation Herrmannsen, 1849): *Clavatula lineata* Lamarck, 1816, present-day, West Africa. Junior homonym of *Tomella* Robineau-Desvoidy, 1830 [Diptera].
- 1943 *Tomellana* Wenz, p. 1383. *Nom. nov. pro Tomella* Swainson, 1840, *non* Robineau-Desvoidy, 1830 [Diptera].

Note – We follow Harzhauser *et al.* (2022, p. 102) in their interpretation of this genus to include species with a beaded suprasutural cord on neanic whorls, as opposed to comma-shaped axial riblets between two adsutural spiral cords in *Perrona*, the siphonal canal of *Tomellana* is much longer and its spire is conical as opposed to slightly gradate in most *Perrona* species. The separation of *Tomellana* from *Perrona* is also supported by molecular data (N. Puillandre pers. comm., in Harzhauser *et al.*, 2022, p. 143), corroborating our interpretation of the systematic value of early teleoconch whorl sculpture in Clavatulidae. The well-known French Atlantic lower Miocene species *Pleurotoma jouannetii* Des Moulins, 1842, which by most authors has been placed in the genus *Perrona*, was shown to belong within *Tomellana*, as well as the species name being misapplied to numerous unrelated taxa in other Neogene basins (see Harzhauser *et al.*, 2022).

***Tomellana postjouannetii* nov. sp.**

Pl. 11, fig. 1.

- 1996 *Perrona (Perrona) jouanneti* [*sic*] (Des Moulins, 1842) – Vera-Peláez (*partim*, Velez-Málaga specimen only), p. 241, pl. 13, figs 1-3, pl. 15, fig. 7; not pl. 7, figs 4-5 (Huelva specimens = *Tomellana onubensis* nov. sp.); not pl. 7, figs 6-7 (Spanish Miocene specimens, undetermined *Perrona* or *Tomellana* sp.) [*non Tomellana jouannetii* (Des Moulins, 1842)].
- 2001a *Perrona (Perrona) jouanneti* [*sic*] (Des Moulins, 1842) – Vera-Peláez & Lozano-Francisco (*partim*, Velez-Málaga specimen only), p. 34, pl. 7, figs 14-

15 (only), pl. 9, fig. 5 (only) [not pl. 7, figs 7-8 (Italian Miocene specimens, undetermined *Perrona* or *Tomellana* sp.), not pl. 7, figs 9-13 (Huelva specimens), pl. 9, figs 1-3, 5 = *Tomellana onubensis* nov. sp.].

Type material – Holotype NHMW 2020/0171/0285, height 18.1 mm, width 5.8 mm.

Other material – One unnumbered specimen from Velez-Málaga in MMPE collection, about 125 km east of Estepona (illustrated by Vera-Peláez & Lozano-Francisco, 2001a, pl. 7, figs 14-15), one incomplete specimen from Velerín.

Type locality – Velerín conglomerates, Velerín Estepona, Spain.

Type stratum – unnamed formation of early Piacenzian age.

Etymology – Species similar but occurring stratigraphically later than *Tomellana jouannetii*. *Tomellana* gender feminine.

Diagnosis – *Tomellana* species of small size, slender, conical spire, bipartite early whorls with narrow, smooth subsutural cord and abapical row of tubercles, mid-whorl concave, later whorls with strongly developed, smooth subsutural cord, smooth concave mid-section, suprasutural cord covered by succeeding whorl, last whorl with broad, sharply delimited, suprasutural collar, shoulder rounded, spiral sculpture restricted to base and siphonal fasciole, anal sinus moderately deep, narrow, asymmetrically U-shaped, siphonal canal long.

Description – Shell small, slender fusiform, with tall conical spire (spire angle 32.2°). Protoconch not preserved. Teleoconch of up to nine whorls, with periphery at abapical suture, separated by superficial, linear suture. Sculpture on early teleoconch with narrow, smooth subsutural cord and slightly wider, beaded suprasutural cord, mid-

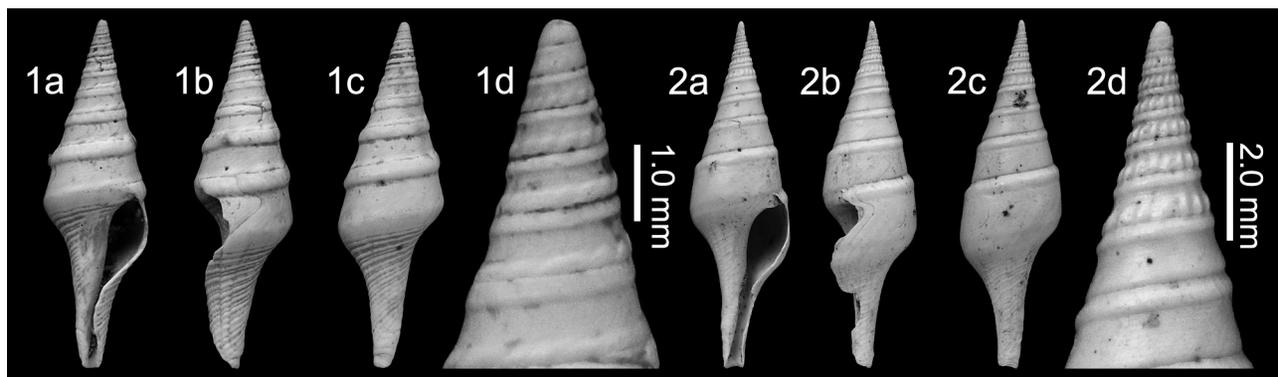


Plate 11. 1. *Tomellana postjouannetii* nov. sp., **Holotype** NHMW 2020/0171/0285, height 18.1 mm, width 5.8 mm, 1d, detail of early teleoconch whorls (digital image). Velerín conglomerates, Velerín, Estepona, lower Piacenzian, upper Pliocene. 2. *Tomellana jouannetii* (Desmoulins, 1842), NHMW 2020/0171/0286, height 27.1 mm, width 7.8 mm, 2d, 1d, detail of early teleoconch whorls (digital image). St-Martin-d'Oney, Meilhan, Landes, France, Falun de St. Avit, Aquitanian, lower Miocene.

whorl smooth, concave. On later whorls subsutural cord broadens to form rounded, subobsoletely tubercular collar, mid-portion weakly concave, smooth, suprasutural cord covered by succeeding whorl on last two whorls. Last whorl 64% of total height, with broad, rounded subsutural collar, weakly concave subsutural ramp, moderately delimited by narrowly rounded shoulder, convex below, moderately constricted at base, base not delimited, fasciole poorly delimited from base; spirals of alternating strength over base and siphonal fasciole. Aperture moderately narrow, 50% of total height, outer lip simple; anal sinus moderately deep, narrow, asymmetrically U-shaped, with apex just below collar; siphonal canal long, straight, narrow, unnotched. Columella smooth, moderately excavated in upper third, straight below, slightly twisted at fasciole. Columellar callus hardly thickened, forming narrow callus margin; parietal callus weakly developed.

Discussion – Pleurotoma jouannetii Desmoulins, 1842 was originally described based on material from Mérignac, lower Miocene Aquitaine Basin of France (1842, p. 143). The specimen illustrated herein from the Aquitanian Lower Miocene of Meilhan, France (Pl. 11, fig. 2) is similar to the topotype illustrated by Peyrot (1931, pl. 8, figs 61, 62, 71 only). Subsequently this name has been misapplied to numerous forms of smooth clavatulids from the Miocene Paratethys (see Harzhauser *et al.*, 2021) and Proto-Mediterranean (Bellardi, 1847, 1877; Montanaro, 1937). Although usually placed in the genus *Perrona* Schumacher, 1817, the early whorl sculpture places it in the genus *Tomellana* Wenz, 1943 (see generic note).

The presence of a ‘*Perrona*’ *jouannetii*-like species in the southern Iberian Pliocene was noted by several authors (Landau, 1984; González Delgado, 1993; Vera-Peláez & Lozano-Francisco, 2001a; Landau *et al.*, 2011). These authors considered the specimens from the Atlantic lower Pliocene Guadalquivir Basin and those from the western Mediterranean Estepona Basin to be conspecific with Desmoulins’s species. This would be an extremely unusually long-lived species for a clavatulid [Note that the true *Pleurotoma jouannetii* Desmoulins, 1842, from the Burdigalian of Merignac in France, was placed in *Tomellana* by Harzhauser *et al.* (2022)].

In the Estepona assemblages, specimens are exceedingly uncommon. However, the single specimen (Pl. 11, fig. 1) from the Velerín conglomerates allows attribution to the genus *Tomellana* rather than *Perrona* (see generic note above), and allows differentiation from *Tomellana jouannetii* (Pl. 11, fig. 2), from which it differs in having the spire less pointed and the beading on the suprasutural cord is weaker and fades earlier (4th to 5th whorls) as opposed to 7th whorl in *T. jouannetii*. On the later teleoconch whorls the subsutural collar is more swollen and prominent than in *T. jouannetii*, resulting in a more concave subsutural ramp. The parietal tubercle present in *T. jouannetii* is not seen in the Estepona specimen, but this is a gerontic character, and it is possible that it is not fully grown.

Specimens identified by authors as *Perrona jouannetii* from the Atlantic Spanish Pliocene Guadalquivir Basin are far more plentiful, but the early whorls are invariably

abraded. However, some fully adult specimens show apertural features typical of *Tomellana* rather than *Perrona* (Pl. 12, fig. 3). They differ from *Tomellana postjouannetii* nov. sp. in the shape of the anal sinus (Fig. 2), which in the Estepona specimen is slightly wider U-shaped and the apex is placed higher. This can also be seen, although less clearly, in Vera-Peláez & Lozano-Francisco [2001a, pl. 9, fig. 3 (Huelva specimen) vs. figs 4-5 (Velez-Málaga specimen)]. For further discussion see under *Tomellana onubensis* nov. sp.

Specimens ascribed to *Clavatula/Perrona jouannetii* from other Miocene basins need to be reassessed. Those from the Paratethys were revised by Harzhauser *et al.* (2022). Those from the middle and upper Miocene of Italy figured by Bellardi (1847, pl. 2, fig. 15) and (1877, pl. 6, fig. 25) differ from *T. pliojouannetii* in having wider apical angle, lower, more gradate spire, much more angular base, and shorter siphonal canal. Bellardi’s two figures look somewhat different, but a series of specimens illustrated by Montanaro (1937, pl. 9, figs 4-15) seem to show intermediates between Bellardi’s two figured. The neanic whorls of these specimens need to be examined to see if they belong to *Perrona* or *Tomellana*. The specimen from the upper Miocene Tortonian of Portugal figured by Pereira da Costa (1867, pl. 26, fig. 16) is similar to those from the Tortonian of Italy. Despite being recorded from the Atlantic upper Miocene Cacula Velha assemblage of southern Portugal by that author, it seems to be extremely uncommon as no specimens are at hand in the extensive NHMW collections (ex BL coll.), nor in the Naturalis collections in Leiden (Netherlands).

Fekih (1975) recorded *Clavatula jouanneti* [*sic*] from the lower Pliocene of Tunisia and erected a new variety *bicincta* (*nomen nudum*). Unfortunately, the entire turrid section of this useful work consists of a species list without comments or illustrations. Therefore, the Tunisian records require further investigation.

Spadini & Manganelli (2010) reported the genus *Perrona* for the first time in the Italian Pliocene. The specimens illustrated (2010, figs 1-5) are all poorly preserved and the neanic whorls are either missing or abraded in all five specimens. The authors concluded that their specimens were most like *Perrona villarrasensis* Vera-Peláez & Lozano-Francisco, 2001, described originally from the Atlantic lower Pliocene Guadalquivir Basin of southwestern Spain. That species is known only from three specimens. It is difficult to conclude from the original figures and description what the neanic whorl sculpture is, but the siphonal canal is much shorter than in *T. pliojouannetii* from Estepona or *Tomellana* sp. from Huelva. The Italian specimens illustrated by Spadini & Manganelli (2010) have a relatively long siphonal canal, and the shape of their anal sinus does not match that of *P. villarrasensis*. It is not clear if Spadini & Manganelli excluded the possibility of these ‘*Perrona*’ species from Italy being reworked Miocene material.

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

***Tomellana onubensis* nov. sp.**

Pl. 12, figs 1-6

- 1984 *Perrona jouanneti* [sic] (Desmoulins, 1842) – Landau, p. 140 [non *Tomellana jouannetii* (Des Moulins, 1842)].
- 1992 *Perrona (Perrona) jouanneti* [sic] (Desmoulins, 1842) – González Delgado, p. 30, pl. 2, figs 9-10. [non *Tomellana jouannetii* (Des Moulins, 1842)].
- 1996 *Perrona (Perrona) jouanneti* [sic] (Des Moulins, 1842) – Vera-Peláez (*partim*, Huelva specimens only), p. 241, pl. 7, figs 4-5; not pl. 13, figs 1-3, pl. 15, fig. 7 (Velez-Málaga specimen = *Tomellana postjouannetii* nov. sp.); not pl. 7, figs 6-7 (Spanish Miocene specimens, undetermined *Perrona* or *Tomellana* sp.) [non *Tomellana jouannetii* (Des Moulins, 1842)].
- 1997 *Perrona jouanneti* [sic] (Desmoulins) – Ruiz Muñoz *et al.*, p. 184, pl. 39, figs 3, 4 [non *Tomellana jouannetii* (Des Moulins, 1842)].
- 2001a *Perrona (Perrona) jouanneti* [sic] (Des Moulins, 1842) – Vera-Peláez & Lozano-Francisco (*partim*, Huelva specimens only), p. 34, pl. 7, figs 9-13 (only), pl. 9, figs 1-3, 5 (only) [not pl. 7, figs 7-8 (Italian Miocene specimens, undetermined *Perrona* or *Tomellana* sp.), not pl. 7, figs 9-13, pl. 9, fig. 4 (Velez-Málaga specimen = *Tomellana pliojouannetii* nov. sp.) [non *Tomellana jouannetii*

(Des Moulins, 1842)].

- 2011 *Perrona jouanneti* [sic] (Desmoulins, 1842) – Landau *et al.*, p. 37, pl. 20, fig. 8 [non *Tomellana jouannetii* (Des Moulins, 1842)].

Type material – Holotype NHMW 2020/0171/0579, height 30.0 mm, width 10.6 mm; paratype 1 NHMW 2020/0171/0578, height 38.3 mm, width 12.6 mm; paratype 2 NHMW 2020/0171/0577, height 33.0 mm, width 9.7 mm.

Other material – NHMW 2020/0171/0580 (50+, ‘yellow sands’ of Landau, 1984), NHMW 2020/0171/0581 (5, ‘grey sands’ of Landau, 1984).

Type locality – Lucena del Puerto, Huelva, Spain.

Type stratum – ‘Yellow sands’ of Landau (1984), ‘Arenas de Huelva Formation’, Zanclean, lower Pliocene.

Etymology – Named after Onuba, the pre-Roman name for the province of Huelva. *Tomellana* gender feminine.

Diagnosis – *Tomellana* species of medium size, moderately slender, conical to gradate spire, bipartite early whorls with narrow, weakly beaded subsutural cord (possibly weakly beaded) and abapical row of tubercles, mid-whorl concave, later whorls with strongly developed but poorly

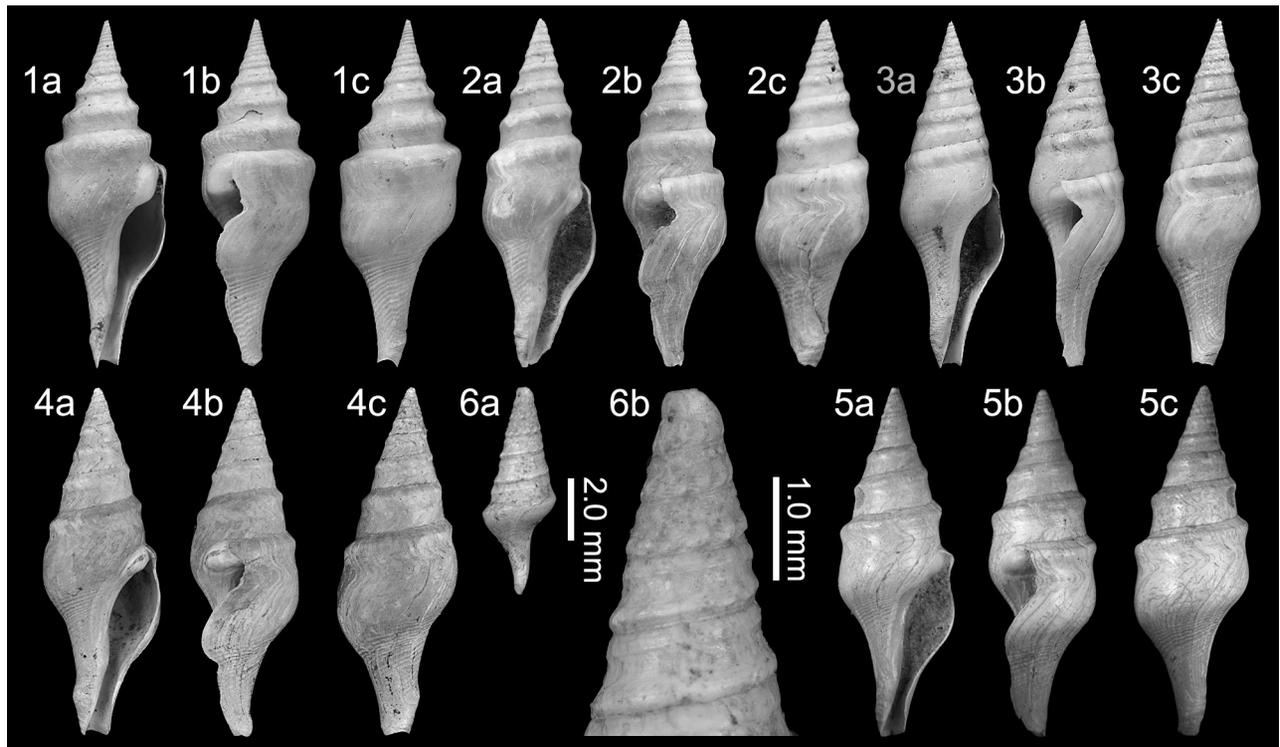


Plate 12. *Tomellana onubensis* nov. sp.; **Holotype** NHMW 2020/0171/0579, height 30.0 mm, width 10.6 mm; **2. Paratype 1** NHMW 2020/0171/0578, height 38.3 mm, width 12.6 mm; **3. Paratype 2** NHMW 2020/0171/0577, height 33.0 mm, width 9.7 mm; ‘Yellow sands’ of Landau (1984). ‘Grey sands’ of Landau (1984). **4. Paratype 3** RGM.1364534, height 38.3 mm, width 12.6 mm; **5. Paratype 4** RGM.1364535, height 26.3 mm, width 9.0 mm; **6. Paratype 5** RGM.1364536, height 6.6 mm (juvenile), **6b**, detail of sculpture early teleoconch whorls (all digital images). ‘Yellow sands’ of Landau (1984), Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, Zanclean, lower Pliocene.

delimited, smooth subsutural cord, smooth concave mid-section, suprasutural cord covered by succeeding whorl, last whorl with broad suprasutural collar, shoulder broadly rounded, spiral sculpture weak, restricted to base and siphonal fasciole, anal sinus moderately deep, narrow, asymmetrically U-shaped, siphonal canal long.

Description – Shell medium-sized, moderately slender fusiform, with tall conical to gradate coeloconoid spire (spire angle 33.2–44.7°). Protoconch not preserved. Teleoconch of up to 9–10 whorls, with periphery at shoulder, separated by superficial, linear suture. Sculpture on early teleoconch with narrow subsutural cord, possibly weakly beaded, and wider, beaded suprasutural cord, mid-whorl smooth, concave. On later whorls subsutural cord broadens to form smooth, rounded, poorly delimited collar, mid-portion weakly concave, smooth, suprasutural cord covered by succeeding whorl. Last whorl 66–68% of total height, with broad, rounded, poorly defined subsutural collar, weakly concave subsutural ramp, poorly delimited by broadly rounded shoulder, convex below, moderately constricted at base, base not delimited, fasciole not delimited from base; weak spirals over base, strengthening slightly over siphonal fasciole. Aperture moderately narrow, 53–57% of total height, outer lip simple; anal sinus moderately deep, narrow, asymmetrically U-shaped, with apex mid-ramp; siphonal canal long, straight, narrow, notched at tip. Columella smooth, broadly excavated in upper half, straight below, slightly twisted at fasciole. Columellar callus hardly thickened, forming narrow callus margin; parietal callus weakly to strongly developed.

Discussion – *Tomellana onubensis* nov. sp. differs from *T. pliojouannetii* nov. sp. in having a broader profile, the subsutural cord, later developed into a broad rounded collar, is not sharply delimited as it is in *T. pliojouannetii*, the shoulder is more broadly rounded, and the spirals on the base and fasciole are weaker and not of alternating strength, as they are in *T. pliojouannetii*. They also differ in the shape of their anal sinus (Fig. 2), the apex of the sinus is placed lower, mid-subsutural ramp in *T. onubensis*, as opposed to just below the collar in *T. pliojouannetii*. The holotype (Pl. 12, fig. 1) has a typical *Tomellana* profile with a broad rounded subsutural collar and strongly developed parietal pad, as seen in the type species *Tomellana lineata* (Lamarck, 1816), which makes it even more clearly different from the Estepona species. However, the development of the collar and parietal pad are variable, as seen in the series illustrated.

Distribution – Lower Pliocene: Atlantic, Guadalquivir Basin, southwestern Spain (Landau, 1984; Vera-Peláez & Lozano-Francisco, 2001a; Landau *et al.*, 2011).

Discussion

This revision of the clavatulids from the upper Pliocene western Mediterranean of Estepona identifies ten clavatulid species; nine within the ‘*Clavatula*’ genus group

representing the genera ‘*Clavatula*’ (*s.l.*) and *Granulatocincta*, of which three are new: ‘*Clavatula iberica*’ nov. sp., ‘*Clavatula pliogradata*’ nov. sp., and ‘*Clavatula nana*’ nov. sp. One species is present representing the ‘*Perrona*’ genus group, which is described as new: *Tomellana postjouannetii* nov. sp. In the course of this revision, one new species was identified from the Atlantic lower Pliocene Guadalquivir Basin assemblage of Huelva, southwestern Spain: *Tomellana onubensis* nov. sp.

In this revision we have attempted to identify species groups within the clavatulids as done by Harzhauser *et al.* (2022). As discussed by those authors, based on morphologic data of early teleoconch whorls (which is supported by unpublished molecular data of Nicolas Puillandre), the present day species in the ‘*Clavatula*’ genus group can be grouped in six different clades. Of those three: the *bimarginata*-clade, *mystica*-clade and the *caerulea*-clade are represented in the Estepona assemblages. The genus *Granulatocincta* persisted in the Pliocene in the Mediterranean and adjacent Atlantic represented by two or three species but does not occur in the extant faunas.

A *Clavatula carinulata* Sacco, 1904 species group is recognised, present in the upper Miocene Proto-Mediterranean and Pliocene western Mediterranean and adjacent Atlantic that also does not occur today, and one species ‘*Clavatula nana*’ nov. sp. is left unassigned.

In the ‘*Perrona*’ species group, based on the molecular data, *Perrona* and *Tomellana* are valid genera. A revision of the fossil Pliocene members of this group, placing taxonomic importance on the neanic whorl morphology, suggest that they were all members of the genus *Tomellana*, and that *Perrona* did not re-enter the Mediterranean or occur along the adjacent Atlantic during the Pliocene. Unpublished molecular data by Nicolas Puillandre suggest that *Clavatula* is polyphyletic, which is supported by conchological data (see Harzhauser *et al.* 2022).

Some of the fossil Pliocene species can be assigned to extant genera and clades, but the group has been more diverse in the past and some clades present in the fossil assemblages are no longer represented in the extant faunas.

At species level the findings herein deviate considerably from those of Vera-Peláez & Lozano-Francisco (2001a, 2001b) (summary given in Table 1). Seven species were recorded by those authors from Estepona (nine in total: *Clavatula implexa* Bellardi, 1877 seems to be a *lapsus*, and two are the same species, = seven species; see Table 1), of which three (44%) were considered endemic. In this work six of the ten species present are considered endemic (60%). Moreover, only two, possibly three of the species extend their range into the middle Miocene, and none survived the end of the Pliocene (Fig. 3).

This high level of endemism and short stratigraphic distribution is in keeping with their non-planktotrophic mode of development.

In the lower Pliocene Atlantic Guadalquivir Basin assemblage reviewed in the same paper (Vera-Peláez & Lozano-Francisco, 2001a) they recorded ten clavatulid species, of

Vera-Peláez & Lozano-Francisco, 2001a	<i>hoc opus</i>
<i>Clavatula interrupta</i> (Brocchi, 1814)	' <i>Clavatula</i> ' <i>iberica</i> nov. sp.
<i>Clavatula rustica</i> (Brocchi, 1814)	<i>Granulatocincta rustica</i> (Brocchi, 1814)
<i>Clavatula implexa</i> Bellardi, 1877 <i>lapsus</i> *	
<i>Clavatula romana</i> (Defrance, 1826)	' <i>Clavatula</i> ' <i>romana</i> (Defrance, 1826)
<i>Clavatula carinulata</i> Sacco, 1890 [<i>sic</i>]	' <i>Clavatula</i> ' <i>munizsolisi</i> (Vera-Peláez & Lozano-Francisco, 2001)
<i>Clavatula martinelli</i> Vera-Peláez & Lozano-Francisco, 2001	<i>Clavatula martinelli</i> Vera-Peláez & Lozano-Francisco, 2001
<i>Perrona jouanneti</i> [<i>sic</i>] (Des Moulins, 1842)	<i>Tomellana postjouanneti</i> nov. sp. (Estepona) <i>Tomellana onubensis</i> nov. sp. (Huelva)
<i>Perrona estebunensis</i> Vera-Peláez & Lozano-Francisco, 2001	' <i>Clavatula</i> ' <i>estebunensis</i> (Vera-Peláez & Lozano-Francisco, 2001)
<i>Perrona munizsolisi</i> Vera-Peláez & Lozano-Francisco, 2001	' <i>Clavatula</i> ' <i>munizsolisi</i> (Vera-Peláez & Lozano-Francisco, 2001)
	' <i>Clavatula</i> ' <i>pliogradata</i> nov. sp.
	' <i>Clavatula</i> ' <i>modesta</i> (Pecchioli, 1864)
	' <i>Clavatula</i> ' <i>nana</i> nov. sp.

Table 1. Taxonomic comparison between Vera-Peláez & Lozano-Francisco (2001a, 2001b) and taxonomy used herein.

**Clavatula implexa* Bellardi, 1877 is registered as occurring in Velerín by Vera-Peláez & Lozano-Francisco (2001a, p. 47, tab. 17) and repeated in Vera-Peláez & Lozano-Francisco (2001b, p. 193, tab. 2), but there is no record or discussion of the species occurring in the Estepona assemblages (2001a, p. 17-18)

which five (50%) were considered endemic. Again, this is an underestimate, as *Clavatula interrupta* (Brocchi, 1814) and *C. carinulata* Sacco 1890 [*sic*] are misidentified, and *Perrona jouanneti* [*sic*] is not that species, but *Tomellana onubensis* nov. sp., which raises the rate of endemism to 80%. The clavatulids from these Spanish Atlantic assemblages require further study. Unfortunately, in these deposits the early whorls are usually poorly preserved. In the Atlantic upper Pliocene, lower Piacenzian of the Mondego Basin two clavatulid species occur (Silva, 2001).

European clavatulid diversity in the Miocene was discussed by Harzhauser *et al.* (2022, p. 153), especially in relation to the Paratethys, and found to be driven by thermophilic conditions, with a maximum in the Paratethys coinciding with the onset of the Miocene Climatic Optimum (Zachos *et al.* 2001).

In the Pliocene, European clavatulid diversity is reduced in comparison with Miocene assemblages at the same latitude. Although the Pliocene assemblages discussed herein vary slightly in age, they all form part of MPP-MU1 (Mediterranean Plio-Pleistocene Molluscan Unit; see Raffi & Monegatti, 1993; Monegatti & Raffi, 2010; Silva *et al.*, 2010; Landau *et al.*, 2011; *inter alia*) which includes the late Zanclean and early Piacenzian and saw frankly tropical conditions in the Mediterranean and adjacent Atlantic. In the Pliocene Mediterranean of Italy six clavatulid species were discussed by Scarponi & Della Bella (2004). This did not include *Clavatula implexa* Bel-

lardi, 1877 described from the lower Pliocene of Italy (or *C. raffaelei* Cipolla, 1914 from the upper Pliocene, which is considered a junior subjective synonym of '*C.*' *romana* herein) and the *Tomellana* species illustrated by Spadini & Manganeli (2010). In the western Mediterranean *Clavatula deperreti* Fontannes, 1880 was described from France and five species were recorded from the Pliocene of north-eastern Spain (Vera-Peláez & Lozano-Francisco, 2001a, 2001b). This information comes primarily from an unpublished thesis by Marquina (1988a) to which we do not have access. We note that *Clavatula acuticostulata* Marquina, 1988 described from Papiol (Baix Llobregat-Barcelona, NE Spain) has strong axial sculpture and is not a Clavatulidae. It is either a species of Borsoniidae Bellardi, 1875 or Pseudomelatomidae Morrison, 1965.

Diversity only increases significantly in the western Mediterranean close to the Strait of Gibraltar and adjacent Atlantic, with ten species each in the Estepona and Guadalquivir Basin assemblages. Further North, in the Mondego Basin assemblage the diversity is drastically reduced to two species. This is to be expected, as at the time this formed part of the more northern subtropical French-Iberian Province. At the northern range of that subtropical province represented by the Assemblage III of northwestern France (see Landau *et al.*, 2019) only one clavatulid species is present (Ceulemans *et al.*, 2018). Therefore, clavatulid diversity is dependent on thermophilia, and in the Pliocene diversity seems to have increased immediately adjacent to the Atlantic Ocean.

Species	Geographical distribution					Stratigraphical distribution							
	Present-day					Miocene		Pliocene		Pleistocene		Hol	
	1	2	3	4	a/c	Lower	Middle	Upper	Lower	Upper	Lower		Upper
<i>'Clavatula' martinelli</i> (Vera-Peláez & Lozano-Francisco, 2001)			●		Ⓜ					■			
<i>'Clavatula' pliogradata</i> nov. sp.			●		Ⓜ				■	■			
<i>'Clavatula' romana</i> (Defrance, 1826)			●		Ⓜ			■	■	■			
<i>'Clavatula' iberica</i> nov. sp.			●		Ⓜ			■	■	■			
<i>'Clavatula' modesta</i> (Pecchioli, 1864)			●		Ⓜ			■	■	■			
<i>'Clavatula' munizsolisi</i> (Vera-Peláez & Lozano-Francisco, 2001)			●		Ⓜ				■	■			
<i>'Clavatula' estebunensis</i> (Vera-Peláez & Lozano-Francisco, 2001)			●		Ⓜ				■	■			
<i>'Clavatula' nana</i> nov. sp.			●		Ⓜ				■	■			
<i>Granulatocincta rustica</i> (Brocchi, 1814)			●		Ⓜ	■	■	■	■	■			
<i>Tomellana postjouanetii</i> nov. sp.			●		Ⓜ				■	■			
<i>Tomellana onubensis</i> nov. sp.		●			Ⓜ			■	■	■			

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

Acknowledgements

Our thanks to Ronald Janssen of the Senckenberg Forschungsinstitut und Naturmuseum Senckenberganlage (Frankfurt am Main, Germany) and Riccardo Giannuzzi-Savelli of Palermo, Italy for their comments and reviews that greatly improved this paper.

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