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The *Inella* group (Gastropoda: Triphoridae, Triphorinae) in the south-western Iberian Pliocene: first records with two new species

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In this paper we record a species of the *Inella* group for the first time in the Pliocene Mediterranean with the description of *Inella bentae* spec. nov. from the Estepona Basin, and *Inella* spec. and *Triphora* (s. l.) *freixiensis* spec. nov. from the Mondego Basin.

Key words: Gastropoda, Triphoridae, *Inella*, Pliocene, Estepona, Mondego

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INTRODUCTION

The family Triphoridae Gray, 1847 is a diversified taxon of small, mostly left-coiled, marine epibenthic spongivorous gastropods mainly occurring in tropical to subtropical waters. The family ranks among the five most diversified families of marine molluscs worldwide (e.g., Bouchet et al., 2002; Albano et al., 2011; Fernandes & Pimenta, 2019).

In the nomenclator of the family, Bakker & Albano (2022) listed 958 species and 75 genus names, of which 771 were known as extant species and 146 as fossil species, 41 known from both the fossil record and today's faunas. However, the expected overall diversity of the group is much higher, with estimates of 2,500 to 5,000 species occurring in the present-day Indo-Pacific alone being put forward by Albano et al. (2011).

Triphorid diversity results from adaptation to feeding on prey showing a high level of structural and textural variability (Marshall, 1978 & 1983; Nützel, 1998), coupled with variable planktotrophic and lecitototrophic larval development strategies, often in the same genus and even within species pairs (Marshall, 1983; Nützel, 2014).

The focus of this paper is the subfamily Triphorinae Gray, 1847 in the Iberian Neogene, where records of this group are scarce. *Triforis perversus* var. *adversa* Montagu was reported by Almera & Bofill (1898) from the Pliocene of Can Albareda, near Barcelona, north-eastern Spain. González Delgado (1986) illustrated a shell from the Atlantic lower Pliocene of the Guadalquivir Basin of southern Spain as *Triphora* (*Triphora*) *perversa* (Linnaeus, 1758). This same species was recorded from the Guadalquivir Basin assemblage as *Marshallora* cf. *adversa* (Montagu, 1803) by Landau et al. (2011).

The Triphorinae Gray, 1847 from the Spanish Estepona Basin Pliocene assemblages were monographed by Landau et al. (2006). Despite the exceptionally rich and diverse fauna recorded in these assemblages, 900 plus species of gastropods, those authors only recognised three triphorid species: *Marshallora* cf. *adversa* (Montagu, 1803), *Obesula protopaucispirata* Landau, La Perna & Marquet, 2006, and *Strobiligera cristulata* (Sacco, 1895).

The group was likewise described from the Pliocene fossil record of the Portuguese Mondego Basin by Silva (2001). Within an assemblage significantly less diversified than that from Estepona, including only around 170 gastropod species, one Triphorinae species was recognized, left in open nomenclature: *Marshallora* aff. *adversa*.

This paper reports three new Pliocene species of Triphorinae – *Inella bentae* spec. nov. from the Estepona Basin and *Inella* spec. (not formally described as based on protoconch only) and *Triphora* (s.l.) *freixiensis* spec. nov. from the Mondego Basin – therefore significantly adding to the paleobiodiversity of this overall species-rich group in the Neogene of the Iberian Peninsula. *Inella bentae* spec. nov. represents the first occurrence of the genus for the Mediterranean Pliocene. We follow Lozouet (1999) in designating these species to the genus *Inella*, although it may be paraphyletic and is referred to as '*Inella* group' herein. The *Inella* group is recorded for the first time in roughly contemporaneous beds from the Atlantic Mondego Basin of central-west Portugal. Interestingly, these are also the last occurrences of the genus in the Neogene north-eastern Atlantic and Mediterranean waters, their importance for the biogeography of the group being discussed herein.

MATERIAL AND METHODS

Estepona Basin assemblage

The study material originates from the Pliocene Velerín site area, located in the Malaga region of southern Spain, some 5 km north-east of the town of Estepona, on the left bank of the Rio del Castor, 1.2 km away from the present-day Mediterranean Alborán Sea coast, with the geographical coordinates 36.45033, -5.097431 (for location map see Landau et al., 2003, text-fig. 1). The Pliocene deposits of the Estepona Basin lie on Sierra Bermeja metamorphic rocks and on sandstones of the Campo de Gibraltar Flysch Complex of Mesozoic to Cenozoic age, both extensively exposed in the region to the north-east of Estepona and the south-west of the nearby town of San Pedro de Alcántara.

The Pliocene deposits in the Velerín site area consist of around 6 m of channelized conglomerates intercalated with sandy and coarse sandy lenses up to 30 cm thick. The conglomerates are made of clasts of metamorphic rocks around 3 to 10 cm in diameter originating from the Sierra Bermeja substrate. Fossils of invertebrate animals are abundant in these deposits, both in the sands and in the conglomerates.

According to Aguirre (1995) and Aguirre et al. (2005), the Estepona Basin deposits represent one single transgressive unit. However, Guerra-Merchán et al. (2002) considered three units for these deposits in the Estepona-San Pedro de Alcántara area, with the Velerín study sequence corresponding to the upper part of the lower conglomeratic section of his 'middle Pliocene unit' deposited – after Aguirre et al. (2005) – in a marine inner fan-delta environment.

Although regarded as Pliocene since the very first studies (e.g., Ansted, 1857), there has been controversy surrounding the precise stratigraphic position of the rich molluscan fossiliferous assemblages of the Estepona Basin, namely those of the Velerín area. Since the late nineteenth century, these deposits have been assigned to the middle to upper Pliocene (e.g., Bertrand & Kilian, 1892; González-Donoso & de Porta, 1977). In early twenty-first century, based on planktic foraminifera, Guerra-Merchán et al. (2002) assigned the 'middle Pliocene unit' to the biozone MPL 4b of Cita (1975), i.e., to the lower Piacenzian (lower upper Pliocene). Later, based on the assemblage of planktic heteropod and pteropod gastropods, Janssen (2004), again, dated these deposits as lower Piacenzian, although for some sites of the Velerín area – where the holoplanktonic gastropod assemblage was poorer – a Zanclean age could not be excluded. Despite the extreme paucity of calcareous nannofossils resulting from shallow depositional conditions, a difficulty already experienced by Janssen (2004), Aguirre et al. (2005) tentatively assigned the Velerín fossil assemblage to the Biozone CN11b of Okada & Bukry (1980), i.e., to the uppermost Zanclean (uppermost lower Pliocene). For more information on the general geological setting and the stratigraphy of the Estepona Basin and the Velerín area in particular see Guerra-Merchán et al. (2002) and Aguirre et al. (2005).

Either way, uppermost Zanclean or lowermost Piacenzian in age, the study molluscan assemblage corresponds to the ecostratigraphic Mediterranean Plio-Pleistocene Molluscan Unit 1 (MPPMU1) of Monegatti & Raffi (2001). Chronologically, this unit spans the Zanclean and the early Piacenzian up to the 3.3 Ma mid-Pliocene major cooling event occurred in Marine Isotope Stage (MIS) M2, during the reversed polarity Mammoth Subchron (Monegatti & Raffi, 2007; Silva & Landau, 2007; Silva et al., 2010; Dolan et al., 2015). The study assemblage from the Mondego Basin (Portugal) also correlates to the MPPMU 1 unit, being roughly coeval.

The Velerín area deposits, both the conglomerates and the sandy beds, yield the richest and most diversified fossil assemblages of the Estepona Basin. The study assemblage includes numerous and well-preserved body fossils of invertebrates, mainly of molluscs (e.g., Janssen, 2004; Aguirre et al., 2005; Estepona ongoing series of gastropod monographs summarized in Landau & Mulder, 2020). The gastropod assemblage includes specimens of *Patella pellucida* (Silva et al., 2006). These extant herbivorous gastropods live on laminarian algae. Their presence in the tropical faunas of the pre-3.3 Ma Pliocene of the northern Alborán Sea suggests a shallow marine infralittoral environment under the influence of upwelling nutrient rich currents (Silva et al., 2006).

Fossils of Scaphopoda (Vera-Peláez et al., 1993) and Polyplacophora molluscs (Dell'Angelo et al., 2004) are also present. Other invertebrates represented include solitary and colonial scleractinian corals, crustaceans, bryozoans, echinoids and brachiopods (Guerra-Merchán et al., 1996; Martinell & Domènech, 2004; Spadini, 2019). The vertebrates are represented by bony fish otoliths and very rare shark teeth (BL personal observations).

The Triphoridae are spongivorous gastropods, therefore poriferans must have been present in the original biocenosis. In fact, the trace fossil record of the Velerín deposits includes *Entobia* bioerosion structures ascribed to the work of boring Clionaidae sponges (e.g., Schönberg, 2008), as well as *Trypanites* and *Sulcichnus* bioerosion structures interpreted as resulting from the boring activity of polychaetes (Martinell & Domènech, 2004).

The Velerín study fossil assemblage and its geological context indicate an infralittoral, tropical shallow marine environment of normal salinity with a mixed pebbly and sandy substrate. The presence of carbonaceous plant remains (Aguirre et al., 2005) also suggests proximity to emerged land. The molluscan faunas represented in the study Estepona Basin assemblages were part of the Pliocene Mediterranean–West African Tropical Province of Silva & Landau (2007) and Landau et al. (2020).

Mondego Basin assemblage

The Mondego study assemblage originates from the Vale de Freixo site, located in central-west Portugal, 20 km east of the present-day coastline, close to the city of Pombal, with the geographical coordinates 39.88392, -8.73136 (for location map see Landau & Silva, 2022: fig. 1). The Neogene beds exposed at this locality are included in the Cainozoic Mondego Basin, the fossiliferous Pliocene sediments corresponding to the basal transgressive sequence of the Carnide Formation (Cachão, 1990; Diniz et al., 2016). Its calcareous nannofossil assemblage indicates placement in the biozone CN12a of Okada & Bukry (1980). Based on calcareous nannofossils and gastropod molluscs, these beds have been assigned to the uppermost Zanclean to lower Piacenzian (Cachão, 1990; Silva, 2001; Diniz et al., 2016). For further information on the geological setting and the stratigraphy of the Vale de Freixo site and supplementary references see Silva et al. (2006, 2010) and Dell'Angelo et al. (2022).

The Mondego Basin assemblage is one of the few Pliocene marine records available along the European Atlantic frontage and, therefore, crucial for understanding the paleobiogeography of Neogene to present-day Atlanto-Mediterranean molluscan faunas (e.g., Silva et al., 2006 + 2010). The gastropods are the most diverse molluscs represented in this rich assemblage (Silva, 2001 + 2002), followed by bivalves (Pimentel, 2018), polyplacophorans (Dell'Angelo & Silva, 2003) and scaphopods. Fossils of other benthic invertebrates such as bryozoans (Carvalho, 1961), echinoids (Silva, 2001; Pereira, 2010), and barnacles (Ferreira et al., 2019), are also present. The Triphoridae are micro-carnivorous gastropods feeding on sponges. In the study fossil assemblage, *Entobia* bioerosion structures ascribed to the work of boring Clionaidae sponges (Schönberg, 2008) are common (Silva, 2001).

The vertebrates are represented by bony fish otoliths and rare shark teeth (Nolf & Silva, 1997; Silva, 2001). Carbonaceous remains of terrestrial plants – seeds, pinecone, and pine needle fragments – are also known, suggesting proximity to terrestrial environments (Silva, 2001). The pollens and spores were investigated by Diniz (1984), Vieira et al. (2006), and Diniz et al. (2016).

The Pliocene fossil assemblage of Vale de Freixo indicates a subtropical infralittoral shallow marine environment of normal salinity sand-pebble shelly substrate, somehow protected from direct influence of the open Atlantic Ocean (Nolf & Silva, 1997; Silva, 2001; Silva et al., 2006; Silva et al., 2010). The molluscan fauna of Vale de Freixo, as well as all the known marine Pliocene Atlantic molluscan assemblages of the Mondego Basin, although Atlantic in distribution and subtropical in nature, correlate to the tropical Mediterranean Plio-Pleistocene Molluscan Unit 1 (MPMU1) as defined by Monegatti & Raffi (2001) for the Mediterranean (Silva et al., 2010). The study assemblage from the Velerín site area (Spain) also correlates to the MPMU1 unit, being roughly coeval. However, contrary to the Estepona West Mediterranean fauna, the Mondego malacofauna was part of the Pliocene French-Iberian Subtropical Province of Silva & Landau (2007) and Landau et al. (2020).

The Estepona Basin material described herein was collected by Henk Mulder at the Velerín site and kindly donated to the Natural History Museum Vienna (NHMW), where it is housed together with the Bernard Landau collection donated to the same institution. The Mondego Basin material was collected by the first author (BL) between 1990 and 2019 from the Vale de Freixo site, and also deposited in the NHMW.

SYSTEMATIC PALEONTOLOGY

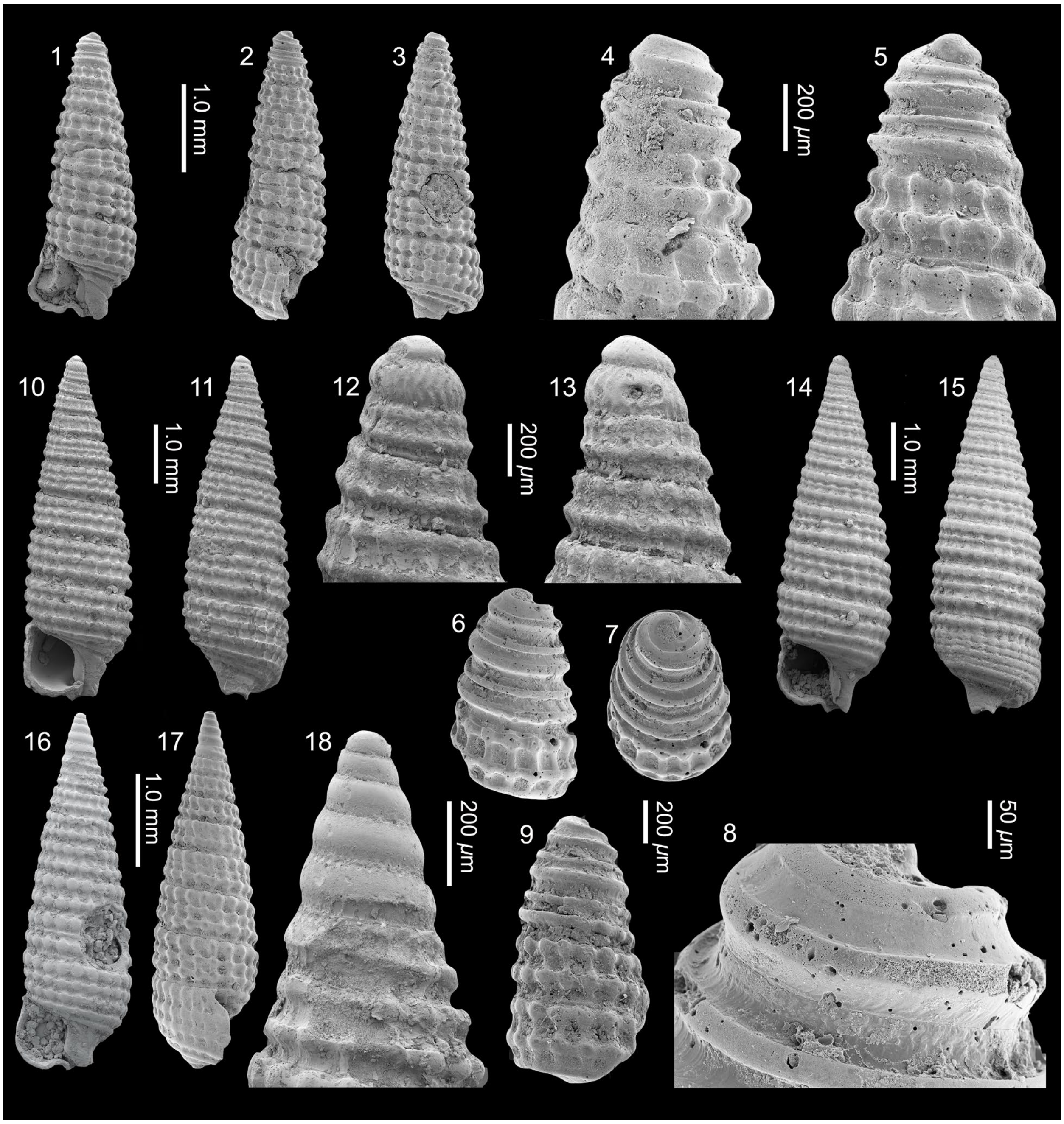
Superfamily Triphoroidea Gray, 1847
Family Triphoridae Gray, 1847
Subfamily Triphorinae Gray, 1847

Genus *Inella* Bayle, 1879

Ino Hinds, 1843: 17. Type species (by subsequent designation, Gray, 1847): *Triphora gigas* Hinds, 1843, present-day, New Guinea. Junior homonym of *Ino* Schrank, 1803 [Crustacea].

Inella Bayle, 1879: 35. Type species (by typification of replaced name): *Triphora gigas* Hinds, 1843, present-day, New Guinea. *Nomen novum* pro *Ino* Hinds, 1843 (non Schrank, 1803 [Crustacea]).

Norephora Gründel, 1975: 155. Type species (by original des-



Figs 1-18. Triphorid gastropods from the Atlanto-Mediterranean Pliocene. **Figs 1-5.** *Inella bentae* spec. nov., holotype NHMW 2022/0070/0025, height 3.2 mm, width 1.2 mm (Figs 4-5 detail of protoconch). Lower Piacenzian, upper Pliocene, Velerín Sands, Velerín, Estepona, Spain. **Figs 6-8.** *Inella* spec., holotype NHMW2022/0070/0026, height 1030 µm, width 610 µm, (Fig. 7 detail of protoconch, Fig. 8 detail of protoconch microsculpture). Lower Piacenzian, upper Pliocene, Vale de Freixo, Mondego Basin, Portugal. **Fig. 9.** *Inella* spec., paratype NHMW2022/0070/0027, height 1.3 mm, width 710 µm. Lower Piacenzian, upper Pliocene, Vale de Freixo, Mondego Basin, Portugal. **Figs 10-13.** *Triphora freixiensis* spec. nov., holotype NHMW2022/0070/0029, height 5.8 mm, width 1.8 mm (Figs 12-13 detail of protoconch). Lower Piacenzian, upper Pliocene, Vale de Freixo, Mondego Basin, Portugal. **Figs 14-15.** *Triphora freixiensis* spec. nov., paratype 1 NHMW2022/0070/0030, height 6.2 mm, width 2.0 mm. Lower Piacenzian, upper Pliocene, Vale de Freixo, Mondego Basin, Portugal. **Figs 16-18.** *Marshallora adversa* (Montagu, 1803), NHMW2022/0070/0031, height 3.8 mm, width 1.2 mm (Fig. 18 detail of protoconch). Lower Piacenzian, upper Pliocene, Vale de Freixo, Mondego Basin, Portugal. All SEM images.

ignation): *Triphora granulata* Strauch, 1967, Oligocene, Germany.

Remarks. — The genus is used here to describe species with blunt protoconch of between two and three whorls, bearing two spiral cords per whorl. According to Marshall (1983: 19), teleoconch spirals 1-3 develop simultaneously, spiral 1 weaker, usually remaining weaker than spirals 2 and 3 throughout (Marshall, 1983: 19). Both Marshall (1983) and Rolán & Fernández-Garcés (2008) commented that the limits of the genus were uncertain.

Species of the genus *Inella* have rarely been reported from European fossil assemblages. In the Neogene, Marquet (1996) described an *Inella* species from the upper Pliocene of Belgium and a second species from the lower Pliocene under the genus *Norephora* Gründel, 1975. We consider the differences given by Marquet (1996: 141) between *Norephora* and *Inella* insufficient to warrant separation. Lozouet (1999) described an *Inella* species from the upper Oligocene of France.

Inella bentae **spec. nov.**

Figs 1-5
urn:lsid:zoobank.org:act:4C9AFF74-E203-42C6-8AAC-D67F31348C7B

Type material. — Holotype NHMW2022/0070/0025, height 3.2 mm, width 1.2 mm (Figs 1-5).

Other material. — Known from holotype only.

Type locality. — Velerín conglomerates, Velerín, Estepona, Andalucía, S. Spain.

Type stratum. — Unnamed beds of lower Piacenzian age, upper Pliocene.

Etymology. — Named after Bente Nieland, granddaughter of Wil and Henk Mulder. *Inella* gender feminine.

Diagnosis. — Shell very elongated with flat sides, protoconch of 2.5 whorls; first half whorl sub-rectangular profile (Fig. 5) with a relatively large nucleus, later whorls bearing two strongly elevated spiral cords, abapical broader, teleoconch with three tubercular cords per whorl, ad- and abapical spirals appear simultaneously at protoconch/teleoconch boundary, middle spiral tardive, appearing on fourth teleoconch whorl, abapically, adapical spiral strengthens and middle and abapical spirals become of similar strength on last whorl, slightly weaker than adapical spiral, three strong smooth spirals over base.

Description. — Shell sinistral, small, cyrtoconoid to slightly ovoid, moderate convex profile. Protoconch of 2.5 whorls: first half whorl, sub-rectangular in profile, later whorls bearing two widely spaced, strongly elevated cords; adapical cord narrower, placed a short distance below suture, abapical cord broader, more elevated, placed a short distance above suture, no protoconch microsculpture present. Beginning of the teleoconch not sharp, marked by beginning of tubercles. Teleoconch of 6.5 flat-sided whorls separated by impressed suture, adapical and abapical spirals appear simultaneously at protoconch/teleoconch junction, adapical spiral slightly weaker, middle spiral tardive, appearing on fourth teleoconch whorl rapidly gaining strength abapically. On penultimate whorl spirals ad- and abapical spirals equal in strength, middle spiral narrower. Axial ribs weak, slightly opisthocline, 16 on penultimate whorl, forming rounded tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, adapical spiral strongest, base somewhat depressed, bearing three strong smooth cords: peribasal adapically delimiting base, weaker mid-basal cord, very strong perifasciolar cord; siphonal fasciole strongly developed, rounded, smooth delimited from base by a deep groove between the fasciole and peribasal cord. Aperture small, ovate; outer lip thin; anal canal marked by small notch; siphonal canal short, open, strongly bent to the right and recurved.

Paleoecology. — Epibenthic vagile spongivorous molluscs living in coastal infralittoral tropical marine environments of normal salinity and sandy-shelly substrates. The extant representatives of the genus are micro-carnivorous, primarily feeding on sponges. In the Velerín site area Pliocene fossil assemblage, *Entobia* bioerosion structures ascribed to the work of boring Clionaidae sponges (Schönberg, 2008) are common (Martinell & Domènech, 2004). The protoconch of *I. bentae* spec. nov. suggests a non-planktotrophic larval development.

Remarks. — Although the protoconch of the new species described herein is typical for the genus, the adult whorl sculpture is not, as the middle spiral is tardive. A molecular phylogeny for the group is not yet available. In the meantime, we follow Lozouet (1999) in including species with this type of protoconch in the genus *Inella*.

In the European fossil record the '*Inella* group' first appears in the Atlantic upper Oligocene Aquitaine Basin of France with *Inella cordata* Lozouet, 1999 which differs from the new Iberian Mediterranean species in having a protoconch with one more whorl and having all three spirals appear simultaneously at the protoconch/teleoconch junction, the adapical spiral only slightly weaker than the others. In the Atlantic Tortonian of north-western Loire Basin of France *Inella alia* Landau, Ceulemans & Van Dingenen, 2018 and *Inella rolani* Landau, Ceulemans & Van Dingenen, 2018 both differ from *Inella bentae* spec. nov. in the same characters: multispiral protoconch of an extra whorl and all three teleoconch spirals appearing at the beginning of the teleoconch, although in *I. rolani*, the adapical spiral starts very weak. In the North Sea Basin lower Pliocene Kattendijk Formation of Belgium *Inella* *pliocaenica* (Marquet, 1996) has a paucispiral protoconch similar to the one of *Inella bentae*, but in the North Sea Basin species the teleoconch adapical spiral is tardive, appearing 2.5 whorls after the protoconch/teleoconch boundary. *Inella vandermarki* Marquet, 1996 from the Luchtbal Sands Member of the Pliocene Lillo Formation of Belgium differs sharply in having a protoconch consisting of three smooth whorls.

***Inella* spec.**

Figs 6-9
urn:lsid:zoobank.org:act:201FA2BB-35A6-4800-8F8C-78EB26E64A6B

Material. — NHMW2022/0070/0026, height 1030 μm, width 610 μm (Figs 6-8); NHMW2022/0070/0027, height 1.3 mm, width 710 μm (Fig. 9); NHMW2022/0070/0028 (15), all juveniles.

Locality. — Vale de Freixo (VFX) site, near the village of Carnide, Pombal municipality, Central-West Portugal.

Stratum. — Pliocene, upper Zanclean to lower Piacenzian, Carnide Formation, basal fossiliferous gray sands, "Bed 3" in Dell'Angelo et al. (2022). Equivalent to the Mediterranean MPPMU1 of Monegatti and Raffi (2001).

Description. — Shell small, sinistral, cyrtoconoid shell. Protoconch of about three whorls: nucleus very small, sunken, post-nucleus whorl develops elevated ridge corresponding to the adapical spiral, abapical spiral develops about one-half whorl later as a second, abapical, elevated ridge, the ridges separated by a deep groove, second protoconch whorl bearing two widely spaced, strongly elevated cords; adapical cord narrower, placed a short distance below suture, abapical cord broader, more elevated, placed a short distance above suture, microsculpture of pustules present between cords. Transition to teleoconch not sharp, marked by beginning of axial sculpture. Teleoconch sculpture of two spiral cords of equal strength, adapical placed just below suture, abapical a short distance above suture, and fine axial ribs, forming large tubercles at sculptural intersections.

Paleoecology. — Epibenthic vagile gastropods living in coastal infralittoral subtropical marine environments (estimated maximum Mean Monthly Sea Surface Temperature (MMSST), of ~23.5°C in September and minimum MMSST of 19°C in January-March; Silva et al., 2010) of normal salinity and sand-pebble shelly substrates. In the Vale de Freixo Pliocene fossil assemblage, *Entobia* bioerosion structures ascribed to the work of boring Clionaidae sponges (Schönberg, 2008) are common (Silva, 2001).

Remarks. — *Inella* spec. is closely similar to the coeval *I. bentae* spec. nov. from the Mediterranean Estepona Basin of southern Spain in having two strong cords on the protoconch, the adapical weaker, and two tubercular cords on the neanic teleoconch whorls. In *I. bentae* the third cord appears tardive. We assume this is also the case in *Inella* spec., but all specimens at hand are juvenile, and the third spiral has not yet developed. However, the protoconch nucleus of the two is different. In *I. bentae* the profile of the first half whorl is sub-rectangular, whereas in *Inella* spec. an elevated ridge appears from the beginning of the post-nuclear whorl which develops into the adapical spiral. Moreover, there is no tubercular microsculpture in the spiral interspaces on the protoconch of *I. bentae*. We refrain to describe this species based on only juvenile specimens, however the protoconch morphology is unique in the European fossil Neogene assembly.

Despite carefully processing over 100 kg of Vale de Freixo sediment through a 0.5 mm mesh sieve, only juvenile specimens of *Inella* spec. have been found. Landau & Micali (2021) made a similar observation regarding the pyramidellid *Clathrella sulcosa* (Brocchi, 1814) which is also represented in the Mondego assemblage by juveniles alone, whereas in the roughly contemporaneous Estepona Basin assemblage adults are plentiful. The Mondego Basin region was part of the subtropical Pliocene French-Iberian Province (see Landau et al., 2011: 49, text-fig. 8). It is possible that larvae arrived here from the warmer tropical southern Pliocene Mediterranean-West African Province, but water temperatures were insufficient for them to mature at the more northern latitudes of Pliocene central-west Portugal.

***Triphora* (s.l.) *freixiensis* spec. nov.**

Figs 10-15
urn:lsid:zoobank.org:pub:52A88B34-DF9D-45EF-AEF1-CBD9081DC1FD

Type material. — Holotype NHMW2022/0070/0029, height 5.8 mm, width 1.8 mm (Figs 10-13). Paratype 1 NHMW2022/0070/0030, height 6.2 mm, width 2.0 mm (Figs 14-15).

Other material. — Known from type series only.

Type locality. — Vale de Freixo (VFX) site, near the village of Carnide, Pombal municipality, Central-West Portugal.

Type stratum. — Pliocene, upper Zanclean to lower Piacenzian, Carnide Formation, basal fossiliferous gray sands, "Bed 3" in Dell'Angelo et al. (2022). Equivalent to the Mediterranean MPPMU1 of Monegatti & Raffi (2001).

Etymology. — Named after the type locality of Vale de Freixo. *Triphora* gender feminine.

Diagnosis. — Shell conical with flat sides, protoconch of two whorls; Protoconch I low, cap-like, depressed, rounded, Protoconch II convex bearing arcuate axial riblets, teleoconch with three tubercular cords per whorl, spirals 1, weaker, and 3, stronger, appear simultaneously at protoconch/teleoconch boundary, spiral 2 tardive, appearing on fourth teleoconch whorl, later in teleoconch, spiral 1 strengthens, all three subequal on last whorl, three strong smooth spirals over base.

Description. — Shell sinistral, small, cyrtoconoid to slightly ovoid, moderate convex profile. Protoconch of two whorls: Protoconch I low, cap-like, depressed, rounded, Protoconch II convex bearing arcuate axial riblets, no protoconch microsculpture visible. Transition to teleoconch marked by appearance of spiral sculpture. Teleoconch of nine flat-sided whorls separated by impressed suture, adapical and abapical spirals appear simultaneously at beginning of teleoconch, adapical spiral slightly weaker, middle spiral tardive, appearing on fourth teleoconch whorl gaining strength abapically. Axial ribs very weak, slightly prosocline, 22 on penultimate whorl, forming small, rounded, spirally elongated tubercles at intersections with spiral sculpture. Last whorl bearing three subequal beaded primary spiral cords, secondaries intercalated on last half whorl in some specimens, base convex, not depressed, bearing three strong smooth cords: peribasal cord delimiting base, weaker mid-basal cord, very strong perifasciolar cord; siphonal fasciole strongly developed, rounded, smooth delimited from base by a deep groove between the fasciole and peribasal cord. Aperture small, ovate; outer lip thin; anal canal marked by small notch; siphonal canal short, open, strongly bent to the right and recurved.

Paleoecology. — Refer to the Paleoecology of *Inella bentae* spec. nov. above.

Remarks. — Generic placement is problematic. Some species related to the genus *Monophorus* Granata Grillo, 1877, such as *Triphora hemileuca* Tomlin, 1931 from present-day South Africa have a similar protoconch (see Albano et al., 2019: 281, fig. 101). Species in the genus *Eutriphora* Cotton & Godfrey, 1931, such as *E. cana* (Verco, 1909) from Australia also have somewhat similarly sculptured protoconchs (see Marshall, 1983: figs 22D-F). *Eutriphora* is also known from the tropical eastern Atlantic (Rolán & Fernández-Garcés, 2008). However, in our opinion, these genera are still not adequatly defined, and we prefer to leave the new species in open nomenclature as *Triphora* (s.l.).

There are no European or West-African extant or fossil species with which we can usefully compare the new taxon. *Triphora* (s. l.) *freixiensis* spec. nov. is immediately separated from all its congeners by its paucispiral protoconch with arcuate axial riblets. There is little intraspecific variability; in the largest specimen (paratype 1), the shoulder is a little more rounded than in the holotype. The sculpture is remarkably consistent.

DISCUSSION

Biogeography

Inella bentae spec. nov. and *Inella* spec. are geologically the last recorded members of the '*Inella* group' to occur in the European Neogene. Members of the '*Inella* group' are no longer present along the eastern Atlantic frontage of Europe or West Africa, nor in the Mediterranean. Akin *Inella* species occur today in shallow marine environments around Saint Helena (Bakker & Albano, 2022); however, St. Helena and Ascension Islands faunas are assigned to a separate biogeographic unit from West Africa (Spalding et al., 2007).

Inella, like *Clathrella sulcosa*, are thermophilic taxa, and managed to thrive in the tropical Pliocene Mediterranean-West African paleobiogeographical provice. The Mondego Basin region was part of the subtropical Pliocene French-Iberian Province (see Landau et al., 2011: 49, text-fig. 8). It is possible that larvae arrived here from the warmer tropical southern Pliocene Mediterranean-West African Province, but water temperatures were insufficient for them to mature at the more northern latitudes of Pliocene central-west Portugal.

Larval development

The Triphorinae are not diverse in the Pliocene Estepona Basin assemblage, where only four species have been recorded: *Marshallora* cf. *adversa* (Montagu, 1803), *Obesula protopaucistiata* Landau, La Perna & Marquet, 2006, *Strobiligera cristulata* (Sacco, 1895), and *Inella bentae* spec. nov. (Landau et al., 2006; hoc opus), nor are they diverse in the Mondego Basin, where three species are known: *Marshallora adversa* (Montagu, 1803) (Figs 16-18), *Triphora* (s. l.) *freixiensis* spec. nov., and *Inella* spec. (Silva, 2001; *hoc opus*).

Even though several extensive studies of the European Cenozoic paleontological record of the Triphoridae have been carried out in the last decades (e.g., Marquet, 1996; Lozouet, 1999; Landau et al., 2018), a state-of-the-art nomenclator of all fossil and present-day triphorids (Bakker & Albano, 2022) did show a marked contrast between their extant (771 spp. in present-day faunas) and fossil diversity (with only 146 spp.). Even considering that the paleontological record for Triphoridae is probably very incomplete, this would suggest a relatively recent explosion in triphorid diversity.

Despite the paucity of Triphorinae species recorded in fossil assemblages, protoconch morphology in them is far more varied than that seen in extant species of the group along the Atlantic coasts of Europe and West Africa (Fernandes & Rolán, 1988), in the Mediterranean (Bouchet, 1985; Rolán & Peñas 2001). All present-day Triphorinae in these regions show tall, multispiral protoconchs, usually with the last whorls keeled and sculptured by ribs and/or tubercles. These protoconchs are typical of gastropods with planktotrophic larval development.

In the fossil record, as early as in the upper Oligocene of France, Lozouet (1999) described species with an *Inella*-type strongly carinate protoconch. Landau et al. (2018) illustrated an enormous diversity in protoconch morphology in triphorids from the Tortonian upper Miocene of north-western France, much more like the sort of protoconch diversity seen in present-day species from South and East Africa (Albano & Bakker, 2016), Caribbean (Rolán & Fernández-Garcés, 2008) and Australia and New Zealand (Marshall, 1983).

In triphorids, as in numerous other gastropod groups, planktotrophy is the ancestral condition, and all non-planktotrophic taxa are derived from planktotrophic ancestors or their non-planktotrophic descendants (e.g., Bouchet, 1990; Krug et al., 2015).

Most species with a planktotrophic larval development are generally more widely dispersed than their non-planktotrophic descendants. The paucispiral protoconchs of non-planktotrophic gastropods are very variable in size, shape and sculpture, and similar morphologies have evolved repeatedly throughout geological time and in present-day faunas (Marshall, 1983; Rolán et al., 2008; Albano & Bakker, 2016; Philippe Bouchet and Bruce Marshall personal communication in Landau et al. 2018: 218). Therefore, sharing a protoconch suggesting a non-planktotrophic larval development does not necessarily imply a phylogenetic relationship. Genetic evidence elucidating triphorid phylogeny is not yet available (Philippe Bouchet pers. comm. in Landau et al. 2018: 218). This phenomenon is not restricted to triphorids, but also applies to the closely related cerithiopsids (Marshall, 1978).

The sharp drop in protoconch diversity from the Neogene to present-day European and West African triphorid species does not seem to be the case in the eastern Atlantic, nor in the southern hemisphere where protoconch diversity is very high, especially around South (and far West) South Africa and Australia (Thiele, 1925; Marshall, 1983; Albano & Bakker, 2016). This circumstance cannot be explained by the decrease in SSTs alone, as the Estepona Basin faunas were part of the tropical Pliocene Mediterranean-West-African Paleobiogeographic Province, and the roughly coeval Mondego Basin fauna was part of the subtropical Pliocene French-Iberian Province. The protoconch diversity seen in triphorids along the Neogene European Atlantic Frontage and adjacent Mediterranean has not been reported from Pliocene assemblages from the Pliocene central and eastern Mediterranean (Brunetti & Cresti, 2018).

At present we do not have an explanation for this paucity in protoconch type along the eastern Atlantic frontage and Mediterranean but highlight this phenomenon as being worthy of further thought.

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