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The genus *Euthria* (Gastropoda, Tudiclidae) in the Pliocene of the Atlantic Mondego Basin of Portugal: a glocal taxon in the Atlanto-Mediterranean Neogene

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Abstract

Today, the range of the genus *Euthria* encompasses the Mediterranean and the eastern Atlantic, the region around southern Africa, and extends into the western Indo-Pacific. The genus, which has a geological history dating back to the Eocene of Europe, has recently undergone taxonomic revision in several European Neogene basins. These studies revealed a pronounced expansion during the Oligocene and Neogene in the Atlanto-Mediterranean region and the Paratethys, and these studies highlighted the overall diversity of the genus combined with a pronounced regional endemism. This paper reviews the fossil record of the genus in the western Iberian Pliocene of the Cainozoic Mondego Basin of Portugal. Two new species endemic to western Iberia with protoconchs showing non-planktotrophic developmental traits have emerged: *Euthria galopimi* n. sp. and *Euthria lockleyi* n. sp. These results reinforce the glocal character of *Euthria*, a genus that is both widespread and diversified, but simultaneously showing a high endemism. The contribution of nonplanktotrophic development to this scenario is discussed. Although well represented in the fossil record of Atlantic France, in present-day European waters, *Euthria* is represented by a single species, *E. cornea* (Linnaeus, 1758), and only in the Mediterranean and the northern shores of the Gulf of Cadiz. As with other warm-water molluscan taxa, the northern distribution limit of *Euthria* in the Atlantic has shifted southward since the Early to mid-Pliocene due to global cooling events and decreasing sea surface temperatures.

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Non-technical Summary

This paper discusses the geological history of the seasnail genus *Euthria* in the eastern Atlantic, Mediterranean, and Paratethys, an inland sea that existed in central-eastern Europe during the Middle Miocene, around 15 million years ago (Ma). The genus has a long geological history dating back to the Eocene, around 47 Ma. Recent studies showed that since the Oligocene, around 44 Ma, it increased in geographic range and in numbers of species. However, despite being present in many locations in this vast territory, a lot of its species were found only in restricted areas. This paper reviews the fossil record of *Euthria* in the western Iberian Pliocene of the Mondego Basin of Portugal. Two new species are described—*Euthria galopimi* n. sp. and *Euthria lockleyi* n. sp.—both endemic, i.e., occurring only in the study area. They both have a larval shell that suggests that these seasnails did not spend a significant amount of time in the plankton as larvae in the early phase of their life. The importance of this mode of larval development to understand their restricted geographical distribution is discussed. Despite being represented by numerous species in the eastern Atlantic and Mediterranean in the past, today a single species of *Euthria* occurs in the Mediterranean, and it is not present in more northern Atlantic waters. As with other seasnail groups that require warm water, the northern distribution limit of *Euthria* in the Atlantic has shifted southward since at least the Pliocene, around 3 Ma, due to decreasing temperatures.

Introduction

The genus *Euthria* Gray, 1850 (Tudiclidae, Buccinoidea) boasts a relatively long geological history, stretching back to the Eocene. Notably, Cossmann (1901, p. 119) documented three *Euthria* species in the Eocene deposits of the Paris and Loire basins of northern and northwestern France. Two species are mentioned from the Lutetian of the Paris Basin: *Euthria decipiens*

Deshayes, 1864 and *Euthria douvillei* Cossmann and Pissarro, 1911 (Le Renard and Pacaud, 1995; Pacaud and Le Renard, 1995). *Euthria decipiens* lacks the typical angulation of the columella at the siphonal canal of typical *Euthria* species, and we exclude it from the genus (see Cossmann and Pissarro, 1911, pl. 37, fig. 181-1). Similarly, *Euthria douvillei* Cossmann and Pissarro, 1911 is unrelated to *Euthria* due to its prominent spiral sculpture (see Cossmann and Pissarro, 1911, pl. 37, fig. 181-2). However, *Euthria reducta* Cossmann, 1897 from the Bartonian of the Loire Basin might be an early *Euthria* (see Cossmann, 1897, pl. 6, figs. 19, 20), which would place the origin of the genus at around 40 million years ago (Ma).

The next unequivocal European records of *Euthria* representatives emerge from the Atlantic lower Oligocene deposits of the Paris Basin of France (Cossmann, 1901). The genus already exhibits a significant presence and diversity in the French Atlantic upper Oligocene of the Aquitaine Basin (Lozouet, 2021), becoming widespread in fossil assemblages of Neogene age across the European Atlantic Frontage (Peyrot, 1928, 1938; Van Dingenen et al., 2017; Landau et al., 2019a; inter alia), the Proto-/Mediterranean (Bellardi, 1873; Brunetti and Della Bella, 2016; Landau and Harzhauser, 2024; inter alia), and the Paratethys (Hoernes and Auinger, 1890; Harzhauser and Landau, 2024; inter alia).

Beets (1986, p. 92), who regarded *Euthria* as a subgenus of *Buccinulum* Deshayes, 1830, identified two primary geographical groups within the extant species of these taxa. He proposed that both groups trace their origins back to the early Cenozoic, the first one spanning from Western and Central Europe to the Indo-Western Pacific region, reaching Japan, and extending across the Mediterranean to the eastern and southern Atlantic, encompassing the region around southern Africa. The second group, existing within a similar chronological range, is centered in the Australo-Tasmanian-New Zealandic realm, possibly indicating a distinct ancestry.

By contrast, Rolán et al. (2003), who treated *Euthria* and *Buccinulum* as autonomous taxa on the basis of radular morphology, slight conchological differences, present-day geographic separation, and different geological record, recognized four main geographical areas of occurrence of *Euthria*–*Buccinulum* gastropods, which they also treated as "radiations": (1) an area of radiation of *Buccinulum* around New Zealand; (2) a typical *Euthria* radiation along the coasts of the Indian Ocean; (3) a third area around New Caledonia, and finally, (4) the East Atlantic *Euthria*–*Euthriostoma* area of "after" radiation, separated from the main group (i.e., from the group in area 2) following the demise of the marine seaway between the Mediterranean Sea and the Indian Ocean in the Middle Miocene. This paper is focused on this last group of representatives of *Euthria*, occurring in the Mediterranean Sea and the eastern Atlantic, extending its range southward to Angola (Schoenherr and Rolán, 2017), with a notable center of diversity around the Cape Verde Islands, where more than 22 endemic species have been described (Rolán et al., 2003; Fraussen and Swinnen, 2016). The determination of whether these "Area 4" species are congeneric with those of the Indo-West Pacific groups falls outside the scope of this paper. It is worth noting that there are no molecular data yet available to shed light on the relationships between these distinct "radiations."

Herein we will examine the biodiversity of *Euthria* from the fossil record of the Pliocene of western Iberia, from the Cenozoic Mondego Basin of Portugal, and discuss the diversity and the endemicity of the group in the European Atlanto-Mediterranean Neogene.

Geological and paleoenvironmental setting

The specimens under investigation originate from the Pliocene deposits of Vale de Freixo. This locality is situated in west-central Portugal, specifically in the Pombal region, with geographic coordinates 39°53’02.1"N, 8°43’52.9"W. The sedimentary sequence exposed at this site spans the Miocene to Pliocene and is part of the Cenozoic Mondego Basin well represented in the Caldas da Rainha, Marinha Grande, and Pombal region (Fig. 1). The basal fossiliferous Pliocene conglomerate and sands at the study site correspond to the initial transgressive beds of the Carnide Formation (Cachão, 1990; Diniz et al., 2016).

The calcareous nannofossil assemblage within the basal sands has been assigned to the biozone CN12a of Okada and Bukry (1980). On the basis of these and of fossil gastropods, these basal transgressive beds were attributed to the uppermost Zanclean to lower Piacenzian (Cachão, 1990; da Silva et al., 2010; Diniz et al., 2016). The molluscan assemblage of Vale de Freixo, as well as all the known marine Pliocene Atlantic molluscan records of the Mondego Basin in the broader Caldas da Rainha, Marinha Grande, and Pombal, correlate to the Mediterranean Plio-Pleistocene Molluscan Unit 1 (MPPMU1), former MPMU1 (Mediterranean Pliocene Molluscan Unit 1) as defined by Monegatti and Raffi (2001) for the Mediterranean (da Silva et al., 2010). For a comprehensive understanding of the geographical location, general geological context, and stratigraphy of the Vale de Freixo site, along with additional references, refer to da Silva et al. (2006, 2010), Diniz et al. (2016), or Dell’Angelo et al. (2022).

The present-day Caldas da Rainha, Marinha Grande, and Pombal region, at the very end of the Zanclean and the onset of the Piacenzian, was occupied by a shallow-marine environment with normal salinity and warm waters, somewhat shielded from the direct influence of the open Atlantic Ocean (Nolf and da Silva, 1997; da Silva et al., 2010). According to molluscan data, during the mid-Pliocene, sea surface temperatures (SSTs) along the western Iberian coast at approximately 40°N latitude, the latitude of Vale de Freixo, had subtropical characteristics. They were comparable to present-day temperatures recorded along the coasts of western Africa at the latitude of Cape Blanc (Morocco/Mauritania, 21°N), that is, with maximum mean monthly SSTs (MMSSTs) of around 23.5°C in September and minimum MMSSTs of 19°C in January–March (da Silva et al., 2010).

The fossil assemblage from the basal beds of the Carnide Formation at Vale de Feixo suggests a marine infralittoral environment, less than 24 m deep, with a sandy, bioclastic substrate, in which the gastropods were the most diverse group, although not the most abundant (da Silva, 2001, 2002), followed by the bivalves (Dollfus and Cotter, 1909, for the Caldas da Rainha, Marinha Grande area; Pimentel, 2018, for the Vale de Freixo site), and the polyplacophorans (Dell’Angelo and da Silva, 2003; Dell’Angelo et al., 2022).

The Pliocene gastropod assemblage of the Caldas da Rainha, Marinha Grande, and Pombal region was investigated by da Silva (2001). The study scrutinized and incorporated all Portuguese Pliocene records known to date, including those of Cox (1936, 1941), Zbyszewski (1959), and Brébion (1971, 1974), and documented a total of 165 species, with 155 of them represented in the Vale de Freixo assemblage.

The western Iberian fauna represented in the Pliocene Mondego Basin fossil assemblage was part of the Pliocene French-Iberian subtropical Province of da Silva and Landau (2007) and Landau

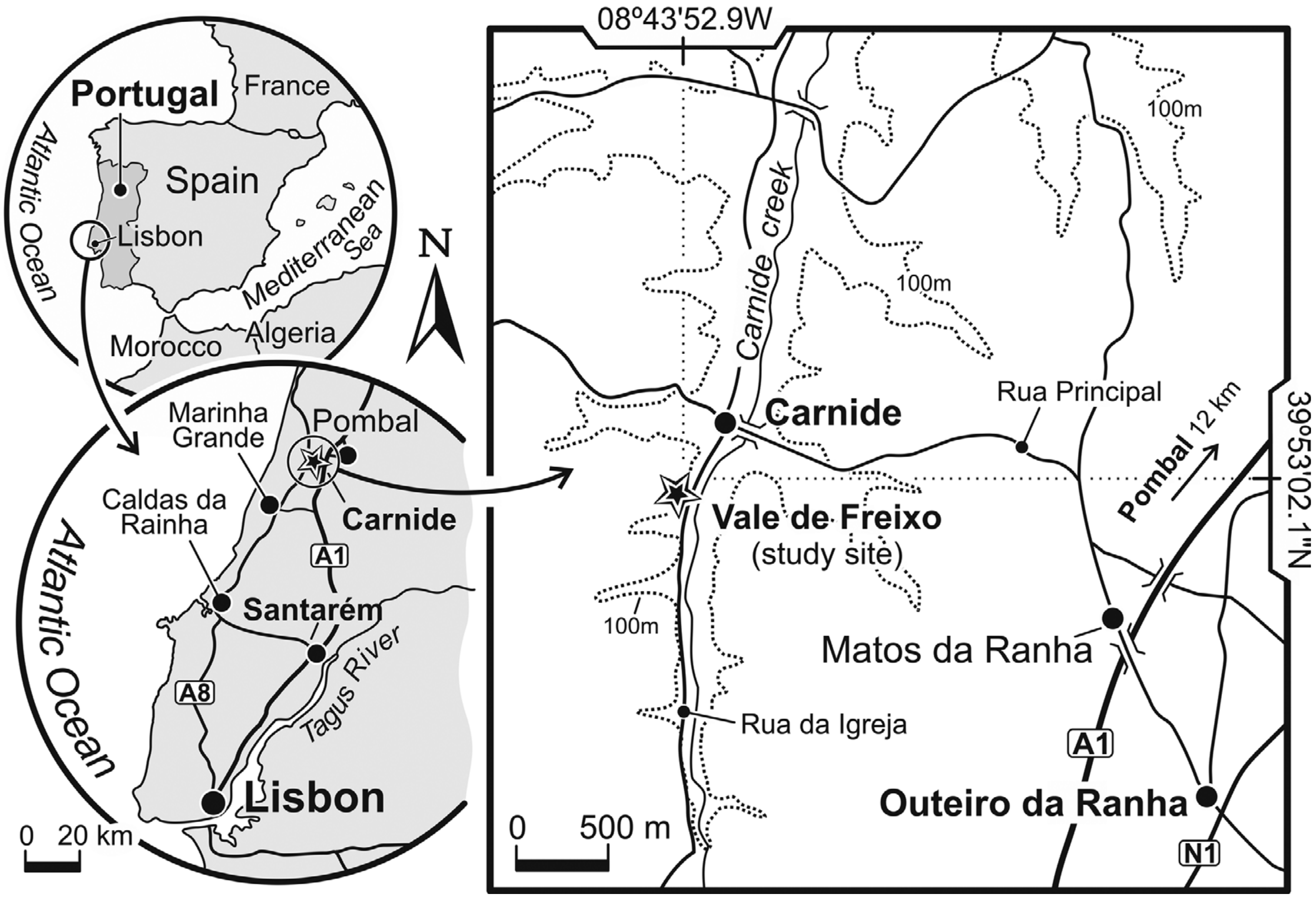

Figure 1. Location of the Pliocene Vale de Freixo locality in the Pombal area of west-central Portugal.

et al. (2019b). It included about 45 thermophilic genera, such as *Xenophora* Fischer von Waldheim, 1807, *Cypraecassis* Stutchbury, 1837, *Distorsio* Röding, 1798, *Bolinus* Pusch, 1837, *Cymbium* Röding, 1798, *Marginella* Lamarck, 1799, *Persicula* Schumacher, 1817, *Granulina* Jousseaume, 1888, *Solatia* Jousseaume, 1887, *Conus* s.l., *Strioterebrum* Sacco, 1891, and *Sveltia* Jousseaume, 1887. However, it lacked the typical tropical indicators common in coeval Mediterranean faunas (e.g., *Thetystrombus* Dekkers, 2008 and diversified Terebridae and Conidae, and so on, after Monegatti and Raffi, 2001).

Materials and methods

The study material was obtained from search sampling conducted in the dark gray sand "Bed 3" of the basal Pliocene sequence at Vale de Freixo. For a stratigraphic log of the sequence, please refer to Dell'Angelo et al. (2022).

Abbreviations. We use the following: hp = height of the protoconch; dp = diameter of the protoconch; pc = protoconch.

Repositories and institutional abbreviations. Types, figures, and other specimens examined in this study are deposited in the following institutions: National Museum of Natural History and Science of the University of Lisbon, Portugal (MNHN/UL), and Natural History Museum Vienna, Austria (NHMW).

Systematic paleontology

Superfamily **Buccinoidea** Rafinesque, 1815
Family **Tudiclidae** Cossmann, 1901
Genus ***Euthria*** Gray, 1850

Type species. *Fusus lignarius* Chiaje [= *Euthria cornea* (Linnaeus, 1758)]; original designation by Gray (1850, p. 67), subsequently *Murex corneus* Linnaeus, 1758 fixed as type species by Petit (2012, p. 99) under Art. 70.4. Present-day, Mediterranean Sea.

Euthria galopimi new species
Figure 2.1–2.4

Holotype. Holotype NHMW 2018/0331/0174, height 35.8 mm, width 18.1 mm.

Diagnosis. *Euthria* species with a small- to medium-sized shell for genus, broad biconic profile, protoconch of two whorls with large nucleus, teleoconch sculpture consisting of broad ribs developed below shoulder on spire whorls, reduced to 10 tubercles placed at strong shoulder on last whorl, fine spiral treads over entire surface, weak cords over base, outer lip weakly lirate within.

Occurrence. Pliocene eastern Atlantic, western Iberian coasts; Mondego Basin (Portugal), uppermost Zanclean to lower Piacenzian (this paper).

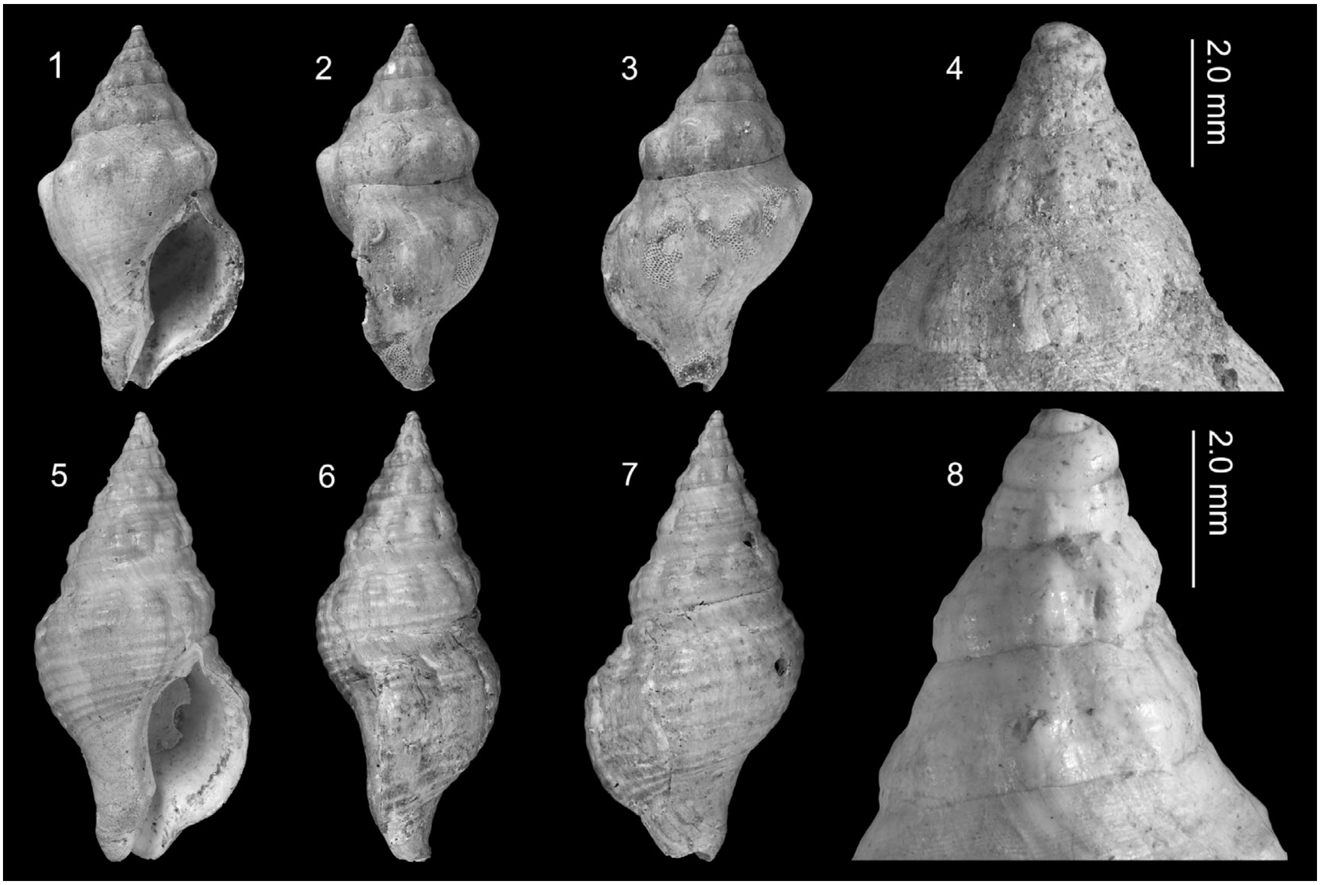

Figure 2. (**1–4**) *Euthria galopimi* n. sp., holotype NHMW 2018/0331/0174, height 35.8 mm, width 18.1 mm: (**1**) apertural view; (**2**) lateral view; (**3**) dorsal view; (**4**) detail of the protoconch. (**5–8**) *Euthria lockleyi* n. sp., holotype MNHN/UL.917, height 47.1 mm, width 23.1 mm: (**5**) apertural view; (**6**) lateral view; (**7**) dorsal view; (**8**) detail of the protoconch. All specimens from the Vale de Freixo locality, Pombal area, Portugal. Carnide Formation, Pliocene, uppermost Zanclean to lower Piacenzian.

Locus typicus. Vale de Freixo site, near the village of Carnide, Pombal municipality, west-central Portugal.

Stratum typicum. Carnide Sandstone Formation, basal fossiliferous gray sands, “Bed 3” in Gili et al. (1995) and Dell’Angelo et al. (2022, text-fig. 2).

Description. Shell small- to medium-sized for genus, solid, relatively broad, squat biconic; apical angle ~60°. Protoconch small, of just over two smooth convex whorls with large nucleus (approximately hp = 1.5 mm, dp = 1.5 mm). Junction with teleoconch delimited by beginning of axial sculpture. Teleoconch of 5.5 whorls separated by weakly impressed undulating suture. First teleoconch whorl bearing 10 broad axial ribs, roughly equal in width to interspaces. Later spire whorls with broad, steep, weakly concave subsutural ramp, weakly delimited by rounded shoulder placed below mid-whorl, periphery at abapical suture. Ribs subobsolete over subsutural ramp, broad and rounded below, weakening toward suture. Spiral sculpture composed of extremely fine, crowded spiral threads covering the entire surface. Last whorl 73% of total height, with broad concave subsutural ramp, roundly angled at prominent shoulder, convex below, strongly constricted at base, fasciole rounded, moderately delimited; ribs reduced to 10 large, rounded tubercles at shoulder; fine spiral threads over surface, slightly broader spiral cords over base, strengthening abapically. Aperture 51% of total height, ovate; anal canal marked by small notch; siphonal canal moderate length and width, open, bent to left and slightly recurved; outer lip concave below subsutural ramp, roundly angled at shoulder, weakly lirate within. Columella broadly and evenly excavated, bearing small fold at upper end of siphonal canal. Columellar callus narrow, hardly thickened, moderately delimited without parietal pad or denticle.

Etymology. Named after António Marcos Galopim de Carvalho (b. 1931), Portuguese geologist and Neogene bryozoan paleontologist at the Department of Earth Sciences of the Faculty of Sciences of the University of Lisbon, Portugal, and Director of the National Museum of Natural History and Science of Lisbon in the late twentieth and early twenty-first centuries. In the 1990s, his geoconservation efforts were crucial for the creation, among others, of the Dinosaur Tracks of Ourém–Torres Novas Natural Monument, also known as the Galinha Quarry track site.

Materials. Known from holotype only.

Paleoecology. Epibenthic vagile gastropods living in coastal infralittoral subtropical marine environments (estimated maximum MMSST of ~23.5ºC in September and minimum MMSST of 19ºC in January–March; da Silva et al., 2010) of normal salinity and sandy, bioclastic substrates. Gastropods with paucispiral protoconch with a large nucleus suggesting non-planktotrophic larval development.

Remarks. Despite the plethora of *Euthria* Gray, 1850 species in the European Neogene, this species differs from all its congeners in its broad biconic profile, broad axial ribs reduced to large tubercles on the last whorl, and the fine crowded spiral threads that cover the entire surface. *Euthria presselierensis* Landau, Ceulemans, and Van Dingenen, 2019 (Landau et al., 2019a) from the Tortonian of northwestern France is similar in its rather squat biconic profile but differs in having the tubercles at the shoulder of the last whorl much weaker, the siphonal canal is longer and narrower, and the outer lip is denticulate within. None of the congeners described from the Paratethyan or Mediterranean Neogene basins can be usefully compared. Neither can any of the extant Cape Verde species illustrated by Fraussen and Swinnen (2016). Rolán et al. (2003, fig. 36) illustrated an unusual tubercular morphotype of *E. cornea* (Linnaeus, 1758) from Turkey. This specimen does not seem to be fully adult (height 29.2 mm as opposed to average adult height of ~55 mm), is slenderer and has more numerous and smaller tubercles at the shoulder.

Euthria lockleyi new species

Figure 2.5–2.8

2001 *Buccinulum aduncum* (Bronn, 1831 [*sic*]); da Silva, p. 371, pl. 16, figs 1, 2 [non *Euthria adunca* (Bronn, 1831)].

Holotype. Holotype MNHN/UL.917, former VFX.03.384 specimen in Carlos Marques da Silva Vale de Freixo (VFX) Pliocene PhD collection, height 47.1 mm, width 23.1 mm.

Diagnosis. *Euthria* species with a small- to medium-sized shell for genus, fusiform, protoconch of 2.25 whorls with large nucleus, teleoconch sculpture consisting of 10 ribs fading on penultimate whorl, obsolete on last whorl, overrun by five spiral cords on spire whorls, secondaries intercalated over subsutural ramp and mid-whorl on last whorl, outer lip with 14 lirate denticles within, columella with weak abapical fold and small bifid parietal denticle.

Occurrence. Pliocene eastern Atlantic, western Iberian coasts; Mondego Basin (Portugal), uppermost Zanclean to lower Piacenzian (this paper).

Locus typicus. Vale de Freixo site, near the village of Carnide, Pombal municipality, west-central Portugal.

Stratum typicum. Carnide Sandstone Formation, basal fossiliferous gray sands, "Bed 3" in Gili et al. (1995) and Dell'Angelo et al. (2022, text-fig. 2).

Description. Shell medium-sized for genus, solid, bucciniform¸ apical angle 45.8°. Protoconch mammillate, of 2.25 smooth convex whorls with large nucleus (hp = 1.67 mm, dp = 1.71 mm). Junction with teleoconch delimited by prosocline scar. Teleoconch of six whorls separated by weakly impressed undulating suture. First teleoconch whorl bearing 10 broad, opisthocline axial ribs, slightly wider than their interspaces, overrun by five spiral cords. Abapically, broad subsutural collar strengthens, concave subsutural ramp poorly delimited by weak shoulder, convex and somewhat swollen lower half of whorls. Axial ribs weaken and broaden abapically, fading on second half of penultimate whorl; adapical cord forms collar, next cord over ramp weaker, shoulder and fourth cord stronger, fourth strongest forming periphery, fifth cord partly covered by subsequent whorl; two secondary spirals appear over subsutural ramp above and below primary cord on penultimate whorl. Sinuous growth lines most strongly developed over subsutural ramp, crowded spiral threads covering entire surface. Last whorl 72% of total height, with relatively broad, rounded subsutural collar, convex subsutural ramp delimited by shoulder cord, evenly convex below, moderately constricted at base; fasciole broad, flattened, poorly delimited; axials obsolete; spiral sculpture of low, rounded cords prominent, single weaker primary cord flanked by single secondary on either side over subsutural ramp, 10 primary cords over mid-whorl and base, narrowing but becoming sharper abapically, single secondary intercalated between primaries just below level of insertion of outer lip; cords flattening over neck, obsolete over fasciole. Aperture 46% of total height, ovate; anal canal marked by deep notch; siphonal canal moderate length, relatively narrow, open, bent slightly to left and slightly recurved; outer lip thickened, with beveled edge, weakly angled at shoulder, bearing 14 denticles at inner edge, extending as lirae deep within aperture. Columella broadly and evenly excavated, bearing weak fold at upper end of siphonal canal and small bifid parietal tooth. Columellar callus narrow, moderately thickened, moderately well delimited.

Etymology. Named after Martin G. Lockley (1950–2023), Welsh Mesozoic dinosaur paleoichnologist at the University of Colorado at Denver and later professor emeritus. In the 1990s, his involvement was paramount for the development of the budding Portuguese dinosaur ichnology and the creation of the Dinosaur Tracks of Ourém–Torres Novas Natural Monument, also known as the Galinha Quarry track site. He was also a good friend.

Materials. Known from holotype only.

Paleoecology. Epibenthic vagile gastropods living in coastal infralittoral subtropical marine environments (estimated maximum MMSST of ~23.5ºC in September and minimum MMSST of 19ºC in January–March; da Silva et al., 2010) of normal salinity and sandy, bioclastic substrates. Gastropods with paucispiral protoconch with a large nucleus suggesting non-planktotrophic larval development.

The cause of death of the type-specimen animal was most likely a lethal attack by a carnivorous gastropod as the shell shows two borings assigned to the ichnogenus *Oichnus* Bromley, 1981. These bioerosion structures are commonly attributed to predatory actions of naticid and muricid gastropods. The Vale de Freixo assemblage contains several such gastropods that could have carried out this predatory act, for example, *Cochlis raropunctata* (Sasso, 1827), a naticid, and *Bolinus brandaris torularius* (Lamarck, 1822), a muricid. A specimen of *Crepidula unguiformis* Lamarck, 1822 can be seen preserved in situ well within the last whorl of the buccinoid specimen, as seen in Figure 5, showing that this *E. lockleyi* shell was occupied postmortem. This shows that it must have been lying on the substrate for a protracted period before being buried, to allow occupation by organisms with cryptic behavior such as *C. unguiformis.*

Remarks. This specimen was originally assigned to *Euthria adunca* (Bronn, 1831), to which it is closely related, by da Silva (2001). However, judging from the series of shells of that species illustrated by Brunetti and Della Bella (2016, fig. 5A–F), the Portuguese exemplar differs in having fewer teleoconch whorls (six versus nine to 10; fide Brunetti and Della Bella, 2016) and narrower and lower axial ribs that fade earlier in ontogeny; the spiral cords are fewer, broader with secondaries intercalated only over the subsutural ramp, and one secondary just below mid-whorl, whereas in *E. adunca* there are more numerous and finer cords over the ramp on the last whorl, and below the shoulder they are finer and more numerous, and of alternating strength. The character of the outer lip is similar in both species that bear lirate denticles; however, the shells of *E. adunca* also bear a row of seven to eight tubercles on the columella, absent in the Portuguese species, which has a smooth columella between the bifid parietal tooth and the abapical fold delimiting the siphonal canal. Last, in *E. lockleyi*, the siphonal canal is considerably shorter. One specimen of *E. adunca* illustrated by Brunetti and Della Bella (2016, fig. 5C) from the lower Pleistocene Calabrian of Italy shows a similarly short siphonal canal. It is unclear whether the canal is complete in this specimen as the authors do not remark on this and describe the canal in *E. adunca* as "lungo, leggermente ripiegata a sinistra [long, slightly recurved and bent to the left]" (Brunetti and Della Bella, 2016, p. 13). Nevertheless, the other differences discussed in the preceding apply.

Paratethyan specimens historically identified as *E. adunca* in the literature (Hoernes and Auinger, 1890; Nikolov, 1994; Bałuk, 1995, inter alia) are not conspecific and were recently described as *E. brunettii* Harzhauser and Landau, 2024. They differ from the Portuguese specimen in their slenderer fusiform rather than bucciniform profile, extremely weak spiral sculpture, and long siphonal canal.

Of the extant species, in having a regularly conical spire, predominant strong spiral sculpture, axials obsolete on the last whorl, and a short siphonal canal, *Euthria lockleyi* n. sp. is most closely similar to *E. darwini* Monteiro and Rolán, 2005 from Boavista and Sal Islands in the Cape Verde Archipelago, but that species has smaller shells, showing a more regularly conical spire, with a more superficial suture and less shouldered whorls, and the siphonal canal is a little longer.

Discussion

Protoconch morphology, environmental constraints, and larval development. The morphological features of the gastropod larval shell, or protoconch, offer valuable insights into the developmental strategies of both extant and extinct gastropod species. In *Euthria*, this is no exception. While these features may exhibit variations across different families, there are consistent traits associated with planktotrophic protoconchs in gastropods with feeding planktonic larvae and non-planktotrophic ones (i.e., those with non-feeding larvae). Representatives of species with planktotrophic development often display a distinctive high, multispiral conical protoconch comprising two to nine whorls.. By contrast, non-planktotrophic species typically exhibit a paucispiral protoconch consisting of 0.5 to two smooth whorls (e.g., Jackson, 1974; Stanley, 1979; Jablonski, 1986; Vendetti, 2007). As a general rule, species with short larval phases are less likely to disperse widely and tend to form genetically isolated populations, leading to species that are geographically restricted and geologically short-lived, whereas planktotrophic development prevents genetic isolation and leads to species with a greater geographic range and geological longevity (Jackson, 1974; Stanley, 1979; Jablonski, 1986). Conversely, planktotrophy—in larvae with longer planktic phases—diminishes genetic isolation, being associated with species with expanded geographic distribution and geological longevity (Jackson, 1974; Stanley, 1979; Jablonski, 1986).

It is widely accepted that the predominant direction of evolutionary change in mode of development is from species with planktotrophic larvae to those with non-planktotrophic development. Moreover, it is thought to be rare or practically impossible for planktotrophic larvae to evolve from non-planktotrophic ones without being obviously distinct from their planktotrophic ancestor (Collin, 2004; Collin et al., 2021). Non-planktotrophic development has evolved independently on multiple occasions (Ponder and Lindberg, 1997), and when this happens, those characters involved in feeding and swimming in the ancestral planktotrophic form are often reduced or lost in benthic nonfeeding larvae or in direct developers (Collin, 2004). This pattern of evolution in mode of development is biased in the direction from planktotrophic to non-planktotrophic (Strathmann, 1985; Hart, 2000) and is widely considered irreversible (Collin et al., 2007).

All extant Atlantic and Mediterranean *Euthria* species show rather bulbous protoconchs with 1.25 to 2.5 whorls (Rolán et al., 2003). These characteristics suggest non-planktotrophy. However, we have not found any papers on present-day *Euthria* gastropods confirming this conclusion by direct observation.

Euthria species documented in the European Neogene fossil record have recently been the subject of comprehensive reviews with protoconch data and, in some cases, illustrations (Lozouet, 1999, 2021; Van Dingenen et al., 2017; Landau et al., 2019a; Harzhauser and Landau, 2024; Landau and Harzhauser, 2024; hoc opus: summary Table 1). Among the species investigated, only the French Atlantic *E. pseudomarginata* Peyrot, 1928, spanning the upper Oligocene to Lower Miocene of the Aquitaine Basin, the *Euthria* sp. 1 as identified by Lozouet (2021) from the upper Oligocene of the French l'Adour Basin, and *E. brunettii* Harzhauser and Landau, 2024, originating from the Middle Miocene Paratethys, exhibit shells featuring characteristics suggestive of planktotrophic development, namely, tall multispiral protoconchs with small nuclei.

These data suggest that *Euthria* evolved away from its primitive planktotrophic mode of development no later than the Late Miocene. Similar shifts away from planktotrophy during the Late Miocene to the present are documented in various gastropod genera within European present-day faunas. Landau and Harzhauser (2024) reported a similar loss of planktotrophy in *Aplus* De Gregorio, 1885 (Buccinoidea, Pisaninae) from the Pliocene to the present, and possibly in *Colubraria* Schumacher, 1817/*Cumia* Bivona e Bernardi, 1838 (Buccinoidea, Colubrariidae), two genera distinguished solely by the presence of paucispiral protoconchs in the latter.

Puillandre et al. (2010) reported a gradual loss of planktotrophy, inferred from protoconch morphology, in the deep-water gastropod genus *Bathytoma* Harris and Burrows, 1891 (Conoidea, Borsoniidae) in the western Pacific. Protoconch characteristics varied across time: Eocene *Bathytoma* species exhibited protoconchs with 3.5–4.5 whorls, Oligocene species had 3.0–3.5 whorls, Pliocene ones showed 3.0 whorls, and contemporary species, now limited to the Indo-Pacific, display protoconchs with 1.5 whorls and a large nucleus. Notably, all but one present-day species exhibits restricted distributions. In the same family Borsoniidae, Landau and Harzhauser (2022b) documented the loss of planktotrophy in *Asthenotoma* Harris and Burrows, 1891 from the Miocene to the Pliocene.

Table 1. *Euthria* species in Oligocene–Pliocene European assemblages that have recently been reviewed and their protoconchs reliably described and/or illustrated, their geological distribution, and number of protoconch whorls. Data from Lozouet (1999, 2021), Van Dingenen et al. (2017), Landau et al. (2019a), Harzhauser and Landau (2024), Landau and Harzhauser (2024)

Species	Geological distribution	Protoconch whorls
Euthria lanotensis (Lozouet, 1999)	Upper Oligocene	2.75
Euthria pseudomarginata (Peyrot, 1928)	Upper Oligocene–Lower Miocene	2.0
Euthria raulini (Peyrot, 1928)	Upper Oligocene	1.5
Euthria tarusatensis (Lozouet, 2021)	Upper Oligocene	1.75
Euthria sp. 1	Upper Oligocene	3.0
Euthria sp. 2	Upper Oligocene	—
Euthria brunettii (Harzhauser and Landau, 2024)	Middle Miocene	2.7
Euthria walaszczyki (Harzhauser and Landau, 2024)	Middle Miocene	—
Euthria dellabellae (Harzhauser and Landau, 2024)	Middle Miocene	2.0
Euthria depressospira (Bandat, 1943)	Middle Miocene	1.5
Euthria diluvii (Eichwald, 1830)	Middle Miocene	2.0
Euthria fuscocingulata (Hoernes and Auinger, 1890)	Middle Miocene	1.5
Euthria koenfrausseni (Harzhauser and Landau, 2024)	Middle Miocene	1.25
Euthria obelixi (Harzhauser and Landau, 2024)	Middle Miocene	1.5
Euthria odiosa (Harzhauser and Landau, 2024)	Middle Miocene	1.5
Euthria puschii (Andrzejowski, 1830)	Middle Miocene	2.5
Euthria stuetzii (Naumann, 1852)	Middle Miocene	1.75
Euthria subnodosa (Hoernes and Auinger, 1890)	Middle Miocene	1.5
Euthria viciani (Kovács, 2018)	Middle Miocene	1.25
Euthria zboroviensis (Friedberg, 1912)	Middle Miocene	—
Euthria yesimae (Harzhauser and Landau, 2024)	Middle Miocene	1.5
Euthria turonensis (Peyrot, 1938)	Middle Miocene–Lower Pliocene	—
Euthria presselierensis (Landau et al., 2019 (Landau et al., 2019a)	Upper Miocene	1.5
Euthria recurvata (Millet, 1865)	Upper Miocene	1.5
Euthria adunca (Bronn, 1831)	Upper Miocene–Lower Pleistocene	2
Euthria palumbina (Van Dingenen et al., 2017)	Lower Pliocene	2
Euthria plioelongata (Sacco, 1890)	Lower Pliocene	1.5
Euthria onubensis (Landau and Harzhauser, 2024)	Lower Pliocene	—
Euthria lucenica (Landau and Harzhauser, 2024)	Lower Pliocene	—
Euthria perpiniana (Fontannes, 1879)	Pliocene	1.5
Euthria ceddensis (Brunetti and Della Bella, 2016)	Pliocene	1.5
Euthria iberoadunca (Landau and Harzhauser, 2024)	Upper Pliocene	—
Euthria inflatissima (Landau and Harzhauser, 2024)	Upper Pliocene	—
Euthria pliovirginea (Landau and Harzhauser, 2024)	Upper Pliocene	2
Euthria pouweri (Landau and Harzhauser, 2024)	Upper Pliocene	2.0
Euthria galopimi (n. sp.	Upper Pliocene	2.0
Euthria lockleyi (n. sp.	Upper Pliocene	2.25
Euthria cornea (Linnaeus, 1758)	Lower Pleistocene–Present day	1.5

Furthermore, Landau et al. (2022, p. 161) described a similar trend for *Clathromangelia* di Monterosato, 1884 (Conoidea, Raphitomidae) from the Middle Miocene to present. Within the genera *Clavatula* s.l. Lamarck, 1801, *Perrona* Schumacher, 1817, and *Tomellana* Wenz, 1943 (Conoidea, Clavatulidae), some upper Oligocene (Lozouet, 2021) and Miocene (Harzhauser et al., 2022) species exhibited multispiral protoconchs. Contrastingly, species from the Pliocene to the present showed paucispiral protoconchs (Landau and Harzhauser, 2022a).

Within the Mediterranean Raphitomidae Bellardi, 1875, Oliverio (1996) and Giannuzzi-Savelli et al. (2018) proposed a speciation event during the early Pleistocene, leading to the emergence of species pairs exhibiting either planktotrophic or non-planktotrophic development. Oliverio (1996) also identified similar species pairs in gastropod genera such as *Alvania* Risso, 1826, *Rissoa* Desmarest, 1814, *Vitreolina* di Monterosato, 1884, *Columbella* Lamarck, 1799, *Nassarius* Duméril, 1805, *Mangelia* Risso, 1826, and *Haedropleura* Bucquoy, Dautzenberg, and Dollfus, 1883, suggesting a widespread occurrence of this phenomenon among Mediterranean prosobranchs. He considered the Pleistocene climatic deterioration a potential trigger for this phenomenon. Moreover, Oliverio (1996) noted that during phases of low sea level, the isolation of the western and eastern subbasins of the Mediterranean resulted in distinct developments. The gastropods of the western subbasin exhibited higher planktotrophy, while in the eastern subbasin they predominantly displayed non-planktotrophic development. This divergence underscores the impact of historical sea-level fluctuations on the reproductive strategies of Mediterranean prosobranch gastropods.

The presence of such species pairs in *Euthria* was not identified during this study. However, it is posited that the underlying forces fostering the loss of planktotrophy, whether manifested spatially (as seen in *Raphitoma*, *Alvania*, *Rissoa*, and so on) or chronologically (as observed in *Euthria*, *Aplus*, *Colubraria*, and so on), remain consistent. The isolation of populations, as discussed by Oliverio (1996), has occurred multiple times for Paratethyan species, driven by pronounced, geodynamically amplified fluctuations in relative sea levels (Harzhauser and Piller, 2007; Kováč et al., 2017). Furthermore, the loss of planktotrophy during the Pliocene correlates with the onset of a global cooling trend (Westerhold et al., 2020), akin to the Pleistocene event described by Oliverio (1996). The decline in sea surface temperatures appears to have exerted stress on the larvae of certain gastropods, prompting a shift to a non-planktotrophic mode of development in species of genera such as *Asthenotoma*, *Bathytoma*, and *Euthria*. Concurrently, numerous planktotrophic species became extinct. The limited dispersal capabilities of the non-planktotrophic species ultimately gave rise to endemic radiations among *Euthria* in the Cape Verde Archipelago (Fraussen and Swinnen, 2016). This phenomenon is exemplified by the genus *Lautoconus* di Monterosato, 1923, which underwent an extraordinary endemic radiation, boasting nearly 50 species confined exclusively to this southern Macaronesian archipelago. Notably, the species of this genus also adopted non-planktotrophic development as their reproductive strategy (Duda and Rolán, 2005).

The impact of water temperature on development strategy is commonly referred to as Thorson's (1950) rule, which posits that higher latitudes and lower temperatures promote lecithotrophy and larger eggs, while planktotrophic species will thrive in tropical waters. Numerous studies have examined and verified Thorson's rule for prosobranch gastropods, including works by Thorson (1950), Picken (1980), Clarke (1992), Gallardo and Penchazadhe (2001), Collin (2003), and Pappalardo et al. (2014). However, during the Miocene and Pliocene, the Paratethys, the Mediterranean, and the adjacent Atlantic region were notably situated at lower latitudes, falling outside the traditional scope of Thorson's rule. Nonetheless, the presumed loss of planktotrophy due to the decline of SSTs in the Central Paratethys and the Mediterranean Sea during this period might have been influenced by similar mechanisms.

Diversity and endemicity in Neogene to Recent Euthria. Today, *Euthria* is present in the Mediterranean Sea and the eastern Atlantic, extending down to Angola (Schoenherr and Rolán, 2017), exhibiting a remarkable center of diversity around the Cape Verde Islands, where more than 22 endemic species have been identified (Rolán et al., 2003; Fraussen and Swinnen, 2016). Endemicity along the West African coast is not as extreme as in the Cape Verde Archipelago, with *Euthria annegretae* Schroenherr and Rolán, 2017 from Angola. The realization of the diversity of the genus coupled with local high endemism in present-day faunas has occurred only relatively recently. Rolán (1987) provided the first comprehensive overview, identifying *Euthria cornea* (Linnaeus, 1758) in the Mediterranean and seven species from the Cape Verde Islands, one left in open nomenclature. Fraussen (1999) echoed this assessment, listing the same number of Atlanto-Mediterranean species while introducing six new Western Indo-Pacific species. Subsequent studies have consistently underscored the genus's highly endemic character in the Cape Verde Archipelago (Rolán et al., 2003; Monteiro and Rolán, 2005; Fraussen and Swinnen, 2016). In this context, the reason for the presence of only one species in the present-day Mediterranean, *Euthria cornea* (Linnaeus, 1758), exhibiting a remarkable degree of variability in shell morphology remains unclear. This becomes particularly perplexing considering that all fossil and remaining extant species exhibit relatively limited intraspecific variation in shell morphology. Despite being highly variable in shell shape and widely distributed in the Mediterranean, preliminary molecular data on *E. cornea* do not suggest the presence of more than one species (P. Bouchet, personal communication, 2024).

Today, *E. cornea* inhabits marine environments of normal salinity at depths ranging from 5 to 30 m, predominantly on rocky substrates. There is no available literature indicating that *E. cornea* has adapted to successfully exploit alternative habitats, such as muddy, sandy, or brackish environments. This observation is further reinforced by personal accounts (K. Fraussen, personal communication, 2024). It is reported to be a carnivorous scavenger (Syrides, 2019), feeding primarily on polychaetes and gastropods (Taylor, 1987). This species exhibits significant variability; axial sculpture may fade early in ontogeny or strengthen on later whorls with the development of tubercles at the shoulder. Moreover, variation in adult shell shape and size is much more marked than in any of its extant congeners (see Fraussen and Swinnen, 2016). While certain forms can be attributed to distinct provenances, more frequently, specimens with diverse shapes and color patterns coexist (K. Fraussen, personal communication, 2024). *Euthria cornea* possesses a protoconch consisting of 1.5 whorls with a bulbous apex characteristic of non-planktotrophic development (Brunetti and Della Bella, 2016, fig. 4D). Its geological history extends back only to the early Pleistocene, Calabrian. Furthermore, in the Mediterranean and in the Iberian shores of the Gulf of Cadiz, it occurs at the northern limit of its water temperature tolerance range, in the present-day subtropical Mediterranean–Moroccan Province (sensu Raffi et al., 1985; da Silva and Landau, 2007), given that *Euthria* is a relatively thermophilic genus.

Therefore, it is likely that *E. cornea* evolved from a Mediterranean Pliocene ancestor, and it appears to be the only species to have survived to the present day in the Mediterranean and the adjacent Atlantic coast of southern Portugal. However, the reason *E. cornea* should have become so abundant, variable, and widespread in that region today is unclear. It is important to emphasize that non-planktotrophic development does not preclude dispersal, yet *E. cornea* is confined mostly to the northern part of the Mediterranean–Moroccan Province. Nevertheless, as far as we are aware, molecular confirmation that all Mediterranean *E. cornea* records pertain to a single species is currently lacking.

Similarly, the recognition of both the diversity and the endemicity of the genus in the European fossil record has also emerged rather recently. Brunetti and Della Bella (2016) revised the Plio-Pleistocene biodiversity of the genus from Neogene basins of northern Italy, documenting four species from the Pliocene (*Euthria perpiniana* [Fontannes, 1879], *E. plioelongata* [Sacco, 1890], *E. ceddensis* Brunetti and Della Bella, 2016, *E. adunca* [Bronn, 1831]). In the past, many Neogene records of these species have been misassigned to the extant *E. cornea*, although it has a confirmed geological record dating back only to the early Pleistocene Calabrian, occurring only in the Mediterranean and on the northern shores of the Gulf of Cadiz (Brunetti and Della Bella, 2016).

In their review of the Atlantic Upper Miocene and Lower Pliocene gastropod fossil record from the Loire Basin in northwestern France, Landau et al. (2019a) reported two *Euthria* species from the Tortonian Assemblage I of Van Dingenen et al. (2015) (*Euthria presselierensis* Landau, Ceulemans, and Van Dingenen, 2019a, and *E. recurvata* [Millet, 1865]), both exclusive to this assemblage and endemic to the Neogene Ligerian Gulf (sensu Landau et al., 2020). In addition, they identified two species within the Zanclean Assemblage III (*Euthria palumbina* Van Dingenen, Ceulemans, and Landau, 2017, exclusive to Assemblage III, and *E. turonensis* Peyrot, 1938, both endemic to the Ligerian Gulf but the later also known from the Middle Miocene Langhian in the Loire Basin).

Lozouet (2021) examined the Buccinoidea from the Atlantic upper Oligocene of southwestern France, revealing a similar level of endemicity. He identified six species documented exclusively from the Chattian Oligocene and the uppermost Chattian and Lower Miocene of the l'Adour Basin (*E. lanotensis* Lozouet, 1999, *E. pseudomarginata* Peyrot, 1928, *E. raulini* Peyrot, 1928, *E. tarusatensis* Lozouet, 2021, alongside two species left in open nomenclature).

Revision of *Euthria* in the Middle Miocene Paratethyan assemblages showed the genus to be not only diverse, represented by 14 species, but also highly endemic, with all species restricted to the Paratethys (*Euthria brunettii* Harzhauser and Landau, 2024, *E. walaszczyki* Harzhauser and Landau, 2024, *E. dellabellai* Harzhauser and Landau, 2024, *E. depressospira* Bandat, 1943, *E. diluvii* [Eichwald, 1830], *E. fuscocingulata* [Hoernes and Auinger, 1890], *E. frausseni* Harzhauser and Landau, 2024, *E. obelixi* Harzhauser and Landau, 2024, *E. odiosa* Harzhauser and Landau, 2024, *E. puschii* [Andrzejowski, 1830], *E. stuetzii* [Naumann, 1852], *E. subnodosa* [Hoernes and Auinger, 1890], *E. viciani* Kovács, 2018, and *E. zboroviensis* Friedberg, 1912). In the same work, Harzhauser and Landau (2024) realized that the specimens from the Serravallian Middle Miocene Karaman Basin of Turkey assigned to *Euthria curvirostris* (de Grateloup, 1845) by Landau et al. (2013) did not represent that species, but a new endemic one described as *E. yesimae* Harzhauser and Landau, 2024.

A study of the genus from the westernmost Mediterranean lower Piacenzian Upper Pliocene Estepona Basin assemblages of southern Spain (Landau and Harzhauser, 2024) resulted in similar findings; the genus was diversified and highly endemic, represented by five species (*Euthria iberoadunca* Landau and Harzhauser, 2024, *E. inflatissima* Landau and Harzhauser, 2024, *E. pliovirginea* Landau and Harzhauser, 2024, *E. pouweri* Landau and Harzhauser, 2024, and one left in open nomenclature). In that paper, the authors also realized that the specimens from the Lower Pliocene Atlantic Guadalquivir Basin of southwestern Spain reported under the name *Euthriofusus* cf. *E. virgineus* (de Grateloup, 1832 [sic]) by Landau et al. (2011) do not correspond to *Euthria virginea* (de Grateloup, 1833). Instead, they represent another endemic: *Euthria onubensis* Landau and Harzhauser, 2024. Similarly, those identified as *E. cornea* (Linnaeus, 1758) also represent an endemic species, *E. lucenica* Landau and Harzhauser, 2024.

Molluscan endemicity in the Pliocene of Western Iberia. Thus, for each revisited Neogene basin, an endemic assemblage of *Euthria* species emerged. This prompted the authors to re-evaluate material from the Upper Pliocene (lower Piacenzian) Mondego Basin of Portugal, with an emphasis on the Vale de Freixo fossil assemblage. Unfortunately, gastropod fossils with larger shells are scarce in these deposits. Nonetheless, two *Euthria* species are represented. Due to the scarcity of material, only one well-preserved specimen of each is so far known, but considering the genus's morphological traits and biogeographical context discussed earlier, their formal description is crucial as it addresses a gap in knowledge concerning its biodiversity along the Pliocene European Atlantic frontage. The Mondego fossil assemblage is the only Pliocene record known along the European Atlantic coast between the Ligerian Basin in northwestern France (Landau et al., 2020) and the Guadalquivir Basin of southwestern Spain (Landau et al., 2011), being paramount for testing the emerging scenario of a diverse yet highly endemic gastropod group in Neogene Atlanto-Mediterranean faunas.

Until recently, few endemic mollusks have been recognized from the Pliocene of the Mondego Basin. In the past century, a handful of new species were described from the localities of Mina, São Pedro de Moel, and Matos, Marinha Grande region by Cox (1936, 1941). However, in recent years the revision of various groups has led to the description of new taxa, suggesting that about 12% of the gastropod species are endemic to the Mondego Basin Pliocene and 25% of the Polyplacophora (Table 2).

Conclusions. The reexamination of the *Euthria* gastropods from the Pliocene of West Iberia, from Mondego Basin (Portugal), resulted in two new species being described, both represented by a single, well-preserved specimen. In these specimens, the protoconchs are well preserved, suggesting non-planktotrophic development. The new species are known only from the type locality (i.e., they are, so far, endemic).

These new results are in line with the pattern that has come to light in recent years as the result of the reappraisal of the biodiversity and the biogeography of Neogene *Euthria* from the Atlanto-Mediterranean region, namely, from the Miocene and Pliocene of the Loire Basin, northwestern France, in the northeastern Atlantic, to the Miocene of the Paratethyan basins, and of the Karaman Basin, Turkey, in the Eastern Proto-Mediterranean, including many other locations along the Atlantic and Mediterranean coasts of Europe. According to this biogeographic scenario, *Euthria* is a diversified group distributed over an extremely wide geographical area, not only in the Atlanto-Mediterranean region but extending as far as the Indian Ocean and reaching the western Pacific. At the same time, however, locally it displays a high degree of endemicity. In general, using a concept more commonly used in sociology to date, this biogeographical duality could be described as glocal because it simultaneously exhibits contrasting global and more local attributes. In opposition to the wide geographical distribution of the genus, the more localized endemic character of its species, as suggested by the morphology of their protoconchs, is probably related to the mostly non-planktotrophic type of larval development that emerged during the Miocene in the Atlanto-Mediterranean *Euthria* species.

In the eastern Atlantic, today, the northern limit of *Euthria* warm-water gastropods extends only as far north as the northern shores of the Gulf of Cadiz, with only one species, *Euthria cornea*, known to occur in what is now the Mediterranean–Moroccan Molluscan Province. No representatives of the group are known from the colder Franco-Iberian Province to the north, diversifying in the southern tropical Mauritano–Senegalese Province, with an endemic diversity hotspot around Cape Verde. *Euthria* was well represented in the Late Miocene to Early Pliocene of the Ligerian Gulf of northwestern France (Mio-Pliocene European–West African Province, sensu da Silva and Landau, 2007) and in the Pliocene of the Mondego Basin of western Iberia (Pliocene French-Iberian Province). None of the Oligo-Pliocene *Euthria* species represented in the European fossil record have survived to the present day. Only *E. cornea*, with a fossil record dating back to the early Pleistocene, persists in the Mediterranean and the northern Gulf of Cadiz.

In conclusion, as for other warm-water gastropod groups, as well as for thermophilic bivalves and polyplacophorans, it is now clear that in the Atlantic, the northern distribution limit of the gastropod genus *Euthria* has experienced a southward shift since at least the Early Pliocene as a consequence of Plio-Pleistocene cooling events that resulted in decreasing SSTs.

Table 2. Molluscan species described as new and known only from the Pliocene of the Mondego Basin fossil assemblages of west-central Portugal, endemics.

Species	Type locality
Gastropods	
Clanculus moelensis (Cox, 1936)	Mina, São Pedro de Moel
Ocinebrina carvalhoi (Cox, 1936), org. comb. *Muricopsis*	Mina, São Pedro de Moel
Aplus moriasi (Cox, 1936), org. comb. *Pollia*	Mina, São Pedro de Moel
Tritia pontisnovi (Cox, 1936), org. comb. *Nassarius* (*Hima*)	Mina, São Pedro de Moel
Mitra melanopsiformis (Cox, 1936)	Mina, São Pedro de Moel
Vexillum moelensis (Cox, 1936), *Vexillum* (*Costellaria*)	Mina, São Pedro de Moel
Nassarius (*Uzita*) *malachiasi* (Cox, 1941[1])	Matos, Marinha Grande
Ancilla marinhensis (Cox, 1941[2])	Matos, Marinha Grande
Granulina choffati (La Perna, Landau, and da Silva, 2003)	Vale de Freixo, Pombal
Tritia cotteri (Landau, da Silva, and Gili, 2009), orig. comb. *Nassarius*	Vale de Freixo, Pombal
Tritia dinizi (Landau, da Silva, and Gili, 2009), orig. comb. *Nassarius*	Vale de Freixo, Pombal
Tritia lusitanica (Landau, da Silva, and Gili, 2009), orig. comb. *Nassarius*	Vale de Freixo, Pombal
Tritia mondegoensis (Landau, da Silva, and Gili, 2009), orig. comb. *Nassarius*	Vale de Freixo, Pombal
Tritia plioholastica (Landau, da Silva, and Gili, 2009), orig. comb. *Nassarius*	Vale de Freixo, Pombal
Demoulia zbysewskii (Landau, da Silva, and Gili, 2009)	Nadadouro, Caldas da Rainha
Persicula mikhailovae (da Silva, Landau, and La Perna, 2011)	Vale de Freixo, Pombal
Gibberula brebioni (da Silva, Landau, and La Perna, 2011)	Vale de Freixo, Pombal
Sveltia sofiae (Landau and da Silva, 2022)	Vale de Freixo, Pombal
Triphora freixiensis (Landau, Bakker, and da Silva, 2023)	Vale de Freixo, Pombal
Euthria galopimi nov. sp., hoc opus	Vale de Freixo, Pombal
Euthria lockleyi nov. sp., hoc opus	Vale de Freixo, Pombal
Polyplacophora	
Ischnochiton zbyi (Dell'Angelo and da Silva, 2003)	Vale de Freixo, Pombal
Ischnochiton loureiroi (Dell'Angelo et al., 2022)	Vale de Freixo, Pombal
Lepidochitona rochae (Dell'Angelo et al., 2022)	Vale de Freixo, Pombal
Bivalvia	
No new species were reported by Pimentel (2018)	
Scaphopoda	
No new species were reported by Zbyszewski (1959), Brébion (1971, 1974)	

[1] Considered subjective junior synonym of *T. turrita* (Borson, 1820) by Landau et al. (2009).
[2] Considered subjective junior synonym of *Amalda elongata* (Deshayes, 1830) by Landau and da Silva (2006).

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Competing interests. The authors declare none.

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