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The genus *Sveltia* (Gastropoda, Cancellariidae) in the Atlantic Pliocene of Iberia with a new species from the Cenozoic Mondego Basin of Portugal

Bernard M. Landau[1,2]* and Carlos Marques da Silva[3]

[1]Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands. <bernardmlandau@gmail.com>
[2]International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal
[3]Departamento de Geologia and Instituto Dom Luiz (IDL), Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal <cmsilva@fc.ul.pt>

Abstract.—The cancellarid genus *Sveltia* Jousseaume, 1887, is widespread in western European and North African Neogene marine fossil assemblages. In Pliocene deposits it is commonly represented by *Sveltia varicosa* (Brocchi, 1814), which until recently was considered a widely distributed taxon in the Mediterranean Sea and adjacent Atlantic faunas. A recent review of the species from the Pliocene of Italy and Spain (Guadalquivir Basin), leading to the erection of *S. confusa*, prompted the reassessment of the *Sveltia* material from the Atlantic Pliocene of the Portuguese Mondego Basin and the subsequent description of *Sveltia sofiae* n. sp. Consequently, a mosaic of species has emerged from what was previously viewed as the broad Atlanto-Mediterranean range of the widespread and quite variable *S. varicosa*. From a biogeographic standpoint, it is now clear that *S. varicosa* was a Mediterranean species, occurring east of the Alboran Sea. *Sveltia confusa* had a mainly Atlantic distribution, from the French Pliocene Ligerian Gulf to the Gulf of Cadiz, at least, and straddling the Strait of Gibraltar into the Alboran Sea. *Sveltia sofiae* n. sp. was endemic to western Iberia, represented today only in the western Portuguese Mondego Basin. *Sveltia* is a thermophilic genus. Since early Pliocene times, because of northeastern Atlantic sea surface temperature decline, it underwent a southward range contraction, occurring today—in the eastern Atlantic—from Cape Blanc, Mauritania, south. This range reduction was coupled with the post mid-Piacenzian southward contraction of the Pliocene Mediterranean-West African tropical molluscan province and the consequent rise of the present-day Mediterranean-Moroccan subtropical province.

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Introduction

The cancellarid genus *Sveltia* Jousseaume, 1887, is represented in most European and North African Neogene shallow-water marine assemblages. In Pliocene deposits, the most commonly reported species is *Sveltia varicosa* (Brocchi, 1814), which was, until recently, considered a widely distributed and variable taxon in the Mediterranean Sea and adjacent Atlantic, along both European and northwestern African coasts (Chavan, 1940; Malatesta, 1974; Fekih, 1975; Martinell, 1979; González-Delgado, 1992; Vera Peláez et al., 1995; Silva, 2001; Chirli, 2002; Landau et al., 2006, 2011).

Brunetti (2016), in a follow-up paper to his review of the genus in the Pliocene of Italy (Brunetti et al., 2011), re-examined the lower Pliocene specimens from the Atlantic Guadalquivir Basin of southwestern Spain assigned to *S. varicosa* and considered them to represent a new species; *S. confusa* Brunetti, 2016. This spurred reassessment of the *Sveltia* material from the Atlantic Pliocene of the Mondego Basin, central-west Portugal, which, in the light of this recent taxonomic revision, represents yet another species of the genus. The results of this re-examination, together with a discussion of the Pliocene to present-day Atlanto-Mediterranean biogeographical evolution of the *S. varicosa* species group is presented herein.

*Corresponding author

Geological and paleoenvironmental setting

The Vale de Freixo site is located in west-central Portugal (Pombal region) with the geographical coordinates 39°53′02.1″N, 8°43′52.9″W (Fig. 1). The Miocene–Pliocene sedimentary sequence exposed at this locality is part of the Cenozoic Mondego Basin, the fossiliferous Pliocene sediments corresponding to the basal transgressive beds of the Carnide Sandstone Formation (Cachão, 1990; Diniz et al., 2016). The calcareous nannofossil assemblage from these beds indicates placement in biozone CN12a of Okada and Bukry (1980). Based on calcareous nannofossils and gastropod mollusks, these beds have been assigned to the uppermost Zanclean to lower Piacenzian (Cachão, 1990; Silva, 2001; Diniz et al., 2016). The molluscan fauna of Vale de Freixo, as well as all the known marine Pliocene Atlantic molluscan assemblages of the Mondego Basin, correlate to the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) as defined by Monegatti and Raffi (2001) for the Mediterranean Sea (Silva et al., 2010). For more information on the general geological setting and the stratigraphy of the Vale de Freixo site and additional references see Silva et al. (2006, 2010) and Diniz et al. (2016).

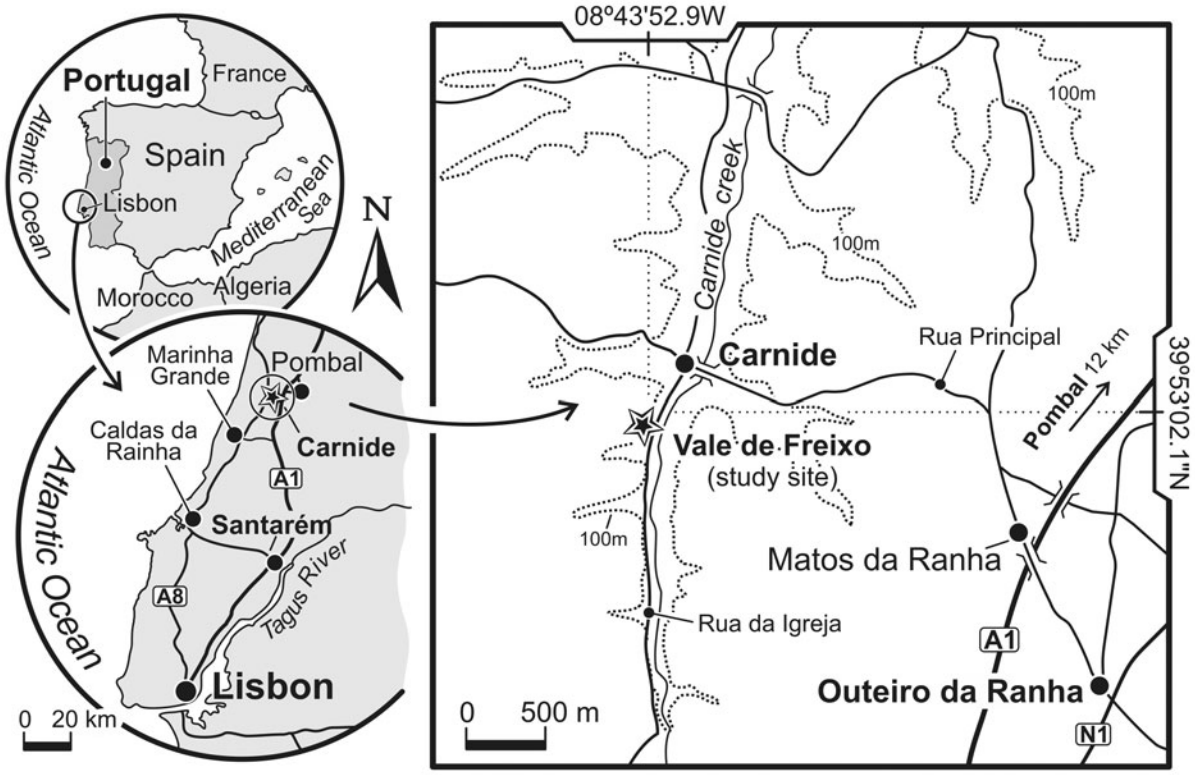

Figure 1. Geographical location of the study site: Vale de Freixo, Carnide, Pombal Municipality (west-central Portugal).

During the very end of the Zanclean and the beginning of the Piacenzian, the Caldas da Rainha-Marinha Grande-Pombal region of western Portugal corresponded, generally speaking, to a shallow marine environment of normal salinity with warm waters, and somehow was protected from the direct influence of open Atlantic Ocean (Nolf and Silva, 1997; Silva et al., 2010). Based on the Pliocene molluscan assemblage, the mid Pliocene Sea Surface Temperatures (SST) along the western Iberian coast at that latitude (Portugal, 40°N) were subtropical, similar to those recorded today on the coasts of western Africa at the latitude of Cape Blanc (Morocco/Mauritania, 21°N; i.e., with maximum Mean Monthly SSTs of ~23.5°C in September and minimum MMSST of 19°C in January–March) (Silva et al., 2010).

The fossil assemblage of Vale de Feixo suggests an infralittoral environment, <24 m deep, in which the gastropods were the most diverse group (Silva, 2001, 2002), followed by the bivalves (Dollfus and Cotter, 1909, for the Caldas da Rainha-Marinha Grande area; Pimentel, 2018, for Vale de Freixo) and the polyplacophorans (Dell'Angelo and Silva, 2003). Other benthic invertebrate groups (i.e., bryozoans, Carvalho, 1961; echinoids, Silva, 2001; Pereira, 2010; and barnacles, Ferreira et al., 2019) were also well represented in the local ecosystem. Vertebrates are represented in the assemblage by bony fish otoliths and rare shark teeth (Nolf and Silva, 1997; Silva, 2001). The gastropod fauna was part of the subtropical Pliocene French-Iberian Province of Silva and Landau (2007) and Landau et al. (2020), including ~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*, but lacking the typical tropical indicators common in coeval Mediterranean faunas (e.g., *Persististrombus* Kronenberg and Lee, 2007, and diversified Terebridae and Conidae, etc., after Monegatti and Raffi, 2001).

Material and methods

The examined material forms part of the collection of the Department of Geology of the Faculty of Sciences of the University of Lisbon, Portugal (C.M. da Silva, Vale de Freixo, Ph.D. collection), and the B. Landau collection, now incorporated in the Natural History Museum Vienna, Austria (NHMW).

Repositories and institutional abbreviations.—NHMW coll. = Natural History Museum Vienna (Austria); GeoFCUL coll. = Department of Geology of the Faculty of Sciences of the University of Lisbon (Portugal), Carlos Marques da Silva, Vale de Freixo (VFX) Ph.D. Collection.

Systematic paleontology

Superfamily Cancellarioidea Forbes and Hanley, 1851

Bouchet et al. (2017, p. 379) synonymized Cancellarioidea Forbes and Hanley, 1851, with Volutoidea Rafinesque, 1815.

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However, the most recent molecular phylogeny of Fedosov et al. (2019, fig. 2) suggests indeed that Cancellariidae are not nested with the rest of the Volutoidea, hence Cancellarioidea is a valid superfamily.

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Cancellariinae Forbes and Hanley, 1851
Genus *Sveltia* Jousseaume, 1887

1887 *Sveltia* Jousseaume, p. 214.

Type species.—*Voluta varricosa* Brocchi, 1814 (currently accepted spelling *varicosa*) by original designation. Pliocene, Italy.

Sveltia sofiae new species
Figures 2.1–2.10, 3.1

2001 *Sveltia varricosa* (Brocchi, 1814) s.l.; Silva, p. 498, pl. 22, figs 17, 18.

Type specimens.—Holotype NHMW 2018/0331/0170, height 20.1 mm, width 9.8 mm (Fig. 2.3, 2.4); paratype 1 NHMW 2018/0331/0305, height 16.0 mm, width 8.3 mm (Fig. 2.5, 2.6); paratype 2 NHMW 2018/0331/0306 (Fig. 2.7–2.10); paratype 3 GeoFCUL VFX.03.130, height 28.0 mm, width 15.1 mm (Fig. 2.1, 2.2); paratype 4 GeoFCUL VFX.03.131, height 17.0 mm, width 9.1 mm; paratype 5 GeoFCUL VFX.03.132, height 14.1 mm, width 7.8 mm; paratype 6 GeoFCUL VFX.03.133, height 12.0 mm, width 6.6 mm; paratype 7 GeoFCUL VFX.04.024, height 12.1 mm, width 6.6 mm. Carnide Sandstone Formation, basal fossiliferous gray sands, "Bed 3" in Gili et al. (1995, text-fig. 2).

Diagnosis.—*Sveltia* specimens of small to medium shell size for genus, multispiral protoconch, teleoconch with scalate spire, sculpture of 14–15 sharp, narrow ribs, fine spiral cords slightly spinous over ribs, subobsolete in interspaces between ribs.

Occurrence.—Vale de Freixo site, near the village of Carnide, Pombal municipality, west-central Portugal. Pliocene northeastern Atlantic, western Iberian coasts; Mondego Basin (Portugal), uppermost Zanclean to lower Piacenzian (this paper).

Description.—Shell of small to medium size and relatively fragile for genus, fusiform with an elevated scalate spire. Protoconch homeostrophic, multispiral, dome-shaped, consisting of three smooth convex whorls, with small smooth nucleus (height: 0.9–1.0 mm; diameter: 1.0–1.1 mm; diameter of nucleus: 0.10–0.14 mm). Transition to teleoconch abrupt, sharply delimited, marked by 2–3 prosocline ribs at end of protoconch and onset of spiral sculpture on teleoconch. Teleoconch consisting of up to 5.5 angular whorls with flattened to weakly convex, subsutural ramp, sharply angled at shoulder, convex below. Suture superficial, undulating. Axial sculpture of 13–15 sharp, narrow, prosocline ribs. Spiral sculpture of narrow, close-set spiral cords of primary to tertiary strength, strengthened over ribs, where primaries slightly spinous; cords weakened or subobsolete in interspaces between ribs. Shoulder cord further strengthened and more strongly spinous, delimiting subsutural ramp. Last whorl 70–72% of total height. Aperture, subtrigonal to ovate, 42–45% of total height. Outer lip not thickened, angled at shoulder, convex below, smooth to lirate within; anal canal hardly developed; siphonal canal short, open. Columella moderately excavated, bearing two oblique folds of equal strength. Columellar and parietal callus continuous, thickened, sharply delimited, closely adpressed and moderately expanded over medial side of venter in adult specimens, closing umbilicus. Siphonal fasciole weakly developed, poorly delimited, rounded.

Etymology.—Named after Sofia Pereira, Portuguese Ordovician trilobite paleontologist at the Geosciences Centre of the University of Coimbra, Portugal.

Additional material.—NHMW 2018/0331/0171 (nine subadults and juveniles), GeoFCUL VFX (eight unnumbered specimens), Vale de Freixo, Pombal, Portugal.

Dimensions.—Measured on the 13 specimens of the GeoFCUL collection. Height: 28 mm (max.) to 4.5 mm (min.), average = 14.3 mm; diameter: 15 mm (max.) to 5.9 mm (min.), average = 8.7 mm; height of the last whorl: 21 mm (max.) to 7.7 mm (min.), average = 12 mm; height of the aperture: 15.5 (max.) to 5.4 mm (min.), average = 8.6 mm.

Variability.—There is little intraspecific variability; in the largest specimen, the shoulder is a little more rounded. The sculpture is remarkably consistent.

Paleoecology.—Epibenthic vagile gastropods living in coastal infralittoral subtropical marine environments (estimated maximum MMSST of ~23.5°C in September and minimum MMSST of 19°C in January–March; Silva et al., 2010) of normal salinity and sandy substrates. Gastropods with multispiral protoconch suggesting planktotrophic larval development.

Remarks.—The careful revision of numerous gastropod species known from the fossil record that were thought to correspond to coherent, widely distributed taxa, either geographically, stratigraphically, or both, has shown them to represent species groups rather than single variable biological entities (e.g., many of the naticid species in the Mediterranean Pliocene, see Pedriali and Robba, 2005, 2008; buccinids, see Brunetti and Della Bella, 2014, 2016; and other cancellarids, see Brunetti et al., 2006, 2008, 2009, 2011).

Difficulties surrounding the *Sveltia varicosa* species group have been repeatedly highlighted in the literature with contrasting conclusions, ranging from Bałuk (1997, p. 48) who considered it pointless to separate species or varieties from various Neogene European basins, to Landau et al. (2006, p. 78) who recognized a Miocene to Pliocene trend for the shells to become larger, more angular, and to lose the abapical columellar fold. Those authors recognized several geographically or

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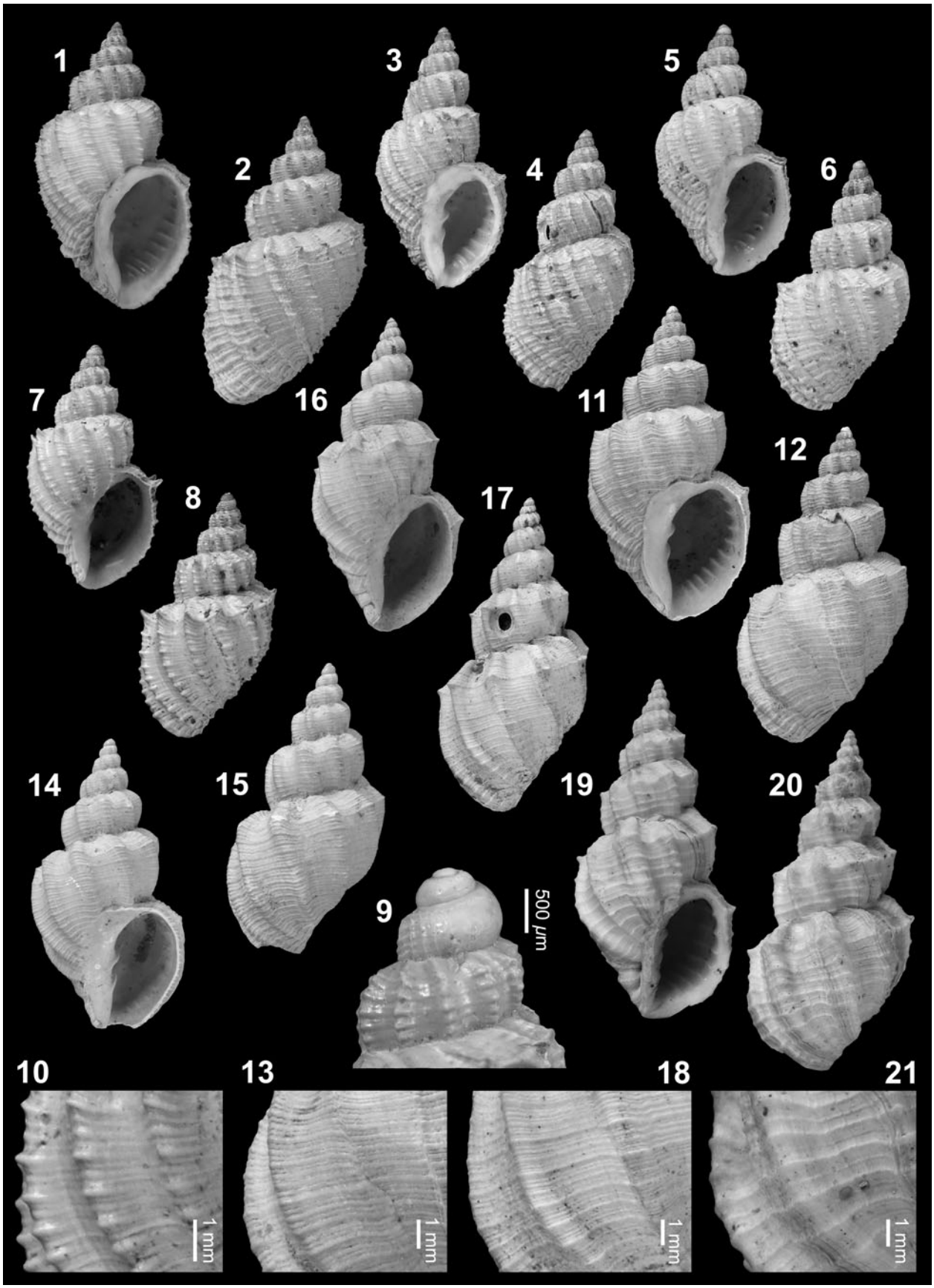

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Figure 2. Gastropods of the *Sveltia varicosa* group from the Atlanto-Mediterranean Miocene and Pliocene. (**1–10**) *Sveltia sofiae* n. sp., Vale de Freixo, Portugal, Carnide Formation; (**1, 2**) (GeoFCUL VFX.03.130) paratype 3 in (**1**) apertural and (**2**) dorsal views, height 28 mm; (**3, 4**) (NHMW 2018/0331/0170) holotype in (**3**) apertural and (**4**) dorsal views, height 20.1 mm; (**5, 6**) (NHMW 2018/0331/0305) paratype 1 in (**5**) apertural and (**6**) dorsal views, height 16 mm; (**7–10**) (NHMW 2018/0331/0306) paratype 2 in (**7**) apertural and (**8**) dorsal views, (**9**) protoconch, and (**10**) detail of the sculpture, height 15.8 mm. (**11–15**) *Sveltia confusa* Brunetti, (**11–13**) (NHMW 2010/0054/0155) Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation, in (**11**) apertural and (**12**) dorsal views, and (**13**) detail of the sculpture, height 28 mm; (**14, 15**) (NHMW unnumbered) La Dixmérie, St-Julien-de-Concelles, Loire Atlantique, France, in (**14**) apertural and (**15**) dorsal views; height 20.4 mm. (**16–18**) (NHMW unnumbered) *Sveltia varicosa* (Brocchi), Poggio alla Staffa, Siena, Italy in (**16**) apertural and (**17**) dorsal views, and (**18**) detail of the sculpture; height 27 mm. (**19–21**) (NHMW1847/0058/0469) *Sveltia dertovaricosa* Sacco, 1894, Yaylasi, Akpinar, Turkey, Serravallian, middle Miocene in (**19**) apertural and (**20**) dorsal views, and (**21**) detail of the sculpture; height 32 mm.

stratigraphically restricted taxa, such as *S. dertovaricosa* (Sacco, 1894) in the middle–upper Miocene Paratethys, Proto-Mediterranean Sea and adjacent Atlantic, *S. burdigalensis* Peyrot, 1928, from the Atlantic Burdigalian lower Miocene of France, and *S. lajonkaireana* (Nyst, 1835) from the Pliocene North Sea Basin. The protoconch in all members of the *Sveltia varicosa* species group is multispiral, composed of three smooth convex whorls, with a small nucleus, and, therefore, not useful to discriminate the various species.

Silva (2001), in his work on the Pliocene Mondego Basin gastropod assemblage, already had expressed doubts about the conspecificity of the Portuguese specimens with "typical" Italian Pliocene *S. varicosa* by recording the species as *Sveltia varricosa* [sic] (Brocchi, 1814) s.l. He pointed out that the Mondego specimens were less elongated, had a lower, more scalate spire with a shallower subsutural ramp, and were closer to the Pliocene Guadalquivir Basin specimens of southern Spain (now *S. confusa*) in shape. Differences in sculpture were also discussed. *Sveltia varicosa* has 8–10 rather broad, rounded axial ribs (Brocchi, 1814; Rossi-Ronchetti, 1955; Brunetti et al., 2011, p. 94), whereas the larger Mondego Basin specimens have 14–15 ribs. The Guadalquivir Basin specimens have 10–11 axial ribs. Apart from the differences highlighted above by Silva (2001), the Mondego specimens are smaller and thinner shelled than either *S. varicosa* or *S. confusa* (maximum size: 51.8 mm *S. varicosa*; 34.6 mm *S. confusa*; 28.0 mm *S. sofiae* n. sp.) and differ in their spiral sculpture.

Brunetti (2016, p. 320) stated: "Compared to the very similar taxon, *S. varicosa*, the new species [*S. confusa*] has spiral sculpture composed of ribbon-like strings of identical thickness (…) while *S. varicosa* shows larger cords alternating with several others much thinner." This is not accurate. All three species show shells with spiral cords of primary to tertiary strength. In *S. varicosa*, the primaries are markedly stronger than the secondaries, and the tertiaries are reduced to fine threads, and there are up to two tertiaries in each interspace between primaries and secondaries, making the distance between the primaries wider (Fig. 3.3). This spiral sculptural arrangement makes the primaries in this species more evident. In *S. confusa*, the primaries are also stronger, but the secondary and tertiary cords are of almost equal strength, giving the impression of more uniform spiral sculpture (Fig. 3.2). Moreover, the spirals are separated by narrower interspaces. In *S. sofiae* n. sp., the spirals are again well separated into those of primary to tertiary strength, slightly spiny where they overrun the ribs, and subobsolete in the interspaces between the ribs (Fig. 3.1). In *S. sofiae* n. sp., the number of ribs is greater than in the other two species. The Mondego Basin specimens represent, without doubt, a separate species, for which the taxon *Sveltia sofiae* n. sp. is herein erected.

Atlantic, Mediterranean, and Paratethyan specimens of this species group have been assigned to *S. dertovaricosa* Sacco, 1894 (Harzhauser and Landau, 2012; Landau et al., 2013). The holotype originates from the upper Miocene Tortonian of Stazzano, Italy (Ferrero-Mortara et al., 1984, pl. 33, fig. 2; Brunetti et al., 2011, figs. 4G, H). It has a regularly fusiform shell with a weak shoulder, two well-developed columellar folds, with a third subobsolete abapical one; and a lirate outer lip. Middle Miocene specimens from the Paratethys and eastern Proto-Mediterranean of Turkey (Fig. 2.19–2.21) are more strongly shouldered and, most importantly, have three well-developed columellar folds, and a lirate outer lip. Therefore, they may represent one or more distinct species. The specimens reported by Pereira da

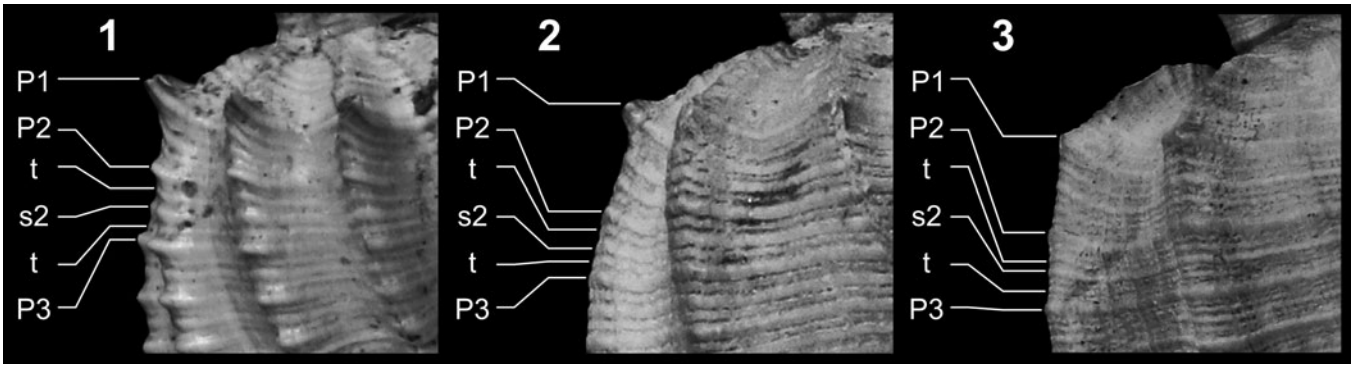

Figure 3. Comparison of spiral sculpture in Pliocene species of the *Sveltia varicosa* group from the Atlanto-Mediterranean Pliocene discussed herein. (**1**) *Sveltia sofiae* n. sp., paratype 2, Vale de Freixo, Portugal, Carnide Formation (NHMW 2018/0331/0306, same specimen as in Fig. 2.7–2.10); scale x2.1. (**2**) *Sveltia confusa* Brunetti, Lucena del Puerto, Huelva, Spain, Arenas de Huelva Formation (NHMW 2010/0054/0155, same specimen as in Fig. 2.11–2.13); scale x2.3. (**3**) *Sveltia varicosa* (Brocchi), Poggio alla Staffa, Siena, Italy (NHMW, same specimen as in Fig. 2.16–2.18); scale x2.4. Terminology after Landau et al. (2019). P1 = primary shoulder cord, P2 = primary cord 2; P3 = primary cord 3; s2 = secondary cord between P2 and P3; t = tertiary cords.

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Costa (1867) from the Tortonian of Portugal, under the name *Cancellaria varicosa*, conform to the shape of *S. dertovaricosa*, the abapical fold is either absent on extremely weak, but the outer lip is smooth, not lirate. We are unsure how important this feature is, because in other groups the presence/absence of lirae may vary intraspecifically. Therefore, we provisionally consider these specimens to represent *S. dertovaricosa*. Apart from the columellar folds, *S. dertovaricosa* further differs from *S. sofiae* n. sp. in being more fusiform, with a weaker shoulder.

Pereira da Costa described an additional member of the *S. varicosa* species group; *Cancellaria adiçana* [sic] (Pereira da Costa, 1867), from the Serravalian–Tortonian transition of Adiça (Almada), south of Lisbon, Portugal. We have not examined specimens of this species, but the shell described and figured by Pereira da Costa is fusiform, with no shoulder, the ribs are weak, the outer lip is smooth within, and it has two columellar folds. These specimens are most like *S. dertovaricosa* from Cacela in being fusiform, having two folds and a smooth outer lip, but the Cacela shells are shouldered with a small spine developed on the shoulder cord.

The genus is represented in the eastern Atlantic by the Pliocene to present-day species *Sveltia lyrata* (Brocchi, 1814). The shell of *S. lyrata* differs from the *S. varicosa* species group discussed herein in having strongly angular whorls, a broad, steeply sloping subsutural ramp, and more or less well-developed spines placed roughly mid-whorl that are more strongly developed than in any of the species in the *S. varicosa* group (e.g., Verhecken, 2007, p. 325, fig. 41).

Discussion

Chronostratigraphic distribution.—Brunetti (2016, p. 323) reported that *S. confusa* has a chronostratigraphic distribution exclusive to the basal Zanclean and a wide geographical distribution, including the Mediterranean Sea (Estepona Basin, southern Spain and Monte Antico, Toscany, Italy) and the adjacent Atlantic (Guadalquivir Basin, southern Spain). In contrast, *S. varicosa* was particularly abundant in the Piacenzian (Pliocene), extending its distribution to the Gelasian (Pleistocene), and only referred to its occurrence in Italian assemblages. However, in the "Examined Material" section, Brunetti (2016, p. 320) clearly stated that *S. varicosa* occurs from the Zanclean to the Piacenzian (Italy) and into the Gelasian of Torrente Stirone (Italy).

It is not clear on what data Brunetti (2016, p. 323) based his chronostratigraphic assignment of the occurrences of *S. confusa* to the basal Zanclean. In the original formalization of the new species, Brunetti (2016, p. 320) did not mention the stratum typicum, stating simply, in the "Distribution," that *S. confusa* occurs in the Zanclean sediments of the Guadalquivir and Estepona basins. In the chresonymy of *S. confusa*, specimens of the Guadalquivir Basin of González-Delgado (1992) and Landau et al. (2011) are included. The *Sveltia* specimens figured in both these publications originate from the Huelva Sands Formation. Moreover, the type material of *S. confusa* originates from Lucena del Puerto, a typical Huelva Sands Formation locality (Landau et al., 2011). Based on planktic foraminifers, this formation was assigned to the *G. margaritae* and *G. puncticulata* biozones (Sierro, 1985; Civis et al., 1987), corresponding to the lower Pliocene, but not to the basal Zanclean (biostratigraphy after Lirer et al., 2019).

Similarly, the chronostratigraphic positioning of the Estepona Basin Pliocene sections does not corroborate a basal Zanclean age. According to Aguirre et al. (2005), the sections exposed in Parque Antena, Velerín, and Velerín-Carretera (Estepona) are assigned to the uppermost Zanclean, while the Velerín-Antena (Estepona) section is assigned to the lower half of the Piacenzian (upper Pliocene). Similarly, other authors assign the Estepona Formation sections to the upper Zanclean (Vera-Peláez et al., 1995) to lower Piacenzian (Guerra Merchán et al., 2002; Janssen, 2004). As to the Monte Antico locality, the origin of the *S. confusa* Italian material examined by Brunetti (2016) was assigned by the author to the lower Pliocene, but not specifically the basal Zanclean. Finally, the fossil assemblage of the La Dixmérie deposits of northwestern France is assigned to Assemblage III of Van Dingenen et al. (2015), which again is dated as Zanclean, but not basal (Landau et al., 2020).

The occurrences of *S. confusa* related to the Pliocene Mediterranean-West African Tropical Province of Silva and Landau (2007) (i.e., the Mediterranean region and Guadalquivir Basin reports) fit into the Zanclean to lower Piacenzian pre-3.0 cooling event, MPMU1 unit of Monegatti and Raffi (2001). The French Assemblage III, representing the subtropical Pliocene French-Iberian Province, fits into the time frame of the MPMU1 in the Mediterranean region. *Sveltia sofiae* n. sp. occurs in the uppermost Zanclean to lower Piacenzian of the Portuguese Mondego Basin (this paper) and correlates to the Mediterranean MPMU1 (Silva, 2001).

Geographical distribution.—For this paper, dozens of Pliocene *Sveltia* specimens spanning the entire Huelva Sands Formation have been revised ("yellow" and "grey" sands, sensu Landau, 1984 and Landau et al., 2011), and all of them represent *S. confusa* (Fig. 2.11, 2.12). Likewise, a small collection of five poorly preserved *Sveltia* shells (NHMW) from the more northern Atlantic lower Pliocene locality of La Dixmérie (Nantes region, France, Assemblage III of Van Dingenen et al., 2015) was examined, all representing *S. confusa* (Fig. 2.14, 2.15).

Brunetti (2016) included the Pliocene specimens from the Estepona Basin, southern Mediterranean Spain, figured by Vera Peláez et al. (1995) as *Sveltia varricosa* [sic], in the chresonymy of *S. confusa*. These specimens are extremely uncommon in the Estepona deposits. A single *Sveltia* specimen from the Velerín Conglomerates (Estepona) was figured recently by Landau and Mulder (2020, fig. 22), and it does indeed represent *S. confusa*.

For this work, the Italian records of Monte Antico given by Brunetti (2016) for *S. confusa* were reassessed. The assemblage was monographed in Brunetti (2014) and the specimen illustrated on page 62 identified as *S. varicosa*. This specimen was later included in the chresonymy of *S. confusa* by Brunetti (2016, p. 320). In our opinion, this specimen represents *S. varicosa*, not *S. confusa*. Although the spiral sculpture resembles that seen in *S. confusa*, the shoulder is far less acute than that seen in specimens of the species from Spain. In light of this

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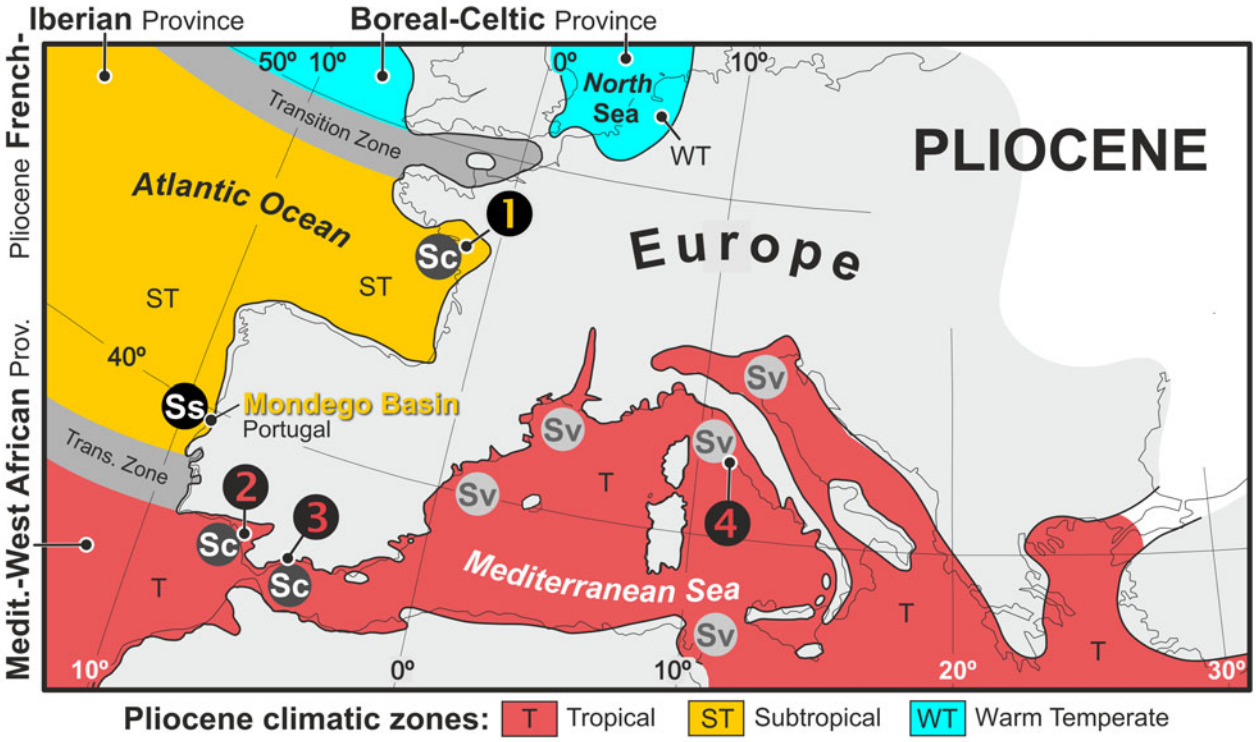

Figure 4. Geographic distribution of *Sveltia sofiae* n. sp. (Ss), *S. confusa* (Sc), and *S. varicosa* (Sv) in the pre-3.0 Ma Atlanto-Mediterranean Pliocene. 1 = Loire Basin, Ligerian Gulf; 2 = Guadalquivir Basin; 3 = Estepona Basin; 4 = Monte Antico, Tuscany. Pliocene biogeographic provinces after Silva and Landau (2007). Paleogeography adapted from Rögl (1999), Silva (2001), and Popov et al. (2006).

revision, *S. confusa* has a geographical distribution restricted to the eastern Atlantic and the adjacent Mediterranean Alboran Sea. Conversely, we re-examined other Mediterranean records of *S. varicosa* (southern France, Fontannes, 1880; Tunisia, Fekih, 1975; Catalonia, north-eastern Spain, Martinell, 1979), all of which represent that species: *Sveltia varicosa* is widespread in the Mediterranean region, east of the Alboran Sea.

Biogeography.—*Sveltia* is a genus of thermophilic gastropods with a wide present-day distribution, including the tropical and temperate eastern and western Atlantic, and eastern Pacific (Verhecken, 2007; Petit and Harasewych, 2011). In the eastern Atlantic, the genus is represented by a single species, *Sveltia lyrata* (Brocchi, 1814), occurring from shallow to relatively deep waters off Cape Blanc, Mauritania to South Africa, off Cape Town (Verhecken, 2007).

From a biogeographical point of view, as a result of the erection of *S. confusa* and *S. sofiae* n. sp., the Zanclean to early Piacenzian pre-3.0 Ma distribution (= MPMU1 time slice) of *S. varicosa* becomes restricted to the Mediterranean sector of the Mediterranean-West African Tropical Province (Fig. 4). Records of *S. varicosa* in the lower Pliocene Atlantic of Dar Bel Hamri (Morocco), although plausible, could not to be confirmed because no figures of specimens are given by either Chavan (1940) or Lecointre (1952).

On the other hand, the coeval *S. confusa* is a predominantly Atlantic Pliocene species, ranging from the northernmost subtropical Pliocene French-Iberian Province (from the Ligerian Subprovince, sensu Landau et al., 2020) to the northernmost Pliocene tropical Mediterranean-Moroccan Province (sensu Silva and Landau, 2007). Its distribution crosses the Strait of Gibraltar, extending into the westernmost Mediterranean Sea only as far as the Alboran Sea. In the Mondego Basin, the *S. varicosa* species group is represented by *S. sofiae* n. sp. The Mondego assemblage, representing the southernmost part of the subtropical Pliocene French-Iberian Province, records a relatively cosmopolitan gastropod fauna with fewer than 10 endemic species (≤6%). This is, therefore, an interesting and relevant addition to the Mondego endemics.

Conclusions

Erection of *Sveltia sofiae* n. sp. from the Pliocene of the Mondego Basin (Portugal), in the wake of the reassessment of the Iberian Atlantic occurrences of *Sveltia* and the previous formalization of *S. confusa*, sheds new light on the biogeography of the *Sveltia varicosa* species group in the Pliocene of the north-eastern Atlantic and the Mediterranean Sea. After this revision, a mosaic of species has emerged from what was previously seen as the broad Atlanto-Mediterranean range of a single widespread and very variable species.

As now understood, *S. varicosa* was a Mediterranean taxon, absent only in the westernmost Alboran Sea. *Sveltia confusa* had a mainly Atlantic distribution, from the northwestern French Pliocene Ligerian Gulf to the Gulf of Cadiz, at least, and straddling the Strait of Gibraltar into the Alboran Sea. *Sveltia sofiae* n. sp. was endemic to western Iberia, represented today only in the western Portuguese Mondego Basin.

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Sveltia is a thermophilic genus. In the eastern Atlantic, since Pliocene times, as a result of sea surface temperature decrease, it underwent a southward range contraction along the western European and African coasts. Today, the genus is represented in the eastern Atlantic by a single species, *Sveltia lyrata*, occurring from Cape Blanc, Mauritania, south. This range contraction was coupled with the post mid-Piacenzian equatorward reduction of the Pliocene Mediterranean-West African tropical molluscan province (resulting in the present-day Mauritanian-Senegalese Province) and the consequent rise of the current Mediterranean-Moroccan subtropical province.

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