

THE GENUS SOLARIELLA
(MOLLUSCA, ARCHAEOGASTROPODA)
FROM THE PLIOCENE OF VALE DE FREIXO, PORTUGAL:
PALAEOBIOGEOGRAPHIC AND PALAEOCLIMATIC IMPLICATIONS

CARLOS MARQUES DA SILVA

Universidade de Lisboa
 Lisboa, Portugal

BERNARD LANDAU

International Health Centres
 Albufeira, Portugal

and

JORDI MARTINELL

Universitat de Barcelona
 Barcelona, Spain

Silva, Carlos Marques da, Bernard Landau & Jordi Martinell. The genus *Solariella* (Mollusca, Archaeogastropoda) from the Pliocene of Vale de Freixo, Portugal: palaeobiogeographic and palaeoclimatic implications. — Contr. Tert. Quatern. Geol., 37(3-4): 57-65, 4 figs. Leiden, December 2000.

In the present paper, the trochid gastropod *Solariella cincta* (Philippi, 1836) is recorded for the first time from Pliocene (Piacenzian) strata exposed at Vale de Freixo (Pombal, central-west Portugal). This record of the species constitutes the first from the Atlantic Neogene; the taxon is here compared with other Miocene to Recent European species of *Solariella*. At present, *S. cincta* is restricted to the coast of West Africa. During the Late Pliocene, it had a much wider distribution, occurring in the Mediterranean and along the European Atlantic coasts, at least as far north as central-west Iberia. The presence of thermophilic benthic gastropods such as *S. cincta*, *Tribia uniangulata* (Deshayes, 1830), *Solatia piscatoria* (Gmelin in Linné, 1790), *Ancilla* sp., *Ficus* sp., and *Strioterebrum* sp. in Pliocene strata at Vale de Freixo, clearly indicates that relatively high water temperatures (*i.e.* warmer than today) still prevailed, at least sporadically, along the European Atlantic coast at this latitude, between *c.* 3.2-3.1 and 2.7 Ma.

Key words — *Gastropoda*, *Trochidae*, *Pliocene*, *Portugal*, *palaeobiogeography*, *palaeoecology*.

C.M. da Silva, Departamento e Centro de Geologia, Universidade de Lisboa, Rua da Escola Politécnica, 58, P-1250 102 Lisboa, Portugal [e-mail: Paleo.Carlos@fc.ul.pt]; B.M. Landau, International Health Centres, Avenida Infante Dom Henrique 7, Areias de São João, P-8200 Albufeira, Portugal [e-mail: bernielandau@netscape.net]; J. Martinell, Departament d'Estratigrafia i Paleontologia, Facultat de Geologia, Universitat de Barcelona, E-08028 Barcelona, Spain [e-mail: jordim@natura.geo.ub.es].

CONTENTS

Introduction	p. 57
Systematic palaeontology	p. 58
Discussion	p. 62
Conclusion	p. 63
Acknowledgements	p. 63
References	p. 64

INTRODUCTION

Although Pliocene marine molluscs from central-west Portugal have been known for more than one hundred years now (see *e.g.* Choffat, 1889), none of the classic localities has produced a fauna as diverse or well preserved as that at Vale de Freixo in the Pombal region (Fig. 1).

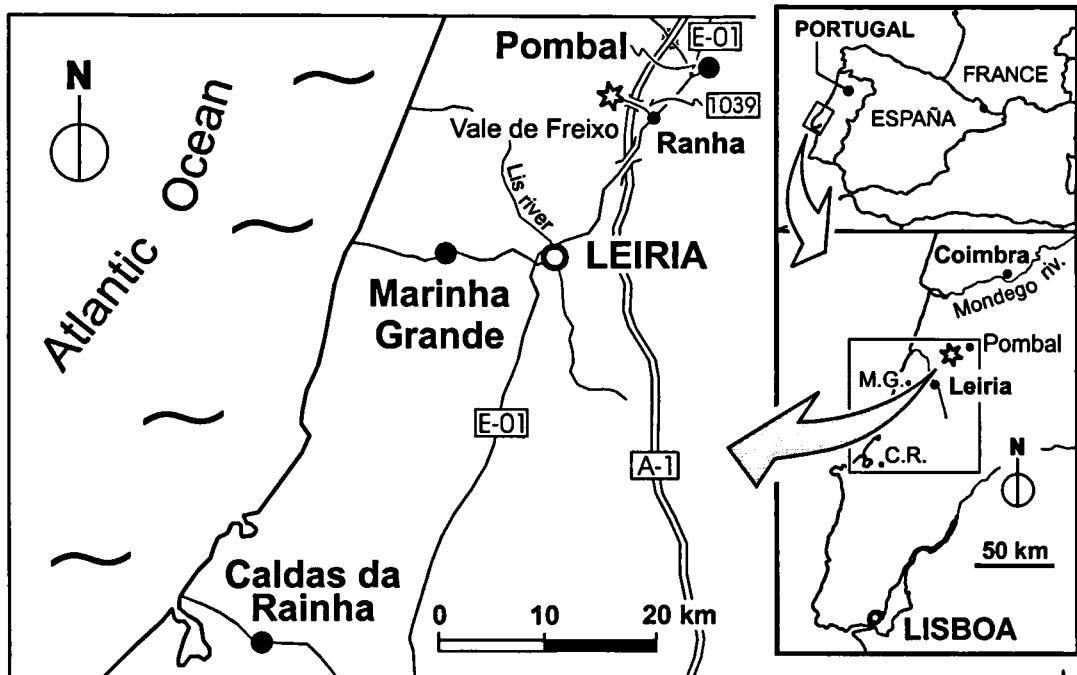


Fig. 1. Map showing the location of the Vale de Freixo outcrop in central-west Portugal.

The Pliocene sequence in this region consists of two members, the Formação Arenito de Carnide below, and Formação Arenito de Roussa-Paredes above. The former unit comprises barren, fine, silty, micaceous sand. Locally, the lowermost portion of this formation contains a basal conglomerate and a sand rich in marine molluscan shells. At Vale de Freixo, the maximum thickness of the basal fossiliferous beds of the Formação Arenito de Carnide amounts to approximately 1 m (Fig. 2). These beds are remarkable for their relatively abundant, well-preserved macrofossils, mostly bivalves and gastropods (see Gili *et al.*, 1995, for more details). The material studied for the present paper was collected from Bed 3.

The molluscan assemblage from Vale de Freixo indicates a shallow marine, infralittoral environment with relatively high water temperatures (Silva, 1993a; Gili *et al.*, 1995; Nolf & Silva, 1997). The fauna shows an interesting combination of Mediterranean and northern European Pliocene species (Gili *et al.*, 1995), in addition to a number of probable endemics, most of which await description.

According to Cachão (1990), the calcareous nanofossil assemblage of Bed 3 at Vale de Freixo indicates placement in the *Discoaster tamalis* Zone (CN12a, see Okada & Bukry, 1980), *i.e.* Upper Pliocene, Piacenzian (*sensu* Berggren *et al.*, 1995). The molluscan faunas from this bed allow assignment to the Mediterranean Pliocene Molluscan Unit 2 of Raffi & Monegatti (1993), *i.e.* postdating the 3.2-3.1 Ma eco-biostatigraphic extinction event (immigration and local extinction) of benthic molluscan taxa of tropical

affinity, as defined by Raffi *et al.* (1989). The chrono-logic overlap between biozone CN12a and molluscan unit MPMU2 provides a more precise time assignment of Bed 3 deposition at Vale de Freixo, *viz.* between 3.2-3.1 and 2.7 Ma, the latter documenting the last appearance datum (LAD) of *Discoaster tamalis* (see Silva, 1995).

SYSTEMATIC PALAEONTOLOGY

Superfamily	Trochoidea Rafinesque, 1815
Family	Trochidae Rafinesque, 1815
Subfamily	Solariellinae Powell, 1951
Genus and subgenus	<i>Solariella</i> Wood, 1842

Solariella (*Solariella*) *cincta* (Philippi, 1836)

Fig. 4

1836 *Trochus cinctus* Philippi, p. 185, pl. 10, fig. 20.
 1898 *Gibbula inoptanda* P. Fischer — Locard, p. 51, pl. 1, figs 24-27.
 1916 *Solariella cincta* (Philippi, 1836) — Cerulli-Irelli, p. 187, pl. 21, figs 23-25 (typical), fig. 26 (var. *depressa* Seguenza), fig. 27 (var. *conica* Cerulli-Irelli).
 1993 *Solariella cincta* (Philippi, 1836) — Warén, p 161, fig. 1b, c.
 1993 *Solariella inoptanda* (Locard, 1897) — Warén, p 161, fig. 2e.
 1993b *Solariella* sp. — Silva, p. 116, pl. 2, figs 1-3.

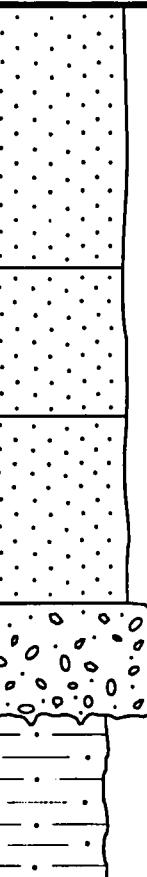
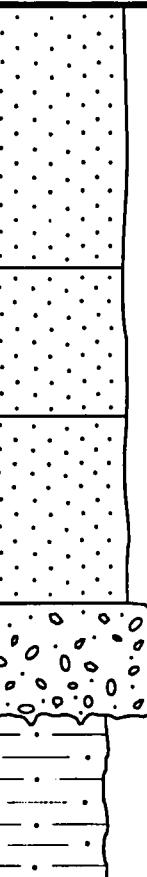
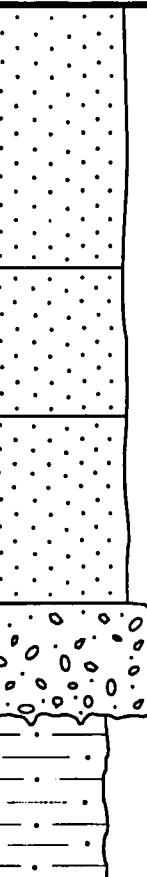
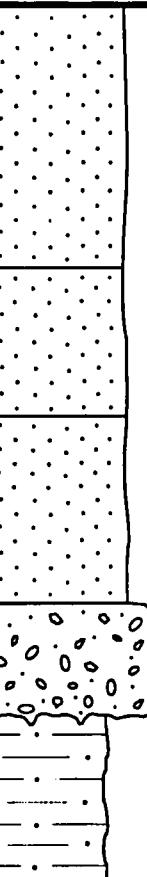
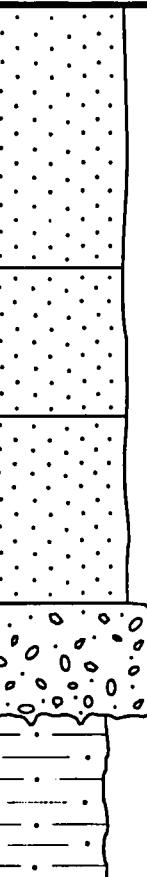
Series	Stage	Formation	Bed	Thickness	Graphic columnar section	Fossils	Description
PLIOCENE	Piacenzian	Arenito de Carnide	5	> 5 m			Sand, yellow, fine well graded, barren
PLIOCENE	Piacenzian	Arenito de Carnide	4	0.3 m			Sand, brown-yellow, fine well graded, fossiliferous
PLIOCENE	Piacenzian	Arenito de Carnide	3	0.4 m			Sand, dark grey, fine, moderately graded, fossiliferous
PLIOCENE	Piacenzian	Arenito de Carnide	2	0.5 m			Conglomerate, dark grey, with fine to medium sand matrix, fossiliferous
PLIOCENE	Piacenzian	Arenito de Carnide	1	> 5 m			Silt, light gray, clayey, with some coarse sand, barren

Fig. 2. Stratigraphy of the Vale de Freixo outcrop, representing the lowermost portion of the Pliocene (Piacenzian) sequence in the Pombal region (central-west Portugal).

Material — Over 30 well-preserved specimens (Silva and Landau collns), representing all growth stages, from Bed 3 at Vale de Freixo (Pombal region, central-west Portugal); Pliocene, Piacenzian.

Diagnosis — A medium-sized *Solariella* with an angular periphery on the spire whorls, rounded body whorl, ornament of three strong primary cords with additional secondaries on later whorls and a wide, deep, ridged umbilicus.

Description — Protoconch homeostrophic, paucispiral, sharply delineated from teleoconch, consisting of about 1.25 whorls with a large, slightly elevated nucleus. Whorl ornament consisting of several (3-4 ?) very fine

spiral cords (Fig. 4d-f). Diameter of protoconch 320-360 μm , of nucleus 180-200 μm . Shell small, trochiform, maximum height 8.6 mm, maximum width 10.0 mm; teleoconch of 6 whorls with a prominent, subhorizontal, concave subsutural ramp, inward sloping in early whorls, outward sloping in subsequent whorls. Whorl profile below subsutural ramp flat on early whorls, concave on body whorl. Teleoconch ornament of two granulose primary spiral cords on the first whorl, with a third appearing towards the end of the second; adapical cord defines outer limit of subsutural ramp. Below, whorl is flattened and slopes at an angle towards adapical cord, from which whorl profile drops vertically to

wards suture, which is narrow, linear and shallow; irregularly spaced spiral secondaries and tertiaries appear in interspaces between the three primaries on later whorls. Axial ornament of numerous weak growth lines overlying spiral ornament and forming granulose cords. Growth lines most prominent over abapical cord, giving it a finely beaded appearance, strongest on the early teleoconch whorls. Body whorl well developed, comprising two-thirds of total shell height; whorl profile rounded rather than angular as in earlier teleoconch whorls. Base flattened, concave with wide, deep umbilicus, occupying half the diameter of base. Ornament of 5-10 subequal spiral cords, wider than interspaces. Umbilicus delimited by a wider perumbilical cord crossed by numerous axial growth lines forming ridges on the cord. Inner face of umbilicus with 7-8 spiral cords, finely ridged by numerous, closely spaced axial growth lines. Aperture circular, with continuous peristome; lip thin and sharp with a sinuous edge, caused by elonga-

tions of spiral cords; parietal lip adherent to body whorl with no callus formation.

Comparisons — *Solariella cincta* is similar to the Recent *S. amabilis* (Jeffreys, 1865), which ranges from southwest Iceland to the coast of western Morocco; however, it has a wider and more coarsely ornamented umbilicus, more convex whorls, a prominent colour pattern and a smaller protoconch (Warén, 1993, p. 161).

There is also a resemblance to *Solariella maculata* Wood, 1842 (p. 531, pl. 5, figs 7, 10), which is endemic to the Lower-Middle Pliocene of the North Sea Basin (Marquet, 1995, p. 64). This form has rounded, rather than angular whorls and evenly spaced spiral keel-shaped cords, and also differs from *S. cincta* in other details of ornament. Traces of coloration are also present in many specimens of *S. maculata* (see Geys & Marquet, 1979, p. 68, pl. 27, fig. 5), but appear as radial spots rather than vertical flammules.

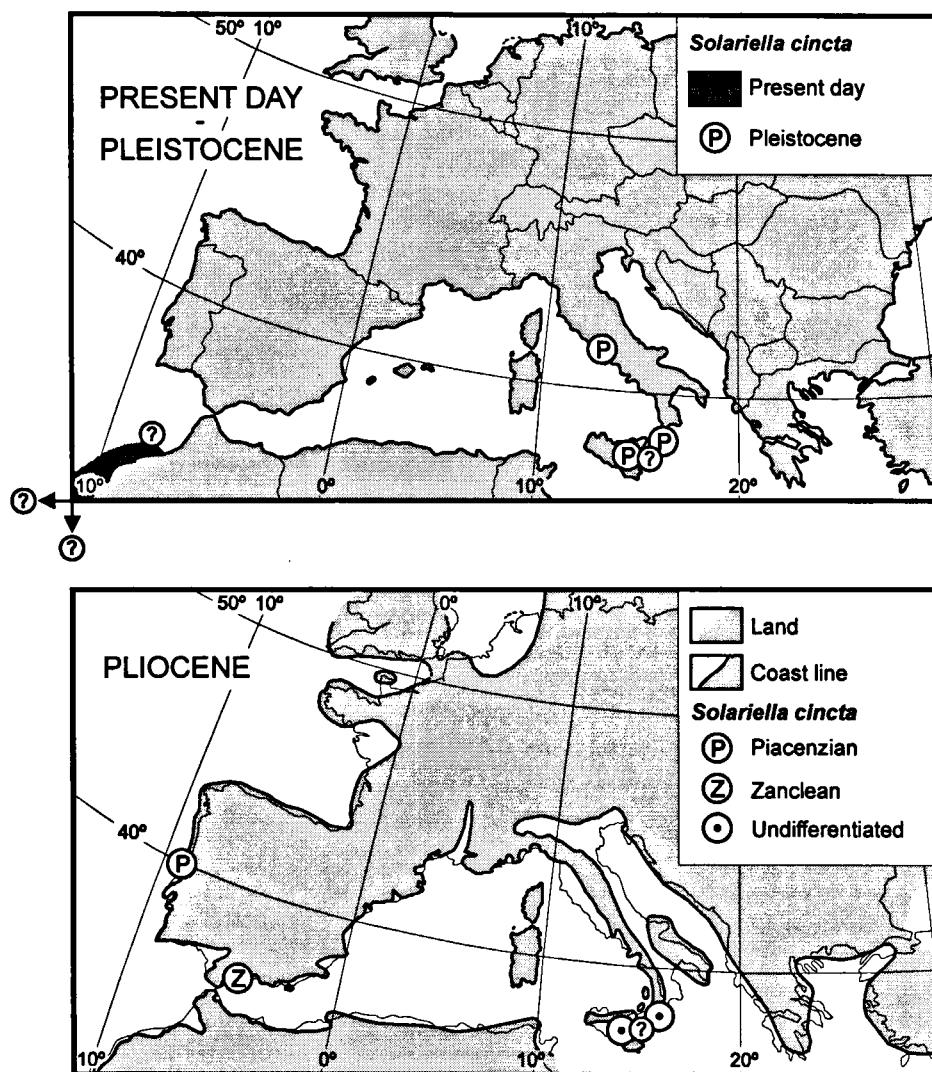


Fig. 3. Stratigraphical and geographical distribution of *Solariella (S.) cincta* (Philippi, 1836).

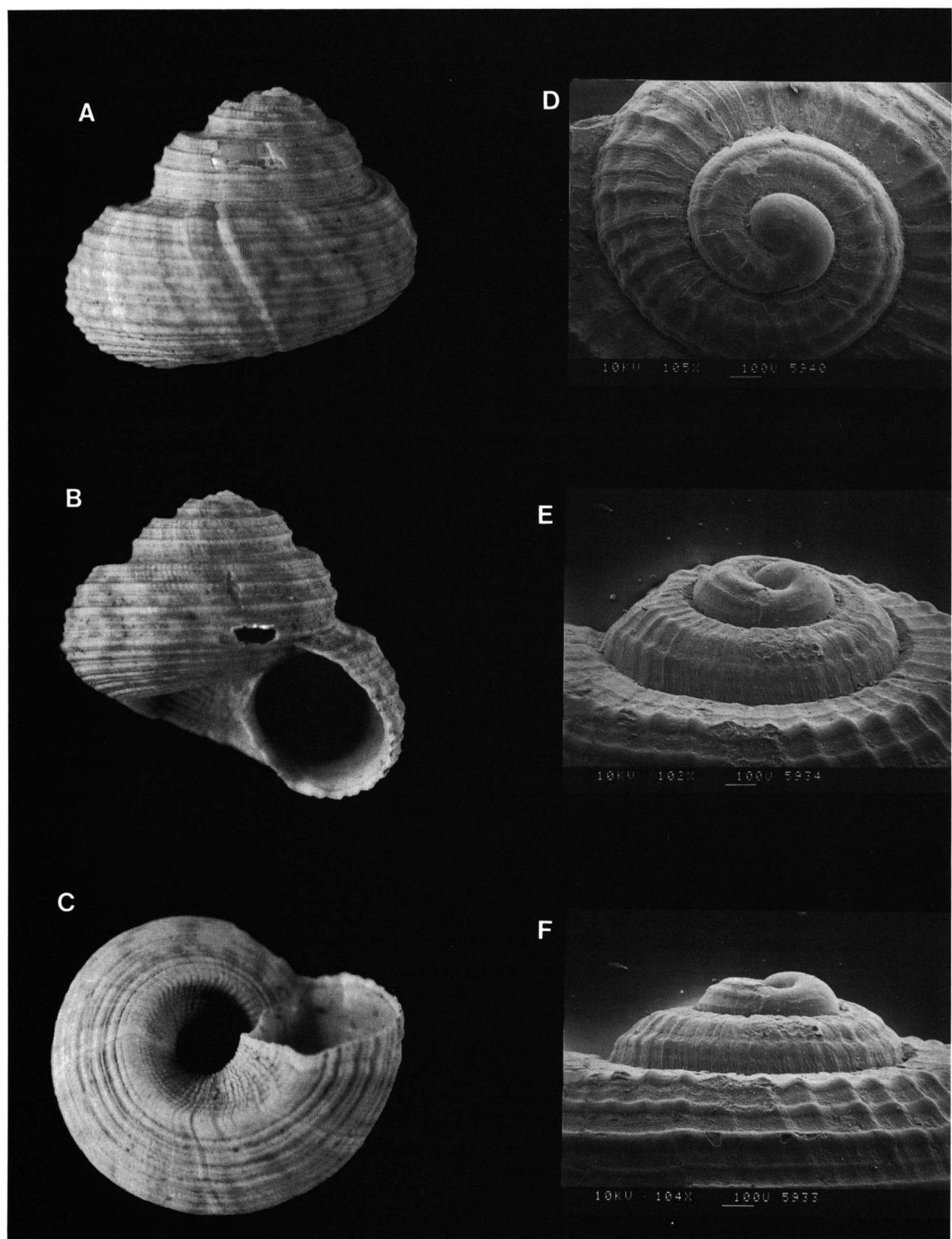


Fig. 4. *Solariella (S.) cincta* (Philippi, 1836), VFX.03.026 (Silva Colln), Upper Pliocene (Piacenzian), Vale de Freixo (Pombal region, central-west Portugal); A - dorsal view (height 8.6 mm, diameter 10.0 mm); B - apertural view; C - umbilical view; D-F - protoconch (scale bar 100 μ m).

Two allied species occur in the Italian Pliocene. One of these, *Solariella peregrina* (Libassi, 1859), which is also known from the Lower Pliocene (Zanclean) of southern Spain, is readily distinguished from *S. cincta* by a stronger axial ornament (see Cavallo & Repetto, 1992; Pavia, 1975). *Solariella pliobscura* Sacco, 1896, has an angular whorl profile, but an ornament consisting of weak, regular, closely spaced spiral cords (see Ferrero-Mortara *et al.*, 1984, pl. 49, fig. 4a-d).

Other related species occur in the Miocene of the North Sea Basin. The specimen assigned to *Solariella aff. duvergieri* Cossmann & Peyrot, 1916 by Janssen (1984, p. 122, pl. 44, fig. 4a-c) has an angular whorl profile, but is less depressed and lacks secondary spiral ornament. *Solariella marthae* Kautsky, 1925 (see Anderson, 1964, p. 197, pl. 12, fig. 93a, b; Janssen, 1984, p. 123, pl. 44, fig. 5a-d) has an ornament which is very similar to that of *S. cincta*, but the shell is less depressed and has stronger axial ornament on the adapical cord and umbilicus. The specimens recorded by Janssen (1984) show these species to be much smaller than the Portuguese one.

From the Miocene of Colli Torinesi (Italy), *Solariella taurocincta* Sacco, 1896 has a depressed shell and beaded adapical cord like *S. cincta*, but stronger keel-shaped spiral cords. This form is most similar to *S. duvergieri*, differing mainly in being more depressed. In the same paper, Sacco (1896) described a second species, *S. taurobella*, from the same horizon. Unfortunately, specimens of this species have not been illustrated nor described in the subsequent literature. With only Sacco's figures in hand, this species appears to be indistinguishable from its congeners. The description suggests a shell with a deeper suture, differing from *S. cincta* in details of ornament.

Solariella duvergieri and *S. contabulata* Cossmann & Peyrot, 1916 from the Burdigalian and 'Helvetian' of France, respectively, are much smaller with less depressed shells, although they have the same elements of axial and spiral ornament as does *S. cincta*.

Remarks — *Solariella cincta* is common at Vale de Freixo, being represented in our collections by over thirty, well-preserved specimens, most of them showing traces of their original colour pattern of vertical stripes or flammules; nacre can be seen where the upper shell layer is missing. There is quite a range of intraspecific variation, both in ornament (with different relative strengths of primaries and secondaries) and shell profile. Both extremes of spire height, i.e. squat *S. cincta* var. *depressa*, and high-spired *S. cincta* var. *conica*, as illustrated by Cerulli-Irelli (1916, pl. 21, figs 26, 27, respectively), are represented at Vale de Freixo, with numerous intermediate gradations.

Stratigraphical and geographical distribution (Fig. 3) — To date, *Solariella cincta* has been recorded from the Pliocene (Piacenzian) of the Atlantic (Portugal, the present paper; see also Silva, 1993b, under the name of

Solariella sp.), the Mediterranean, southern Spain (Estepona, Zanclean, pers. obs.), and ?Italy (Sicily and Calabria, ?Pliocene; see Cerulli-Irelli, 1916; Warén, 1993), and the Pleistocene of the Mediterranean, Italy (Monte Mario, ?Sicily and ?Calabria, Lower Pleistocene; see Cerulli-Irelli, 1916; Warén, 1993). At present, *S. cincta* occurs off the coast of West Africa, under the name of *S. inoptanda* (see Warén, 1993).

Palaeoecology — At Vale de Freixo, *S. cincta* is found in fine sandy sediments, co-occurring with molluscs (Silva, 1993a; Gili *et al.*, 1995) and fish (Nolf & Silva, 1997) that indicate a normal salinity, shallow (infralitoral) marine environment with a fine sandy substrate. Associated with *S. cincta* are other trochid gastropods such as *Clanculus corallinus* (Gmelin, 1791), *Clelandella miliaris* (Brocchi, 1814), *Gibbula* cf. *subcineraria*(?) (d'Orbigny, 1852), *Gibbula* cf. *adansoni*(?) (Payraudeau, 1826), and *Calliostoma* cf. *zizyphinum* (Linné, 1758).

Extant members of genus *Solariella*, e.g. *S. amabilis* (see Graham, 1988), normally are infralitoral to bathyal (up to 1,000 m deep) in their distribution, being epibenthic on sandy and gravelly bottoms. According to Fretter & Graham (1977), *S. amabilis* is either a ciliary feeder or collects detritus from the bottom. Graham (1988, p. 100) wrote, 'Its way of life is unknown (.....)'.

DISCUSSION

The Miocene-Recent genus *Solariella* (see Knight *et al.*, 1960) is widely distributed in Neogene faunas of Europe, with records from the North Sea Basin as follows: Miocene (Burdigalian-Lower Langhian) of the Netherlands (Janssen, 1984), Miocene (Upper Serravalian-Messinian) of Denmark (Rasmussen, 1968) and Germany (Anderson, 1964), Pliocene (Piacenzian) of East Anglia (England) (Wood, 1842, 1848; Harmer, 1923) and Pliocene (Zanclean-Piacenzian) of Belgium (Nyst, 1878-1881; Marquet, 1995). In the Atlantic Neogene, there are records from the Miocene (Burdigalian) of Aquitaine (SW France) (Cossmann & Peyrot, 1916-1919) and the Pliocene (Piacenzian) of Portugal (Silva, 1993b; present paper).

There are also records from the Pliocene of north-west Africa (Dar-bel-Hamri, Morocco; Zanclean, see Lecointre, 1952), the Miocene of Italy (Piedmont; 'Helvetian', see Sacco, 1896) and the Pliocene of southern Spain (Estepona; Zanclean, see Vera-Peláez *et al.*, 1995) and Italy (Piedmont; Zanclean-Piacenzian, see Sacco, 1896; Pavia, 1975; Cavallo & Repetto, 1992; Monte Mario, Sicily and Calabria, ?Plio-Lower Pleistocene, see Cerulli-Irelli, 1916). The last representatives of *Solariella* in the Mediterranean occurred during the Pleistocene.

In extant European faunas, the genus is represented by a single species, *S. amabilis* (Jeffreys, 1865), which

is restricted to the Atlantic coast, being found from the Bay of Biscay to the Shetland Islands (Graham, 1988; Poppe & Gotto, 1991). Although now confined to the Atlantic, *S. amabilis* extended into the Mediterranean during Early Pliocene times and is commonly found in strata of Zanclean age exposed at Velerín (Estepona, southern Spain; pers. obs.).

Solariella cincta was first described from the Sicilian Plio-Pleistocene; it occurs in Lower Pleistocene deposits of mainland Italy (Cerulli-Irelli, 1916; Warén, 1993). At present, *S. cincta* is found off the coast of West Africa, under the name of *Solariella inoptanda* (Locard, 1897), now considered a junior synonym of *S. cincta* (see Warén, 1993).

The present record of the species is the first from the Iberian Neogene, and extends the palaeogeographic range from the Mediterranean into the Atlantic.

Palaeoclimatic implications — The presence in the Portuguese Pliocene (Piacenzian) of representatives of thermophilic genera and species that at present occur only further south (*i.e.* off the coast of West Africa), does not exclusively relate to *S. cincta*. Other species and genera, such as *Tribia uniangulata* and *Solatia piscatoria*, both found at the same locality and at present missing from the European Atlantic and Mediterranean coasts, but occurring off the West African coast. Similarly, genera such as *Ficus*, *Ancilla* and *Strioterebrum*, also represented in Vale de Freixo fauna, disappeared from European waters during the Late Pliocene. This southerly migration and local extinction of Pliocene thermophilic gastropods from the Pliocene European Atlantic coast and the Mediterranean reflects successive climatic cooling events during the Pliocene (see Raffi & Monegatti, 1993; Barnes *et al.*, 1995; Stanley & Ruddiman, 1995).

The taxonomic composition of the Vale de Freixo malacofauna, with several thermophilic elements still present, but without clear indicators of tropical conditions (*sensu* Raffi *et al.*, 1989; Raffi & Monegatti, 1993) such as a high number of tropical species and a high diversity of Terebridae and Conidae in particular, is the result of the first Pliocene climatic cooling event. This first pulse of cooling occurred in the Northern Hemisphere at high and mid-latitudes relatively suddenly, at about 3.2-3.1 Ma, presaging the onset of the Plio-Pleistocene ice age, but still without the buildup of major ice sheets (Raffi & Monegatti, 1993; Barnes *et al.*, 1995; Stanley & Ruddiman, 1995). However, the presence at Vale de Freixo of thermophilic benthic gastropods suggests that relatively high water temperatures (warmer than today) still prevailed along the European Atlantic coast at this latitude between *c.* 3.2-3.1 and 2.7 Ma, *i.e.* the age assignments for the Vale de Freixo fossiliferous beds.

The next Pliocene climatic cooling event took place at *c.* 2.5 Ma, and marked the formation of large ice sheets and the transition to the modern ice age (Barnes

et al., 1995; Stanley & Ruddiman, 1995). This second Pliocene cooling pulse resulted in the total disappearance of Terebridae from the European Atlantic coast and the Mediterranean (Raffi & Monegatti, 1993). The above-mentioned thermophilic taxa probably migrated southwards, leaving the European and Mediterranean coasts, as a result of this particular event. These Early/Late Pliocene migration and local extinction (ecobiostatigraphic) events of western and eastern North Atlantic thermophilic molluscs are collectively classified by Barnes *et al.* (1995, p. 320) as a Global Event of relatively small order (E'L' Plio event; third rank in a total of five), in what they labelled as a '(...) very rough and relative classification.'

CONCLUSION

At present, *Solariella cincta* occurs only off the coast of West Africa. During the Late Pliocene this species had a much wider distribution, occurring in the Mediterranean and along the European Atlantic coast, at least as far north as central-west Iberia.

The presence of thermophilic benthic gastropods such as *Solariella cincta*, *Tribia uniangulata*, *Solatia piscatoria*, *Ancilla* sp., *Ficus* sp., and *Strioterebrum* sp. in the Portuguese Pliocene (Piacenzian) at Vale de Freixo, clearly indicates that relatively high water temperatures (warmer than today) still prevailed, at least sporadically, along the European Atlantic coast at this latitude between *c.* 3.1-3.2 and 2.7 Ma. The presence of several thermophilic genera and species in the Portuguese Pliocene and their subsequent disappearance, would favour climatic change as a trigger of these local extinctions and southerly migrations of marine benthic gastropods of tropical affinity. In this respect, it does not appear necessary to evoke the possibility of different Pliocene palaeobiogeographic distributions based on distinct palaeoecological requirements for these thermophilic molluscs, thus undermining the general applicability of Dodd & Stanton's (1981) principle of taxonomic uniformitarianism, which was suggested by Aguirre (1998) to interpret bioconstructions of the oyster *Saccostrea cucullata* Born, 1778, a west African/Indo-Pacific thermophilic species, in the Upper Pliocene of Cádiz (southwest Spain, Atlantic coast).

ACKNOWLEDGEMENTS

The authors wish to thank Dr Anders Warén (Swedish Museum of Natural History, Stockholm) for his kind advice on classification and assistance in photography. SEM micrographs were kindly prepared by Sr. Octávio Chaveiro (Estação Agronómica Nacional, Oeiras, Portugal). This is Contribution 36 of the 'Grupo Paleo' (Palaeontology Group of the National Natural History

Museum of Lisbon University). This work was supported by Research Project 1999SGR 00348 of the 'Pla de Recerca de Catalunya' (Catalonia, Spain).

REFERENCES

Aguirre, J., 1998. Bioconstrucciones de *Saccostrea cuccullata* Born, 1778 en el Plioceno Superior de Cádiz (SO de España): Implicaciones paleoambientales y paleoclimáticas. — Rev. esp. Paleont., 13(1): 27-36.

Anderson, H.-J., 1964. Die Miocene Reinhart-Stufe in Nord- und Westdeutschland und ihre Mollusken-Fauna. — Fortschr. Geol. Rheinl. u. Westf., 14: 31-368, 58 pls.

Barnes, C., A. Hallam, D. Kaljo, E.G. Kauffman & O.H. Walliser, 1995. Global Event Stratigraphy. In: O.H. Walliser (ed.) Global Events and Event Stratigraphy. Berlin (Springer), pp. 319-333.

Berggren, W.A., D.V. Kent, C.C. Swisher III & M.-P. Aubry, 1995. A revised Cenozoic geochronology and chronostratigraphy. In: W.A. Berggren, D.V. Kent, M.-P. Aubry & J. Hardenbol (eds). Geochronology, Time Scales and Global Stratigraphic Correlation. SEPM Spec. Publ., 54: 129-212.

Cachão, M., 1990. Posicionamento bioestratigráfico da Jazida Pliocénica de Carnide (Pombal). — Gaia, 2: 11-16.

Cavallo, O. & G. Repetto, 1992. Conchiglie Fossili del Roero, Atlante Iconografico. — Mem. Ass. Natural. Piemontese (Ass. Amici Mus. 'Federico Eusebio'), 2: 1-251.

Cerulli-Irelli, S., 1916. Fauna malacologica Mariana, Parte Ottava. — Paleontogr. It., Mem. Paleont., 22: 171-220, pls 20-24.

Choffat, P., 1889. Observations sur le Pliocène du Portugal. — Mém. Soc. belge Géol., Paléontol., Hydrol., 3: 119-123.

Cossmann, M. & A. Peyrot, 1916-1919. Conchyliologie Néogénique de l'Aquitaine. — Actes Soc. linn. Bordeaux, 69: 1-709 (1916), pls 1-17 (1919).

Dodd, J.R. & R.J. Stanton Jr., 1981. Paleoecology, concepts and applications. New York (John Wiley & Sons), 559 pp.

Ferrero-Mortara, E., L. Montefameglio, M. Novelli, G. Opesso, G. Pavia & R. Tampieri, 1984. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, 2. — Cataloghi Museo Reg. Sci. nat. Torino, 7: 1-484, 56 pls.

Fretter, V. & A. Graham, 1977. The prosobranch molluscs of Britain and Denmark, 2. Trochacea. — J. moll. Stud., Suppl. 3: 39-100.

Geys, J.F. & R. Marquet, 1979. Veldatlas voor Cenozoische fossielen van België, 1. Neogeen. — Publ. Belg. Ver. Palaeont., 2: 1-123, pls 1-45.

Gili, C., C.M. da Silva & J. Martinell, 1995. Pliocene nasariids (Mollusca: Neogastropoda) of central-west Portugal. — Tert. Res., 15(3): 95-110, 2 pls.

Graham, A., 1988. Molluscs: prosobranch and pyramidelid gastropods: keys and notes for the identification of the species. — Synop. Brit. Fauna (n.s.). D.M. Kermack & R.S.K. Barnes (eds), 2nd ed. (E.J. Brill/Dr. W. Backhuys), 662 pp.

Harmer, F.W., 1923. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's Monograph of the Crag Mollusca. — Monogr. Palaeontogr. Soc. Lond., 2: 705-856, pls 57-64.

Knight, J.B., L.R. Cox, A.M. Keen, R.L. Batten, E.L. Yochelson & R. Robertson, 1960. Systematic descriptions. In: R.C. Moore (ed.). Treatise on Invertebrate Paleontology, Part I, Mollusca 1: I169-I331. Lawrence (Univ. Kansas Press), Boulder (Geol. Soc. Am.).

Janssen, A.W., 1984. Mollusken uit het Mioceen van Winterswijk-Miste. Een inventarisatie met beschrijvingen en afbeeldingen van alle aangetroffen soorten. Leiden (KNNV, NGV & RGM), 451 pp., 82 pls.

Lecointre, G., 1952. Recherches sur le Néogène et le Quaternaire marins de la côte atlantique du Maroc, 2. Paléontologie. — Notes Mém. Serv. géol. Maroc, 99: 5-170, 28 pls.

Locard, A., 1898. Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883. Mollusques testacés, 2. Paris (Masson), 515 pp.

Marquet, R., 1995. Pliocene gastropod faunas from Kallo (Oost-Vlaanderen, Belgium) - Part 1. Introduction and Archaeogastropoda. — Contr. Tert. Quatern. Geol., 32(1-3): 53-85, 6 pls.

Nolf, D. & C.M. da Silva, 1997. Otolithes de poissons plio-cènes (Plaisancien) de Vale de Freixo, Portugal. — Rev. Micropaléont., 40(3): 273-282, 3 pls.

Nyst, P.H., 1878-1881. Conchyliologie des terrains tertiaires de la Belgique, première partie. Avec un atlas de 28 planches in-folio. Terrain Pliocène Scaldien. — Ann. Mus. r. Hist. nat. Belg., 3: 1-263 (1881), 28 pls (1878).

Okada, H. & D. Bukry, 1980. Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation. — Mar. Micropaleont., 5: 321-325.

Pavia, G., 1976. I Molluschi del Pliocene inferiore di Monteu Roero (Alba, Italia NW). — Boll. Soc. paleontol. It., 14(2) (1975): 99-175, 14 pls.

Philippi, R.A., 1836. Enumeratio Molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, 1. Berlin (S. Schroppi), 268 pp., pls 1-12.

Poppe, G.T. & Y. Goto, 1991. European Seashells, 1. Polyplacophora, Caudofoveata, Solenogastra, Gastropoda. Wiesbaden (Christa Hemmen), 352 pp., 40 pls.

Raffi, S., D. Rio, R. Sprovieri, G. Valleri, P. Monegatti, I. Raffi & P. Barrier, 1989. New stratigraphic data on the Piacenzian stratotype. — Boll. Soc. geol. It., 108: 183-196.

Raffi, S. & P. Monegatti, 1993. Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climatic-oceanographic and stratigraphic inferences. Proc. 1st RCANS Congr., Lisbon 1992. — Ciências da Terra, 12: 45-50.

Rasmussen, L.B., 1968. Molluscan faunas and biostratigraphy of the marine younger Miocene formations in Denmark, 2. Palaeontology. — Geol. Surv. Denm., (2)92: 1-265, 27 pls.

Sacco, F., 1896. I Molluschi dei Terreni Terziari del Piemonte e della Liguria, 21. Torino (Carlo Clausen), 1-65, 4 pls.

Silva, C.M. da, 1993a. Gastropod palaeoecology and palaeoenvironment of the Pliocene of Vale de Freixo (central-west Portugal). — Abstr. 1st Europ. Palaeontol. Congr., Lyon 1993: 77.

Silva, C.M. da, 1993b. Gastrópodes pliocénicos marinhos de Vale de Freixo (Pombal, Portugal). Sistemática, tafonomia, paleoecologia. Lisboa (MSc thesis, Fac. Ciênc., Univ. Lisboa), 313 pp., 8 pls (unpubl.).

Silva, C.M. da, 1995. Significado ecobioestratigráfico da malacofauna marinha pliocénica de Vale de Freixo (Pombal, Portugal). — Mem. Mus. Lab. min. geol. Univ. Porto, 4: 127-131.

Stanley, S. & W.F. Ruddiman, 1995. Neogene ice age in the North Atlantic region: climatic changes, biotic effects, and forcing factors. In: AAVV, Effects of Past Global Change on Life, Washington DC [Studies in Geophysics, Board on Earth Sci. and Resources, Comm. on Geosci., Environment and Resources, Natl. Res. Council, Natl. Acad. Press], pp. 118-133.

Vera-Peláez, J.L., M.C. Lozano-Francisco, R. Muñiz-Solís, C. Gili, J. Martinell, R. Domènech, P. Palmqvist, & A. Guerra-Merchán, 1995. Estudio preliminar de la malacofauna del Plioceno de Estepona (Málaga, España). — Iberus, 13(2): 93-117.

Warén, A., 1993. New and little known Mollusca from Iceland and Scandinavia, 2. — Sarsia, 78: 159-201.

Wood, S.V., 1842. A catalogue of shells from the Crag. — Ann. Mag. nat. Hist., 9: 455-462, 527-544, pl. 5.

Wood, S.V., 1848-1874. A monograph of the Crag Mollusca, with descriptions of shells from the Upper Tertiaries of the British Isles, 1-3. — Monogr. Palaeontogr. Soc. Lond., 1 (Univalves): xii + 1-208, pls 1-21 (1848); 2: 1-150, pls 1-12 (1851); 151-216, pls 13-20 (1853); 217-342, pls 21-31 (1857); 1-2 (1861); 3 (Suppl.): xxxi + 1-98, pls 1-7 (1872); 99-231, pls 8-11; suppl. pls (1874).

Manuscript received 19 May 2000, revised version accepted 9 October 2000.