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NOTA BREVE

SPIRORBID POLYCHAETES AS BOREAL GUESTS IN THE MEDITERRANEAN PLEISTOCENE

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Riassunto. Sono stati trovati numerosi tubi di policheti spirorbidi attribuibili alle specie *Spirorbis spirorbis* (Linnaeus, 1758) e *Spirorbis corallinae* de Silva & Knight-Jones, 1962, provenienti vari depositi del Pleistocene freddo della Sicilia, nonché da sedimenti würmiani del Mar Tirreno. Tali spirorbidi vivono lungo le coste dell'Atlantico settentrionale, in acque basse della piattaforma continentale, e sono assenti nell'attuale Mediterraneo. Nei sedimenti pleistocenici questi sono invece associati a faune di media piattaforma ed epibatiali, probabilmente perché spiazzati da biotopi più superficiali. Viene attribuito a *S. spirorbis* e *S. corallinae* un significato paleobiogeografico e paleoclimatico, in base alla loro attuale distribuzione biogeografica. Tali specie, entrate in Mediterraneo durante una o più fasi fredde del Pleistocene, assumono quindi il significato di Ospiti Nordici. Speciale attenzione è stata, infine, rivolta alla morfologia e struttura del tubo, le quali hanno portato all'individuazione di caratteri diagnostici a livello specifico.

Abstract. A first report of *Spirorbis spirorbis* (Linnaeus, 1758) and *Spirorbis corallinae* (de Silva & Knight-Jones, 1962) from Early and Middle Pleistocene deposits in Sicily and submerged Late Glacial sediments in the Western Mediterranean is presented. Today both species live on shores and very shallow bottoms in the North Atlantic and are unknown from the Recent Mediterranean. Such differences in their present and past biogeographic distributions suggest that these species were Boreal Guests (BGs) in the Mediterranean Pleistocene. Special attention is paid to tube morphology and structure, which bear some diagnostic features for species identification.

Introduction.

The appearance in the Mediterranean of boreal shelf species, together with the progressive disappearance (since the Piacenzian) of warm-temperate taxa is a distinctive element of the cold Pleistocene phases (Raffi, 1986; Raffi & Marasti, 1982).

These cold-water species are currently known as "Northern Guests" or "Boreal Guests" (BGs) as they spread mainly in the North Atlantic Ocean, from Arctic latitudes southward to the southern British Isles and the Bay of Biscay.

During cold phases the BGs funnelled into the Mediterranean, superimposing on the Mediterranean autochthonous temperate faunas. Their migration occurred in successive, cumulative, increasingly cold floods, which correspond in part to the chronostratigraphic repartition of the Early Pleistocene (Raffi, 1986).

BG species, early used as stratigraphic markers (Mars 1963; Ruggieri et al. 1976), were employed subsequently as palaeoclimatic tools (Di Geronimo, 1974; Malatesta & Zarlenga, 1986; Raffi, 1986; Taviani et al., 1991).

Deposits rich in BGs have been studied since the last century and crop out extensively in southern Italy. Records of boreal species are known from the colder periods of both the Mediterranean and the Atlantic Ocean (Taviani et al., 1991). Nevertheless, BGs are quite poorly documented within the East Atlantic Pleistocene sediments (submerged thanatocoenoses) and are recorded mainly from the Mediterranean Quaternary.

Most BGs are molluscs, such as the bivalve *Arctica islandica*, the best known North Atlantic species in the Mediterranean, which is now regarded as a marker for the Plio-Pleistocene boundary (Ruggieri et al., 1984). Other taxonomic benthic groups, notably serpulids (Zibrowius, 1979; Zibrowius & ten Hove, 1987) have been considered sporadically as palaeoclimatic-oceanographic tools. However, these Plio-Pleistocene taxa, are more widely distributed, belong to the deep-sea Mediterranean benthos and have an Atlantic or more generally oceanic affinity.

In the present work, the first Mediterranean fossil records of two North Atlantic spirorbid species are discussed, together with an account of their present-day geographic distributions and ecology.

Material and methods.

The material examined (Fig. 1) originates from Early to Middle Pleistocene sandy deposits, cropping

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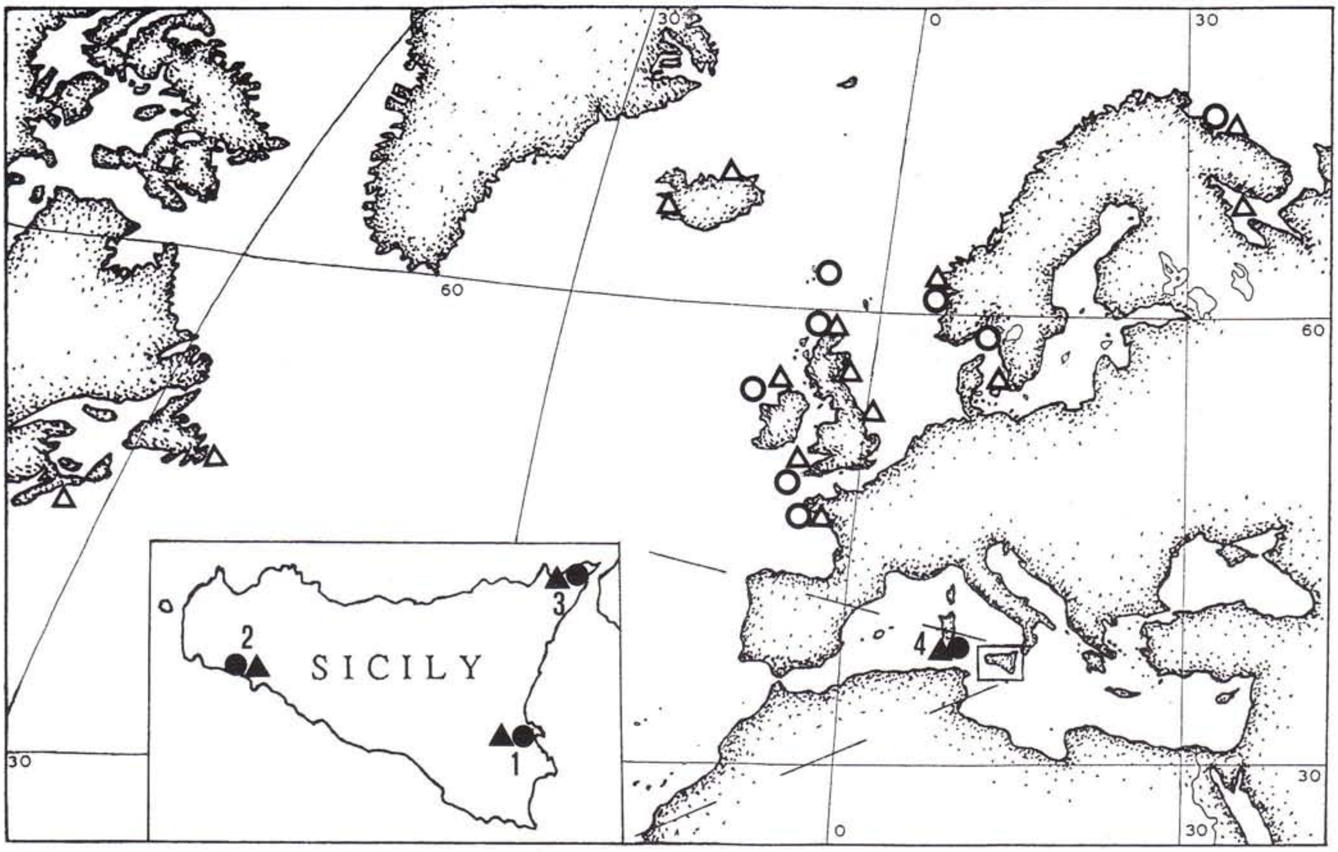


Fig. 1 - Fossil (closed symbols) and Recent (open symbols) records of *Spirorbis spirorbis* (triangles) and *Spirorbis corallinae* (circles). 1) Augusta; 2) Valle del Belice; 3) Salice; 4) Canyon del "Toro".

out in western (Valle del Belice) and eastern (Augusta and Salice) Sicily, and from submerged Late Glacial sediments in the Tyrrhenian Sea (canyon "del Toro").

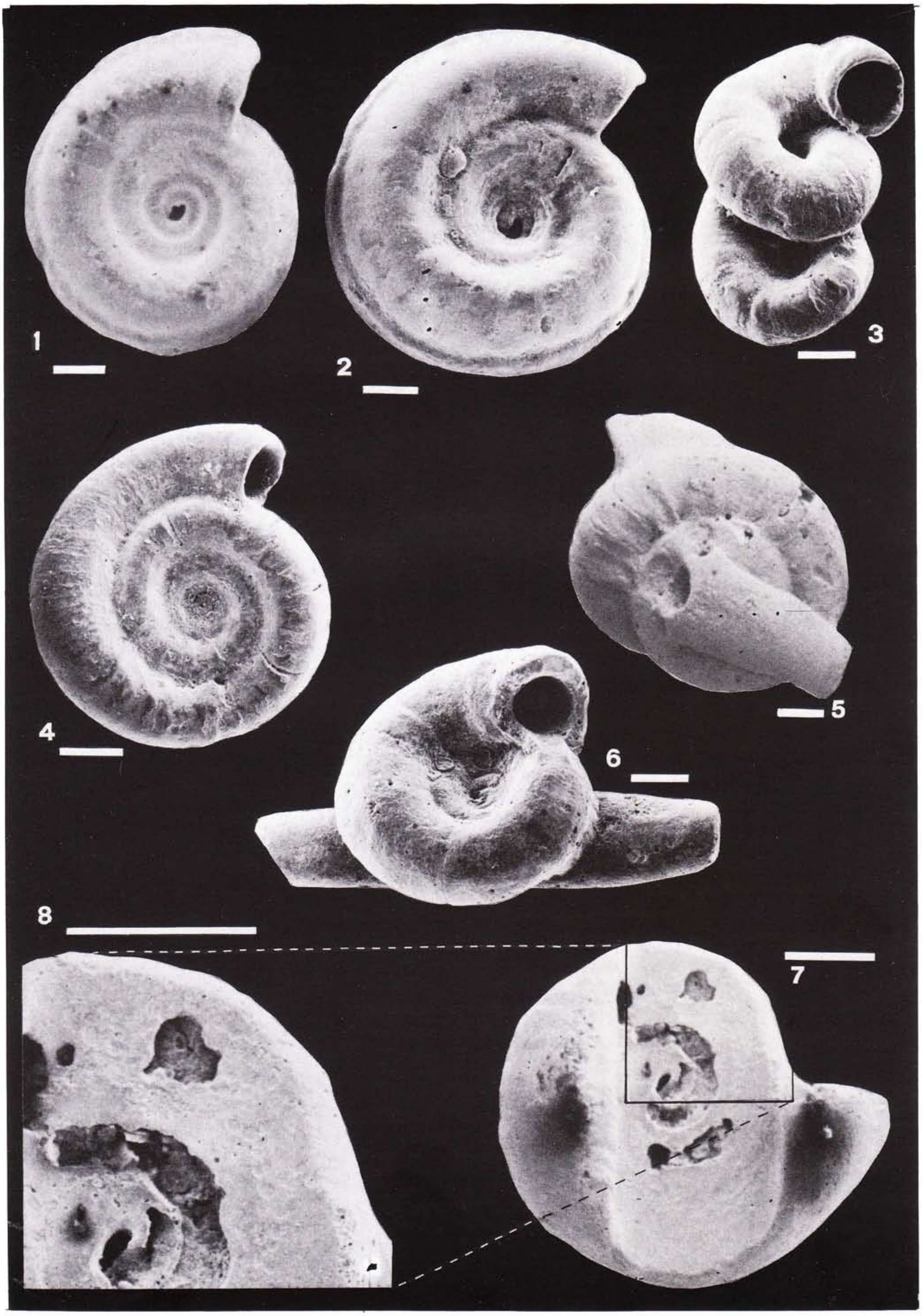
The Valle del Belice section crops out along the right side of the Belice river, in southwestern Sicily (Fig. 1). It consists of a biogenic sandy succession, ca. 3.5 m thick, within a clayey sequence of uppermost Early Pleistocene age. The sands are highly fossiliferous, with corallinaceous algae, rhodoliths and molluscs. The spirorbid tubes were found in a bed with *Arctica islandica*. Palaeoecologic indications inferred from the benthic macrofaunistic assemblages, suggest an upper-circalittoral soft bottom (ca. 35-40 m depth) (Di Geronimo et al., 1994). Several species of North Atlantic origin are present. *S. spirorbis* (10 specimens) and *S. corallinae* (71 specimens) are associated with other serpulids, i.e. *Hydroides norvegicus, Spirobranchus polytrema, Serpula concharum* and *Pomatoceros triqueter*. Most *S. corallinae* tubes show a concave attachment surface, indicating growth on articulate coralline stems (Pl. 1, Fig. 7, 8), while some *S. spirorbis* tubes have flat attachment surfaces, suggesting that they may have been attached to kelp fronds.

The Augusta outcrop is located along the left side of the Marcellino river (SE Sicily), ca. 7 km SW of Augusta (Fig. 1). It consists of an organogenic sequence of muddy-gravelly sands of uppermost Early Pleistocene age (Di Geronimo et al., in press), over 1 m thick, contained in bluish sandy muds. Palaeoecologic observations from the sandy levels indicate a mid-shelf area (upper Circalittoral) with palaeocommunities characterized by North Atlantic immigrant species, among which *A.*

PLATE 1

Scale bar = 400 μm

Fig. 1 - *Spirorbis spirorbis* (Linnaeus, 1758). Augusta, Early Pleistocene.
Fig. 2 - *Spirorbis spirorbis*. Valle del Belice, Early Pleistocene.
Fig. 3 - *Spirorbis corallinae* de Silva & Knight-Jones (1962), forming irregular ascending coils. Salice, Early Pleistocene.
Fig. 4 - *Spirorbis corallinae*, with regularly flat coils. Valle del Belice, Early Pleistocene.
Fig. 5 - Tube of *Spirorbis corallinae* on a *Corallina* stem. Valle del Belice, Early Pleistocene.
Fig. 6 - Tube of *Spirorbis corallinae*, attached on *Corallina* stem. Belice, Early Pleistocene.
Fig. 7 - Bioimmuration of *Corallina* stem *by Spirorbis corallinae*. Augusta, Early Pleistocene.
Fig. 8 - Detail of Fig. 7 showing casts of sporangiae.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islandica is dominant (Di Geronimo et al., in press). Some layers of the sequence supplied tubes of *S. spirorbis* (6 specimens) and *S. corallinae* (14 specimens). They are mostly detached from the original substrata, probably coming from neighbouring shallower biotopes. Among the associated serpulids, *Hydroides norvegicus* is the more abundant species. Moreover, several tubes of an undetermined *Circeis* species occur.

The Salice section crops out near the town of Salice, ca. 15 km W of Messina (Fig. 1). The Middle Pleistocene outcrop (Di Stefano & Lentini, 1996) is an organogenic sandy sequence, 13 m thick, overlying in unconformity limestones with bathyal corals. The sands are often cross-bedded and increase in muddy fraction upwards. The same two spirorbid species (13 *S. spirorbis* and 25 *S. corallinae* specimens) were obtained within some layers of the sands, becoming more abundant in their upper part. The associated benthic assemblages indicate an epibathyal palaeoenvironment swept by currents, with infra- and circalittoral elements transported down from shallower biotopes located on top of the steep sides of the palaeobasin. Faunas are characterised by species with a markedly Atlantic affinity (such as *Neovermilia falcigera* among serpulids). *Placostegus tridentatus* and *Serpula lobiancoi* are the dominant associated serpulids. Some tubes of *Circeis* sp. are also present. *S. corallinae* tubes are usually detached from the substrate, showing a concave area of attachment, suggesting an original settlement on cylindrical substrata like *Corallina* stems.

S. spirorbis and *S. corallinae* were found also in a sample dredged from "del Toro" canyon, off southwestern Sardinia (Stn. DG03, 38°43.78'N, 8°20.59'E, 195 m). The sample consists of muds rich in oyster shells and scleractinians, indicating a Late Glacial age. *S. spirorbis* and *S. corallinae* (both with 6 specimens) occur together with deep circalittoral and bathyal serpulids (*Metavermilia multicristata, Semivermilia agglutinata, Hyalopomatus variorugosus* and *Filogranula stellata*). As in the previous sample, spirorbids seem to have been displaced from the infralittoral environment, down to epibathyal depths. Some specimens of spirorbids are free in the mud, showing limited areas of attachment, as though they had been attached to comparatively thin stems of algae, hydroids or bryozoans.

A stock of living specimens of *S. spirorbis* from Iceland, collected by Drs. P. and E.W. Knight-Jones, was used for observations and comparison of tube structures. They are densely settled on a blade of *Fucus serratus*.

For SEM observations, before coating with gold palladium, fossil and Recent tubes were cleaned with H_2O_2. Some tubes were broken to investigate the wall structure.

Tube morphology and structure.

Differences between the tubes of *S. spirorbis* and *S. corallinae* are seemingly slight, both tubes being sinistrally coiled, smooth and similar in shape. Nevertheless, careful observations of tube morphology allow a distinction at the species level to be made, even when only fossil material is available.

Size is also similar, the outer coil diameter being ca. 2-3 mm in *S. spirorbis* and 2-2.5 mm in *S. corallinae*. The opening is simple, without peristomes, in both species (Pl. 1, Figs. 1, 2, 4).

A weak sculpture occurs only in *S. corallinae*, consisting of wide-spaced rounded growth ridges, indicating the previous openings (Pl. 1, fig. 4).

In *S. spirorbis* the outer edge of the tube spreads out to form a more or less evident peripheral flange (Pl. 1, Figs. 1, 2). This feature is distinctive for *S. spirorbis* (see Rzhavsky, 1994), but lacking in *S. corallinae*, the cross section of which is regularly circular (Pl. 1, Figs. 3, 4, 5).

When attached to the small and convex fronds of *Corallina*, a tube of *S. corallinae* grows often as irregular ascending coils (Pl. 1, Figs. 3, 5, 6). On fronds of larger algae it is regularly flat and planispirally coiled. The tube diameter of the external coil does not increase toward the opening (Pl. 1, Fig. 4). The outer coil of *S. spirorbis*, however, lies partly over the inner ones and the tube diameter increases more rapidly with growth (Pl. 1, Figs. 1, 2). On the attachment surface of *S. corallinae*, on casts of *Corallina* stems and sporangia are often visible (Pl. 1, fig. 7, 8).

PLATE 2

Scale bar = 400 μm (Fig. 1), 20 μm (Figs. 2-7)

Fig. 1 - *Spirorbis spirorbis* on *Fucus serratus*. Iceland, Recent.

Fig. 2 - Transverse section of tube wall of *Spirorbis spirorbis* showing an inner chitinous layer, a mid opaque and an outer glossy calcareous layer. Iceland, Recent.

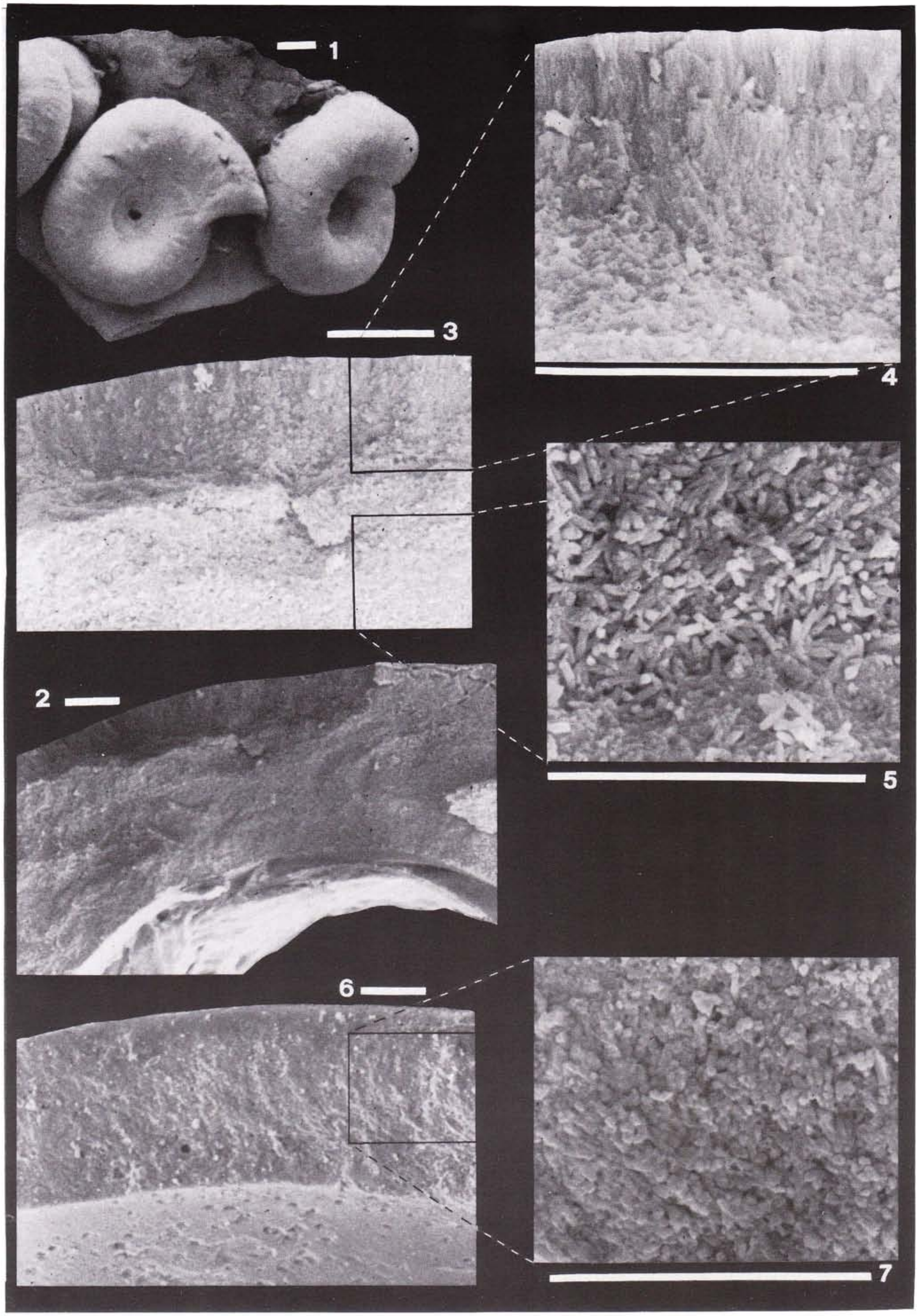
Fig. 3 - Microstructure of the two calcareous layers. Opaque layer with crystals arranged in a criss-cross pattern. Outer glossy with isorientated crystals. Iceland, Recent.

Fig. 4 - Detail of outer glossy layer. Needle-like crystals, perpendicular to the outer surface.

Fig. 5 - Detail of mid opaque layer. Crystals of prismatic shape and criss-cross arrangement.

Fig. 6 - Transverse wall section of fossil *Spirorbis spirorbis*, with homogeneous structure without layers. Augusta, Early Pleistocene.

Fig. 7 - Detail of Fig. 6. Crystals have lost the original shape structure and have crowded together.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The tube wall of living *S. spirorbis* specimens has a glossy surface and is composed of two calcareous layers (Pl. 2, fig. 2, 3). The inner layer is opaque, ca. 50 µm thick, and with crystals arranged in a criss-cross pattern (Pl. 2, Fig. 5); the outer layer is porcellaneous or almost vitreous, ca. 20 µm thick, with larger crystals, showing a common axis orientation. At higher magnification, crystals appear needle-like and perpendicular to the outer tube surface (Pl. 2, fig. 4). This kind of structure results in transparency (Zibrowius & ten Hove, 1987). A third chitinous layer rarely occurs around the lumen of the tube (Pl. 2, Fig. 2). Several burrows, probably by boring algae, are visible near the outer surface (Pl. 2, Fig. 2).

Fossil tubes of both species are thick and rather porcelaneous, with a glossy surface. They are always recrystallized. SEM micrographs show a unique homogeneous layer, 70 µm thick, in which crystals are closely packed without a regular orientation (Pl. 2, fig. 6, 7). The original wall structure is lost.

Biogeography and ecology.

The present geographic distribution of the two species investigated is Atlantic, north of latitude 40°N.

S. spirorbis is a boreal-arctic species (Fig. 1), ranging from the Arctic Sea to the northeast coast of the U.S. (Knight-Jones *et al.*, 1991). It is frequent in the Celtic and North Seas (Knight-Jones & Knight-Jones, 1977; Knight-Jones, pers. comm.). It was found also in the White and Barents Seas (Rzhavsky, 1992).

S. corallinae is boreal-arctic too, but less widely distributed, ranging from the Barents Sea (Rzhavsky, 1992) to southern Brittany (Fig. 1). It is particularly common in the Celtic Sea, from Ireland to the Scilly Isles (Knight-Jones & Knight-Jones, 1977).

In the southern area of distribution of both species (English Channel) the mean bottom water temperature is 6-10° C in winter and does not exceed 16° C in summer (Holmes, 1966).

Both species are mesolittoral to upper infralittoral, occurring from rock pools to shallow depths (Knight-Jones et al., 1975; Knight-Jones & Knight-Jones, 1977; Rzhavsky, 1992). They are mainly epiphytic on fronds of various algae. *S. spirorbis* typically settles on brown fucoids (especially *Fucus serratus*) but may occur also on kelps (*Laminaria*, *Sacchorhiza*) (Knight-Jones et al., 1975). *S. corallinae* settles almost exclusively on *Corallina officinalis*, and rarely on other red algae. Exceptionally it was found on the soft red alga *Chondrus*, in higher pools (Knight-Jones & Knight-Jones, 1977). Gregariousness is seen in both species and the larvae swim for no more than a few hours (Knight-Jones, 1951).

The boreal distribution of *S. spirorbis* and *S. corallinae* is a character common to many species belonging to the genus *Spirorbis* Daudin. *S. rupestris*, *S. inornatus* and *S. tridentatus* are exclusively boreal (Knight-Jones *et al.*, 1991; Knight-Jones & Knight-Jones, 1995). *S. strigatus*, as well as the recently described *S. (Velorbis) gesae*, live in the Atlantic at mid-latitudes (off west Africa). Only three species live in the Mediterranean: *S. infundibulum*, which is probably endemic, *S. cuneatus* which lives also in NE Atlantic, and the circumtropical *S. (Spirorbella) marioni*, whose recent introduction into the Mediterranean was by ship transport (Zibrowius & Bianchi, 1981). The last species, and three other eastern Pacific spirorbids (*S. spatulatus, S. bifurcatus, S. rothlisbergi*) are dextrally spiraled. Only two other *Spirorbis* are tropical, *S. placophora* and *S. bidentatus*, the former known only from the Galapagos and the latter having a circumtropical distribution (Knight-Jones et al., 1991).

In the fossil assemblage the association of *S. spirorbis* and *S. corallinae* with a deep water fauna can be explained easily by post-mortem down slope displacement from shallower bottoms. It is very unlikely that these shallow water spirorbids were fossilized within their original environment, exposed to dispersing wave action.

Discussion.

The present boreal and arctic distribution of *S. spirorbis* and *S. corallinae*, here reported as Pleistocene fossils, suggests significantly colder conditions than today. Their immigration into the Mediterranean Pleistocene probably took place by a gradual southward expansion of their biogeographic range, in step with the progressive cooling. The movement of their populations into the Mediterranean would have been helped by their short planktonic larval phase and gregariousness during settlement. *S. spirorbis* and *S. corallinae* probably made a relatively "late" appearance in the Mediterranean during the cold Pleistocene. They are recorded from sediments not older than the uppermost Early Pleistocene (Sicilian age), corresponding to the third molluscan migration flood (Raffi, 1986). As already stressed by Buccheri (1985) this age could be correlated to the first cold Pleistocene peak recognised by Shackleton & Opdyke (1976) at about 0.8 Ma.

A similar southward movement of *Spirorbis* was invoked to explain the recent finding of a species which may be endemic to Madeira, *S. (Velorbis) gesae* Knight-Jones & Knight-Jones (1995). This is quite like *S. spirorbis*, and the authors suggest that a common ancestor of both species may have reached Madeira during an ice age, and that *S. (Velorbis) gesae* may be its modified descendent.

As mentioned above, tubes of *Circeis* and of the serpulid *H. norvegicus* occur together with the fossil *Spirorbis* under study. *Circeis* is a circumboreal spirorbid genus, quite common in northeastern Atlantic infralittoral waters, but not represented in the present-day Mediterranean (Knight-Jones & Knight-Jones, 1977). It may thus have the same palaeoclimatic significance as the two other spirorbids. *H. norvegicus*, still common in the Recent Mediterranean (Zibrowius, 1972), appears more abundant in Pleistocene mid-shelf deposits. This could also suggest lower Pleistocene temperatures.

The diagnostic value of shape and other morphologic features of spirorbid tubes is demonstrated here. Identification at the species level is possible only when empty or fossil tubes are available. SEM observations of the tube wall of *S. spirorbis* show a particular microstructure, not observed in other spirorbids (two distinct layers). This suggests that at least in Recent material, not affected by diagenetic changes, tube microstructure can also be a diagnostic character at the species level.

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